
12 Power Generation during Locomotion in *Anolis* Lizards: An Ecomorphological Approach

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12.1 INTRODUCTION

Movement requires the generation of muscular power. How much mechanical power a muscle can produce is determined by its physiological properties, such as force-velocity relationship, pattern of stimulation, and strain waveform and

amplitude [1–5]. High power outputs are typically associated with explosive movements such as fast starts, jumping, or take off in flying organisms [6–8]. Among species or higher taxa, mechanical power output and muscle physiology can vary dramatically. For instance, Wakeling and Johnston [9] showed that among six teleost fish species, total (hydrodynamic) power output during fast starts varied 10-fold, i.e., from around 16 W kg⁻¹ to over 160 W kg⁻¹, and that this interspecific variation was associated with differences in body shape and natural temperature regime. Moreover, muscle power output limits the fast-start performance of these animals [9]. Similarly, large differences in muscle power output have been measured in other studies comparing species, such as birds [10] and lizards [11], or life-history stages within one species, such as eels [12] and frogs [13].

Muscle power output is determined by the interaction between the active muscles and the external environment through which the organism is moving [2]. This becomes clear when comparing muscle power output in individuals moving through different media, such as water and air [14,15]. Ducks, for instance, produce less power when they are swimming than when they are walking, and their work, forces, and muscle strains differ between the two locomotor modes [15]. Additionally, different locomotor modes in the same medium, such as walking vs. running or running vs. jumping, might impose different power requirements on the locomotor musculature of an organism. Similarly, in legged animals, the configuration or movement pattern of a limb during different locomotor behaviors can affect muscle power output. *In vivo* changes in configuration or posture and power output can be studied by measuring muscle performance, such as power output, in concert with morphological and/or kinematical analyses [16,17].

At an even larger scale, different (micro) habitats might impose demands on the locomotor muscle system with regard to power output. For instance, arboreal habitats are extremely complex and often require organisms to jump from branch to branch. Because jumping requires high power outputs [8,18], arboreal organisms are expected to be able to generate high muscular powers. Similarly, lizards such as geckoes that often move on vertical substrates against gravity while escaping from predators [19] are expected to have high muscle mass-specific power outputs [20].

Given the potential for differences in limb configuration during different locomotor modes and its potential effect on power output, we compare mechanical power output in *Anolis* lizards while accelerating from a standstill and while jumping. We examined these two locomotor modes because *Anolis* lizards typically use burst running and jumping to escape from predators or when searching for food [21], suggesting that the selective forces acting on the generation of high mechanical power output should be strong. For two of the *Anolis* species, we furthermore quantify joint angles during running and jumping to investigate whether differences in limb configuration might explain differences in power output.

Additionally, we investigate whether muscle mass-specific power output has evolved within *Anolis* lizards in response to variation in microhabitat use and behavior. Previous ecomorphological studies have shown that *Anolis* lizards have evolved into ecologically and phenotypically distinct forms termed *ecomorphs*, including trunk-ground, trunk-crown, crown-giant, and twig ecomorphs [22–25]. Thus, although most species are classified as “arboreal,” some are more ground

dwelling, while others occur almost exclusively in vertical microhabitats. Consequently, we expect higher mechanical power outputs to evolve in species frequently occupying arboreal habitats because they often have to move against gravity. Similarly, we expect high power outputs to evolve in species that escape upward toward the canopy when threatened by a predator. Therefore, we expect to find correlations between muscle power output during locomotion and the habitat occupied by these animals. Specifically, we address the following questions: (1) Have muscle mass-specific power output during running and jumping coevolved? (2) Are interspecific differences in muscle mass-specific power output correlated with differences in ecology, i.e., microhabitat use? (3) Do differences in limb configuration explain differences in power output?

12.2 MATERIAL AND METHODS

12.2.1 ANIMALS

We captured male individuals of 10 species *Anolis* by hand or noose at different field sites between November 2001 and June 2002. *A. carolinensis*, *A. sagrei*, *A. distichus*, and *A. garmani* were captured at mainland U.S. sites (*A. carolinensis* at New Orleans, LA; all the others at Miami, FL); *A. grahamsi*, *A. lineatopus*, and *A. valencienni* were caught in Jamaica (Discovery Bay), and *A. evermanni*, *A. gundlachi*, and *A. pulchellus* were caught in Puerto Rico (El Verde). We transported these species back to the laboratory at Tulane University. Upon arrival in the laboratory, we kept the lizards in pairs in 40-L terraria lined with leaf litter. We fed them live crickets dusted with calcium three times a week and sprayed them with water daily.

