

## ORIGINAL PAPER

# Comparative analysis of *Dipodomys* species indicates that kangaroo rat hindlimb anatomy is adapted for rapid evasive leaping

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## Abstract

Body size is a key factor that influences antipredator behavior. For animals that rely on jumping to escape from predators, there is a theoretical trade-off between jump distance and acceleration as body size changes at both the inter- and intraspecific levels. Assuming geometric similarity, acceleration will decrease with increasing body size due to a smaller increase in muscle cross-sectional area than body mass. Smaller animals will likely have a similar jump distance as larger animals due to their shorter limbs and faster accelerations. Therefore, in order to maintain acceleration in a jump across different body sizes, hind limbs must be disproportionately bigger for larger animals. We explored this prediction using four species of kangaroo rats (*Dipodomys* spp.), a genus of bipedal rodent with similar morphology across a range of body sizes (40–150 g). Kangaroo rat jump performance was measured by simulating snake strikes to free-ranging individuals. Additionally, morphological measurements of hind limb muscles and segment lengths were obtained from thawed frozen specimens. Overall, jump acceleration was constant across body sizes and jump distance increased with increasing size. Additionally, kangaroo rat hind limb muscle mass and cross-sectional area scaled with positive allometry. Ankle extensor tendon cross-sectional area also scaled with positive allometry. Hind limb segment length scaled isometrically, with the exception of the metatarsals, which scaled with negative allometry. Overall, these findings support the hypothesis that kangaroo rat hind limbs are built to maintain jump acceleration rather than jump distance. Selective pressure from single-strike predators, such as snakes and owls, likely drives this relationship.

## KEYWORDS

allometry, body size, morphology, muscle, performance, segment length

## 1 | INTRODUCTION

Predation is a fundamental evolutionary force that shapes the behavior and morphology of animals. Factors that influence the dynamics of predator-prey interactions vary from system to system, but physical performance is often a crucial component of a

successful antipredator strategy. Performance is directly affected by morphology, so predation thereby shapes morphology through selective pressure on performance (Arnold, 1983). For example, Bronze Frog tadpoles (*Lithobates clamitans*, Latreille) exhibit variation in morphology based on the dominant predators in the local habitat; those morphological differences relate directly to

fast-start escape performance and presumably the tadpoles' ability to escape from the respective dominant predators (Johnson et al., 2015). Therefore, in order to understand why organisms look the way they do, and the role natural selection plays in driving the diversity of body plans observed in nature, an integrative approach combining detailed examinations of performance and morphology is necessary.

One fundamental aspect of morphology that shapes prey performance is body size (Dangles et al., 2007; Domenici & Blake, 1993; Landberg & Azizi, 2010; Martín & López, 1995). In a variety of comparative studies, relative prey body size can affect both the encounter rate and the capture rate by predators (Asquith & Vonesh, 2012; Holmes & McCormick, 2009; Kotler et al., 1988; Osenberg & Mittelbach, 1989). For animals that rely on jumping to escape from predators, there is a theoretical trade-off between jump distance and acceleration as body size changes. Therefore, the selective pressures on jump escape maneuvers can be inferred by comparing jump performance across individuals of different body sizes at the inter- and/or intraspecific level.

Hill (1950) laid the foundation on which many studies have tested the competing demands of jump distance and acceleration. In theory, if an animal maintains geometric similarity (i.e., isometry) in morphology as it gets larger, the acceleration of the body will be lower; mass (which is proportional to volume) increases more quickly than area, and the force produced by a muscle is proportional to its cross-sectional area (CSA) (Powell et al., 1984). Therefore, larger animals produce proportionally smaller forces, which in turn lead to overall slower accelerations (Hill, 1950). However, larger animals can accelerate for a longer period because they also have longer legs, so theoretically both large and small animals achieve similar velocities at the time when the limbs leave the ground (take-off velocity) and therefore would be expected to jump similar distances and heights. If the purpose of an animal's jump is to put as much distance as possible between predator and prey, the capacity of a small animal to jump as far as a larger animal would be most beneficial. On the other hand, if the purpose of the jump is to accelerate out of a predator's attack trajectory as fast as possible, then muscle CSA should scale with positive allometry, resulting in the maintenance of acceleration across a range of body sizes as well as longer jumps as body size increases. While the theoretical trade-off between jump acceleration and distance is somewhat simplistic and does not always hold (reviewed in Biewener & Patek, 2018), this framework has served as the backbone of numerous studies of jumping in animals, primarily in anurans or invertebrates (e.g. Emerson, 1978; Katz & Gosline, 1993; Ryerson, 2013; Wilson et al., 2000).

