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Kinematics and Mechanics of Jumping Lizards: the Modulation of Jump Power

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Kinematics and Mechanics of Jumping Lizards: the Modulation of Jump Power

A Thesis submitted in partial satisfaction
of the requirements for the degree of

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in

Evolution, Ecology, and Organismal Biology

by

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Introduction

Locomotion is used by many animals for avoiding predators, obtaining resources, and interacting with conspecifics (Swingland and Greenwood, 1983). Animals use multiple types of locomotion to move through habitats that are often complex and highly variable (Cartmill, 1985; Kohlsdorf and Biewener, 2006; Olberding et al., 2012; Tucker and McBrayer, 2012). In order to understand how locomotor behaviors are adapted to the environments in which animals live, researchers often investigate relationships within the morphology-performance-fitness paradigm (Arnold, 1983; Garland and Losos, 1994). However, a correlation between morphology and performance does not necessarily establish a causal link. Biomechanical studies are used to determine the relationships between the function of locomotor morphology and the resulting performance (Fieler and Jayne, 1998; Irschick and Jayne, 1998; Jayne and Irschick, 1999).

Some morphological features may be beneficial for one type of locomotion yet reduce some other form of locomotor performance (Vanhooydonck and Van Damme, 2001; Vanhooydonck et al., 2011). For example, the reduction of mass in the distal limb is considered beneficial for sprint running where the distal limb mass would increase the inertia the must be overcome to accelerate the limb (Coombs, 1978; Hildebrand, 1985). However, in a jump, increased muscle mass of the distal joint extensors may increase jump performance (Hildebrand, 1985; Toro et al., 2004). The morphology that prevails will depend upon the strength of selection acting on each type of locomotor performance. Alternatively, some features with no relationship, positive or negative, with one type of performance may be neutral or beneficial for some other type of performance (Van

Damme et al., 1997; Vanhooydonck and Van Damme, 2001). For example, the long toe of many lizards is not likely to be beneficial for running when using a plantigrade posture, yet it could increase jump performance by increasing the effective length of the hindlimb (Brinkman, 1981; Rewcastle, 1981; Reilly and Delancey, 1997b; Fieler and Jayne, 1998; Irschick and Jayne, 1999). By understanding these functional relationships and quantifying the mechanical demand placed on locomotor morphology during different behaviors, we may gain insight into the selective pressures that animals might be facing and make hypotheses regarding the evolution of locomotor morphology and behavior.

Rather that using some ecological measure of performance, it can be useful to quantify locomotion in terms of the mechanical demand placed on the locomotor apparatus because it allows for easy comparison between different behaviors in different situations (Nauwelaerts et al., 2003). For example, jumping is a form of locomotion found in many terrestrial vertebrates distinguished by a single acceleratory event that rapidly changes the position of the center of mass (COM) relative to the starting position (Alexander, 2003; Biewener, 2003; Toro et al., 2006). Animals use jumping for escaping predators, catching prey, competing with conspecifics, or simply moving through the habitat (Alexander, 2003). Jump performance is often measured as vertical jump height or horizontal jump distance, both of which may be ecologically relevant in different situations and both jump height and jump distance can be calculated by knowing only the instantaneous velocity at the time the animal leaves the ground (take-off velocity) and the angle of the trajectory relative to horizontal (take-off angle). The take-off angle simply determines the proportion of take-off velocity that is directed vertically and the proportion that is directed horizontally. Take-off velocity is the result of the work done during the jump. The work required to achieve a certain take-off velocity and thus jump height or distance is a measure of the mechanical demand on the locomotor morphology.

Jumping is a form of locomotion that may place high demands on the locomotor apparatus because of the high peak power requirements (Aerts, 1998; Demes et al., 2005; Vanhooydonck et al., 2006b). In a jump, the duration of power generation is necessarily limited by the time of limb contact with the ground and power must be generated quickly enough to result in an acceleration that overcomes the pull of gravity. Therefore, it is the magnitude of the power that tends to define the work that is done in a jump (Aerts, 1998; Vanhooydonck et al., 2006b). In limbed vertebrates, jumping is accomplished by rapidly extended one or more limbs to propel the body into the air (Bobbert and van Ingen Schenau, 1988; Ashby and Heegaard, 2002; Toro et al., 2006). If the joints are moving simultaneously, the peak power of the COM must equal the sum of the peak power from each joint. If the power production in the joints is not simultaneous, then the sum of the peak power from each joint will exceed the peak power of the jump. Within the muscles of the hindlimb joints, there is a given value of shortening velocity and force production at which muscle power output is greatest (Alexander, 2003). The muscles of the limbs used during the jump power this high acceleration and the limits of muscular performance may thus limit jump performance (Aerts, 1998; Biewener, 2002; Vanhooydonck et al., 2006b; Roberts et al., 2011). This peak muscle power output can be measured using in vitro or in situ techniques where the muscle or muscle fibers are isolated and maximally stimulated while simultaneously measuring length changes and force production (Josephson, 1985; Johnson et al., 1993; Curtin et al., 2005). The morphological and functional traits of the limbs of vertebrates may therefore determine jump performance, and if jumping is important for fitness, these traits may change in response to selection (Arnold, 1983).

We often use lizards as model systems to examine relationships between morphology, performance, and fitness in locomotion because of the wide diversity in both morphology, behavior, and ecology in the lizard clade (Arnold, 1983; Garland and Losos, 1994; Irschick and Losos, 1998; Bonine and Garland, 1999; Melville and Swain, 2000; Zani, 2000; Vanhooydonck and Van Damme, 2001; Herrel et al., 2002; Toro et al., 2003; Elstrott and Irschick, 2004; Calsbeek and Irschick, 2007; Higham and Russell, 2010; Tulli et al., 2012). The ability of lizards to perform successfully during locomotion can have impacts on fitness (Husak, 2006; Husak and Fox, 2006; Husak et al., 2006; Calsbeek and Irschick, 2007; Irschick and Meyers, 2007; Irschick et al., 2008). Measures of locomotor performance, such as maximum sprint speed, are often examined in conjunction with morphology or habitat use to gain understanding of how lizards are adapted for moving in their environment (Losos, J. B., 1990; Losos, Jonathan B., 1990; Sinervo et al., 1991; Sinervo and Losos, 1991; Garland and Losos, 1994; Bauwens et al., 1995; Bonine and Garland, 1999; Melville and Swain, 2000; Zani, 2000; Vanhooydonck and Van Damme, 2001; Vanhooydonck et al., 2006a; Gifford et al., 2008; Goodman et al., 2008; Tulli et al., 2012). Various biomechanical studies have sought the causal links between morphology and these types of performance in various ecologically relevant settings and have supported the hypothesized relationships between locomotor function and habitat (Higham and Jayne, 2004; Spezzano and Jayne, 2004; Foster and Higham, 2012; Olberding et al., 2012).

The locomotion of many lizard species is not characterized by long bouts of steady-speed running over level terrain, but rather by quick bursts of movement in a complex environment (Irschick, 2000; Mattingly and Jayne, 2005; McElroy et al., 2007; McElroy and McBrayer, 2010). Animals may use a number of different types of locomotion to deal with the variation in the habitat on the small scale. In studies of obstacle negotiation and maneuverability, lizards used running, climbing, jumping, and turning to deal with complex habitats (Kohlsdorf and Biewener, 2006; Tucker and McBrayer, 2012). Many species of lizards use jumping as a means of moving through their habitat, but compared to steady running, it has received relatively little attention (Losos, J. B., 1990; Bels et al., 1992; Toro et al., 2003; Toro et al., 2004, 2006; Vanhooydonck et al., 2006b). Because jumping may place unique demands on the locomotor apparatus, we may expect it to shape the morphology of the limbs in lizards where the ability to jump is important for fitness (Demes et al., 2005), but the mechanisms linking the kinematics of individual limb joints and jump performance are not well understood for lizards.

