

A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean *Anolis* lizards

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Summary

Scaling models predict how functional variables change as animals grow or increase in size evolutionarily. However, few experimental studies have found support for the predictions of these models. Here, we use a force plate to investigate the scaling of functional variables associated with jumping within (for three species) and across adults of 12 species of *Anolis* lizards. Both ontogenetically (with the exception of *Anolis carolinensis*) and across the 12 species examined, limb dimensions increased geometrically, making *Anolis* lizards an ideal study system to test the predictions of geometric scaling models. However, both the ontogenetic and interspecific scaling of functional variables deviated in several aspects from model predictions. Unexpectedly, the scaling of functional variables such as acceleration differed for different species. Whereas acceleration capacity increases with

hindlimb length for *A. carolinensis*, no relationship was detected for the other two species. Interspecifically, the inclusion of two large species in our analysis appears to drive the absence of a correlation between acceleration capacity and hindlimb length across species. These data suggest that selection for enhanced jumping performance is relaxed in larger anoles and support the notion that no scaling model seems to be able to comprehensively predict changes in function with size across species; rather, natural selection seems to drive changes in the scaling relationships of some key variables such as force output or acceleration capacity.

Key words: geometric scaling model, jumping, hindlimb, acceleration capacity, morphology, lizard, *Anolis*, biomechanics, force plate technology.

Introduction

The size of an organism is an important attribute that has profound consequences on its ecology, physiology and behaviour (e.g. Pedly, 1977; Schmidt-Nielsen, 1984; Brown and West, 2000; Schmid et al., 2002). Moreover, most organisms must cope with the consequences of changes in size on the functioning of their musculo-skeletal system. In the case of simple geometric growth (i.e. larger organisms simply being scaled-up versions of smaller organisms), changes in linear dimensions are often not matched by changes in function; for example, a doubling of linear dimensions will result in a fourfold increase in surface area and an eightfold increase in volume or mass. Theoretically, this pattern should lead to a discrepancy between the increase in force (proportional to muscle cross-sectional area) and segment mass during growth (Hill, 1950; Schmidt-Nielsen, 1984). The consequence of this discrepancy in growth trajectory between force and mass should be a decrease in the acceleration capacity and ultimately the speed of movement of the segment. Clearly, differences in the maximal speeds of movement can have strong implications for the ecology and survival of an organism (Irschick and

Garland, 2001). In some cases, animals undergo behavioural or ecological changes to overcome these constraints (e.g. McMahon, 1984; Carrier, 1996).

Given the importance of size on animal function, several authors have proposed models that predict the effects of size on the physiology and function of animal movement (e.g. Hill, 1950; McMahon, 1984). If these predictive models are valid, they could shed light on ontogenetic changes in ecology or behaviour, as well as variation in animal function among species. Although universal quarter power scaling laws have been proposed in the past decade (e.g. Brown et al., 2000), these scaling laws appear unable to explain the observed scaling patterns of functional data. Indeed, to date, no single general scaling model can explain the range of observed scaling patterns in morphology, function and behaviour (Biewener, 2000). However, given specific conditions and assumptions, certain models may still apply. Geometric scaling models (i.e. models based on the assumption of isometric growth) might be such an example. Because many ectothermic vertebrates tend to scale geometrically for most characters,

they provide an excellent study system for testing the predictions of these models (Wainwright and Richard, 1995; Meyers et al., 2002). Hill (1950) proposed a scaling model for geometric systems based on the premise that velocity does not change with increases in body size (Hill, 1950). However, little experimental support has been obtained for this model, even when using ectothermic study organisms (Reilly, 1995; Richard and Wainwright, 1995; Wainwright and Richard, 1995; Wainwright and Shaw, 1999; Nauen and Shadwick, 1999, 2001; Hernandez, 2000; Quillin, 2000; Wilson et al., 2000; Meyers et al., 2002). One notable exception is a study investigating the scaling of toad tongue kinematics (O'Reilly et al., 1993). Still, most experimental studies tend to support an alternative model that also assumes geometric scaling but differs in the assumption that velocity increases linearly with increases in linear dimensions (Richard and Wainwright, 1995).

Lizards are good models for scaling studies because much of their growth is geometric (e.g. Meyers et al., 2002). Moreover, lizards in general, and *Anolis* lizards in particular, show substantial variation in adult body size. For example, adult body size ranges from 0.5 g (*Anolis occultus*; Losos, 1990a) to almost 100 g (e.g. *Anolis equestris*). Furthermore, within species, body size increases dramatically from newly hatched lizards to adults, typically by more than one order of magnitude (or a more than threefold increase in hindlimb length). As lizards typically do not display parental care, they need to function from the day they hatch, and thus the selection for high performance at all sizes will probably be strong (Carrier, 1996; Irschick, 2000; Irschick et al., 2000).

Locomotion is of particular interest in scaling studies because of its obvious ecological relevance (e.g. Van Damme and Vanhooydonck, 2001; Irschick and Garland, 2001). Moreover, as the biomechanics of locomotion in general, and jumping in particular, are fairly simple and reasonably well understood (Alexander, 2000; Harris and Steudel, 2002), one can generate specific predictions concerning the effects of size on the dynamics (i.e. displacements, forces, velocities and accelerations) and performance aspects (i.e. distance, jump angle and time) of jumping (see also Table 1; Hernandez, 2000). As *Anolis* lizards are highly arboreal and jump in a variety of behavioural contexts (e.g. escape and feeding; Moermond, 1979; Losos, 1990a,b; Irschick and Losos, 1998), the study of jumping behaviour in anoles is relevant. Another advantage of studying jumping behaviour is that the forces generated during jumping are easily and accurately measured using force plate technologies (Wilson et al., 2000). The accurate measurement of forces is of particular interest, as previous studies have found large differences in the scaling of forces with body size (Wilson et al., 2000; Nauen and Shadwick, 2001; Harris and Steudel, 2002; Meyers et al., 2002).