12.2.2 MORPHOLOGY

We used digital calipers (Mitutoyo CD-15DC; ± 0.01 mm) to measure snout-vent length (measured from the tip of the snout to the cloaca) on all individuals used in the running trials. Between 1 and 3 individuals of the 10 species included in our analysis were sacrificed for morphological analysis. Specimens were preserved in 10% aqueous formalin and stored in 70% aqueous ethanol solution. Before dissection, we weighed the intact specimens to the nearest 0.01 g on an electronic balance (A & D Instruments, FX 3200; ± 0.01 g). We subsequently dissected out all the hind limb muscles of one hind limb. We then weighed all femur retractor muscles and all knee and ankle extensor muscles separately on a Mettler MT 5 electronic balance (± 0.00001 g). We used the mass of these muscles in further analyses because these are the only muscles potentially responsible for generating propulsion. Muscle and body masses were averaged per species.

12.2.3 RUNNING TRIALS

We induced the lizards to run up a 2-m long dowel (diameter of 8 cm) by clapping our hands and/or by tapping the base of their tails. The plastic dowel, covered with a mesh to provide sufficient traction, was placed against the wall at an angle of 45°. Individual lizards were filmed laterally using a high-speed video camera (Redlake

Motionscope PCI camera) at 250 Hz. We conducted between 5 to 10 trials per individual over several nonconsecutive days. Prior to experimentation and in between trials, we placed the lizards in an incubator set at 32°C for at least 1 h to attain body temperatures similar to their preferred field body temperatures [26].

The running trials for the Puerto Rican species (i.e., *A. pulchellus*, *A. gundlachi*, and *A. evermanni*) were conducted at the field station in Puerto Rico within 24 hr of capture. The experimental setup differed from the laboratory setup in the following ways: lizards were filmed at 240 Hz using a JVC high-speed video camera. Prior to filming and in between trials, the lizards were placed in individual bags in the shade to attain temperatures equal to or near the environmental temperature (30°C).

For analysis, we selected sequences in which the lizard (1) started from a complete standstill, (2) ran over a total distance of at least 25 cm, and (3) ran on top of the dowel (i.e., in a straight line). For these sequences, we digitized the tip of the lizard's snout for every frame using MOTUS software by Peak Performance. A sequence began 20 frames before the first movement and lasted until the lizard ran out of view or stopped. We subsequently smoothed the data using the Quintic Spline Processor implemented in MOTUS. Only data from individuals that performed at least three "good" trials were used in further analyses.

Based on the smoothed displacement data, instantaneous speed and acceleration (i.e., per frame) were calculated in MOTUS. Instantaneous body mass-specific power output for level locomotion can be calculated as the product of instantaneous velocity and instantaneous acceleration, and is derived by using the following formulas:

$$\text{Power output} = \text{rate of doing work} = \text{force} \times \text{distance/time} = \text{force} \times \text{velocity}$$

and

$$\text{Force} = \text{mass} \times \text{acceleration}$$

Then,

$$\text{Power output} = \text{mass} \times \text{acceleration} \times \text{velocity}$$

and

$$\text{Body mass-specific power output} = \text{acceleration} \times \text{velocity}$$

Because the animals were running at an angle of 45°, we had to take into account gravitational forces. Specifically, we used the following formula to calculate body mass-specific power output:

$$\text{Power output (W Kg}^{-1} \text{ body mass)} = [(\text{instantaneous acceleration}) + (\text{acceleration due to gravity} \times \cos 45^\circ)] \times \text{instantaneous velocity}$$

The maximal value of body mass-specific power output was selected from each sequence.

To estimate peak muscle mass-specific power output, we took into account which step in each running sequence was associated with peak body mass-specific power output. If peak power output occurred within the first step, then both hind limbs were considered to be generating the propulsion because lizards typically started running from standstill with both hind limbs pushing off the substrate simultaneously. Muscle mass-specific power output was then calculated as body mass-specific power output divided by the ratio of the propulsive muscle mass of both hind limbs to total body mass. However, if peak power output occurred in later steps, then only one hind limb at a time was responsible for generating propulsion, and muscle mass-specific power output was calculated by dividing body mass-specific power output by the ratio of the propulsive muscle mass of only one hind limb to total body mass. The front limbs were not considered as contributing to the propulsion because they do not contribute to acceleration [27].