Toro et al. suggested that the control strategy in lizards for increasing jump performance differ depending on the task, with jump distance being largely modulated by peak force during the jump. As the authors note, however, this is largely unsurprising because force is a term in the calculation of jump distance, and peak force would be related to jump height of jump velocity, as well. Jumping for angle is controlled by is controlled less by peak force and more by trunk, head, and elbow angle. However, lizards may not jump "for" a particular angle, and as a measure of performance, jump angle, may not be ecologically relevant. Rather, the combination of jump height or jump distance (the ratio of which is determined by jump angle) could a more ecologically relevant measure of performance, and in either of these cases, peak jump force should be important for modulating performance because of its importance in determining power and work. Therefore, although the ecological context of individual jumps may differ, they still must meet the mechanical demand of power and work in order to produce high forces that result in greater jump heights, distances, and velocities. Here I investigate how the joint kinematics are modulated to meet this mechanical demand regardless of the ecological measure of performance.

Within an individual animal, the peak power output of the muscles (per unit muscle mass) is limited by the physiological characteristics of muscle (Alexander, 2003) but some animals have mechanisms by which these limits can be bypassed to increase the power of locomotor movements (Roberts, 2002). The storage and recovery of energy through elastic elements has been a recent focus of study in biomechanics and muscle physiology (Biewener, 1998, 2002; Roberts, 2002; Biewener and Daley, 2007). Energy may be loaded into elastic structures such as tendons, ligaments, or muscle itself, which can then be recovered through elastic recoil (Roberts, 2002). This is the basis for models of energetically efficient locomotion via the mass-spring model (Cavagna et al., 1971; Cavagna et al., 1977; Roberts et al., 1997; Biewener, 1998, 2006). If the elastic structures can somehow be prevented from recoiling, however, energy can be stored over a long period of time at low power then recovered quickly with high power (Roberts, 2002). Evidence for elastic power amplification has been found in vertebrate groups including amphibians and mammals (Marsh and John-Alder, 1994; Aerts, 1998)

To understand the relationships between jumping kinematics and mechanics in lizards, I used the desert collared lizard, *Crotaphytus bicinctores*, which is considered a lizard jump specialist. These animals live in rocky habitats where they often use jumping to move from rock to rock rather than scramble down and back up (Fitch, 1956). In the laboratory and the wild, desert collared lizards regularly jump from a standstill to heights three to four times their snout-vent length (SVL). I examined jumping in the desert collared lizard to address the following questions: Which kinematic variables are modulated to increase jump power? Do jumps exceed the power that could be provided by muscle alone? Is jump power enhanced through the use of countermovements?

If only the multi-segmented limbs of a lizard contribute to jumping, jump power could be provided by any combination of one or more joint movements (James et al., 2007). The power generated by a particular joint can by is equal to the angular velocity of that joint movement multiplied by the rotational force (moments) exerted by the muscles of that joint. When the loading, or mass being moved, of a joint remains constant, greater force acting at that joint will result in greater angular velocity. Higher power jumps should result in greater peak angular velocities of joint motions when loading remains constant.

I hypothesize that collared lizards are utilizing elastic mechanism to amplify muscle power in their jumps. If power amplification mechanisms are used, then peak power output measured during the jumps will exceed the peak power output of lizard muscle fibers alone. Even without the temporal separation of loading and recoil, elastic mechanisms can contribute to increased power generation (Roberts, 2002). Some animals utilize countermovements when jumping, which is simply the movement of the limb joints in the opposite direction of the desired motion immediately prior to the jump (Bobbert et al., 1996; Aerts, 1998). Flexion of the joints will cause stretching of the extensor muscles and energy may be stored in the elastic elements of the extensors, which is the recovered simultaneously with contraction of the extensors. Therefore, I also hypothesize that the lizards are utilizing countermovements to increase their jump power.

Methods

I used four desert collared lizards obtained from a commercial supplier, which were housed in the vivarium for a period of five weeks (AUP #A-20110038E). Each individual was tested daily in the morning and fed immediately after experiments. Lizards were placed on a custom-built force plate consisting of a six-axis force/torque sensor (Nano17, ATI Industrial Automation, Apex, NC, USA) fitted with a carbon-fiber top plate (DragonPlate, Allred & Associates, Elbridge, NY, USA) then made to jump using light taps on the tail. The top surface of the force plate measured 15.2 cm by 15.2 cm and was located 10 cm above the surrounding surface in order to eliminate alternative

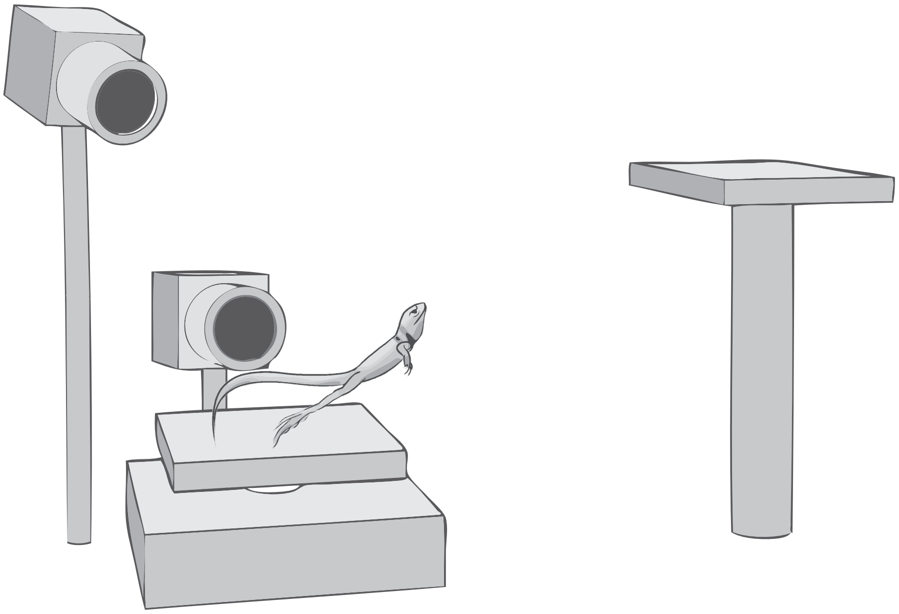


Figure 1. Schematic showing a collared lizard positioned on the force plate set-up with two cameras positioned for a lateral view of the left side of the animal.

locomotor options (Fig. 1). The target destination was a carbon fiber plate of similar dimensions to the force plate. The distance and height of the destination relative to the force plate were randomly altered in order to elicit a range of jump heights and distances. The lizard often jumped over the destination even when placed at its maximum height indicating that the motivation and resultant performance were to some degree independent of the target destination.

Video recordings of the jumps from two high-speed cameras (1080× 1080 pixels, Photron APX-RS, Photron USA Inc., San Diego, CA, USA) were collected at 1000 frames/s along with simultaneous ground reaction force (GRF) recordings at 5000 Hz (down-sampled to 1000 Hz). The high-speed video recordings were digitized using the

DLTdv3 program (Hedrick, 2008) to determine the three-dimensional coordinates of a number of markers painted on the body and left hindlimb. The positions of these paint markers were photographed *post mortem* and related to the anatomical axes of the animal. All digitized data were filtered using low-pass fourth-order Butterworth filtering with a cutoff frequency of 40 Hz. A custom MATLAB (v. R2010A, The MathWorks, Natick, MA, USA) script was used to determine the angles of the hip, knee, and ankle joints around three axes of rotation by constructing 3D rotation matrices from one limb segment to the next then extracting Euler angles. The first time derivatives of the joint angles were calculated as joint angular velocities. The same MATLAB script related the GRF measurements to the axes of the body and calculated the position and velocity of an estimated COM located in the middle of the body, 30% of SVL forward of the vent.