In the present study, we test whether hindlimb dimensions and the dynamics of jumping in *Anolis* lizards scale as predicted by geometric growth models (see Table 1; Hill, 1950; Richard and Wainwright, 1995). To investigate this issue, we

Table 1. *Scaling predictions of two geometric scaling models versus a linear indicator of size such as body length*

Variable	Hill (1950)	Richard and Wainwright (1995)
Linear dimensions	1	1
Force	2	2
Mass	3	3
Velocity	0	1
Acceleration	-1	1
Durations and timing	1	0
Linear displacements	1	1
Jump distance	0	1
Angles	0	0
Angular velocity	-1	0
Angular acceleration	-1	0

will examine intraspecific scaling patterns for three species of *Anolis* lizard that differ in body size and ecology. Additionally, we investigate whether the evolution of body size in 12 West Indian *Anolis* species is accompanied by proportional increases in limb dimensions and jumping dynamics as predicted by two theoretical models of geometric growth (Table 1).

Materials and methods

Animals

We examined size series of *Anolis carolinensis* (Voigt 1832), *Anolis sagrei* (Dumeril and Bibron 1837) and *Anolis equestris* (Merrem 1820) to investigate ontogenetic scaling. Additionally, adults of a total of 12 species of *Anolis* lizards were used in a comparative analysis. The *A. sagrei*, *A. equestris*, *Anolis garmani* (Stejneger 1899) and *Anolis distichus* (Cope 1861) used in this study were captured in the vicinity of the University of Miami (Miami, FL, USA) and transported to the laboratory at Tulane University. After the experiments, the animals were euthanised and preserved. The *A. carolinensis* were captured in New Orleans, transferred to the laboratory, measured and subsequently returned to the field. All other animals were captured in the field [Jamaica: *Anolis lineatopus* (Gray 1840), *Anolis grahami* (Gray 1845), *Anolis valencienni* (Dumeril and Bibron 1837); Puerto Rico: *Anolis evermanni* (Stejneger 1904), *Anolis cristatellus* (Dumeril and Bibron 1837), *Anolis gundlachi* (Peters 1877), *Anolis pulchellus* (Dumeril and Bibron 1837)], transferred to the laboratory at Tulane University and sacrificed and preserved at the end of the experiments. All experiments were approved by the Institutional Animal Care and Use Committee at Tulane University (IAUCUC approval 0189-2-16-0301).

Jumping data

All animals were induced to jump in 3–5 jumping sessions, each on different days. At least three good trials were obtained per individual in each session. Before and in-between each jumping trial, animals were placed in an incubator set at 32°C (28°C for *A. gundlachi*; see Hertz, 1981, 1992; Huey, 1983;

Huey and Webster, 1976) for at least 1 h. This temperature is close to the preferred field temperatures of these 12 anoles (see references above; D. J. Irschick, unpublished data). During jumping trials, animals were removed from the incubator, placed on the force plate and induced to jump to a horizontal branch positioned at the level of the force plate and placed just outside of the presumed maximal reach of each individual. Maximal efforts were further elicited by startling the animals using a sudden clapping of hands or a slight tap on the base of the tail (only for larger individuals). We only included jumps in which all four feet were squarely on the force plate and for which the tap on the tail did not coincide with the timing of the jump. We only included the maximal jump (longest distance) for each individual obtained in all trials and sessions combined as our estimate of maximum jumping performance.

Jumping in *Anolis* lizards consisted of a preparatory phase, the actual take-off phase, a flight phase and the landing (see Bels and Theys, 1989). The preparatory phase involves the positioning of the feet anterior to the pelvic girdle, just posterior to, or at the level of, the hands. During this phase, the lizards also align their bodies with the jump direction. The actual take-off phase involves the rapid extension of the hindlimbs from a standstill and the stretching of the vertebral column (see also Bels and Theys, 1989). The take-off phase ends when the toes no longer touch the force plate. Only the forces exerted during the take-off phase were analysed here.

A custom-designed force plate (30 cm×18 cm×1 cm, length × width × height) was used to measure the three-dimensional ground reaction forces during jumping (see Heglund, 1981). The output of the strain gauges was sent to a 12-bridge, 8-channel amplifier (K & N Scientific, Greenfield, MA, USA) and subsequently A–D converted at 10 kHz (Instrunet, model 100B). Digital traces were read into a G4 Macintosh computer using Superscope (GW Instruments, Somerville, MA, USA). Force traces were smoothed using a low-pass filter before further analysis. First, body mass was subtracted from the forces in the vertical direction (*Z*). Next, the resultant force vector was calculated using the vector sum of the individual *X*-, *Y*- and *Z*-forces. The acceleration of the centre of mass was obtained by dividing the resultant ground reaction force (3-D) by the body mass of the animal. Numerical integration of the acceleration profile yielded the instantaneous velocity of the centre of mass. As the animals started the jump from a standstill (i.e. no movement or dip in the force trace was noted prior to rapid extension of the hindlimbs in all species examined), the integration constant for the velocity integration was set to zero. Instantaneous mass-specific power was calculated by multiplying the instantaneous velocity and acceleration profiles. The displacement of the centre of mass was obtained by numerical integration of the instantaneous velocity during take-off. The angle of take-off was determined using the horizontal (*X*+*Y*) and vertical (*Z*) ground reaction forces during jumping.

From these traces, we extracted the peak acceleration during take-off, the velocity at take-off (i.e. the terminal velocity at the end of the take-off phase), the peak power during take-off,

the time to peak power, the time to peak acceleration, the displacement of the centre of mass during take-off (further referred to as contact time distance) and the duration of the entire take-off phase. Using the take-off angle (θ), the take-off velocity (V_t) and the horizontal displacement of the centre of mass during take-off (D_h), we calculated the horizontal jump distance as $D=D_h+D_a+D_f$, where D_f is the horizontal distance travelled from take-off height back to resting height, and D_a is the distance travelled during the ballistic phase of jumping [$D_a=(V_t^2 \times \sin 2\theta)/g$; see Marsh and John-Adler, 1994]. The output of the force plate (i.e. calculations of acceleration, velocity, take-off angle and jump distance) was validated using high-speed video recordings (250 frames s^{-1}) of maximal jumps for seven individuals of *A. valencienni* (see Wilson et al., 2000).