As an estimate of an individual's maximal muscle mass-specific power output, we selected the single highest peak muscle mass-specific power output from all the sequences for that individual, i.e., one value per individual. We subsequently averaged these values per species. We refer to this variable as "muscle mass-specific power output during running."

12.2.4 JUMPING TRIALS

Jumping trials were performed on the same individuals and under similar laboratory settings as the running trials. As opposed to running, jumping is a single, discrete event making it possible to use a force platform to record the forces and ultimately power output (see further). We recorded forces of individual lizards jumping from a custom-made force platform to a branch positioned just outside the presumed reach of the individual (see Ref. [26] for detailed description). The lizards were induced to jump by clapping our hands or by tapping slightly on the tail. Prior to experimentation, lizards were placed in an incubator set at 28°C for *A. gundlachi* and 32°C for all the other species for at least 1 h [26,28]. Each animal was subjected to five separate trials, each on a different and nonconsecutive day. In each trial, we induced the lizard to perform as many separate jumps as possible until it was exhausted. In most cases, the animals performed three or more good jumps per trial. Body mass-specific peak (i.e., instantaneous) power output was calculated using an algorithm written in Superscope 11 (see Ref. [26,28] for details of the calculations). Because lizards always used both hind limbs to push off the substrate during jumping, we calculated muscle mass-specific power output by taking into account the propulsive force of two hind limbs as described above. As an estimate of an individual's maximal muscle mass-specific power output, we selected the single highest instantaneous muscle mass-specific power output from all jumping trials for that individual, i.e., one value per individual. We subsequently averaged these values per species. We refer to this variable as "muscle mass-specific power output during jumping."

For two of the species (*A. valencienni* and *A. carolinensis*), jumping trials were filmed in lateral view at 250 frames s⁻¹ using the Redlake camera.

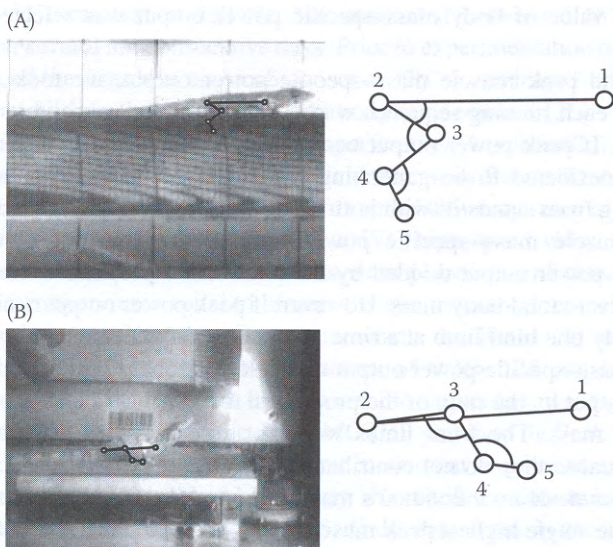


FIGURE 12.1 Lateral view and stick figures of *A. valencienni*. (A) Footfall prior to peak power (running). (B) Takeoff (jumping). In the right panel, the stick figure (enlarged) is shown with the three two-dimensional angles that were measured. Numbers refer to anatomical landmarks on the body: (1) shoulder, (2) pelvis, (3) knee, (4) ankle, and (5) base of the second toe.

12.2.5 CONFIGURATION OF HIND LIMBS

We quantified three joint angles for the two species (*A. valencienni* and *A. carolinensis*) for which movies of both running and jumping were available. In both cases, we only used those sequences in which the individual was producing the highest power output. For the running trials, joint angles were quantified on the frame of footfall of the step in which peak power was reached; in those sequences in which peak power was reached in the first step, joint angles were quantified on the frame prior to the start of any movement. For jumping trials, we used the last frame prior to the start of the jump.

The frames were subsequently imported into CorelDraw (version 10; Corel Corporation 2000), and four lines were drawn connecting (1) the hip to the shoulder, (2) the knee to the hip, (3) the ankle to the knee, and (4) the base of the second toe to the ankle. We then calculated the three angles between the different lines, i.e., the hip, knee, and ankle angles (Figure 12.1).

12.2.6 ECOLOGY

We quantified the time each species spent off the ground, i.e., its degree of arboreality, by observing individual lizards in their natural habitat. Observations were done on the same populations as those sampled for the locomotor trials. Whenever we observed an animal, we noted the substrate type (ground, leaf litter, grass, trunk, branch, or boulder or stone wall) and dimensions (height and width) of the perch it

was on at first sight. An individual was subsequently scored as being “on the ground” if the substrate type was ground, leaf litter, or grass; perch height was less than 10 cm; and perch width was greater than 400 cm. We subsequently approached the lizard and noted in which direction it fled (up, down, or horizontally).