Variables

Power of the COM was calculated as the product of the GRF and COM velocity measured per unit hindlimb extensor muscle mass from both hindlimbs based on muscle proportions from the closely related species, *C. collaris* (Snyder, 1954). Each jump was considered to begin at the time at which 5% of the peak COM power had been reached and the jumps ended when the limb left contact with the ground. All data recorded prior to the start of the jump were considered to be part of the preparatory phase, though these recorded data did not always start at a standardized point restricting the possible comparisons between kinematics during the preparatory phase.

Observation of the jump behaviors in these lizards make it clear that femur retraction, knee extension, and ankle extension are likely powering the movement of the COM in a forward and upward direction. The majority of the mass of the hindlimb muscles is predicted to function for these movements or their antagonist movements (Snyder, 1954); therefore, I test the relationships of these hindlimb movements specifically with jump power. Power could be modulated by altering magnitude of angular velocity of motions in any combination of these three joints. Additionally, making each of the three motions more simultaneous, so that each individual peak power occurs at the same time, could increase peak jump power. Although these three movements are the only ones likely to influence power directly, vertebrate limbs are complex structures that function in three dimensions. It is possible that the movements of the limb segments in other axes may influence the ability to effectively extend at the appropriate times. For example, the depression of the femur could influence the orientation of the flexion-extension axis of the knee. Therefore, I investigate the potential influences of these secondary kinematic variables on peak COM power output.

Statistical Methods

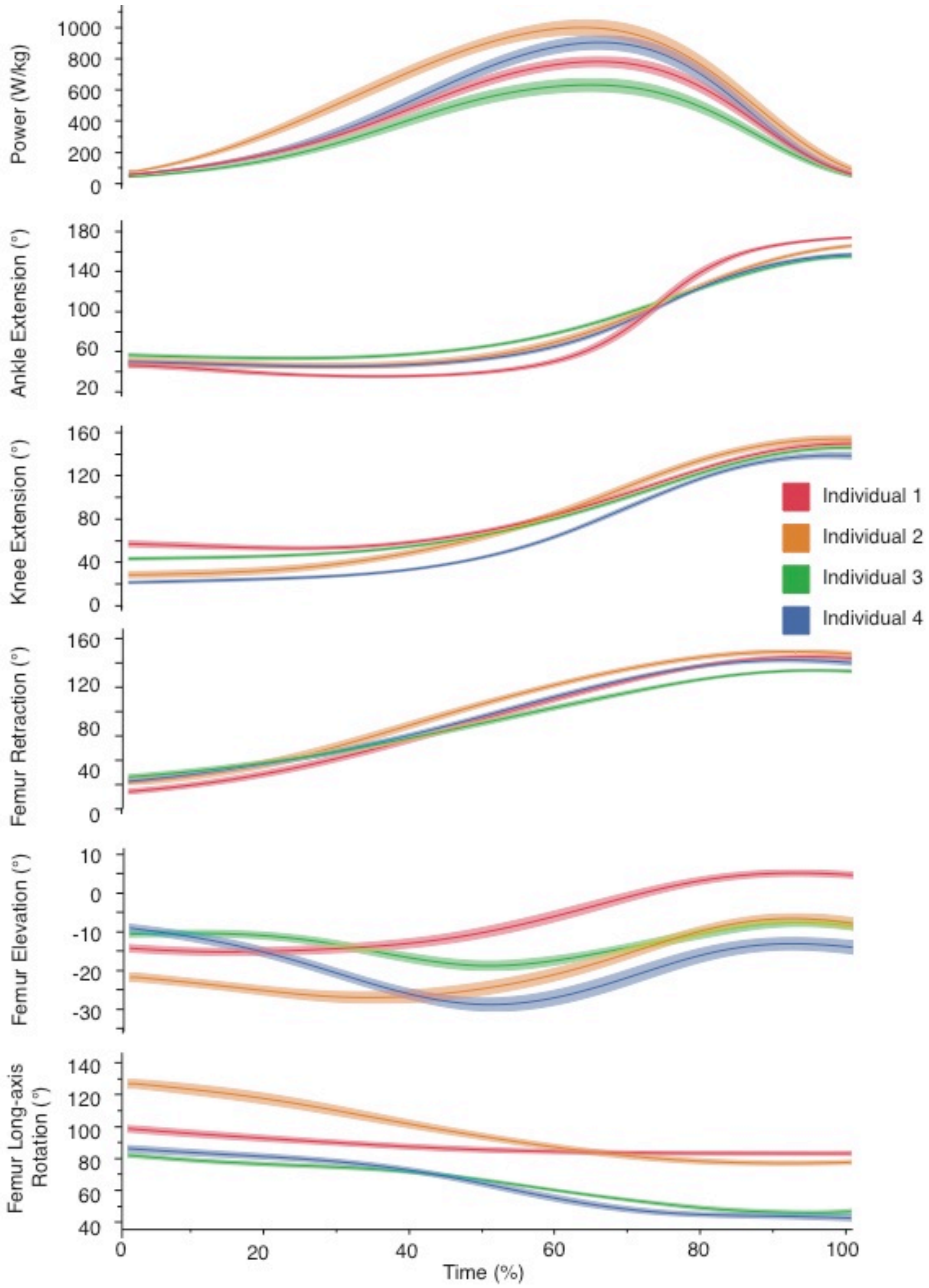
Differences in muscle mass-specific peak COM power generated during the jump between individuals were assessed using a one-way ANOVA and a Tukey-Kramer HSD test was used to examine pairwise differences. Because this test revealed high individual variation in power output, I performed separate analyses for each individual to assess relationships between kinematics and jump power. In order to determine which joint motions contributed to the modulation of jump power, I used stepwise multiple linear regressions to determine the best model for predicting peak COM power using ankle extension velocity, knee extension velocity, and femur retraction velocity based on AICc. To assess the relationship between timing of joint motions and jump power, I performed regressions of the total time between the first and last peak angular velocity of a jump and peak COM power. I used linear regression to assess the role of femur elevation and long-axis rotation in determining peak COM power.

I tested general linear models (GLMs) of peak muscle mass specific COM power with the residuals of peak flexion regressed against joint angular velocity in each joint as a fixed factor and individual as a random factor to examine the role of countermovement on jump power independent of its effects on joint angular velocity. In order to understand the importance of individual variation in the modulation of jump power, the relationships between joint flexion and power were tested for each individual using linear regression. All statistical analyses were performed using JMP (version 10.0.0, SAS Institute Inc., Cary, NC, USA).

Results

The lizards utilized a preparatory phase when jumping from a standstill similar to that observed in other jumping lizards (Bels et al., 1992). The lizards typically rested in a sprawled posture with the limbs directed laterally from the body, but prior to jumping, the limbs were repositioned so that the feet were directed anteriorly with the long-axis of the foot almost parallel with the long-axis of the body. This put the limbs into a position where extension of the hindlimb joints would propel the animal in a forward (anterior) direction. Each jump trial was categorized based on the details of the preparatory phase to examine the effects of each behavior on kinematics and performance. Sometimes the lizards moved their limbs into position then paused for a period of a few seconds to several minutes before jumping (standstill, SS). Other times the lizards would step into position with one limb and then the other, then without pausing spring into the jump as soon as the second limb had contacted the ground (left-right, LR, or right-left, RL depending on the order of the limbs). Finally, the lizards sometimes moved both limbs into position at the same time so that both hindlimbs were out of contact with the ground for at least some point during the movement (double-set, DS). The type of jump used was included as a factor in analyses to account for kinematic variation potentially introduced by difference in the preparatory phase. I collected 120 separate jump events from the four individuals including 63 DS, 13 SS, 28 LR, and 16 RL jumps. The kinematics of the jumps followed a general pattern of proximal to distal extension of the hindlimb joints. Femur retraction began at the start of the jump followed by knee extension at 10.4 ± 1.1 % total jump duration total jump duration, then ankle extension at 28.3 ± 1.1 % total jump duration (Fig. 2).