Morphometrics

Immediately after measuring their jumping performance, all animals were weighed (to the nearest 0.0001 g using an M-220 electronic balance; Denver Instruments, Denver, CO, USA) and measured (to the nearest 0.01 mm using digital callipers; Mitutoyo, Sakato, Japan). For each individual, the following morphological variables were measured on the right side (from a dorsal perspective): snout-vent length, forelimb length (length of the entire, fully extended forelimb, including the length of the longest toe), hindlimb length (length of the entire, fully extended hindlimb, including the length of the longest toe),

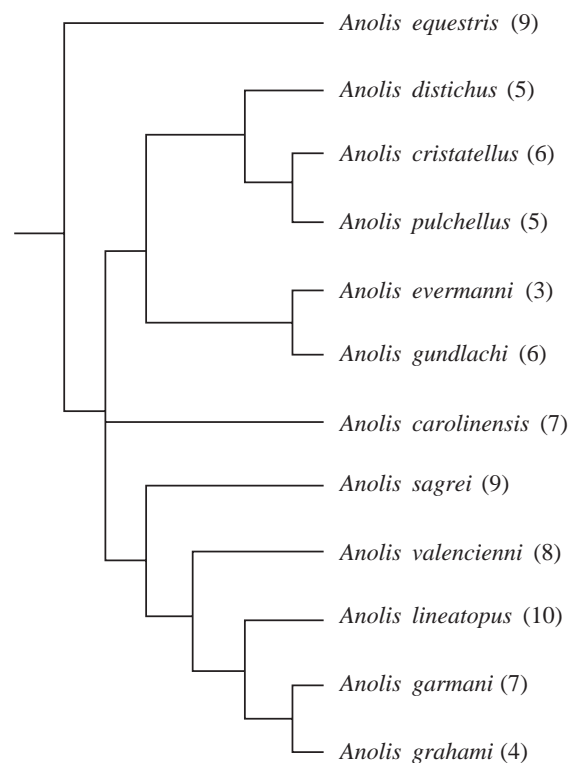


Fig. 1. Phylogenetic tree depicting the relationships between the species in our analysis. Numbers in parentheses represent sample sizes for each species. Based on Jackman et al. (1999, 2002).

femur length (from the articulation of the femur with the hip to the end of the femur), tibia length (from the joint with the femur to the articulation with the metatarsi), metatarsus length (from the articulation with the tibia to the base of the longest toe) and the length of the longest toe (see also Losos, 1990a). Additionally, the length of the tail, including regenerated parts, was measured from vent to tail tip. All measurements were taken externally. To increase our sample size, morphometric data were collected for an additional 17 *A. sagrei* and 12 *A. equestris* using preserved specimens.

Analyses

All data were analysed using reduced major axis regressions. Deviations of predicted slopes were considered significant if the predicted slope fell outside the 95% confidence interval of the reduced major axis regression slope. To investigate whether limb proportions in each species increased isometrically, we regressed the \log_{10} -transformed limb proportions against the \log_{10} -transformed snout-vent length for each individual. We did not use body mass, as it was subject to substantial day-to-day variation in small animals. The scaling of jumping performance was investigated by regressing

the \log_{10} -transformed jumping performance data against the \log_{10} -transformed hindlimb length for all individuals. Hindlimb length was chosen as the independent variable in these regressions as (1) it is functionally related to the performance variables investigated and (2) to allow a comparison of data across species, given that hindlimb length scaled with significant negative allometry relative to snout-vent length in *A. carolinensis* only. All regression analyses were performed using SPSS (version 10; Statsoft Inc., Tulsa, OK, USA).

To investigate the interspecific scaling of limb dimensions and jumping performance, we gathered data on a wide range of species differing in body size (Fig. 1). However, as species are not independent data points but are related evolutionarily (Felsenstein, 1985; Harvey and Pagel, 1991), we used independent contrast analysis to investigate the interspecific scaling of morphological and functional data (see also Blob, 2000; Van Damme and Vanhooydonck, 2001). Only data for adults of all species (i.e. reproductively active animals) were included in the interspecific analysis. We used the PDAP package (Garland et al., 1999) to calculate the independent contrasts of all variables of interest using the \log_{10} -transformed

Table 2. Ontogenetic scaling of limb and body proportions in three species of *Anolis* lizards using data from both live and preserved specimens

Variable	N	Intercept	Slope	r	Confidence limits	
<i>Anolis equestris</i>						
Hindlimb length	21	0.00	0.92	0.97	0.78	1.07
Forelimb length	21	-0.18	0.93	0.97	0.79	1.06
Femur length	21	-0.64	0.98	0.93	0.63	1.34
Tibia length	21	-0.63	0.97	0.97	0.86	1.07
Metatarsus length	21	-1.06	1.06	0.90	0.75	1.37
Longest toe length	21	-0.59	0.89	0.84	0.39	1.40
Mass	21	-8.04	3.10	0.96	2.26	3.94
Tail length	21	-0.85	1.49	0.63	0.82	2.16
<i>Anolis sagrei</i>						
Hindlimb length	30	0.07	0.89	0.97	0.76	1.02
Forelimb length	30	-0.31	0.98	0.97	0.91	1.05
Femur length	30	-0.47	0.89	0.95	0.77	1.02
Tibia length	30	-0.62	0.99	0.97	0.83	1.15
Metatarsus length	30	-0.75	0.95	0.96	0.78	1.12
Longest toe length	30	-0.46	0.80	0.89	0.56	1.04
Mass	30	-8.11	3.31	0.99	3.05	3.58
Tail length	30	0.01	1.11	0.78	0.73	1.49
<i>Anolis carolinensis</i>						
Hindlimb length	52	0.05	0.85	0.98	0.78	0.92
Forelimb length	52	-0.22	0.90	0.96	0.84	0.95
Femur length	52	-0.51	0.88	0.95	0.77	0.99
Tibia length	52	-0.53	0.89	0.98	0.85	0.94
Metatarsus length	52	-0.74	0.89	0.96	0.82	0.95
Longest toe length	52	-0.60	0.83	0.92	0.72	0.94
Mass	52	-7.62	2.96	0.99	2.80	3.12
Tail length	52	0.11	1.07	0.84	0.88	1.25

