

Relationship between myological variables and different take-off and landing behaviours in frogs

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Abstract

Although landing behaviour in anurans differs significantly among species, a take-off behaviour seems to be largely conserved in the evolution of frogs and toads. The ancestral mode of landing is hypothesized to involve the body crash-landing on the substrate, after which the anuran cycles the limbs forward and then backward to their resting position. The part of the body that first contacts the substrate may vary among taxa. The limbs and pectoral girdle muscles as well as those of the caudopelvic region, involved with landing and take-off behaviours, are investigated. The existence of a relationship exists between myology and different take-off and landing behaviours is explored. The results suggest that most of the muscles involved in both take-off and landing are conserved morphologically, with only few differing, depending on the locomotor behaviour. Two muscles tend to be longer; the *m. coracobrachialis*, which is involved with landing, and the *m. coccygeosacralis*, related to the take-off.

KEYWORDS

anuran, caudopelvic mechanism, landing, myology, take-off

1 | INTRODUCTION

So far as is known, all anurans that jump take-off from the substrate in the same way; however, there is variation in the way in which they land. The ancestral landing behaviour is thought to resemble that of the basal frogs, *Ascaphus* and *Leiopelma*; both frogs first crash-land on the ventral surface of their body, and then move their limbs forward and then back to their resting position (Essner, Suffan, Bishop, & Reilly, 2010; Reilly et al., 2016). Variation in landing behaviour involves the body part that first comes in contact with the substrate. Thus, jumping frogs, such as species of *Leptodactylus*, typically land on their hands, whereas climber-walker frogs, such as species of *Phyllomedusa*, usually land on their belly. Azizi, Larson, Abbott, and Danos (2014) reported that a controlled landing, in which an animal neither crashes nor

topples, requires enough stability to allow muscles to dissipate mechanical energy.

Many organisms, such as primates and birds, use the same limbs for taking-off and landing; thus, they generate a similar distance of potential acceleration and deceleration. In frogs, the forelimbs are shorter than the hindlimbs; accordingly, the impact forces on the forelimbs are expected to be higher and the potential acceleration and deceleration distances different (Nauwelaerts & Aerts, 2006).

To take-off anurans completely extend the hindlimbs, keeping the arms stiff stay over the full jumping range. Meanwhile, landing is accomplished when each hand touches the ground and forelimb forms a pivot engaging the glenoid joint while rotating the entire pectoral girdle (Emerson, 1983; Griep et al., 2013). Nauwelaerts and Aerts (2006) found that frogs flex the elbows and use the force

of the extensor muscles to reduce the force of the landing impact. As in jumping mammals, frogs can modulate the stiffness of limb muscles to absorb the impact of landing before they take-off; thus, they seem to be aware of how far they are jumping (Gillis, Akella, & Gunaratne, 2010; Gillis, Ekstrom, & Azizi, 2014).

Soliz, Tulli, and Abdala (2017) found that in species that jump, such as *Dendropsophus nanus*, the scapulae are long and broad proximally and distally, with the clavicles and coracoids also long. According to Emerson (1984), the clavicle or the coracoid may function to absorb the impact when the frog lands. Several scapular muscles such as the anconeus (triceps scapularis medialis) are critical to provide resistance to the impact forces of landing; these are activated before take-off, to prepare (i.e., tense) the forelimbs so that they do not collapse at landing (Akella & Gillis, 2011; Ekstrom & Gillis, 2015; Gillis et al., 2010; Gillis et al., 2014; Shearman, 2008).

Jenkins and Shubin (1998) stressed the importance of pelvic girdle joints in take-off and landing. The longissimus dorsi muscles, aided by forelimb thrust, act on the joint between the ilia and the sacrum, along with the presacral vertebral column. Additionally, the coccygeoiliacus muscles stabilize the urostyle between the ilia, thereby transmitting the propulsive thrust from the ilia to the urostyle (Jenkins & Shubin, 1998).

Considering the importance of girdle movements to anuran take-off and landing mechanisms, and the limited information available about interspecific variation in these mechanisms (Akella & Gillis, 2011), we explore whether morphometric variation in girdle muscles correlate with proposed differences in the roles of these muscles in take-off and landing mechanisms in anurans. In this context, we predict that muscles directly linked to take-off will be highly conserved through anuran evolution, given that is a single mechanism. We also predict more variation in muscles directly linked with landing mechanisms, which seem to be more plastic.

2 | MATERIALS AND METHODS

2.1 | Data collection

From the 62 adult female and male anurans that we examined, 19 species belong to independent evolutionary lineages (Figure 1). Specimens were selected to represent different specialized landing behaviours. All the specimens examined are deposited in systematic collections and listed in Supporting Information Data S1.

2.2 | Morphology

We select active muscles involved in the different landing behaviours; besides, considering that Reilly et al. (2016)

postulated that the pelvic girdle also might play an important role in landing, we also include data about those muscles involved in the caudopelvic mechanism (Jenkins & Shubin, 1998) (Table 1, Figure 2) which are also active during take-off. Dissections of the muscles were performed under a binocular microscope (Nikon SMZ645). Muscles were removed intact and measured between the corresponding origin and insertion points in mm with digital calipers (± 0.01 mm; Mitutoyo CD-15B, Mitutoyo Corp., Kure, Japan). Body length was measured from tip of snout to tip of urostyle. To minimize the error measurements, three replicates of each measurement were made with digital calipers; the values reported here are means of the replicates. Given that the force that a muscle can develop is largely proportional to its cross-sectional area (CSA) (Biewener, 1998), we tested for differences in anatomical CSA among muscles of different landing behaviour of anurans. Since, the muscles are all the same with their fibres parallel to the medial axis of the body were transversally cut across their maximum diameter and photographed in dorsal view with a high-resolution digital camera under a binocular microscope (Leica ID M-Series). Each image was taken using the same magnification and from the same distance. The CSA of the muscles were measured in square millimetres using the software LAS V4.8. Ink, Leica M205 stereomicroscope, following the same protocol used to obtain length measures. The terminology used follows Abdala and Diogo (2010), Diogo and Ziermann (2014), and Prikryl, Aerts, Havelková, Herrel, and Roček (2009). Muscles mean values, body size and the numbers of individuals used per species, are detailed as necessary (Supporting Information Table S1).