As an estimate of “degree of arboreality,” we used the ratio of number of observations the individual lizards were not sitting on the ground against the total number of observations for that species. As an estimate of “proportion of observations fleeing upward,” we used the ratio of number of observations fleeing upward against the total number of observations for that species.

Each individual was only observed once. Except for *A. garmani*, only observations on males were included in the analyses. Since we were unable to observe any undisturbed *A. garmani* male in the field, we used observations on females instead.

12.2.7 STATISTICAL ANALYSIS

Because the values for the variables under study were not normally distributed, muscle mass–specific power output during running and jumping and all morphological variables were logarithmically ($\log_{10}$) transformed and the ecological variables were transformed by taking their arcsine [29] before statistical analyses.

To compare muscle mass–specific power output during running to muscle mass–specific power output during jumping for all 10 species, we performed a two-way ANOVA with the locomotor mode (i.e., running or jumping) and species as the factors. Two species, *A. carolinensis* and *A. valencienni*, were further analyzed in detail for two reasons: (1) They showed marked differences in muscle mass–specific power output during running and jumping (see Section 12.3), and (2) movies of both jumping and running were available, thus allowing the quantification of the two-dimensional joint angles. For just *A. carolinensis* and *A. valencienni*, we repeated the two-way ANOVA as described above. Since the analysis showed a significant locomotor mode–species interaction effect and species effect (see Section 12.3 for details), we performed one-way ANOVA (with species as factor) on the three joint angles for each locomotor mode separately.

We followed the procedure described below to test whether muscle mass–specific power output during running and/or jumping were intercorrelated and whether the variation in muscle mass–specific power output was explained by the variation in ecology (i.e., degree of arboreality and proportion of time escaping upward). In the latter case, we only used the maximal muscle mass–specific power output for each species, regardless of whether it was attained running or jumping. We refer to this variable as “maximal muscle mass–specific power output.”

Because species share parts of their evolutionary history, they cannot be regarded as independent data points in statistical analyses [30–32]. Various methods and computer programs have been developed over the years, however, in which phylogenetic relationships among different species are taken into account in statistical analyses [30–33]. In this study, we used the independent contrast approach [30,31].

We calculated the standardized independent contrasts using the PDTree program [34] on the transformed means per species of muscle mass–specific power output during running and jumping, maximal muscle mass–specific power output

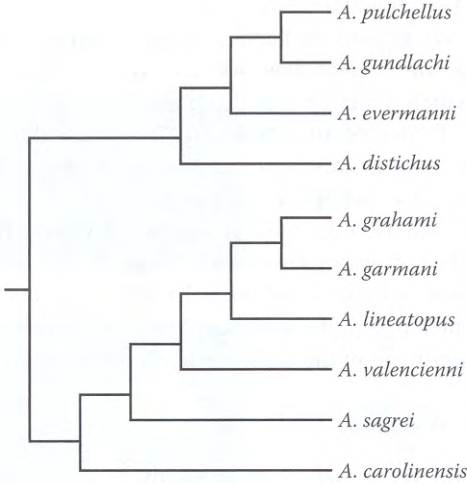


FIGURE 12.2 Phylogenetic tree of the 10 *Anolis* species used in this study. Relationships are based on mitochondrial DNA data by Harmon L.J. et al., *Science*, 301, 961, 2003. Branch lengths are not to scale.

snout-vent length (SVL), degree of arboreality, and proportion of time escaping upward. We subsequently performed two multiple regression analyses (backward method). In the first regression, we used the contrasts in muscle mass-specific power output during running as the dependent variable and the contrasts in muscle mass-specific power output during jumping as the independent variable. In the second regression, we used the contrasts in maximal muscle mass-specific power output as the dependent variable, and the contrasts in SVL, degree of arboreality, and proportion of time escaping upward as the independent variables. All the regressions were forced through the origin [35].