Kangaroo rats (*Dipodomys* spp.) are a group of bipedal rodents that exhibit notable variation in body size: the smaller species, such as Merriam's kangaroo rats (*Dipodomys merriami*, Mearns) average approximately 40 g, whereas the giant kangaroo rat (*Dipodomys ingens*, Merriam) can reach 160 g. All kangaroo rat species exhibit a suite of antipredator adaptations which aid in their ability to rapidly detect and avoid predators, such as enlarged auditory bullae that allow them to detect the low-frequency sounds produced by snake

strikes and owl swoops (Webster, 1962) as well as thick ankle extensor tendons that can withstand high forces associated with rapid, powerful leaps (Biewener et al., 1981; Biewener & Blickhan, 1988). In general, bipedality in rodents appears to have evolved as a means of enhancing predator evasion (McGowan & Collins, 2018), and kangaroo rats perform impressive, acrobatic leaps that aid in their escape from predators (Higham et al., 2017; Webster, 1962; Whitford et al., 2019). During these escapes, kangaroo rats rely on their large hindlimbs to jump up to a meter into the air with maximal velocities exceeding 4 m/s, which is equivalent to 27 body lengths per second (Freymler et al., 2017, 2019). That said, it is not clear if kangaroo rats are morphologically adapted to optimize jump distance or acceleration.

Kangaroo rats use evasive jumps as their primary means of avoiding the attacks of single-strike ambush predators, such as snakes or owls. Given that attacks from these predators occur in less than a second and over small spatial scales (often less than a meter), we expect that kangaroo rats maximize their ability to displace their body from the attack trajectory as quickly as possible (i.e., acceleration). For example, rattlesnakes can reach their prey in as little as 54 ms once they initiate a strike (Whitford et al., 2019), giving prey very little time to evade the strike, especially after factoring in the prey's reaction time (for kangaroo rats, however, the reaction time can be as short as 8–16 ms; Freymiller et al., 2017; Freymiller, 2021). Furthermore, rattlesnakes rarely initiate a second strike immediately following a first attempt (Clark, 2006; Hayes, 1993; Kardong & Bels, 1998), so a jump maneuver that removes the kangaroo rat from an attack trajectory quickly would be more beneficial than a jump which trades off speed to move the kangaroo rat further from the rattlesnake (either horizontally or vertically). Similarly, owls can reach their prey in approximately 1.13 s (Ilany & Eilam, 2007) and their swoops typically cover short distances (Edut & Eilam, 2004). Unlike rattlesnakes, owls are capable of initiating a second attack when their first attempt misses, but the window of time between attacks provides prey with an opportunity to escape to cover; therefore, dodging the initial attack as quickly as possible then fleeing to cover would likely increase survival probability more so than jumping far from the owl. As all kangaroo rat species (regardless of body size) are preyed on by snakes, owls, and other ambush predators, it is crucial that larger species can displace their bodies from a predator's attack path just as quickly as smaller species.

In this study, we compared the jump performance and hindlimb morphology of four species of kangaroo rat. We utilized well-established methods to elicit startle responses from kangaroo rats in the field, coupled with morphological analyses of hindlimb muscle mass and segment length. Since kangaroo rats primarily use jump maneuvers when escaping single-strike predators, we hypothesized that kangaroo rat hindlimbs maximize jump acceleration rather than jump distance or height. Thus, we predicted that the cross-sectional area of kangaroo rat hind limb muscles would scale with positive allometry and the functional segment lengths would scale isometrically, resulting in a maintenance of average acceleration during jumps and an increase in jump distance and height as body mass

increases. We also predicted that positive allometric scaling would be biased toward the proximal muscles, as they produce a large portion of the work during jumps (Schwaner et al., 2018).