2.3 | Behavioural assignments

2.3.1 | Landing behaviour

Three landing mechanisms are currently recognized in anurans (Bijma, Gorb, & Kleinteich, 2016; Essner et al., 2010): (a) a belly hit, when the body of the frogs stretches its limbs out and lands on the substrate; (b) a hand hit, in which the frog makes contact with the substrate with the palmar surface of the hand; and (c) a digit hit, the digit of either the forelimbs or the hindlimbs performed a cartwheel around the stick (Figure 3). However, we are aware that anuran species are capable of a range of landing behaviours, and that they seem to be related to different modes of locomotion. Thus, we decided to treat the landing settings as a continuum and created indexes within each category (i.e., inside each category the proportion of landing styles would gradually range from zero to one). This categorization (Table 2) follows Grizante, Navas, Garland, and Kohlsdorf (2010) and Soliz et al. (2017), who also searched for a way to incorporate more subtlety

in the ecological settings of the taxa studied. For example, landing behaviour of *Scinax fuscovarius* is recorded as hand hit and digit hit following descriptions of movements implied in jumping (Manzano, Herrel, Fabre, & Abdala, 2017) (Figure 3). Our field observations indicate that, occasionally, this species also exhibits belly hit. Thus, we combine in our Table 2 all these records and assignate to this species arbitrary values of 0.2 to belly hit, 0.5 to hand hit and 0.3 to digit hit. Values of each category were inferred considering the recorded frequency of each behaviour. Likewise, climber-walker species, as *Phyllomedusa sauvagii*, walk across narrow substrates using their arms, they use their digits to grip the branches while climbing, but they are also able to jump in order to escape predators and in that case, they land with their body (Manzano et al., 2017). Thus, we assigned them

0.6 for digit hit and 0.4 for belly hit. Meanwhile, for those species exhibiting strict hand touchdown, as jumper species as *Leptodactylus fuscus*, we assigned 1 for hand hit and zero for the remaining behaviours (Table 2). Quantitative assignations are arbitrary to some extent, although we consider that an assignation of present (1) or absent (0) is also arbitrary and imply loss of valuable information available in the literature, checked in many cases by personal observations.

2.3.2 | Take-off behaviour

It has been recorded only one take-off behaviour, universally observed (Emerson & Jongh, 1980; Reilly et al., 2016). The jump begins with the extension of hindlimbs and stiffness of the arms, while the alignment of the vertebral column