The independent contrast method requires information on the topology and branch lengths of the phylogenetic tree. The phylogeny of the 10 *Anolis* species under study here is based on a phylogenetic analysis of a much larger number of anole species by Harmon et al. [36], using mitochondrial DNA sequences (Figure 12.2). Branch lengths are available upon request from L. Harmon. Moreover, checks of branch lengths, using the diagnostics in the PDTREE program, did not show any significant correlation between the absolute values of the standardized contrasts and their standard deviations [35]. Recently, the phylogenetic relationships among *Anolis* lizards have been reexamined, resulting in minor changes [37]. Because, however, branch lengths have not been made available for this phylogeny, we preferred to use the phylogeny data of Harmon et al. [35].

12.3 RESULTS

The 10 species varied 10-fold in body mass, 15-fold in hind limb muscle mass, and about 2-fold in muscle mass-specific power output both during running and jumping (Table 12.1). As for interspecific variation in field behavior, the degree of arboreality

varied between 45 and 100%, while the incidence of escaping upward varied between 27 and 100% (Table 12.1).

The 10 species of *Anolis* lizards differed significantly in muscle mass-specific power output (two-way ANOVA, species effect, $F_{9,178} = 9.76$, $p < 0.0001$) (Figure 12.3). Muscle mass-specific power output, however, did not differ between jumping and running (two-way ANOVA, locomotor mode effect, $F_{1,178} = 0.06$, $p = 0.80$), and the difference among species was similar in both locomotor modes (two-way ANOVA, locomotor mode-species effect, $F_{9,178} = 1.56$, $p = 0.13$). Additionally, the contrasts in muscle mass-specific power output during running were positively correlated with the contrasts in muscle mass-specific power output during jumping ($r = 0.86$, $F_{1,8} = 6.94$, $p = 0.030$) (Figure 12.4).

A multiple regression model (backward method) with the independent contrasts of maximal muscle mass-specific power output as the dependent variable and the independent contrasts of SVL, degree of arboreality, and proportion of time escaping upward as independent variables was performed; only an analysis of the latter independent variable was found to be significant ($r = 0.68$, $F_{1,8} = 7.05$, $p = 0.029$). Thus, only the variation in (contrasts in) the relative numbers escaping upward explained a significant proportion of the variation in (contrasts in) maximal muscle mass-specific power (Figure 12.5). Separate bivariate regressions showed the same results, i.e., only the contrasts in proportion of time escaping upward show a significant correlation with the contrasts in maximal power output.

In the two-species comparison, muscle-mass specific power output differed significantly between *A. carolinensis* and *A. valencienni* (two-way ANOVA, species effect, $F_{1,31} = 4.71$, $p = 0.038$), and the interspecific difference in muscle mass-specific power output varied significantly according to locomotor mode (two-way ANOVA, locomotor mode-species effect, $F_{1,31} = 4.88$, $p = 0.035$). Muscle mass-specific power output during running, however, did not differ significantly from the muscle mass-specific power output during jumping (two-way ANOVA, locomotor mode effect, $F_{1,31} = 0.12$, $p = 0.73$). Because there were no significant differences in power output between locomotor modes, only between species, we further compared muscle mass-specific power output for each locomotor mode separately between the two species using one-way ANOVA. During running, muscle mass-specific power output did not differ between *A. carolinensis* and *A. valencienni* (one-way ANOVA, $F_{1,26} = 0.94$, $p = 0.34$). Muscle mass-specific power output during jumping, on the other hand, was significantly greater in *A. valencienni* than in *A. carolinensis* (one-way ANOVA, $F_{1,21} = 5.31$, $p = 0.031$).

Because of the significant species-locomotor mode interaction effect and species effect (two-way ANOVA, see above), we compared the three joint angles for the two species for each locomotor mode separately using one-way ANOVA. For running, both the hip and knee angle were not significantly different between *A. valencienni* and *A. carolinensis* (one-way ANOVA for both, $F_{1,16} < 0.27$, $p > 0.61$). The ankle angle in running trials, however, was significantly smaller in *A. valencienni* ($F_{1,16} = 5.76$, $p = 0.029$). For jumping, all three joint angles were significantly different between the two species (hip: $F_{1,18} = 11.84$, $p = 0.003$; knee: $F_{1,18} = 38.11$, $p < 0.0001$; ankle: $F_{1,18} = 15.55$, $p = 0.001$). Whereas the femur was more protracted

TABLE 12.1
Descriptive Statistics for Muscle Mass–Specific Power during Running and Jumping Trials, Propulsive Muscle Mass (of One Hind Limb), Body Mass, Degree of Arboreality, and Proportion of Time Escaping Upward per Species