For individual 1, the best model based on AICc included the peak velocity of knee extension and the peak velocity of femur retraction (Table 3), and these were both significantly positive related to peak COM power of the jump (Table 4). The best model for individual 2 included only the peak velocity of ankle extension which was positively



Power (W/kg)
1000
800
600
400
200
0
Ankle Extension (°)
180
140
100
60
20
Knee Extension (°)
160
120
80
40
0
Individual 1
Individual 2
Individual 3
Individual 4
Femur Retraction (°)
160
120
80
40
0
Femur Elevation (°)
10
0
-10
-20
-30
Femur Long-axis Rotation (°)
140
120
100
80
60
40
0
20
40
60
80
100
Time (%)

Figure 2. Average values of kinematic variable for all trials through time for each individual. Trials are scale to relative time with 0% being the point at which 5% of peak muscle mass-specific COM power has been developed and 100% the time at which the limbs leave contact with the ground (A) muscle mass specific COM power (B) ankle extension (C) knee extension (D) femur retraction (E) femur elevation (F) long-axis femur rotation

related to peak COM power (Table 3, 2). For individual 3, the best model included both ankle extension velocity and peak knee extension velocity, both of which had a significant positive relationship with peak COM power (Table 3,2). The best model for individual 4 included both peak ankle extension velocity and peak knee extension velocity, but only peak knee extension velocity had a significant positive relationship with peak muscle mass-specific COM power (Table 3, 2).

In individual 3, the timing of peak joint angular velocities became more separated (Table 5,Fig. 3) in jump of greater peak COM power. There was a significant positive relationship between the maximum elevated position of the femur prior to depression and peak COM power for one individual (Table 6, Fig. 4). The maximum depressed position of the femur had a significant positive relationship with peak COM power in another individual (Table 6, Fig. 4). The rotation of the femur about its long axis had no relationship with peak COM power in any individual (Table 6, Fig. 4).

For all four individuals, the maximum peak muscle mass-specific COM power output observed exceeded the limit of lizard muscle peak power output of ~950 W/kg, though the average values for three individuals were below this muscle limit (Fig. 5, Table 7). The maximum peak muscle mass specific COM power output differed significantly between individuals (Table 1), and between types of jump preparatory behaviors with DS type jumps having significantly higher COM power than LR ($p = 0.021$) and SS ($p = 0.041$) type jumps (Tukey-Kramer HSD) (Table 2). There were no general relationships

Table 1. Mean values ± SEM for each individual. Statistical results for two-way ANOVAs with type as a fixed factor and individual as a random factor (see Table 7 for results for type).

Variable	1	2	3	4	F (3,107)	p
Power (W/kg)	811.06±40.03	1026.44±39.42	655.17±42.79	922.82±41.34	9.69	**<0.001**
Ankle flexion (°)	32.25±0.93	43.60±2.47	51.60±1.36	43.69±1.49	13.77	**<0.001**
Knee flexion (°)	49.59±1.81	22.48±2.92	37.58±2.33	16.03±1.84	15.34	**0.013**
Femur protraction (°)	22.70±1.07	32.03±1.60	29.18±1.62	28.73±1.39	1.90	0.134

Table 2. Mean values ± SEM for each jump preparatory behavior. Statistical results for two-way ANOVAs with type as a fixed factor and individual as a random factor (see Table 6 for results for individual).

Variable	DS	SS	LR	RL	F (3,9)	p
Power (W/kg)	898.95±31.21	802.34±64.62	718.61±50.22	998.20±52.99	10.04	**0.003**
Ankle flexion (°)	44.36±1.92	32.51±3.92	41.81±2.48	44.78±2.15	2.51	0.125
Knee flexion (°)	37.18±2.21	22.90±2.88	32.89±3.50	14.17±1.95	3.76	0.053
Femur protraction (°)	26.45±1.61	30.43±2.31	32.86±1.76	24.91±1.51	5.41	**0.021**

Table 3. Model selection for each individual for the relationship between joint angular velocity and muscle mass-specific peak power output. Ext. = extension, Vel. = velocity, Ret. = retraction.

Individual	Variables	R^2	RMSE	AICc	BIC
1	Knee Ext. Vel., Femur Ret. Vel.	0.56	122.9	392.7	396.8
	Ankle Ext. Vel., Knee Ext. Vel., Femur Ret. Vel.	0.58	121.7	393.8	398.6
	Ankle Ext. Vel., Knee Ext. Vel.	0.53	127.1	394.8	399.0
	Ankle Ext. Vel., Femur Ret. Vel.	0.48	133.9	398.0	402.2
	Knee Ext. Vel.	0.43	138.1	398.3	401.7
	Femur Ret. Vel.	0.40	140.7	399.5	402.9
	Ankle Ext. Vel.	0.38	143.5	400.7	404.1
2	Ankle Ext. Vel.	0.16	227.6	456.6	460.3
	Knee Ext. Vel.	0.12	232.4	458.0	461.7
	Ankle Ext. Vel., Femur Ret. Vel.	0.18	227.9	458.2	462.8
	Ankle Ext. Vel., Knee Ext. Vel.	0.18	228.5	458.4	463.0
	Knee Ext. Vel., Femur Ret. Vel.	0.15	232.1	459.4	464.0
	Ankle Ext. Vel., Knee Ext. Vel., Femur Ret. Vel.	0.20	229.3	460.3	465.6
	Femur Ret. Vel.	0.05	241.1	460.4	464.1
3	Ankle Ext. Vel., Knee Ext. Vel.	0.81	100.5	344.2	347.8
	Ankle Ext. Vel., Knee Ext. Vel., Femur Ret. Vel.	0.81	102.4	347.1	351.0
	Knee Ext. Vel.	0.76	109.5	347.4	350.4
	Knee Ext. Vel., Femur Ret. Vel.	0.77	110.6	349.6	353.1
	Ankle Ext. Vel., Femur Ret. Vel.	0.74	117.6	353.0	356.6
	Ankle Ext. Vel.	0.69	124.6	354.6	357.6
	Femur Ret. Vel.	0.57	146.8	363.8	366.8
4	Ankle Ext. Vel., Knee Ext. Vel.	0.62	164.9	371.9	375.5
	Knee Ext. Vel.	0.58	170.0	372.0	375.0
	Knee Ext. Vel., Femur Ret. Vel.	0.58	172.6	374.5	378.1
	Ankle Ext. Vel., Knee Ext. Vel., Femur Ret. Vel.	0.62	168.0	374.8	378.8
	Ankle Ext. Vel.	0.34	213.0	384.6	387.6
	Ankle Ext. Vel., Femur Ret. Vel.	0.38	210.1	385.5	389.1
	Femur Ret. Vel.	0.28	222.1	386.9	389.9

between joint flexion and peak COM power (Table 8), but there were some relationships within individuals (Table 9, Fig. 6). For two individuals, a more protracted position of the femur at the start of retraction was related to higher peak COM power when the effect of angular excursion was removed. Peak flexion of the knee and ankle occurred after the jump began, rather than during the preparatory phase, but both had no relationship with jump power overall or separately by individual (Table 9, Fig. 6).