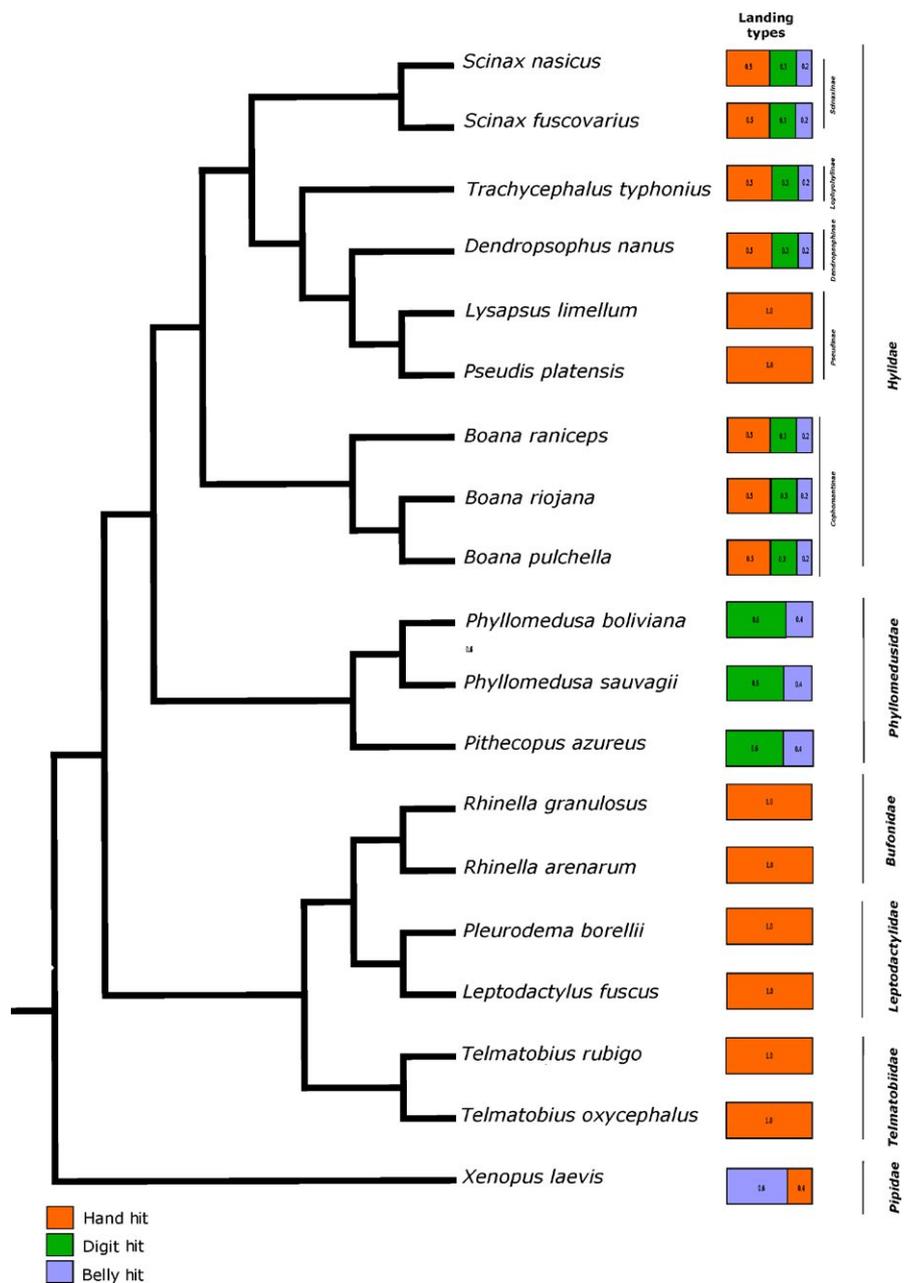


FIGURE 1 Composite tree based on Duellman et al. (2016) and Pyron and Wiens (2011)

occurs. Then, the forelimbs leave the ground, the foot contacting broadly with the ground and the knees are extended. Afterwards, only the distal tips of the toes are in contact with the ground, the forelimbs are extended and are pressed against the sides of the body. Finally, the legs are maximally extended and the animal is off the ground (Emerson & Jongh, 1980).

2.4 | Phylogeny

Phylogenetic Comparative Analyses were performed using a composite tree (Figure 1) based on Pyron and Wiens (2011) and the phylogenetic hypothesis of Hylidae proposed by Duellman, Marion, and Hedges (2016). Branch lengths were not available, so we assumed all of them were equal to 1, and we transformed branch lengths using Pagel's methods (Tulli, Cruz, Kohlsdorf, & Abdala, 2016). Branch lengths were not available, and our composite tree is based on the topological relationships among species, thus we used arbitrary branch lengths (all branch lengths equal to 1 and branch length transformations were performed using Pagel's, Nee and Grafen's methods). For testing the adequacy among the three branch lengths, we performed an independent contrast analysis (Garland, Harvey, & Ives, 1992) using the PDTREE module of Mesquite v2.74 (Maddison & Maddison, 2015; Midford,

Garland, & Maddison, 2005). We selected branches length equal to one because they showed the lower number of significant trends and they gave the best standardization of phylogenetically independent contrasts (Garland et al., 1992).

2.5 | Statistical analysis

Mean values of muscle variables were \log_{10} , transformed prior to analyses to meet normality requirements (Zar, 1999). As landing behaviour is expressed in proportions, data were transformed to the arcsin of the square root of each value (Martin & Bateson, 1993). Because muscle variables require body size corrections based on their phylogenetic context, we performed the phylogenetic size correction analysis described by Revell (2009). Residuals were calculated from least square regression analyses of muscle traits on body size (BL), while controlling for phylogenetic non-independence by using phylo.resid (a module of Phytools for R developed by Revell, 2012). The resulting residuals were then used for the subsequent analyses.

2.6 | Phylogenetic signal

To determine whether there was a pattern of phylogenetic signal in the variables, we calculated the phylogenetic signal

TABLE 1 List of muscles measurements examined in this study, including muscles involved in caudopelvic mechanism and pectoral muscles involved in landing (derived from Abdala & Diogo, 2010; Diogo & Ziermann, 2014)

Muscles	Origin	Insertion	Function
Longissimus dorsi (LD)	Presacral vertebrae	Urostyle	Dorsal rotation of the urostyle (Přikryl et al., 2009)
Coccygeosacralis (CS)	Sacral diapophyses	Urostyle	Lateral bending of the body at the iliosacral Joint, trunk stiffness and moderately dorsal rotation of urostyle (Přikryl et al., 2009)
Coccygeoilacus (CI)	Urostilo	Iliac shaft	Anterior gliding of the ilium along the sacral diapophysis, ventral rotation of urostyle or posteriorly pelvis shifts (Přikryl et al., 2009)
Procoracohumeralis (pars episternalis; Ppe)	Procoracoids/epicoracoids	Humerus	Flexion of the shoulder joint by pulling the humerus forward (Duellman & Trueb, 1994) and it could be important in positioning the arms during a jump and shoulder joint stabilization during landing (Akella & Gillis, 2011)
Procoracohumeralis (pars clavicularis; Ppc)	Clavicle	Humerus	Flexion of the shoulder joint by pulling the humerus forward (Duellman & Trueb, 1994)
Coracobrachialis (C)	Coracoids	Humerus	Contraction of this pulls the arm posteroventrally, therefore, it is antagonistic to the muscle deltoideus (Duellman & Trueb, 1994)
Triceps scapularis medialis (Tsm)	Scapula	Humerus	Extension of the elbow joint and it is presumed to be important in moving the forelimb (Duellman & Trueb, 1994). It is important for arm positioning before landing and for resisting impact during landing, regardless of jump distance. Not important for increasing propulsive forces during take-off in toad hopping (Akella & Gillis, 2011)