## 2 | METHODS

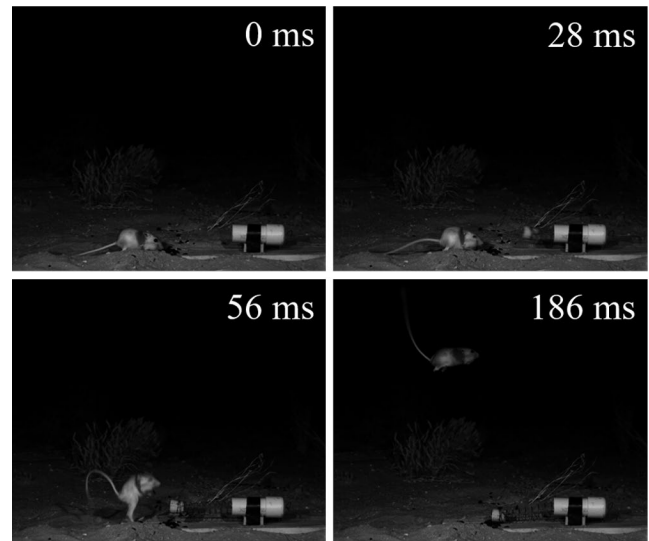
### 2.1 | Study sites and animals

All methods were approved by the San Diego State University Institutional Animal Care and Use Committee [APF 16-08-014C]. We focused on four species of kangaroo rat: the desert kangaroo rat (*Dipodomys deserti*, Stephens; DIDE), Merriam's kangaroo rat (*Dipodomys merriami*; DIME), Dulzura kangaroo rat (*Dipodomys simulans*, Merriam; DISI), and banner-tailed kangaroo rat (*Dipodomys spectabilis*, Merriam; DISP). These species were chosen as they encompass the relatively large variation in body size among kangaroo rats (average mass range of 40–150 g). Field measurements of performance took place at several locations throughout southwestern North America. Data were collected from mid-May through early August in 2018 at Rodeo, New Mexico, USA (21 DISP, 15 DIME) and in Animas, New Mexico, USA (13 DISP). We collected data from June to July of 2019 in the Mojave Desert of California at a site south of the California State University's Desert Studies Center located in Zzyzx, California, USA (20 DIDE and 15 DIME). Lastly, we attempted to collect data for Dulzura kangaroo rats from mid-March to early May of 2020 in the Rancho Jamul Ecological Reserve, California, USA. However, we were unable to gather performance data for this species, so they were only retained in the morphological analyses.

Kangaroo rats were captured using Sherman live traps baited with sterilized black oil sunflower seeds. Traps were set between sunset and sunrise near burrows. Trapped individuals were sexed and measured (mass, snout-anus length, tail length, and hind foot length), then marked with fingerling ear tags (National Band and Tag #1005-1) and a unique fur dye mark using Nyanzol dye. The fur dye allowed individuals to be visually identified without recapture. Individuals were processed in the field and immediately released at the site of capture. Additionally, two to five specimens for each species were collected from each population for morphological analyses, providing a total of 5 DISP, 6 DIME, 5 DIDE, and 2 DISI. Specimens were either salvaged from incidental mortalities during field data collection or euthanized with isoflurane. Specimens were immediately frozen to preserve the muscles for morphological analyses.

### 2.2 | Performance experiments

All performance experiments were conducted in the field with free-ranging individuals. Once a marked kangaroo rat was relocated, an experimental set-up (Figure 1) was placed in the vicinity of the known individual's location. The set-up consisted of a rattlesnake strike simulator (RSS), infrared lighting outside of the rodents' visual spectrum (850 nm wavelength), a GoPro video camera (Hero 4 Black)