Results of reduced major axis regressions of \log_{10} -transformed morphometric data against \log_{10} of snout-vent length for ontogenetic series of the three species included in the ontogenetic scaling part. All regressions are significant at the $\alpha=0.01$ level. Slopes indicated in bold are significantly different from model predictions.

species means of all variables. To do so, we constructed a tree depicting the phylogenetic relationships among the species included in our analysis based on literature data (see Jackman et al., 1999, 2002; Fig. 1). As no data on divergence times are available for all the species in the analysis, all branch lengths were set to unity. To check that constant branch lengths were adequate for all traits, we inspected the diagnostic graphs in the pdtree program (Garland et al., 1999). To calculate the slopes of the regressions, the standardised contrasts of all morphometric variables were regressed against the standardised contrasts of snout-vent length, and the standardised contrasts of jumping performance were regressed

against the standardised contrasts of hindlimb length, using a reduced major axis regression analysis forced through zero (Garland et al., 1992).

Results

Ontogenetic scaling of morphology

The assumptions of geometric scaling models are that linear dimensions should scale with a slope of one, surfaces with a slope of two and masses with a slope of three relative to a linear measure of overall size such as snout-vent length (Hill, 1950; Richard and Wainwright, 1995; Table 1). Whereas nearly all

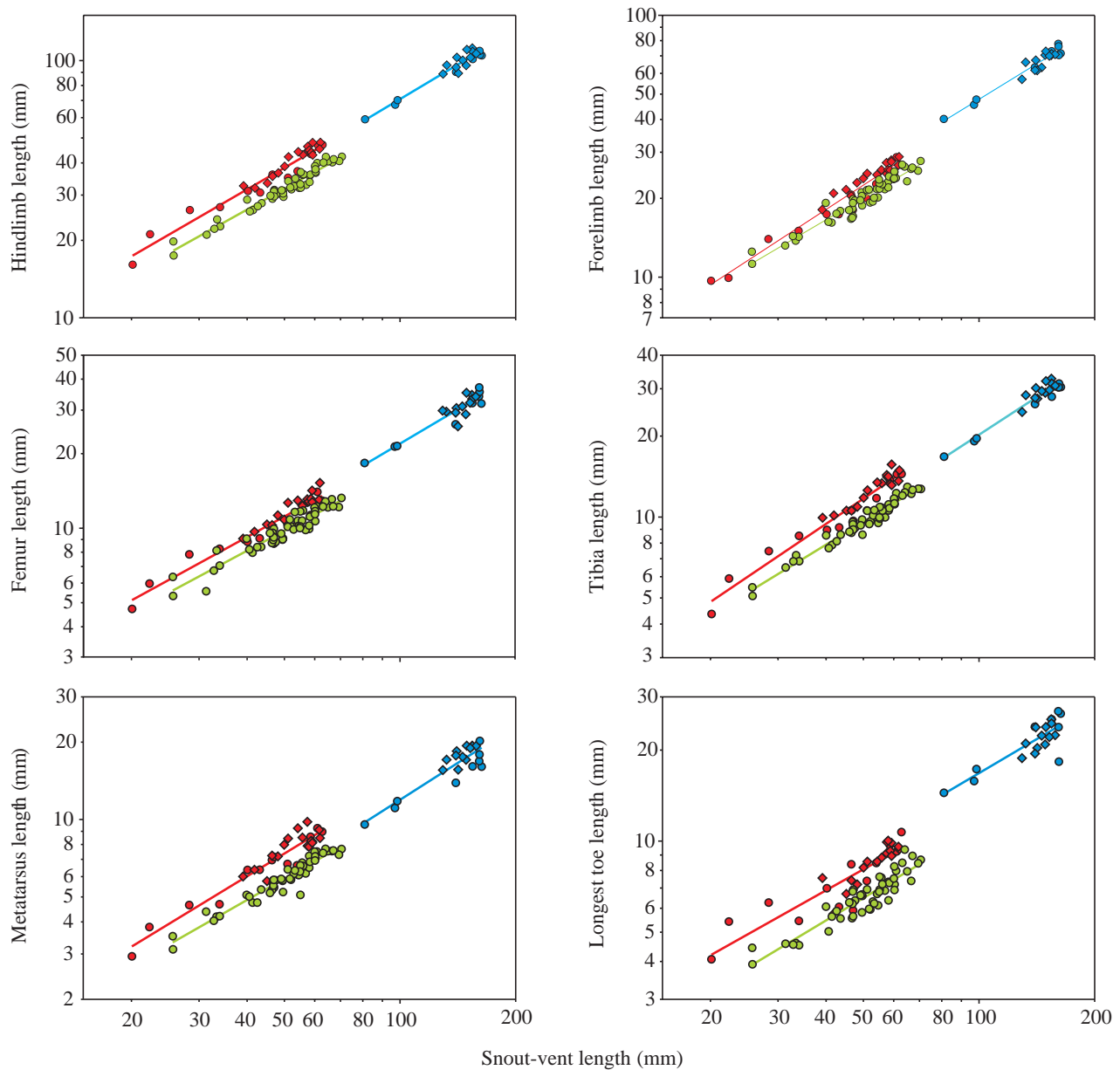


Fig. 2. Ontogenetic scaling of limb proportions in three species of *Anolis* lizard: *Anolis carolinensis* (green), *Anolis sagrei* (red) and *Anolis equestris* (blue). Circles represent data for live animals, which were also used for the force plate trials. Diamonds represent data for preserved specimens. Note that the regression lines depicted on the graphs are linear least-squares. Slopes and r values of the reduced major axis regressions are presented in Table 2.

measures increased geometrically for both *A. equestris* and *A. sagrei* (with the exception of body mass in *A. sagrei*), limb dimensions increased with significant negative allometry in *A. carolinensis* (Table 2; Fig. 2).