Species	Muscle Mass–Specific Power (W kg ^{−1})			Mass (g)			Field Behavior			
	N	Running	N	Jumping	N	Muscle	Body	N	Arboreality	Escaping up
<i>A. pulchellus</i>	16	574.32 ± 26.96	5	472.26 ± 36.49	2	0.076 ± 0.003	2.37 ± 0.07	23	0.78	0.43
<i>A. gundlachi</i>	18	524.84 ± 44.98	6	516.42 ± 65.83	3	0.317 ± 0.030	6.68 ± 0.21	35	0.97	0.69
<i>A. evermanni</i>	15	671.71 ± 46.25	3	767.66 ± 17.85	3	0.201 ± 0.006	5.42 ± 0.35	23	0.83	0.48
<i>A. distichus</i>	12	735.46 ± 61.73	5	647.43 ± 13.32	3	0.075 ± 0.025	2.97 ± 0.15	25	1	0.72
<i>A. grahami</i>	13	438.26 ± 40.47	4	601.50 ± 64.28	3	0.241 ± 0.040	5.54 ± 0.13	23	0.86	0.78
<i>A. garmani</i> ^a	8	570.55 ± 57.59	7	598.01 ± 58.51	1	1.054	26.31	6	1	0.83
<i>A. lineatopus</i>	14	540.73 ± 37.91	10	543.98 ± 31.94	1	0.247	5.19	14	0.93	0.42
<i>A. valencienni</i>	8	725.21 ± 70.36	8	848.71 ± 57.82	2	0.159 ± 0.021	6.93 ± 0.96	5	1	1
<i>A. sagrei</i>	19	419.61 ± 24.49	9	373.68 ± 39.69	2	0.226 ± 0.057	4.19 ± 0.45	22	0.45	0.27
<i>A. carolinensis</i>	12	714.90 ± 37.32	7	595.91 ± 89.60	3	0.222 ± 0.012	7.33 ± 0.33	30	0.97	0.57

Note: Given are the number of individuals (*N*) and — where applicable — means and standard errors (mean ± SE) per species.

^a Observations of behavior are of females only. We were unable to gather data on males for this species.

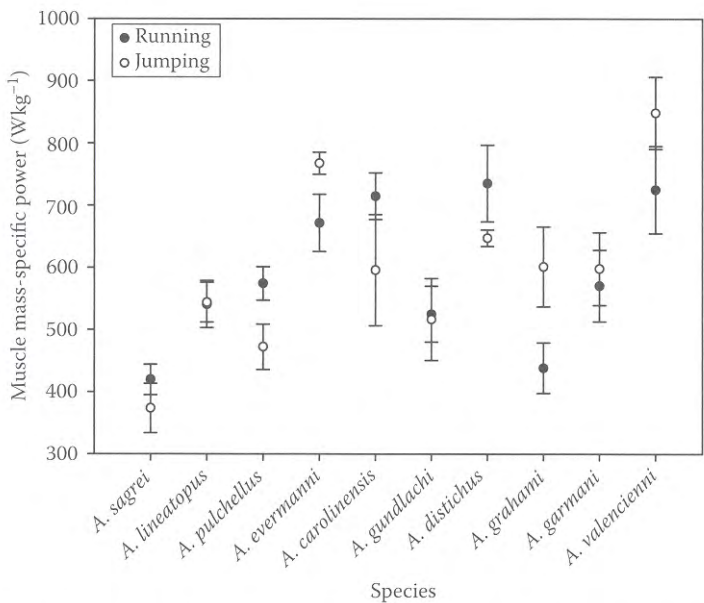


FIGURE 12.3 Mean and standard error of muscle mass–specific power output during running (closed symbols) and jumping (open symbols) per species. Species are ordered from low to high incidence of escaping upward when confronted with a (human) predator.

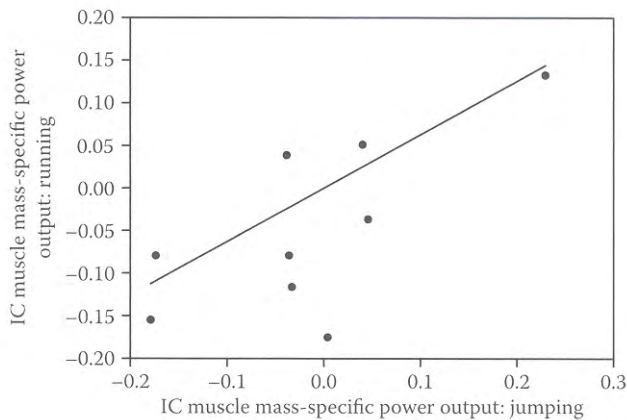


FIGURE 12.4 Regression through the origin of the independent contrasts (IC) of muscle mass–specific power output during running against the independent contrasts of muscle mass–specific power output during jumping ($r = 0.86$, $p = 0.030$).