Discussion

Individual Variation in the Modulation of Jump Power

Individual variation in the relationship between kinematics and performance in a species is often dismissed as an error term in biomechanical studies, despite the potential ecological and evolutionary consequences (Bolnick et al., 2003). It is recognized that selective pressures can differ between the sexes and through ontogeny, changing the relationship between performance and fitness (Husak, 2006; Husak and Fox, 2006), and some studies have assessed the differences in morphology and kinematics between different sexes or different age classes (Dill et al., 2013). However, individuals may also differ in habitat specialization and past experiences causing changes in the relationship between morphology, kinematics, and performance within that individual relative to the rest of the species that may lead to ecological and evolutionary consequences (Bolnick et al., 2003).

Individuals in the current study differ in their relationship between hindlimb kinematics and jump mechanical performance. The extension of the knee is important for determining jump power in three individuals, the extension of the ankle is important for jump power in two individuals, but only one individual seems to use femur retraction to increase jump power (Table 4). Only in one individual did the timing of peak angular

Table 4. Effects from individual regressions based on best model from model selection using AICc.

Individual	Variable	Slope±SEM	t	p
1	Knee Extension	0.21±0.07	3.16	**0.004**
	Femur Retraction	0.25±0.08	2.93	**0.007**
2	Ankle Extension	0.17±0.07	2.4	**0.022**
3	Ankle Extension	0.14±0.06	2.43	**0.022**
	Knee Extension	0.24±0.06	3.87	**<0.001**
4	Ankle Extension	0.07±0.04	1.62	0.117
	Knee Extension	0.24±0.06	4.29	**<0.001**

velocities have a relationship with peak COM power of the jump, but it was opposite of what was expected (Table 5). Although more overlap in joint motions should result in peak power generation of each joint occurring simultaneously, mechanical considerations may preclude this. For example, the biarticular muscles spanning both the ankle and knee joints may make simultaneously power generation at each joint difficult (Snyder, 1954). The timing of the movements may still be critical to producing high power jumps, but perhaps in a more complex way than the simultaneous generation of peak joint powers.

Table 5. Individual relationships between the elapsed time between the first and last peak angular velocities and muscle mass-specific peak power output.

Individual	R^2	Slope±SEM	t	p
1	0.00	0.02±2.87	0.01	0.99
2	0.07	-5.17±3.34	-1.55	0.13
3	0.15	10.04±4.69	2.14	**0.04**
4	0.04	-5.28±5.38	-0.98	0.34

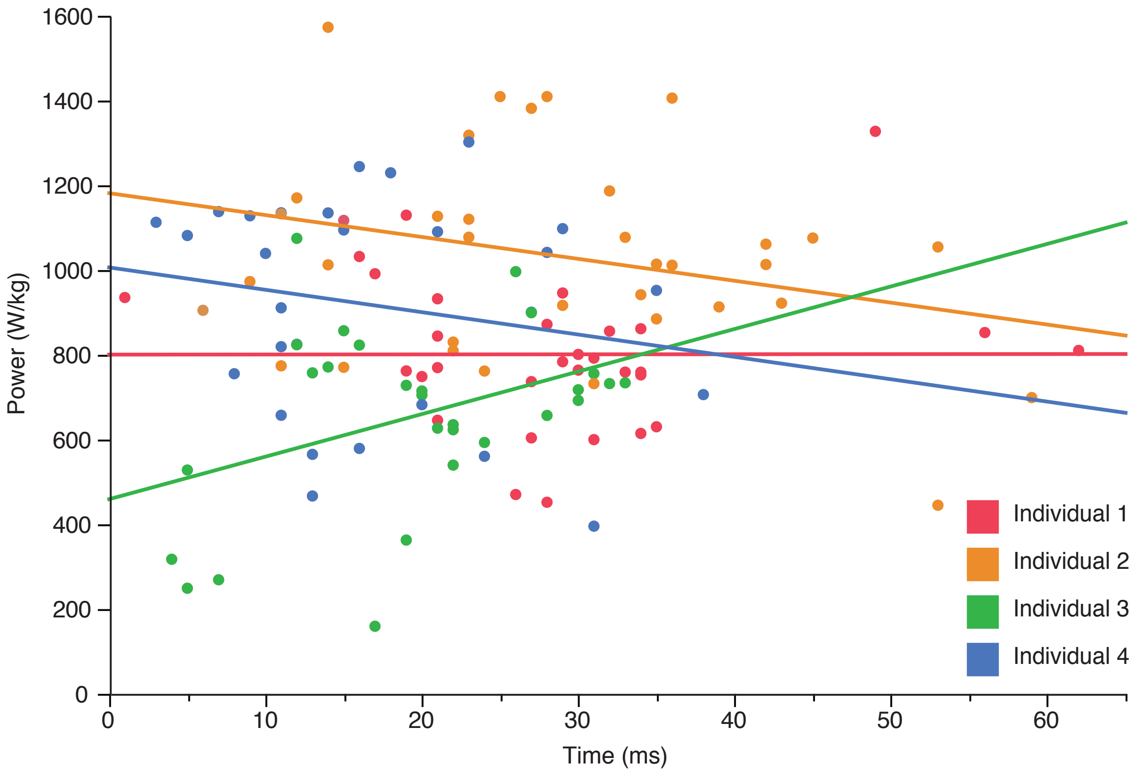


Figure 3. Linear regressions of the elapsed time between the first and last peak angular velocity and muscle mass-specific peak power output for each individual. Statistical results reported in Table 3.

Although, it is unlikely that femur depression is contributing directly to jump work, because the muscles that depress the femur are also hypothesized to protract it (Snyder, 1954), depression of the femur could potentially enhance the ability of femur retraction to do work by changing the moment arm of the femur retractors. The position of the femur along its elevation-depression axis was an important predictor of jump power in some individuals, but not all. Long axis rotation of the femur should be important for the ability of knee extension to do work because rotation of the femur will align the knee such that the flexion-extension axis is kept in line with the long axis of the

Table 6. Individual relationships between secondary kinematic variables and muscle mass-specific peak power output. Femur Elevation 1 is the maximum elevation of the femur prior to depression during the jump, Femur Depression is the maximum depressed position, and Femur Elevation 2 is the elevated position of the femur attained after depression. Femur Post. Rot. is the posteriorly rotated position of the femur prior to the jump and Femur Ant. Rot. is the anteriorly rotated position of the femur about its long-axis after the jump.