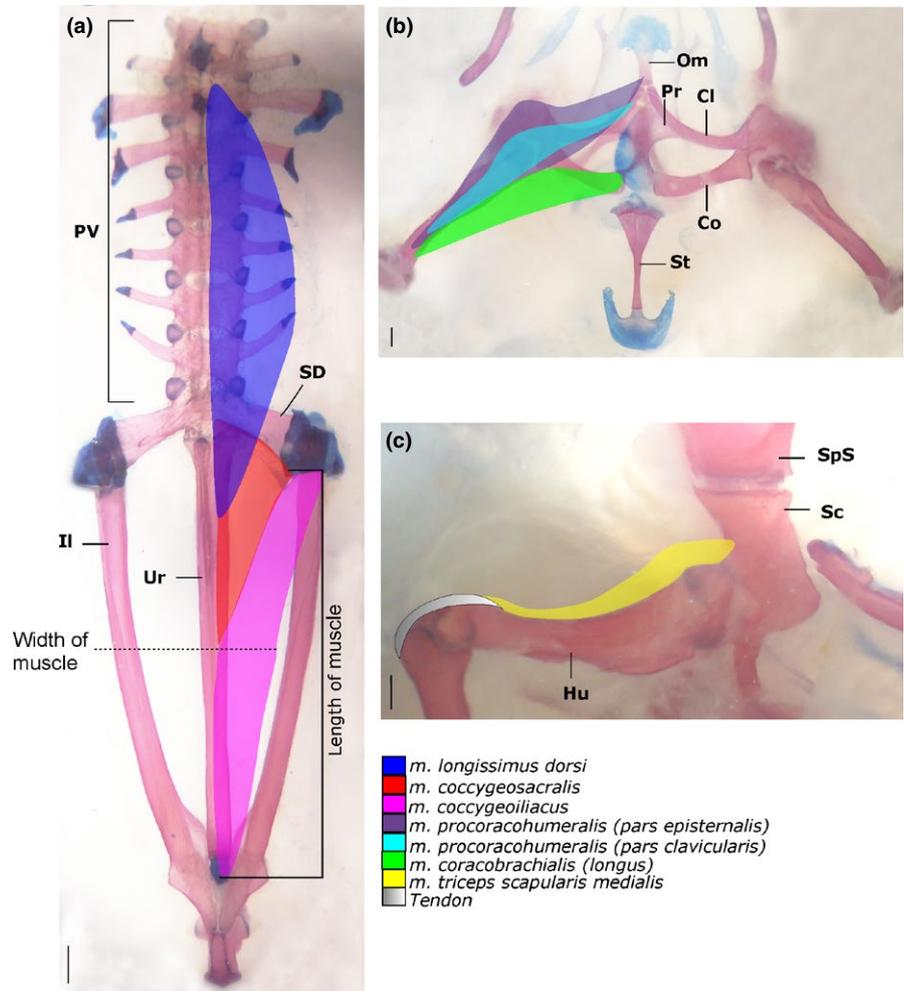


FIGURE 2 Myological variables. (a) *Scinax fuscovarius*, muscles involved in the caudopelvic mechanism. (b, c) *Leptodactylus fuscus*, pectoral muscles involved to landing. Cl: clavicle; Co: coracoid; Hu: humerus; Il: ilium; Om: omosternum; Pr: procoracoid; PV: presacral vertebrae; Sc: scapula; SD: sacral diapophyses; SpS: suprascapula; Ur: urostyle. Scale bars: 1 mm

of these variables using Pagel's λ . The phylogenetic signal is a measure of the tendency of related species to resemble each other, and Pagel's λ is a quantitative measurement of this pattern. Pagel's λ is a scaling parameter that ranges from 0 to 1. Lambda (λ) values equal to 0 indicate no phylogenetic signal, whereas values equal to 1 indicate a strong phylogenetic signal, matching the trait evolution expected under Brownian motion.

Subsequently, we tested three different evolutionary models to explore the processes that best explain the evolution of these muscle traits. The first model, known as the Brownian Motion evolutionary model (BM), supposes that the evolution of a trait results from random fluctuations through time (Felsenstein, 1988; Harmon et al., 2010). The second Ornstein-Uhlenbeck (OU) model focuses on sections of lineages where a trait varies in relation to an optimum or stabilizing selection



FIGURE 3 Landing behaviour of *Scinax fuscovarius*: (a) Belly hit. (b) Digit hit. (c) Hand hit. Table 2 show ecological index assigned to each landing behaviour