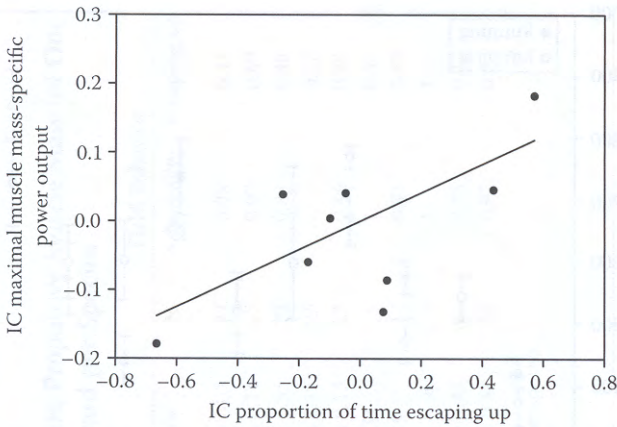


FIGURE 12.5 Regression through the origin of independent contrasts of maximal muscle mass-specific power output against the independent contrasts of the proportion of time lizards escape upward ($r = 0.68$, $p = 0.029$). Evolution toward higher incidence of escaping upward has been paralleled by evolution toward higher power outputs among the 10 *Anolis* species.

in *A. valencienni*, the knee and ankle angle in this species were significantly smaller than in *A. carolinensis* (Figure 12.6).

12.4 DISCUSSION

The aim of this study was to investigate whether muscle mass-specific power output has evolved within a closely related group of organisms in response to variation in microhabitat use and behavior. To our knowledge, ours is the first study that quantitatively links the variation in muscle power output to variation in ecology using a comparative approach. Our data show that muscle mass-specific power output varies considerably among species (more than twofold) and is indeed linked to the ecology and behavior of the species investigated.

12.4.1 ECOLOGICAL CORRELATES OF POWER OUTPUT

Our results show a significant correlation between maximal power output and ecology across 10 species of *Anolis* lizards. More specifically, the evolution toward a higher incidence of escaping upward has been paralleled by the evolution toward higher muscle mass-specific power output. Muscle mass-specific power output, however, does not seem to correlate with an arboreal lifestyle *per se*. *Anolis* lizards are typically “active” lizards that run and jump around their natural habitat to search for food and/or partners, to defend their territories, or to escape predators [21]. However, it is clear that, on top of the large ecological variation, such as the degree of arboreality, there is also a large behavioral variation, such as antipredator behavior. Moreover, perching off the ground does not necessarily mean that the animals move up and down a lot, i.e., in a vertical direction. While some species typically jump down to other trees or to the ground, others “squirrel” to the opposite side of the

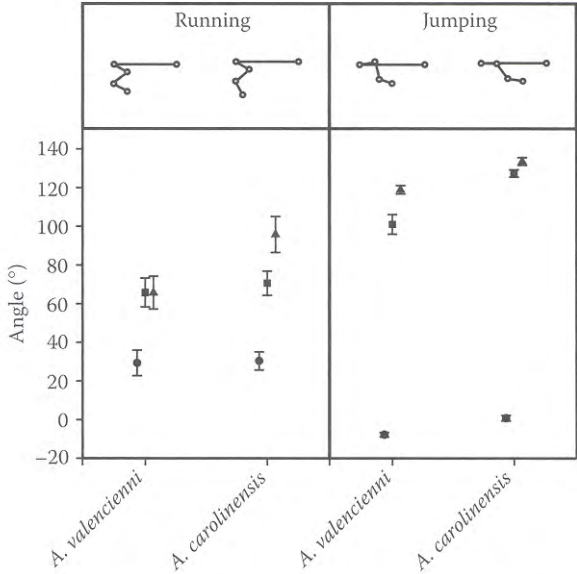


FIGURE 12.6 Plot of two-dimensional angles at footfall in running trials (left) and takeoff in jumping trials (right) for *A. valencienni* and *A. carolinensis*. Shown are means and standard error bars. For running, only the ankle angle differs between the two species ($F = 5.76$, $p = 0.029$), whereas all three angles differed significantly for jumping (all $F > 11.84$, all $p < 0.003$). Stick figures representing the mean configuration of the limb segments during running and jumping, per species are shown in the top panel. ● = hip; ■ = knee; ▲ = ankle.

trunk, i.e., stay at the same height, and/or run up [38]. In our sample, for instance, *A. lineatopus* typically does not escape upward when confronted with a (human) predator while *A. valencienni* does, although both show similar degrees of arboreality. Moreover, maximal power output is greater in *A. valencienni* (see Table 12.1 for raw values). Thus, it seems that higher power outputs are selected for in arboreal microhabitats, specifically in those species that frequently need to move rapidly by running or jumping against gravity.