Ontogenetic scaling of jumping performance

Although the different species showed differences in the scaling of functional variables relative to body size (Table 3), overall trends were similar (see Fig. 3; Table 3). On average, our experimental data supported the Richard and Wainwright (1995) model more closely than the Hill (1950) model (see Tables 1, 3). Interestingly, the data for both acceleration capacity and peak power showed different trends when comparing data for *A. carolinensis* with the data for the other two species. Whereas peak acceleration capacity and peak power scaled significantly with hindlimb length in *A. carolinensis*, no significant correlations could be observed in the other two species. Moreover, peak power scaled with significant positive allometry in *A. carolinensis* (Table 3). Peak

acceleration scaled according to the Richard and Wainwright (1995) model (see Tables 1, 3). The scaling of peak force (all species) is predicted by neither of the two models. Peak force scaled with significant positive allometry relative to hindlimb length in all three species.

Interspecific scaling of morphology and jumping performance

The interspecific scaling of hindlimb dimensions, tail length and body mass did not show any significant deviations from the predicted values. Thus, across species, evolutionary increases in snout-vent length change in concert with evolutionary increases in limb, body and tail dimensions, as predicted for geometrically growing systems (Table 4; Fig. 4). Take-off angle did not scale with hindlimb length, as predicted by both models (Table 1). Both jump distance and peak force production also scaled in accordance with model predictions (i.e. slopes not significantly different from 1 and 2, respectively; Table 4). The other functional variables all scaled with slopes intermediate between those predicted by the Hill

Table 3. *Ontogenetic scaling of functional variables associated with jumping in three species of Anolis lizards*

Variable	<i>N</i>	Intercept	Slope	<i>r</i>	Confidence limits	
<i>Anolis equestris</i>						
Take-off velocity	9	-1.18	0.72	0.73*	0.33	1.12
Peak acceleration	9	-	-1.01	0.37	-	-
Peak power	9	-	1.35	0.17	-	-
Peak force	9	-6.78	3.42	0.93*	2.78	4.07
Duration of take-off phase	9	-2.28	0.74	0.64*	0.30	1.18
Take-off angle	9	-	1.09	0.30	-	-
Jump distance	9	-3.04	1.36	0.88*	-0.55	3.27
Contact time distance	9	-3.46	1.25	0.98*	0.87	1.63
Time to peak power	9	-	0.98	0.55	-	-
Time to peak acceleration	9	-	1.06	0.14	-	-
<i>Anolis sagrei</i>						
Take-off velocity	13	-0.92	0.73	0.65*	0.31	1.14
Peak acceleration	13	-	0.91	0.25	-	-
Peak power	13	-	1.42	0.47	-	-
Peak force	13	-7.39	4.10	0.97*	3.24	4.96
Duration of take-off	13	-	0.74	0.48	-	-
Take-off angle	13	-	1.14	0.33	-	-
Jump distance	13	-2.65	1.39	0.72*	0.67	2.12
Contact time distance	13	-3.24	1.33	0.62*	0.50	2.17
Time to peak power	13	-	0.92	0.43	-	-
Time to peak acceleration	13	-	-0.47	0.45	-	-
<i>Anolis carolinensis</i>						
Take-off velocity	52	-1.12	0.82	0.71*	0.69	0.95
Peak acceleration	52	0.01	0.95	0.37*	0.72	1.19
Peak power	52	-0.10	1.59	0.59*	1.22	1.97
Peak force	52	-6.99	3.89	0.95*	3.49	4.29
Duration of take-off	52	-2.01	0.62	0.48*	0.43	0.80
Take-off angle	52	-	0.92	0.14	-	-
Jump distance	52	-2.90	1.50	0.71*	1.23	1.78
Contact time distance	52	-3.10	1.17	0.67*	0.90	1.43
Time to peak power	52	-2.28	0.73	0.40*	0.54	0.92
Time to peak acceleration	52	-	2.95	0.24	-	-

Results of reduced major axis regressions of log₁₀-transformed kinesiological data against log₁₀ of hindlimb length for ontogenetic series of the three species included in the present study. * denotes significant regressions at the $\alpha=0.05$ level.