Species	Landing behaviour			Literature source
	Belly hit	Hand hit	Digit hit	
<i>Scinax nasicus</i>	0.2	0.5	0.3	Pers. Obs., Manzano et al. (2017)
<i>Scinax fuscovarius</i>	0.2	0.5	0.3	Pers. Obs., Manzano et al. (2017)
<i>Trachycephalus typhonius</i>	0.2	0.5	0.3	Pers. Obs.
<i>Dendropsophus nanus</i>	0.2	0.5	0.3	Pers. Obs., Manzano et al. (2017)
<i>Pseudis platensis</i>	0.0	1.0	0.0	Pers. Obs., Manzano et al. (2008), Sustaita et al. (2013)
<i>Lysapsus limellum</i>	0.0	1.0	0.0	Pers. Obs., Manzano et al. (2017)
<i>Hypsiboas raniceps</i>	0.2	0.5	0.3	Pers. Obs.
<i>Boana riojana</i>	0.2	0.5	0.3	Pers. Obs., Manzano et al. (2017)
<i>Hypsiboas pulchellus</i>	0.2	0.5	0.3	Pers. Obs., Manzano et al. (2017)
<i>Phyllomedusa boliviana</i>	0.4	0.0	0.6	Pers. Obs., Manzano et al. (2017), Vaira (2001)
<i>Phyllomedusa sauvagii</i>	0.4	0.0	0.6	Pers. Obs., Manzano et al. (2017)
<i>Pithecopus azureus</i>	0.4	0.0	0.6	Pers. Obs., Manzano et al. (2017)
<i>Rhinella granulosa</i>	0.0	1.0	0.0	Pers. Obs., Manzano et al. (2017)
<i>Rhinella arenarum</i>	0.0	1.0	0.0	Pers. Obs., Manzano et al. (2017)
<i>Pleurodema borellii</i>	0.0	1.0	0.0	Pers. Obs.
<i>Leptodactylus fuscus</i>	0.0	1.0	0.0	Pers. Obs., Manzano et al. (2017)
<i>Telmatobius rubigo</i>	0.0	1.0	0.0	Barrionuevo (2016), Manzano et al. (2017)
<i>Telmatobius oxycephalus</i>	0.0	1.0	0.0	Barrionuevo (2016), Manzano et al. (2008), Sustaita et al. (2013)
<i>Xenopus laevis</i>	0.6	0.4	0.0	Measey (2016)

TABLE 2 Ecological index assigned to each species according to the landing behaviour

(Butler & King, 2004; Harmon et al., 2010). The third hypothesis predicts intensified trait modifications, early in the evolutionary tree, followed by a gradual deceleration of the evolutionary rate, in a model called Early Burst (EB; Harmon et al., 2010). To test which evolutionary model best fits each variable, a fitContinuous analysis was run using GEIGER (Harmon et al., 2010) and analysis of phylogenetics and evolution (Paradis, Claude, & Strimmer, 2004) packages for R. The command “fitContinuous” describes the rate of character modification within the three aforementioned evolutionary

models, while providing an Akaike criterion value (AIC) for each procedure. The best fit among the candidate evolutionary models was then obtained from the AIC (Angilletta, 2006; Burnham & Anderson, 2002) using the weights (wAICc) as a measure of strength for each model, and indicating the probability that a given model is the best among a series of candidate models (Burnham & Anderson, 2002).

Pagel's phylogenetic signal (λ) was estimated using the residual errors simultaneously on the regression parameters of phylogenetic generalized least squares models (PGLS)

analyses. These analyses were performed in “caper” (Orme et al., 2012) and “ape” (Paradis et al., 2004) packages for R. Models were built using the ecological data as the independent variable, as a proportion of landing behaviour, either individually or in combination (e.g., LD ~ belly hit + hand hit + digit hit), and using the morphological information as the dependent variable. Model choice was based on the model fit using the AIC mentioned above. Statistical analyses were carried out in R (R version 3.4.1; R Development Core Team, 2013).

3 | RESULTS

Body length and some muscle variables showed significant phylogenetic signal with high λ -values (Table 3). Pagel's values (λ) from the residual errors on the regression of PGLS were significant for 18 of the 98 recovered associations related to muscle variables (Table 4) and showed a λ -value closer to 0, suggesting that variability could be a consequence of adaptation to ecological requirements.

3.1 | Evolutionary models

The length of the muscles and the CSA seem to have evolved through similar evolutionary processes. Some traits fitted

TABLE 3 Phylogenetic signal using Pagel's lambda estimate

Variables	λ	<i>p</i>
Body length	0.578	<0.032
Longissimus dorsi length	0.74	0.11
Longissimus dorsi CSA	0.93	0.06
Coccygeosacralis length	1.51	<0.013
Coccygeosacralis CSA	0.344	0.628
Coccygeoilicus length	0.791	0.12
Coccygeoilicus CSA	0.863	0.103
Procoracohumeralis (pars episternalis) length	0.68	0.142
Procoracohumeralis (pars episternalis) CSA	1.13	<0.02
Procoracohumeralis (pars clavicularis) length	0.97	<0.05
Procoracohumeralis (pars clavicularis) CSA	0.84	0.083
Coracobrachialis length	1.004	0.07
Coracobrachialis CSA	1.03	0.06
Triceps scapularis medialis length	0.84	<0.02
Triceps scapularis medialis CSA	0.74	0.092

Notes. Boldface denotes the presence of phylogenetic signal in the variable. CSA: anatomical cross-sectional area.

to more than one evolutionary model, as BM and OU were equally possible under the AIC (Table 5). For example, the lengths of the coccygeosacralis, pars episternalis of procoracohumeralis, triceps scapularis medialis and the body length (Table 5). The evolution of the CSA of the all muscles was best explained by OU model (Table 5). None of the morphological variables showed a best fit under EB evolutionary model.

3.2 | Ecomorphological relationships

The PGLS analysis produced a total of 98 possible models for associations between muscle variables and landing behaviour (Supporting Information Table S2), and 16 associations were considered informative according AIC (Table 4). Four significant models were for muscles length and 12 for CSA (Table 4), for example, a significant association between coracobrachialis muscle CSA and digit and belly hit landing behaviours. In this example, we detected that those species that land with both digit and belly tend to have higher values for the lengths and CSA of coracobrachialis in relation to digit hit and lower CSA for belly hit (Table 4). We have identified an association between the coracobrachialis muscle CSA and the concomitant digit and belly landing behaviours, where frogs having such behaviours tend to exhibit wider and elongate coracobrachialis muscle. Another association identified occurred between coccygeoilicus CSA with hand hit and digit hit, where climber-jumper frogs tend to have a bigger coccygeoilicus (Table 4). None of the morphological variables fit exclusively to any hit behaviour.