**FIGURE 1** Series of stills illustrating the simulation device. The strike simulator consisted of a PVC pipe which housed a spring-propelled cork. When released, the spring-propelled cork startled the kangaroo rat and elicited an evasive response. For video samples of the device, see Freymiller et al. (2017)

retrofitted with an IR-sensitive lens (Peau Productions, 2.97 mm f/4.0 90d HFOV 5MP, no IR filter), and recording at approximately 240 frames per second (fps), and a second IR-sensitive video camera (Sony Handycams, model SR-65 or SR-300) recording at 30 fps. The RSS consists of a 1-inch diameter PVC pipe containing a compressed spring that projects a cork toward a target with a peak velocity of 2.8 m/s, approximately the same velocity as a rattlesnake strike (Higham et al., 2017; Penning et al., 2016; Whitford et al., 2019). The spring was held in a compressed state with monofilament nylon line that was tied on one end to the spring and on the other end to a camera tripod operated by an observer 3–5 m away.

At the beginning of a trial, the kangaroo rat was encouraged to feed near the RSS by baiting it with sunflower seed. Trials were not conducted on individuals that behaved apprehensively around the RSS (e.g., through anti-predator displays), as vigilance affects jump performance (Freymiller et al., 2017; Putman & Clark, 2015). Once the kangaroo rat left to cache, more seed was placed in a small pile directly in front of the cork. When the kangaroo rat began to feed from the seed pile, the monofilament nylon line was cut which released the spring, and the kangaroo rat's response was recorded (Figure 1). If the kangaroo rat jumped, the jump distance (distance between the take-off and landing positions, measured in meters) was immediately measured in the field with a measuring tape using the video playback of the landing location for guidance. Trials in which the individual did not jump were excluded from analyses. No individual was ever tested twice to prevent the possibility that learning would affect the response to the RSS. All trials were recorded between sunset and sunrise.

In order to calculate average acceleration and jump height from the videos, we used the jump distance measured in the field, the amount of time spent airborne (amount of time, in seconds, between

take-off and landing), and the contact time (amount of time, in seconds, between the kangaroo rat's first visible movement and toe-off) with the following equations:

$$\text{Velocity}_h \text{ (m/s)} = \frac{\text{jump distance}}{\text{time spent airborne}} \quad (1)$$

$$\text{Velocity}_v \text{ (m/s)} = g \left( \frac{\text{time spent airborne}}{2} \right) \quad (2)$$

$$\text{Take-off velocity (m/s)} = \sqrt{\text{Velocity}_h^2 + \text{Velocity}_v^2} \quad (3)$$

$$\text{Average acceleration (m/s}^2\text{)} = \frac{\text{Take-off velocity}}{\text{Contact time}} \quad (4)$$

$$\text{Jump height (m)} = \frac{\text{Velocity}_v^2}{2 \times g} \quad (5)$$

where  $g$  = acceleration due to gravity ( $9.8 \text{ m/s}^2$ ). It is important to note that our method of using standard ballistic equations to calculate jump velocity (and therefore acceleration and jump height) does not capture the movement of the kangaroo rat immediately prior to toe-off (i.e., leg extension) and immediately after landing (i.e., compression), and the distance covered during these phases becomes more significant when the overall jump distance is shorter. Additionally, video image quality was not sufficient to determine the frame of toe-off for eight trials out of 84 trials, and therefore we omitted these trials from the jump height analyses. Finally, we could not determine the frame in which the kangaroo rat initiated its response for 26 trials, and therefore we also omitted these trials from the acceleration analyses.

### 2.3 | Morphological data

Overall body mass and tail length were recorded for each specimen. Muscle and segment length data were collected from the left hindlimb of each specimen. Muscle measurements were made for the major extensors of the hindlimb. Hip extensors included the biceps femoris, semitendinosus, and semimembranosus. Knee extensors included the rectus femoris, vastus lateralis, and vastus medialis. Ankle extensors included the plantaris and the medial and lateral heads of the gastrocnemius. For each individual muscle, we measured the wet mass (g) using an analytical balance (0.001-g precision) and the fiber length using digital calipers (0.01-mm precision). For pennate muscles (rectus femoris, vastus lateralis, vastus medialis, medial and lateral gastrocnemius, and plantaris), we also measured the pennation angle ( $^\circ$ ) by slicing the muscle belly with a scalpel and visually inspecting the fiber directionality, then using a small ruler and protractor to measure the fiber angle. Although we acknowledge that fiber length can vary along a pennate muscle, the small size of the muscle constrained us to measuring pennation angle and fiber length in one location along the muscle. For consistency,