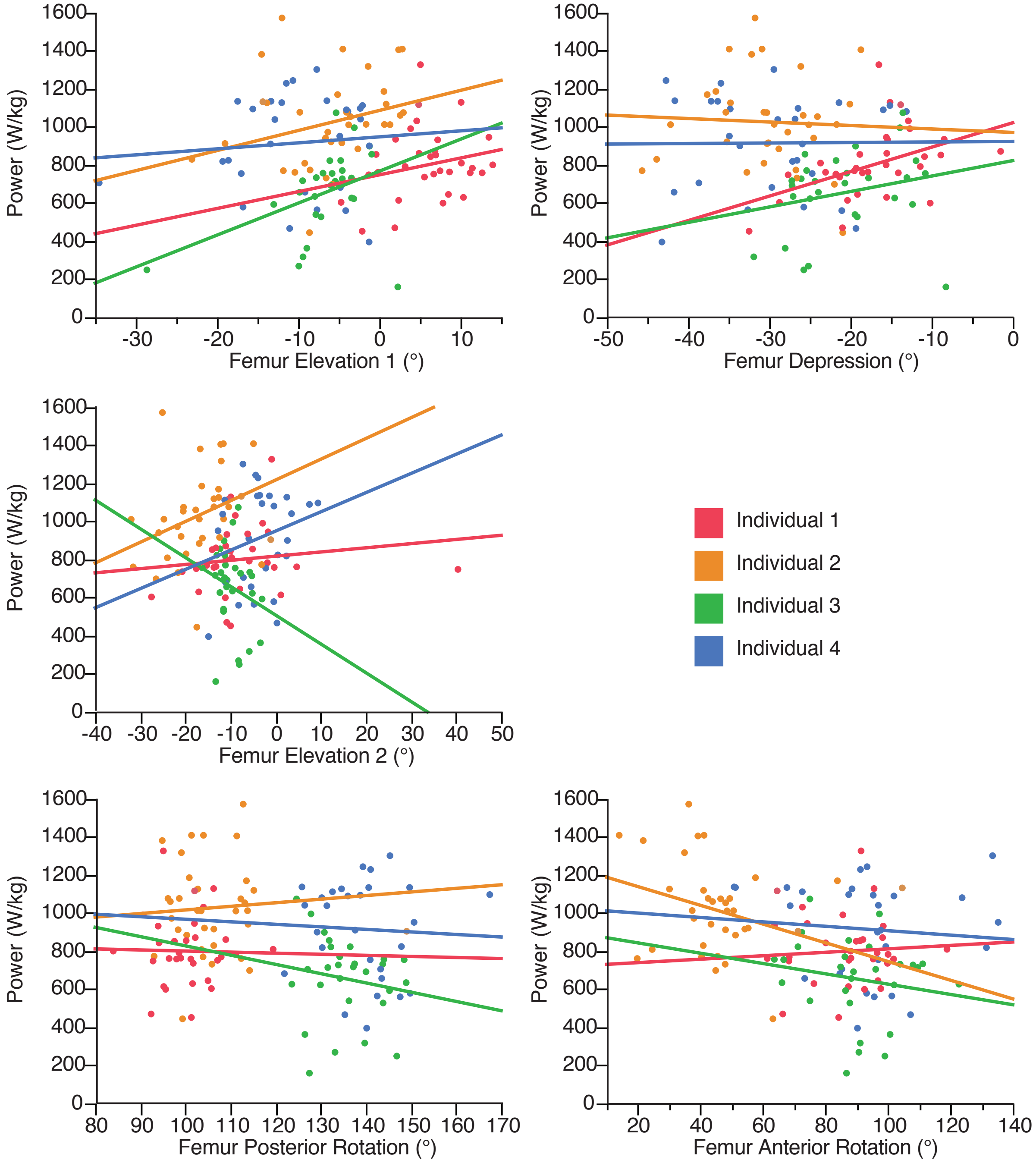
Individual	1		2		3		4	
	R^2	Slope±SEM	R^2	Slope±SEM	R^2	Slope±SEM	R^2	Slope±SEM
Femur Elevation 1 (°)	0.05	8.8±6.8	0.07	10.6±6.7	0.17	16.8±7.3*	0.01	3.2±6.7
Femur Depression (°)	0.21	12.9±4.7*	0.00	-1.8±6.6	0.05	8.1±6.6	0.00	0.3±5.9
Femur Elevation 2 (°)	0.02	2.2±2.9	0.09	10.9±6.2	0.05	-15.1±12.9	0.05	10.1±8.2
Femur Post. Rot. (°)	0.00	-0.6±4.7	0.00	1.9±6.6	0.03	-4.9±5.8	0.00	-1.3±5.3
Femur Ant. Rot. (°)	0.00	0.9±2.5	0.07	-4.9±3.2	0.03	-2.7±2.9	0.01	-1.2±2.4

*$p<0.05$

body (Rewcastle, 1981; Gatesy, 1991; Reilly and Delancey, 1997b, a; Jayne and Irschick, 1999). However, no femur rotation variables were significantly related to jump power (Table 6, Fig. 4).

Because I do not have detailed ecological data for each individual, it is impossible to suggest specific ecological sources of this variation. Likewise, although the individuals differ in mechanical performance, the ecological measure of jump performance important for fitness is unknown making it impossible to conclude that different strategies for the modulation jump work result in increased or decreased performance. Additionally, I did not attempt to elicit maximum performance so individual differences may be due entirely to difference in motivation in a laboratory setting. If individuals differ as a result of some sort of ecological specialization, then the selective pressure experienced by each individual may be different.

The ability to impart kinetic energy to the COM during jumping is not dependent of a specific set of kinematic parameters between individuals, but kinematics are also highly variable within an individual. Although the peak angular velocities of the joint motions explained a large amount of variation in jump power in some individuals (Table 4) there is still a great deal of variation in joint kinematics within individuals. Highly variable kinematics could still effectively modulate jump work if correlated with joint kinetics. The unmeasured component of joint power, joint moment, may vary correspondingly with joint angular velocity so that a slow joint extension can be coupled with a large joint moment to produce that same power as a fast extension/ low force movement. The relationship between joint moment and joint angular velocity



Power (W/kg)
1600
1400
1200
1000
800
600
400
200
0
-30
-20
-10
0
10
Femur Elevation 1 (°)
-50
-40
-30
-20
-10
0
Femur Depression (°)
-40
-30
-20
-10
0
10
20
30
40
50
Femur Elevation 2 (°)
Individual 1
Individual 2
Individual 3
Individual 4
80
90
100
110
120
130
140
150
160
170
Femur Posterior Rotation (°)
20
40
60
80
100
120
140
Femur Anterior Rotation (°)

Figure 4. Linear regressions of secondary joint kinematics with muscle mass-specific peak COM power. Statistical results are reported in Table 4. Femur Elevation 1 is the maximum elevation of the femur prior to depression during the jump, Femur Depression is the maximum depressed position, and Femur Elevation 2 is the elevated position of the femur attained after depression. Femur Post. Rot. is the posteriorly rotated position of the femur prior to the jump and Femur Ant. Rot. is the anteriorly rotated position of the femur about its long-axis after the jump.

determined by the mass being moved by that joint and could depend on the motion occurring both proximal and distal to the joint. Measuring the joint moment during jumps and calculating joint power could demonstrate such variation in the modulation of joint work. Because the total work of the jump is the sum of the work done at each individual joint, the relative contributions of these joints may be variable between jumps in an individual yet able to produce the same level of jump performance. The variability of the individual joints with regard to total jump work would suggest that neural control of the jump behavior is not a rigid action pattern by may operate under feedback mechanisms. Because the joint movements proceed from proximal to distal along the limb, the perceived efficacy of femur retraction at accelerating the body may result in changes to the work output of the knee and ankle joints in order to achieve the desired level of performance.

Peak Power Output

The muscle-mass specific peak COM power measurements exceeded the *in vitro* limits previously recorded for lizard muscle, supporting the hypothesis that these lizards are utilizing elastic power amplification (Fig. 5, Table 7) (Curtin et al., 2005). Measurement of power at the individual joints would be needed to specifically pinpoint where power is being generated in the hindlimb. If high power were generated at the ankle and knee joint where extensor muscles tend to be pennate with large associated tendons, this would provide further support to the hypothesis of elastic power amplification. Alternatively, these analyses could reveal additional sources of power,