4 | DISCUSSION

One of the most interesting outcomes of our work is that, in general terms, in spite of having eight species that perform exclusively hand hit, we did not find a relationship between a particular muscle variable and a particular landing behaviour. These results indicate that frogs exhibit a functionally generalized morphology (Arnold, 1983) having the ability to perform adequately all landing types (Gans, 1974; Gould & Lewontin, 1979). This seems to be the most appropriate morphology to assure that all these behaviours are safely performed.

Reilly et al. (2016) showed that frogs with forelimb landing exhibit many morphologies, locomotor modes, habitats, etc., with controlled landing to improve their escape behaviour. However, we noticed that muscles, structures deeply involved in any type of movement, related to digit hit and hand hit exhibit a remarkable similarity in their variables irrespective of the landing type.

Emerson (1984) proposed that the function of the impact absorption upon landing could be carried out by the clavicle

TABLE 4 Best fitting phylogenetic generalized least squares models for myological traits and landing behaviour

Model	λ	Adj r^2	Intercept	Variable	Slope	Pp	Pt	AICc	Wi																																																																																																																																																																																												
CS length ~ BH + DH	0.001	0.551	0.746	BH	0.46	0.001	0.0006	10.42	0.374																																																																																																																																																																																												
				DH	-0.644	0.002				CS length ~ HH + DH	0.001	0.557	2.034	HH	-0.445	0.001	0.0005	10.18	0.423	DH	-1.015	0	C length ~ BH + DH	0.001	0.272	-0.27	BH	-0.111	0.08	0.03	-13.82	0.272	DH	0.224	0.02	C length ~ HH + DH	0.001	0.268	-0.579	HH	0.106	0.08	0.03	-13.71	0.256	DH	0.312	0.009	LD CSA ~ BH + DH	0.001	0.384	-1.017	BH	-0.453	0.02	0.008	27.1692	0.3236	DH	0.840	0.008	LD CSA ~ HH + DH	0.001	0.395	-2.301	HH	0.447	0.02	0.006	26.8153	0.3863	DH	1.214	0.002	CI CSA ~ BH + DH	0.001	0.303	-0.866	BH	-0.399	0.05	0.02	27.7535	0.2942	DH	0.734	0.01	CI CSA ~ HH + DH	0.001	0.308	-1.988	HH	0.389	0.05	0.02	27.6216	0.3142	DH	1.058	0.006	C CSA ~ BH + DH	0.001	0.335	-0.675	BH	-0.428	0.02	0.01	22.5444	0.2825	DH	0.601	0.02	C CSA ~ HH + DH	0.001	0.360	-1.903	HH	0.430	0.01	0.01	21.8111	0.4077	DH	0.962	0.004	Ppc CSA ~ BH + DH	0.001	0.285	-0.507	BH	-0.500	0.01	0.02	27.1734	0.2241	DH	0.502	0.08	Ppc CSA ~ HH + DH	0.001	0.321	-1.953	HH	0.508	0.01	0.01	26.1762	0.3690	DH	0.930	0.01	Ppe CSA ~ BH + DH	0.001	0.247	-0.836	BH	-0.385	0.07	0.04	30.1856	0.2521	DH	0.697	0.03	Ppe CSA ~ HH + DH	0.001	0.263	-1.943	HH	0.388	0.01	0.01	29.7799	0.3088	DH	1.022	0.01	Tsm CSA ~ BH + DH	0.001	0.342	-0.881	BH	-0.350	0.01	0.04	23.0464	0.3009	DH	0.725	0.08	Tsm CSA ~ HH + DH	0.001	0.354	-1.880	HH	0.349
CS length ~ HH + DH	0.001	0.557	2.034	HH	-0.445	0.001	0.0005	10.18	0.423																																																																																																																																																																																												
				DH	-1.015	0				C length ~ BH + DH	0.001	0.272	-0.27	BH	-0.111	0.08	0.03	-13.82	0.272	DH	0.224	0.02	C length ~ HH + DH	0.001	0.268	-0.579	HH	0.106	0.08	0.03	-13.71	0.256	DH	0.312	0.009	LD CSA ~ BH + DH	0.001	0.384	-1.017	BH	-0.453	0.02	0.008	27.1692	0.3236	DH	0.840	0.008	LD CSA ~ HH + DH	0.001	0.395	-2.301	HH	0.447	0.02	0.006	26.8153	0.3863	DH	1.214	0.002	CI CSA ~ BH + DH	0.001	0.303	-0.866	BH	-0.399	0.05	0.02	27.7535	0.2942	DH	0.734	0.01	CI CSA ~ HH + DH	0.001	0.308	-1.988	HH	0.389	0.05	0.02	27.6216	0.3142	DH	1.058	0.006	C CSA ~ BH + DH	0.001	0.335	-0.675	BH	-0.428	0.02	0.01	22.5444	0.2825	DH	0.601	0.02	C CSA ~ HH + DH	0.001	0.360	-1.903	HH	0.430	0.01	0.01	21.8111	0.4077	DH	0.962	0.004	Ppc CSA ~ BH + DH	0.001	0.285	-0.507	BH	-0.500	0.01	0.02	27.1734	0.2241	DH	0.502	0.08	Ppc CSA ~ HH + DH	0.001	0.321	-1.953	HH	0.508	0.01	0.01	26.1762	0.3690	DH	0.930	0.01	Ppe CSA ~ BH + DH	0.001	0.247	-0.836	BH	-0.385	0.07	0.04	30.1856	0.2521	DH	0.697	0.03	Ppe CSA ~ HH + DH	0.001	0.263	-1.943	HH	0.388	0.01	0.01	29.7799	0.3088	DH	1.022	0.01	Tsm CSA ~ BH + DH	0.001	0.342	-0.881	BH	-0.350	0.01	0.04	23.0464	0.3009	DH	0.725	0.08	Tsm CSA ~ HH + DH	0.001	0.354	-1.880	HH	0.349	0.01	0.01	22.6744	0.3624	DH	1.017	0.01						