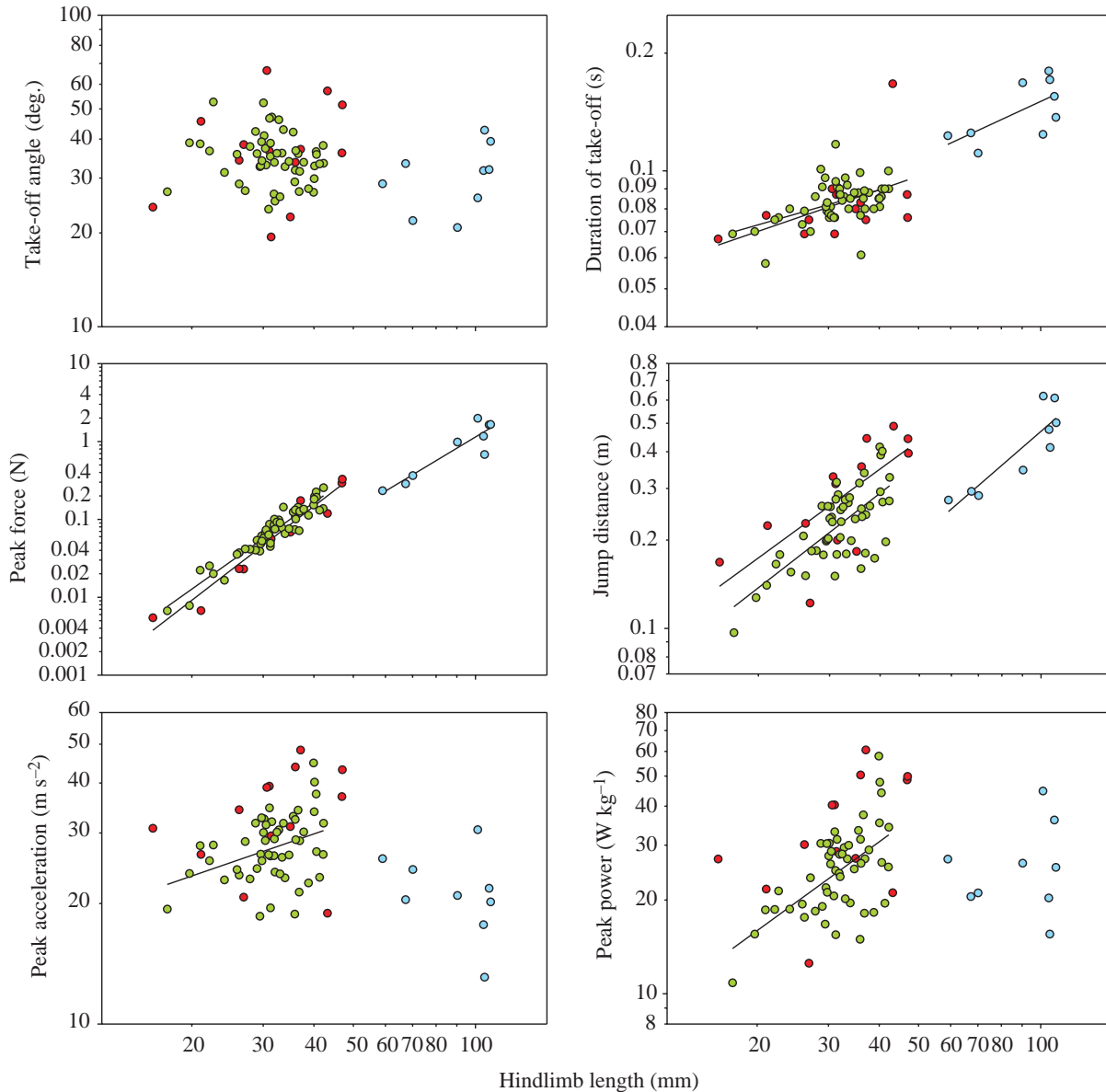


Fig. 3. Ontogenetic scaling of jumping performance in three species of *Anolis* lizard: *Anolis carolinensis* (green), *Anolis sagrei* (red) and *Anolis equestris* (blue). Note that the regression lines depicted on the graphs are linear least-squares. The broken line indicates that the regression approached significance. Slopes and r values of the reduced major axis regressions are presented in Table 3.

(1950) or Richard and Wainwright (1995) models (see Tables 1, 4).

Discussion

Models of growth

A fundamental assumption of the models tested here is that morphological scaling is geometric. If this assumption is not met, then the model predictions for the scaling of functional variables will not hold. Our data for the intraspecific scaling for three species of *Anolis* lizard indicated that limb dimensions grew geometrically for two out of three species examined, with only *A. carolinensis* exhibiting negative

allometry for the hindlimb. Based on the fact that both body mass and tail length scale geometrically with body length, our results show that for *A. carolinensis*, larger individuals will have relatively short limbs. Negative allometric growth of the hindlimb has also been documented in other lizard species (e.g. *Dipsosaurus dorsalis*; Irschick and Jayne, 2000). In general, interpreting the adaptive significance of allometric trends is difficult. One possibility is that, because adult *A. carolinensis* rely heavily on crypsis as a predator-avoidance strategy and move undisturbed in nature at very slow speeds (see Irschick and Losos, 1998), selection for long limbs in adults is either weak or non-existent. However, selection for relatively long limbs in the juvenile life stages of *A. carolinensis* may be

Table 4. Interspecific scaling of limb proportions and jumping performance across 12 species of *Anolis* lizards

Variable	<i>N</i>	Slope	<i>r</i>	Confidence limits	
Morphometrics					
Hindlimb length	11	1.02	0.93*	0.80	1.24
Forelimb length	11	1.10	0.96*	0.96	1.24
Femur length	11	1.03	0.95*	0.81	1.25
Tibia length	11	0.98	0.93*	0.74	1.22
Metatarsus length	11	0.96	0.92*	0.65	1.28
Longest toe length	11	1.20	0.86*	0.76	1.64
Mass	11	2.85	0.98*	2.43	3.27
Tail length	11	1.22	0.86*	0.90	1.55
Jumping performance					
Take-off velocity	11	0.34	0.75*	0.09	0.59
Peak acceleration	11	-0.48	0.30	-	-
Peak power	11	0.66	0.16	-	-
Take-off angle	11	-0.22	0.36	-	-
Jump distance	11	0.67	0.79*	0.18	1.16
Peak force	11	2.47	0.93*	1.71	3.23
Duration take-off	11	0.38	0.78*	0.27	0.49
Time to peak power	11	0.45	0.82*	0.29	0.61
Time to peak acceleration	11	0.33	0.77*	0.20	0.46
Contact time distance	11	0.47	0.90*	0.37	0.58

Results of reduced major axis regressions of the standardised contrasts of \log_{10} -transformed morphometric data against the standardised contrasts of \log_{10} -transformed snout-vent length (morphometrics) and of the standardised contrasts of the \log_{10} -transformed jumping performance variables against the residual contrasts of the \log_{10} -transformed hindlimb length (jumping performance) for a comparative data set of 12 species. Note that the intercept of the regression on the contrast data equals 0 by definition (Garland et al., 1993). * denotes a significant regression at the $\alpha=0.05$ level.

strong for several reasons: (1) juvenile *Anolis* lizards frequently escape by jumping to nearby perches, and the ability to jump quickly or far may be important for evading predators or capturing prey (Irschick, 2000; Irschick et al., 2000) and (2) selection is often very strong during the juvenile life stages (Carrier, 1996). Nevertheless, across all the species in our analysis, we detected geometric scaling of limb proportions with snout-vent length. Thus, in general, *Anolis* lizards are a good system to test the predictions of geometric scaling models.