12.4.2 INTERSPECIFIC VARIATION

When comparing all 10 species, we found no overall difference in muscle mass-specific power output between jumping and running. Moreover, both power outputs seem to have coevolved. This might be explained by the fact that the same muscles are used in running and jumping.

Still, it is striking that even within a very closely related group of lizards such as *Anolis* lizards, large variation in muscle mass-specific power output exists. In our sample of 10 species, muscle mass-specific power output varies between 374 and 849 W kg⁻¹, i.e., more than a twofold difference (Table 12.1). In general, differences in maximal power output, when executing the same task, are attributed to differences in the physiological properties of the muscle. At the moment, we do not have data on the physiology, for example muscle fiber-type of the different muscles in the

different species. However, it does seem likely that differences in muscle fiber-type composition are present because similar results have been found in other lizard species [11,39]. On the contrary, while (theoretically) also being of great importance to muscular power output, the configuration of the musculoskeletal system, such as the origin and insertion of the muscles, is generally considered to be more conservative, i.e., less variation is found among species. We have some evidence that this might not be the case among *Anolis* lizards. When comparing the hind limb musculature of two extreme *Anolis* species — a ground-trunk anole, *A. sagrei*, and a twig anole, *A. valencienni* — we found distinct differences in the insertion of the hip retractor and knee extensor muscles between these two species [40]. Thus, our limited data set on *Anolis* lizards at least suggests that muscular morphology might be more variable than previously thought.

Surprisingly, the values for muscle mass-specific power output we find for some *Anolis* species, such as jumping in *A. valencienni*, are within the range of so-called extremely high power outputs in jumping frogs [41,42] and flying or running birds [5,10,43]. In the past, it has been generally assumed that power amplifiers are necessary to produce such high powers at the whole animal level [18,41,42]. Recently, however, it has been shown that power outputs of around 1000 W kg^{-1} are possible at the muscular level [5,44]. Although likely, it remains to be tested whether in *Anolis* lizards high power outputs at the whole animal level reflect power output at the muscular level. However, our data do show that high power outputs, i.e., in the range of 500 to 800 W kg^{-1} , might not be as exceptional as previously claimed [5,10,41–43].

12.4.3 POWER OUTPUT DURING RUNNING AND JUMPING: A TWO-SPECIES COMPARISON

The comparison between *A. carolinensis* and *A. valencienni* shows that while muscle mass-specific power output is similar during running, it differs significantly during jumping. We suggest that biomechanical differences lie at the basis of this discrepancy. While the configuration of the hind limb segments is similar in both species in running trials, it differs greatly in jumping events. In the species producing the highest muscle mass-specific power during jumping, i.e., *A. valencienni*, the femur is significantly more protracted, i.e., the hip angle is negative (Figure 12.6), while the knee and ankle are more flexed, i.e., the knee and ankle angles are smaller (Figure 12.6). Could these differences be responsible for the differences in muscle mass-specific power output between the two species? The different configuration of the hind limbs may indeed result in changes in the instantaneous moment arms of the hip retractors and knee and ankle extensors that power locomotion. For example, inspection of Figure 12.6 shows that in, e.g., *A. valencienni*, the femur is maximally protracted. In this configuration, the dominant femur retractor (m. caudofemoralis) has a negligible moment arm and initially cannot contribute to femur retraction. This opens up the possibility for elastic energy storage in the broad tendon of the *M. caudofemoralis* inserting on the femur. However, for this to be the case, the muscle has to be active prior to femur retraction such that energy can effectively be stored. In *A. carolinensis*, the femur is significantly less protracted prior to the onset of the

jump and may thus have less potential for energy storage. Although these differences may explain the observed differences in power output (and also the magnitude of power output in these animals), this hypothesis needs to be investigated further by electromyographic and sonometric recordings of the *M. caudofemoralis* during jumping.

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