we measured both the fiber length and pennation angle at the same location on the muscle. Muscle cross-sectional area ( $\text{CSA}_m$ ) was calculated in  $\text{cm}^2$  for each muscle using the following equation:

$$\text{CSA}_m = \frac{m \cos\theta}{\rho l} \quad (6)$$

where  $m$  is the mass (g),  $\theta$  is the pennation angle (converted to radians),  $\rho$  is the muscle density (assumed value of  $1.06 \text{ g cm}^{-3}$ ; Méndez, 1960), and  $l$  is the fiber length (cm). Free tendon mass and length were measured for the plantaris and gastrocnemius tendons; in most instances, these tendons could not be separated and were measured as a single unit ("ankle extensor tendon"). Tendon cross-sectional area ( $\text{CSA}_t$ ) was calculated in  $\text{cm}^2$  using the following equation:

$$\text{CSA}_t = \frac{m}{\rho l} \quad (7)$$

where  $m$  is the tendon mass (g),  $\rho$  is the tendon density (assumed value of  $1.12 \text{ g cm}^{-3}$ ; Ker, 1981), and  $l$  is the tendon length (cm). Functional segment lengths (mm) were measured for the femur, tibia, metatarsals, longest toe (phalanx), and calcaneus. We also calculated the lever arm ratio about the ankle by dividing the sum of the metatarsal length and half the phalanx length (assuming that the middle of the toes is the center of pressure during a jump) by the length of the calcaneus.

### 2.4 | Statistical analyses

All statistical analyses were performed in R (version 4.0.3). Scaling relationships were determined by regressing each variable against body mass. For the performance analyses, scaling coefficients (a) and exponents (b) were obtained for both pooled species and each species individually using model II regression analyses (with the package "lmodel2") on log-transformed data. For the morphological analyses, scaling coefficients and exponents were obtained for only pooled species using model II regression analyses on log-transformed data (due to the relatively small number of specimens for each species, we could not conduct individual scaling analyses for each species). For the muscle mass analyses only, we examined each muscle individually as well as each functional group of muscles (i.e., hip extensors, knee extensors, and ankle extensors). Scaling exponents were determined as significantly different from the expected value under isometry if the 95% confidence interval did not include the isometric value ( $b = 1.0$  for mass,  $b = 0.67$  for area, and  $b = 0.33$  for length). Based on our *a priori* hypothesis that kangaroo rats maintain acceleration during jumps, we tested the obtained exponents from the performance regressions against the expected exponents under the morphological isometry model ( $b = -0.33$  for acceleration,  $b = 0$  for distance and height; Emerson, 1978). In other words, we tested the slopes to see if they significantly differed from the expected values under the null hypothesis that distance is relatively constant across body sizes and acceleration decreases as body size increases.

### 3 | RESULTS

#### 3.1 | Jump performance

Average acceleration did not show a significant relationship with body mass for pooled species ( $R^2 = 0.01$ ,  $p = 0.40$ ; Figure 2a; Table 1) nor for each individual species (DIME  $n = 27$ ,  $R^2 = 0.06$ ,  $p = 0.22$ ; DIDE  $n = 18$ ,  $R^2 = 0.02$ ,  $p = 0.61$ ; DISP  $n = 13$ ,  $R^2 = 0.13$ ,  $p = 0.22$ ). Additionally, the estimated scaling exponent for acceleration differed significantly from the expected value under isometry ( $b = -0.33$ ) in the pooled species comparison, but not in any of the individual species comparisons (Table 1).