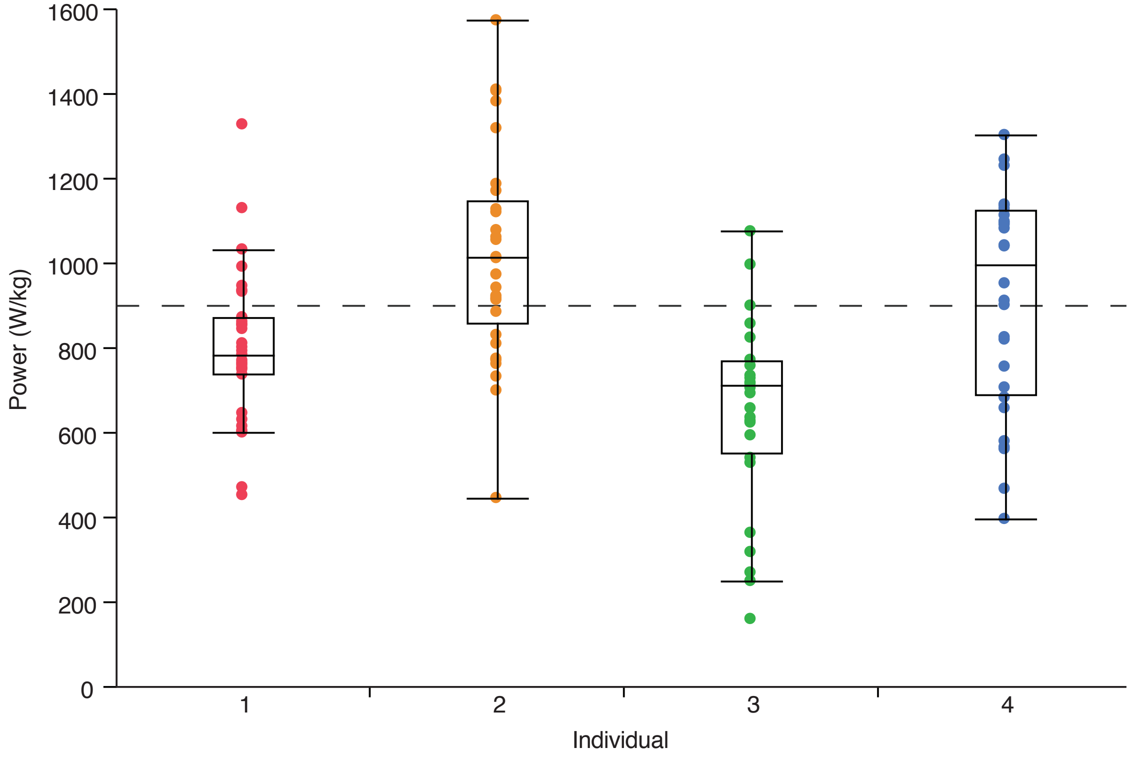


Figure 5. Peak muscle mass specific COM power of the jumps for each individual. The dotted line indicates the literature value for *in vitro* mass specific power output for lizard hindlimb muscle of 952 W/kg. Summary statistics reported in Table 5.

such as the back or the tail. Jumping anoles flex their trunks during a jump, which could provide power to the jump through trunk extension via the action of epaxial muscles (Bels 1992). There is no obvious evidence of body bending in jumping collared lizards, but inverse dynamic analysis and EMG recordings would be necessary to confirm that muscles outside the hindlimbs are not contributing to the energy of the jump. Finally, the only values for peak muscle power output in lizards come from measurements on isolated muscle fibers of the caudofemoralis muscle (a femur retractor) in a distantly related species of lizard (Curtin, 2005). It could be that the muscles of *C. bicinctores* are simply

Table 7. Peak muscle mass-specific COM power for each individual in W/kg.

Individual	Max	Min	Mean±SEM
1 (N = 32)	1327.4	452.2	811.1±32.7
2 (N = 33)	1573.0	445.1	1026.4±42.5
3 (N = 28)	1074.8	159.5	655.2±41.6
4 (N = 30)	1302.2	395.7	922.8±45.9

more powerful or that distal muscle are more powerful than proximal ones, though this is unlikely given that a peak power output of 950 W/kg is already much higher than muscle power measured in other groups of animals (Lutz and Rome, 1996).

These values of muscle-mass specific peak power output are likely underestimates because they were calculated using the mass of all of the muscles of the hindlimbs that are predicted to cause femur retraction, knee extension, and ankle extension (Snyder, 1954). This assumes that every fiber in every muscle is recruited simultaneously and that peak power of each joint occurs at the same time. Because I did not attempt to elicit maximum performance and a large portion of the range of jump powers obtain are above the physiological limit of muscle, it is unlikely that all hindlimb muscles were maximally recruited. The evidence for a proximal-distal sequence of joint movements suggest that these values are likely underestimates of muscle-mass specific peak power output because the instantaneous power from each joint motion contributing to the peak power of the jump would not be maximal for each movement (Fig. 2). Electromyographical recordings of the level of muscle recruitment, as well as the timing of muscle activity, would be needed to verify that all muscle was recruited simultaneously. Additionally, elastic power amplification could be used in jumps even though the same level of peak power could have been produce using only muscle. Simultaneously recording of in vivo forces and length changes in both muscle and tendon are necessary in order to determine the role of elastic mechanisms in submaximal jumps (Roberts et al., 1997).

Countermovements

The degree to which the femur is protracted prior to retracting during the jump has positive effects on jump power independent of its relationship with femur retraction excursion in two individuals (Fig. 6, Table 9). This is consistent with my hypothesis that countermovements are used to increase jump power, but the importance of a proximal joint movement rather than a distal joint movement is surprising considering that the difference in muscle architecture suggest a great ability for elastic storage in the knee and ankle extensors (Snyder, 1954). However, a greater protraction angle of the femur may allow the femur retractors to operate closer to an optimum length, producing higher forces and thus greater power (Alexander, 2003). Additionally, if the extensor muscles are activated while flexion is still occurring, the force generation will start which the muscle is lengthening. Because of the force-velocity properties of muscle, force production will be higher during an eccentric contraction (Cavagna et al., 1968). The degree of flexion in the ankle and knee is not related to jump power in any individual, but because extension occurs immediately following the countermovement flexion, these