C length ~ BH + DH	0.001	0.272	-0.27	BH	-0.111	0.08	0.03	-13.82	0.272																																																																																																																																																																																												
				DH	0.224	0.02				C length ~ HH + DH	0.001	0.268	-0.579	HH	0.106	0.08	0.03	-13.71	0.256	DH	0.312	0.009	LD CSA ~ BH + DH	0.001	0.384	-1.017	BH	-0.453	0.02	0.008	27.1692	0.3236	DH	0.840	0.008	LD CSA ~ HH + DH	0.001	0.395	-2.301	HH	0.447	0.02	0.006	26.8153	0.3863	DH	1.214	0.002	CI CSA ~ BH + DH	0.001	0.303	-0.866	BH	-0.399	0.05	0.02	27.7535	0.2942	DH	0.734	0.01	CI CSA ~ HH + DH	0.001	0.308	-1.988	HH	0.389	0.05	0.02	27.6216	0.3142	DH	1.058	0.006	C CSA ~ BH + DH	0.001	0.335	-0.675	BH	-0.428	0.02	0.01	22.5444	0.2825	DH	0.601	0.02	C CSA ~ HH + DH	0.001	0.360	-1.903	HH	0.430	0.01	0.01	21.8111	0.4077	DH	0.962	0.004	Ppc CSA ~ BH + DH	0.001	0.285	-0.507	BH	-0.500	0.01	0.02	27.1734	0.2241	DH	0.502	0.08	Ppc CSA ~ HH + DH	0.001	0.321	-1.953	HH	0.508	0.01	0.01	26.1762	0.3690	DH	0.930	0.01	Ppe CSA ~ BH + DH	0.001	0.247	-0.836	BH	-0.385	0.07	0.04	30.1856	0.2521	DH	0.697	0.03	Ppe CSA ~ HH + DH	0.001	0.263	-1.943	HH	0.388	0.01	0.01	29.7799	0.3088	DH	1.022	0.01	Tsm CSA ~ BH + DH	0.001	0.342	-0.881	BH	-0.350	0.01	0.04	23.0464	0.3009	DH	0.725	0.08	Tsm CSA ~ HH + DH	0.001	0.354	-1.880	HH	0.349	0.01	0.01	22.6744	0.3624	DH	1.017	0.01																			
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				DH	0.312	0.009				LD CSA ~ BH + DH	0.001	0.384	-1.017	BH	-0.453	0.02	0.008	27.1692	0.3236	DH	0.840	0.008	LD CSA ~ HH + DH	0.001	0.395	-2.301	HH	0.447	0.02	0.006	26.8153	0.3863	DH	1.214	0.002	CI CSA ~ BH + DH	0.001	0.303	-0.866	BH	-0.399	0.05	0.02	27.7535	0.2942	DH	0.734	0.01	CI CSA ~ HH + DH	0.001	0.308	-1.988	HH	0.389	0.05	0.02	27.6216	0.3142	DH	1.058	0.006	C CSA ~ BH + DH	0.001	0.335	-0.675	BH	-0.428	0.02	0.01	22.5444	0.2825	DH	0.601	0.02	C CSA ~ HH + DH	0.001	0.360	-1.903	HH	0.430	0.01	0.01	21.8111	0.4077	DH	0.962	0.004	Ppc CSA ~ BH + DH	0.001	0.285	-0.507	BH	-0.500	0.01	0.02	27.1734	0.2241	DH	0.502	0.08	Ppc CSA ~ HH + DH	0.001	0.321	-1.953	HH	0.508	0.01	0.01	26.1762	0.3690	DH	0.930	0.01	Ppe CSA ~ BH + DH	0.001	0.247	-0.836	BH	-0.385	0.07	0.04	30.1856	0.2521	DH	0.697	0.03	Ppe CSA ~ HH + DH	0.001	0.263	-1.943	HH	0.388	0.01	0.01	29.7799	0.3088	DH	1.022	0.01	Tsm CSA ~ BH + DH	0.001	0.342	-0.881	BH	-0.350	0.01	0.04	23.0464	0.3009	DH	0.725	0.08	Tsm CSA ~ HH + DH	0.001	0.354	-1.880	HH	0.349	0.01	0.01	22.6744	0.3624	DH	1.017	0.01																																
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				DH	0.725	0.08				Tsm CSA ~ HH + DH	0.001	0.354	-1.880	HH	0.349	0.01	0.01	22.6744	0.3624	DH	1.017	0.01																																																																																																																																																																															
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Notes. See Supporting Information Table S2 for all possible models. Pagel's λ (phylogenetic signal), adjusted r^2 (Adj r^2), intercept, slopes were considered for those informative variables based on the Akaike criterion (AICc and Wi).

Boldface denotes significant results. For muscle abbreviations see Table 1. Landing behaviour: BH: belly hit; DH: digit hit; HH: hand hit.

Pp: means the partial p value for each variable; Pt: is the p value for the complete model.

or the coracoid. Our results show that the coracobrachialis is the widest muscle that governs the movements of the humerus. The fact that this muscle originates on the coracoid would indicate that this is the bone that drives the support of the impact in landing.