Jump distance exhibited a significant positive relationship with body mass for pooled species ( $R^2 = 0.06$ ,  $p = 0.03$ ; Figure 2b; Table 1). Additionally, the scaling exponent differed significantly from the expected isometric exponent ( $b = 0$ ). However, there was no relationship between body mass and jump distance in the individual species comparisons (DIME  $n = 30$ ,  $R^2 = 0$ ,  $p = 0.80$ ; DIDE  $n = 20$ ,  $R^2 = 0$ ,  $p = 0.85$ ; DISP  $n = 34$ ,  $R^2 = 0$ ,  $p = 0.81$ ; Table 1). There was no significant relationship between body mass and jump height for pooled species or for each individual species (Table 1). Furthermore, the scaling exponent did not significantly differ from the expected isometric exponent ( $b = 0$ ) in any of the jump height analyses. Body mass for all individuals in the performance analyses ranged from 21 to 155 g (Table 2).

#### 3.2 | Hindlimb morphology

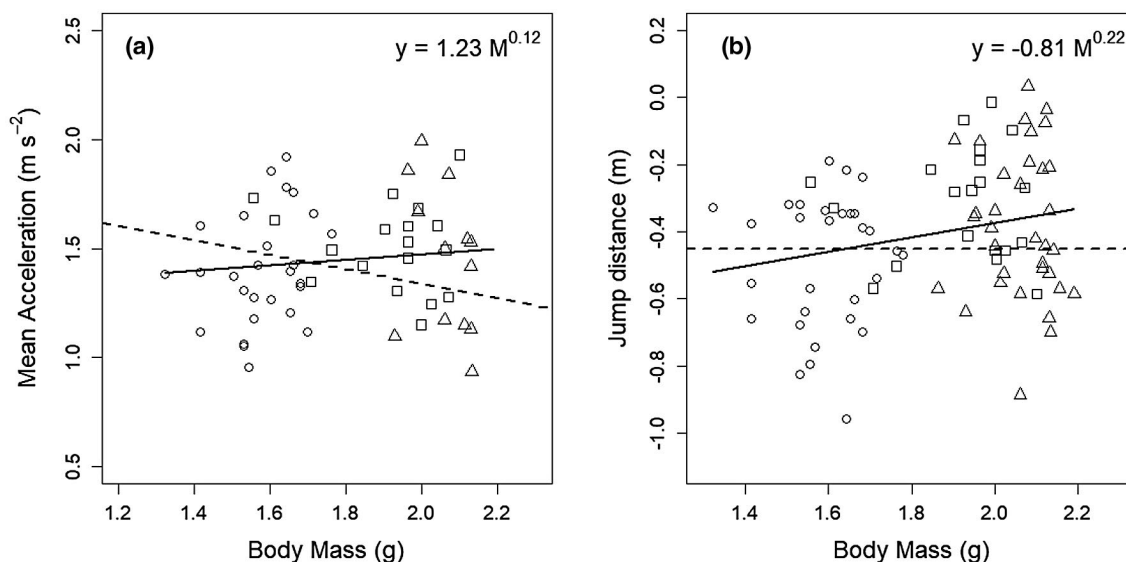
Summary information for the morphological measurements is provided in the supporting documents (Tables S1–S4). Muscle CSA scaled with significant positive allometry in the biceps femoris, semitendinosus,

vastus lateralis, and plantaris (Table 3). Total muscle mass for all functional groups scaled with significant positive allometry (Figure 3). Individual muscle mass scaled with significant positive allometry in the biceps femoris, semitendinosus, rectus femoris, vastus lateralis, and plantaris (Table 3). Thus, there was greater positive allometry in muscle mass for the proximal muscles (hip and knee extensors), and less pronounced positive allometry in the distal muscles (ankle extensors). Fiber length was only significantly allometric for the vastus lateralis, which scaled with negative allometry (Table 3). Therefore, positive allometry in muscle CSA was driven primarily by changes in muscle mass. Ankle extensor tendon CSA (combined plantaris and gastrocnemius tendons) scaled with significant positive allometry (Table 4).

With the exception of the metatarsals, which scaled with significant negative allometry, all the other segment lengths scaled isometrically with body mass (Table 4). Although they were insignificant, the femur, tibia and phalanges had positive allometric exponents, while the calcaneus had a negative allometric exponent. The lever arm ratio about the ankle did not show any relationship to body mass ( $R^2 = 0.02$ ,  $p = 0.61$ ).