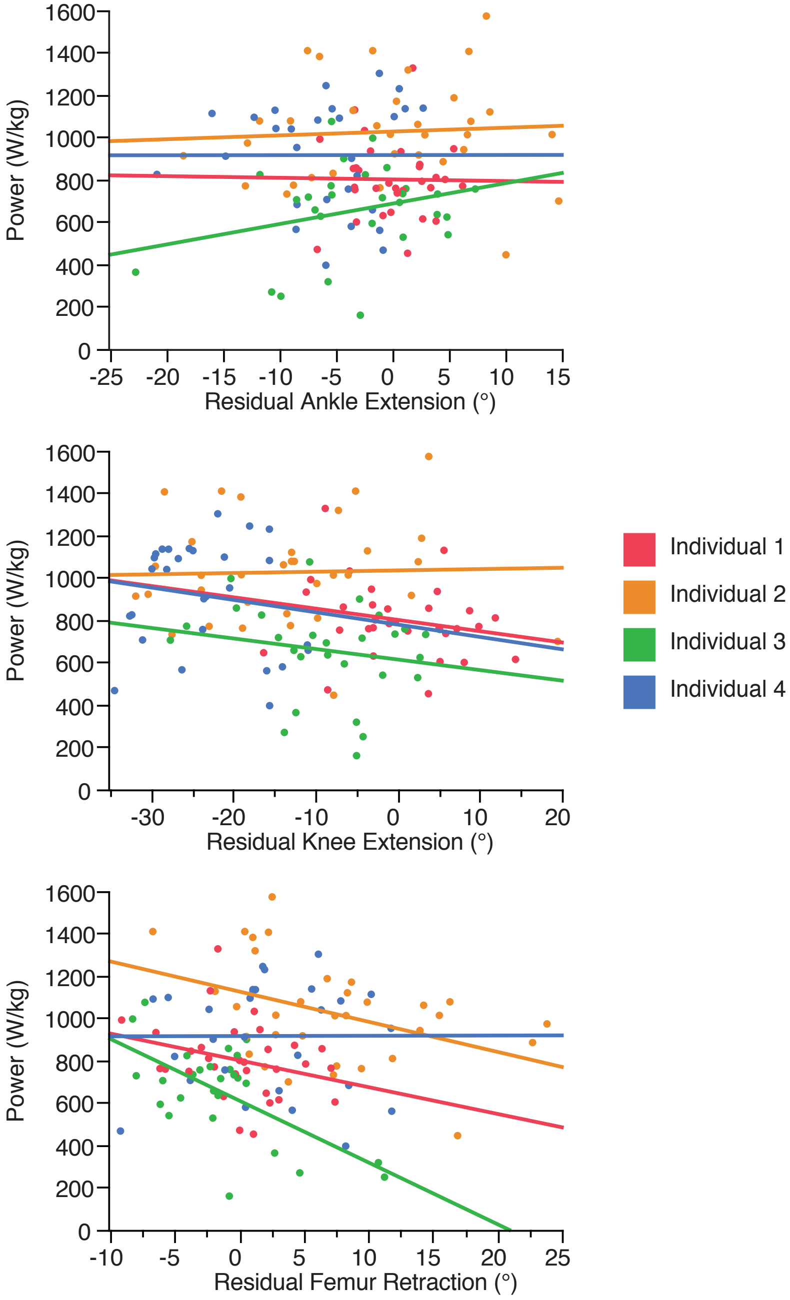

Power (W/kg)
1600
1400
1200
1000
800
600
400
200
0
-25
-20
-15
-10
-5
0
5
10
15
Residual Ankle Extension (°)
Power (W/kg)
1600
1400
1200
1000
800
600
400
200
0
-30
-20
-10
0
10
20
Residual Knee Extension (°)
Power (W/kg)
1600
1400
1200
1000
800
600
400
200
0
-10
-5
0
5
10
15
20
25
Residual Femur Retraction (°)
🟥 Individual 1
🟧 Individual 2
🟩 Individual 3
🟦 Individual 4

Figure 6. The relationship between residual ankle extension, knee extension, and maximum femur retraction and peak muscle mass specific COM power output for each individual. Statistical results reported in Table 9.

Table 8. GLMs of peak muscle mass-specific COM power during the jump with residual max joint flexion prior to extension after regression against joint angular excursion as a fixed factor and individual as a random factor. Individual was highly significant for all three models (p <0.0001)

Variable	F(1,3)	P-value
Residual Ankle Flexion (°)	12.79	0.393
Residual Knee Flexion (°)	4.11	0.136
Residual Femur Protraction (°)	5.57	0.099

individuals could still be storing elastic energy or allowing muscles to operated eccentrically during the beginning of contraction. A comparison of jumps starting from different levels of joint flexion in which extension occurs either immediately or following some pause could reveal a power increase due to countermovements, but behavioral considerations make these data virtually impossible collect except unless using human subjects (Bobbert et al., 1996). Alternatively, direct measurement of muscle and tendon lengths during these behaviors could directly reveal the potential for power enhancing mechanisms.

Jumps which were preceded by the DS type preparatory behavior are associated with high peak COM power output compared to LR and SS jumps, but this is not associated with an increased flexion of the joints prior to the jump. Rather than influencing kinematics and thus jump power, perhaps the preparatory behaviors differ in some unmeasured aspect such as the total time from stimulus to take off. Moving both limbs simultaneously could be a faster way to move the limbs into position compared to moving one limb then the other. Maybe simply performing the preparatory behavior quickly is important for fitness rather than the details of the movements and the

Table 9. Linear regression of residual maximum joint flexion after regression with joint angular excursion versus peak muscle mass-specific power separately for each individual.

Individual	1		2		3		4	
	R^2	Slope±SEM	R^2	Slope±SEM	R^2	Slope±SEM	R^2	Slope±SEM
Residual Ankle Flexion (°)	0.00	-0.8±9.9	0.00	1.8±5.3	0.08	9.6±6.6	0.00	0.1±9.1
Residual Knee Flexion (°)	0.05	-5.3±4.4	0.00	0.6±3.7	0.04	-5.0±4.9	0.02	-5.8±7.3
Residual Femur Protraction (°)	0.08	-12.7±8.0	0.17	-14.2±5.7*	0.39	-29.2±7.2**	0.00	0.1±9.1

*p<0.05, **p<0.001

motivation that triggers a high performance jump also drives the lizard to accomplish the overall behavior as quickly as possible.

Morphology and Performance

In lizards, limb morphology has been related to locomotor performance (Losos, 1990b, a; Sinervo et al., 1991; Sinervo and Losos, 1991; Garland and Losos, 1994; Bauwens et al., 1995; Bonine and Garland, 1999; Melville and Swain, 2000; Zani, 2000; Vanhooydonck and Van Damme, 2001; Toro et al., 2004; Vanhooydonck et al., 2006; Gifford et al., 2008; Goodman et al., 2008; Tulli et al., 2012). Specifically, longer hindlimbs have been associated with increased jump distance and velocity, as well as increased sprint speed on both level and inclined surfaces (Losos, 1990b; Bonine and Garland, 1999; Vanhooydonck and Van Damme, 2001; Goodman et al., 2008; Toro, 2004). In mammals, the elongation of the distal most segment has been associated with increased performance during jumping (Aerts, 1998) with the explanation that elongation of the relatively low mass distal segment provides the greatest increase in total limb length with the lowest increase in mass (Coombs, 1978; Hildebrand, 1985). For jumping lizards, the relative lengths of the individual segments could have impacts on joint angles in a given position. For example, at starting position a relatively longer shank could increase the flexion of the knee and ankle unless the elevation of the femur were increased. In jumping anoles, however, the relative lengths of the limb segments are not related to jump performance, only the total length of the hindlimb (Toro et al., 2004). In the absence of any segment-specific considerations, morphological modifications to increase jump performance would simply be a longer and more powerful hindlimb achieved through any combination of limb segment alterations (Toro, 2003, Toro, 2004).

The high variation in the kinematics of jumping collared lizards and the differences between individuals in the relationships between kinematics and jump work make forming joint specific predictions of the relationship between muscle morphology and performance difficult. All three joint motions, ankle extension, knee extension, and femur retraction are implicated as important for modulating power output in this species (Table 4). If all joints are capable of modulating the power generated in a jump, then the muscles of an individual joint would not be any more likely to respond to selection than any other joint. Inversely, limb morphology may change in response to selection for other types of locomotor performance without necessarily having negative impacts on jump performance. However, the detailed ways in which habitat use interacts with locomotor behavior, kinematics, and mechanics may influence selection on hindlimb morphology. The constraints imposed by habitat on morphology may differ between the segments of the same limb (Snyder, 1954, 1962; Vanhooydonck and Van Damme, 1999; Herrel et al., 2002) and differentially elongating one segment over the others may allow for a beneficial elongation of the hindlimb while circumventing the constraints of habitat. Hypotheses regarding the relationship between limb morphology and performance must therefore include consideration of habitat use and possible trade-offs with other limb functions.

Conclusions

The differences in relationships between limb kinematics and jump work between individuals highlight the importance of individual variation in locomotor biomechanics. In studies relating locomotor function to performance, individuals in a species are often implicitly assumed to be functionally similar (Bolnick et al., 2003). In jumping lizards, there are multiple strategies for increasing jump power (and thus performance) with differences between individuals in the relative importance of each joint motion. Regardless of the specific source of power, peak power outputs exceeding the physiological limits of muscle indicate a source of power besides the muscles of the hindlimb, potentially through elastic power amplification. Additionally, the use of countermovements may increase jump power, though possibly through mechanisms other than elastic energy storage. The results of this study are likely to be critical for future studies hoping to examine the relationship between morphology, mechanics, and performance during jumping. Biomechanical variation between individuals should ultimately be considered a source of information rather than a problem that needs to be eliminated.

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