Predicting jumping dynamics from hindlimb length

Given its obvious and direct relevance to jumping (Losos, 1990a; Wilson et al., 2000; Harris and Steudel, 2002), we used hindlimb length as a size indicator to investigate the scaling of jumping dynamics. Hindlimb length is often considered a good indicator of jumping and running performance and is often used in ecomorphological and evolutionary studies as a proxy for locomotor capacity (e.g. Losos, 1990a,c; Garland and Losos, 1994; Vanhooydonck and Van Damme, 1999; Melville and Swain, 2000). However, within the species of *Anolis* studied here, the dynamics of jumping were generally poorly predicted by scaling models based on limb length (i.e. compare Table 1 with Table 3). Velocity increased with hindlimb length as predicted by Richard and Wainwright (1995) in both *A. equestris* and *A. sagrei*. However, in *A. carolinensis*, velocity increased with significant negative allometry (slope less than 1; see Table 3). Jump distance again

increased with hindlimb length, as predicted, in *A. sagrei* and *A. equestris* but scaled with positive allometry in *A. carolinensis* (see Table 3). Given that velocity scaled with negative allometry relative to hindlimb length in *A. carolinensis* and that jump distance (scaling with positive allometry relative to hindlimb length) is proportional to take-off velocity and take-off angle (invariant with hindlimb length), this suggests that variables other than limb length affect take-off velocity in this species. Across species, both take-off velocity and jump distance increased significantly with hindlimb length. However, whereas take-off velocity scaled with significant negative allometry, jump distance increased isometrically with hindlimb length. Here too, hindlimb length does not seem to be the sole predictor of take-off velocity.

Scaling of jumping dynamics

The maximal forces generated during take-off scaled with significant positive allometry for all species. However, interspecifically, peak force scaled as predicted by both scaling models (see Tables 1, 4). The deviations of the ontogenetic scaling of forces from model predictions indicate that as animals grow, muscle physiological cross section increases disproportionately with hindlimb length. This could, in turn, be the result of disproportionate increases in muscle mass with size and/or could be the result of changes in muscle architecture throughout ontogeny. The existing data for the interspecific scaling of leg muscles in mammals indicate that

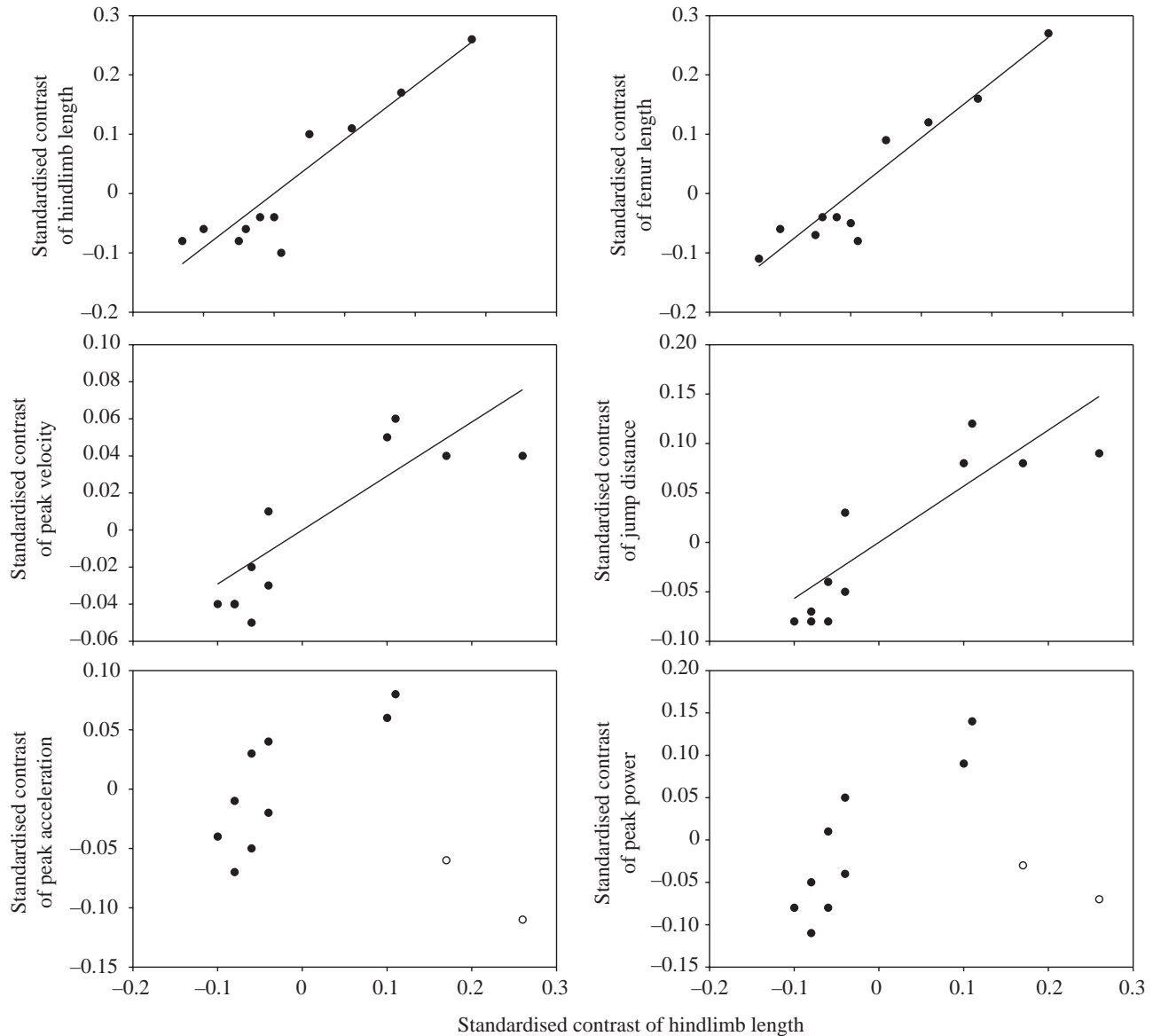


Fig. 4. Comparative scaling of limb proportions and jumping performance in *Anolis* lizards. Data represent standardised contrasts. Note that the regression lines depicted on the graphs are linear least-squares. Open circles indicate the contrasts between the two large species in our analysis and their respective sister nodes (see Discussion). Slopes and r values of the reduced major axis regressions are presented in Table 4.

allometries in the scaling of fibre lengths, muscle masses and moment arms can potentially all occur (Castiella and Casinos, 1990). Other parameters that might be important in determining the scaling of force output are the pennation angle of the muscle (Gans and De Vree, 1987) and fibre type (Peters, 1989). To our knowledge, no data are available on the intraspecific scaling of functional properties of muscle in ectotherms (but see Zimmerman and Lowery, 1999). Given that deviations from model predictions for scaling of forces are common (Quillin, 1999; Herrel et al., 1999; Nauen and Shadwick, 2001; Meyers et al., 2002), these kinds of data would be especially useful.