Muscles involved in the caudopelvic mechanism active during take-off behaviour exhibit similar relative sizes in accordance with the stereotyped hindlimb function during take-off found by Reilly et al. (2016). Our results show that all those muscles involved in the urostyle movement/

stabilization and in the caudopelvic mechanism (Jenkins & Shubin, 1998) need to be well developed, especially in relation to their anatomical CSA. Thus, regardless of their locomotor requirements, anurans exhibit wide coccygeoiliacus and longissimus dorsi, while the coccygeosacralis tends to be short. Considering that during the propulsive thrust, the force is transmitted from the forelimbs to the hindlimbs through the longissimus dorsi (Jenkins & Shubin, 1998), which supposedly should be able to conduct as much force as needed. At the same time, the m. coccygeoiliacus fixes the urostyle

TABLE 5 Values of Akaike criterion (AICc) and Log Likelihood (LogL) that correspond to the evolutionary models tested [Brownian motion (BM), Ornstein-Uhlenbeck (OU) and Early Burst (EB)] for all the muscles and body traits

Morphology	BM			OU			EB			BeMo
	LogL	AICc	wAICc	LogL	AICc	wAICc	LogL	AICc	wAICc	
BL	5.10	-5.45	0.43	-5.55	-3.687	0.45	-2.60	-0.551	0.1	BM-OU
LD length	-1.24	7.24	0.16	1.76	4.07	0.79	-1.24	10.08	0.03	OU
LD CSA	-17.22	39.19	0.27	-14.90	37.41	0.66	42.04	-62.26	0.06	OU
CS length	-7.77	20.29	0.43	-6.28	20.17	0.45	-7.72	23.04	0.10	BM-OU
CS CSA	-15.38	35.51	0.13	-12.17	31.95	0.82	-15.38	38.36	0.03	OU
CI length	1.87	1.00	0.26	4.20	-0.81	0.66	1.87	3.85	0.06	OU
CI CSA	-17.36	39.48	0.18	-14.51	36.63	0.77	-17.36	42.33	0.04	OU
Ppe length	6.57	-8.40	0.53	7.55	-7.50	0.33	6.57	-5.55	0.12	BM
Ppe CSA	-16.97	38.69	0.39	-15.30	38.20	0.50	-16.97	41.54	0.09	OU
Ppc length	3.82	-2.90	0.20	6.55	-5.50	0.74	3.82	-0.05	0.04	OU
Ppc CSA	-15.38	39.02	0.21	-14.51	36.62	0.72	-17.13	41.87	0.05	OU
C length	3.35	-1.95	0.17	6.27	-4.95	0.78	3.35	0.89	0.04	OU
C CSA	-14.37	33.50	0.26	-12.04	31.68	0.66	-14.37	36.35	0.06	OU
Tsm length	4.07	-3.40	0.41	5.64	-3.68	0.48	4.07	-0.55	0.10	BM-OU
Tsm CSA	-16.32	37.39	0.11	-12.91	33.42	0.85	-16.32	40.24	0.02	OU

Notes. BeMo indicates the evolutionary model that best fitted the data based on the wAICc values.

C: coracobrachialis; CI: coccygeiliacus; CS: coccygeosacralis; CSA: cross-sectional area; LD: longissimus dorsi; Ppc: pars clavicularis; Ppe: pars episternalis; Tsm: triceps scapularis medialis; wAICc: weight of the different models.

between the ilia and transmits the propulsive force from the ilia to the urostyle and to the vertebral column (Jenkins & Shubin, 1998). During the muscular contraction, the coccygeiliacus also participates in the posterior gliding of the ilium along the sacral diapophysis, projecting the vertebral column forward (Přikryl et al., 2009). The coccygeosacralis and the coccygeiliacus are both attached to the urostyle, being both antagonist in relation to the movement of the urostyle. The coccygeosacralis rotates the urostyle dorsally, while the coccygeiliacus rotates it ventrally (Přikryl et al., 2009; Table 1), generating probably some kind of trade-off.

We further found that the triceps scapularis medialis is thick in species that land with hand hit and digit hit, such as *Trachycephalus typhonius*. This supports the results of Akella and Gillis (2011) who suggest that this muscle would prevent collapse of the elbow joints as the hindlimbs are lowered to the ground. Akella and Gillis (2011) also showed that the triceps scapularis medialis presents greater activity during most of the landing phases compared to others muscles such as the coracoradialis and procoracohumeralis. It is also the only muscle that exhibits its highest average intensity during the landing phases, and its more intense activity after forelimb has touched the ground (Akella & Gillis, 2011). In accordance with all these data, both Brownian Motion and OU models were equally possible under the AIC. According to Manzano, Abdala, and Herrel (2008), the procoracohumeralis in *Litoria caerulea* and *Phyllomedusa bicolor* showed

a pronounced activity during the swing and stance phases in walking, indicating that the function of this muscle should be more deeply considered.

5 | CONCLUSIONS

Overall, our results indicate a similar conservative myology needed for landing and take-off, with only some muscles exhibiting clear trends associated to these behaviours. An interesting trend that we found was that two muscles tend to be longer, one related to landing, the coracobrachialis, and the other, the coccygeosacralis, related to the take-off. The importance of some muscles such as the procoracohumeralis in landing behaviour and coccygeosacralis in the take-off should be further considered. More studies are needed to shed light about the combined action of muscles and their related tendons which allow a versatile response to the biomechanical challenging actions of take-off and landing in anurans.

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