As a consequence of the scaling of forces and body mass versus hindlimb length (see Tables 2, 3), maximal acceleration

capacity increased significantly with hindlimb length in *A. carolinensis* (force increasing proportionally to body mass) but did not change with 'size' for the other two species. Despite the fact that body mass increased disproportionately with length in *A. sagrei* (Table 2) and that increases in force are not as dramatic in *A. equestris* when compared with the two other species (Table 3), we still would have expected a significant positive relationship between limb length and acceleration capacity with a slope of approximately 1, as predicted by the Richard and Wainwright (1995) model. Whereas we observed a slope of approximately 1 in *A. sagrei* (not significant, however), the regression of hindlimb length versus acceleration capacity was negative in *A. equestris* (see Table 3; Fig. 3). Clearly, more experimental data on jumping in *A.*

sagrei and *A. equestris* are needed to determine whether the absence of a correlation between hindlimb length and acceleration is a real phenomenon or simply a sampling artefact (note the broad confidence limits in Table 3 and spread of the data in Fig. 3).

Size and the evolution of jumping capacity in Anolis lizards

Across species, we also did not detect a significant relationship between maximal acceleration capacity and size. Inspection of the relationship between acceleration and hindlimb length across species (Fig. 4) suggests that the absence of a correlation is largely driven by the inclusion of two large species in the analysis (i.e. large contrast in hindlimb length but small contrast in acceleration capacity between *A. garmani* and *A. equestris* and their respective sister nodes/taxa). Indeed, when rerunning the independent contrast analysis without the two large species (*A. equestris* and *A. garmani*), we obtain a highly significant positive relationship with a slope not significantly different from 1 ($r=0.83$, $P<0.01$, $N=10$, slope=0.72, confidence limits=0.3–1.12). Why is there this disproportionate scaling of force to body mass in small versus big species? The data gathered here indicate that there might be a size limit above which a positive allometric scaling of limb muscle force is no longer possible or, alternatively, no longer required. Along these lines, two explanations are possible. First, there is some mechanical limit to the absolute amount of force that can be exerted by the limbs, which in turn might be driven by the scaling of bone or tendon strength. Given that forces scale with length to the fourth power (in the two smaller species), the stresses exerted on the bones and tendons will become disproportionately large if bone or tendon surface area scales geometrically (i.e. as length to the second power). Consequently, larger animals will be operating at lower safety factors (see also Biewener, 2000), which may limit the scaling of force output of the system. Alternatively, there might be a lack of selective pressure for disproportionately strong muscles in large lizards. Because large animals have absolutely long limbs, they are capable of jumping long distances in nature, and increasing jumping performance even more may not be ecologically relevant (but see Van Damme and Van Dooren, 1999). On the other hand, large anoles might also be big enough such that alternative anti-predator strategies become feasible. Indeed, large *Anolis* lizards such as *A. equestris* or *A. garmani* often attempt to bite with their powerful jaws when confronted with (human) predators (A. Herrel, personal observation).

A similar pattern was observed for the scaling of peak mass-specific power. Whereas a significant increase with hindlimb length was observed for *A. carolinensis*, mass-specific power output did not scale with hindlimb length in the other two species. Again, low sample sizes for *A. equestris* and *A. sagrei* do not allow us to speculate whether these differences are real or not. Interestingly, also across species, mass-specific power output did not scale with hindlimb length. Here too, the absence of a relationship seems to be driven by the inclusion of the two large species in our analysis. Given that take-off

velocity increases with hindlimb length across all species, this suggests that force production (and thus acceleration capacity) is limited in the largest species.

Interestingly, Wilson et al. (2000) found similar results for the scaling of jumping in frogs using methods comparable to ours. Whereas across small sizes of frogs (metamorphs up to 1 g), forces, velocities and accelerations scaled as observed for *A. carolinensis* (strong positive relationships with size), the data for the larger post metamorphs corresponded more closely to the scaling patterns observed for the largest species in our analysis. Wilson et al. (2000) suggested that these trends could be explained by relaxed selection for jumping performance in larger animals. However, whereas in large frogs jump distance was invariant across different body sizes, in the larger lizards acceleration capacity and power output did not change with body size (see Fig. 3). If length or mass independence is indeed the criterion to determine which performance parameters are critical (Emerson, 1978) then this indicates differences in selective pressures for frogs and lizards. Whereas for some frogs (Wilson et al., 2000) jump distance seems to be the critical variable, for the large lizards studied here, as well as for the frogs studied by Emerson (1978), acceleration capacity, and thus quickness of movement, seems to be more important. Also, across species, acceleration capacity and power output are invariant of hindlimb length, indicating that acceleration capacity (rather than jump distance) might be the key aspect of jumping, driving the evolution of jumping performance in *Anolis* lizards.

In summary, our data indicate that scaling laws cannot be applied universally to predict changes in function with size, even when considering closely related species that grow according to model assumptions. Whereas no universal laws seem to apply, deviations from general laws or predictions seem to be common (see also Biewener, 2000). However, once the scaling of certain key functional aspects (e.g. velocity and forces) has been derived experimentally, other functional parameters can be predicted. Our data, together with data from previous studies, suggest that natural selection may have driven some aspects of the evolution of jumping among anole species of varying sizes, but much variation remains to be explained (Tyler-Bonner and Horn, 2000; Alexander, 2000). Further studies investigating the limits on scaling of forces, muscle architecture and geometry and muscle contraction characteristics might prove to be especially insightful in explaining the differential scaling of force output across different body sizes (see Wilson et al., 2000).

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