### 4 | DISCUSSION

Average acceleration of kangaroo rat jumps was maintained in larger-bodied species, suggesting that kangaroo rat morphology favors acceleration rather than distance in jump escapes from single-strike predators. Similarly, contact time showed no relationship to body size (Table 1), suggesting that the larger species are applying relatively higher forces and therefore extending their legs faster than smaller species. This is supported by the finding that kangaroo rat hindlimb muscle cross-sectional area generally scales with positive allometry such that the muscles of larger kangaroo rat species are capable of producing



**FIGURE 2** Log-log plots of jump performance with body size for pooled species comparisons. Average acceleration (a) shows no relationship with body mass ( $p = 0.4$ ), whereas jump distance (b) shows a significant positive relationship with mass ( $p = 0.03$ ). Open circles represent DIME, open squares represent DIDE, and open triangles represent DISP. Solid lines show obtained regression line for equation in top right corner, and dashed line shows the expected trend based on morphological isometry ( $b = -0.33$  for acceleration,  $b = 0$  for distance)

TABLE 1 Results from performance scaling analyses. Equations are in the form  $y = aM^b$ . Bold values indicate significant difference from isometric exponents under the morphological isometry model (acceleration = -0.33, distance/height = 0)

	a	b	R <sup>2</sup>	±95% CI	P
<i>Pooled species</i>					
Avg. Acceleration (m/s <sup>2</sup> )	1.23	<b>0.12</b>	0.01	0.29	0.40
Jump distance (m)	-0.81	<b>0.22</b>	0.06	0.19	0.03
Jump height (m)	-1.15	-0.02	0	0.33	0.92
<i>DIME</i>					
Avg. Acceleration (m/s <sup>2</sup> )	0.46	0.60	0.06	0.97	0.22
Jump distance (m)	-0.63	0.09	0.00	0.71	0.80
Jump height (m)	-2.29	0.7	0.02	1.17	0.23
<i>DIDE</i>					
Avg. Acceleration (m/s <sup>2</sup> )	1.83	-0.16	0.02	0.67	0.61
Jump distance (m)	-0.41	0.05	0.00	0.55	0.85
Jump height (m)	-1.34	0.16	0	1.24	0.79
<i>DISP</i>					
Avg. Acceleration (m/s <sup>2</sup> )	4.97	-1.70	0.13	2.89	0.22
Jump distance (m)	-0.14	-0.12	0.00	0.99	0.81
Jump height (m)	-0.23	-0.5	0.01	1.69	0.55

TABLE 2 Summary statistics from performance experiments. Results are mean ± standard error

Species	Mass (g)	Contact time (ms)	Avg. Acceleration (m s <sup>-2</sup> )	Jump distance (m)	Jump height (m)
DIME	40 ± 2	90 ± 9	30 ± 4	0.35 ± 0.03	0.09 ± 0.02
DIDE	91 ± 5	83 ± 7	39 ± 4	0.54 ± 0.04	0.12 ± 0.02
DISP	117 ± 3	92 ± 15	36 ± 8	0.47 ± 0.04	0.07 ± 0.01

more force (Powell et al., 1984), resulting in higher accelerations and faster take-off times than expected under isometry. The increase in cross-sectional area was driven by positive allometric scaling of muscle mass as most fiber lengths scaled isometrically. As a result of the disproportionately large muscle mass, the larger kangaroo rat species also jumped farther. However, there was no observed increase in jump height as body mass increased. A larger proportion of proximal muscles exhibited positive allometric scaling, which is expected considering that the proximal muscles produce a substantial amount of work that is then transferred to the ankle joint by the biarticular ankle extensors during jumps (Schwaner et al., 2018).

The large variation in acceleration and distance resulted in relatively low R<sup>2</sup> values in each performance analyses (Figure 2, Table 2). It should be noted that the jumps elicited here are not necessarily representative of maximal performance; kangaroo rats in a baseline state of vigilance (such as the kangaroo rats in this study) exhibit slower reaction times and take-off velocities, do not jump as high, and take longer to displace their bodies from an attack trajectory when compared to kangaroo rats that have recently interacted with a rattlesnake and are in a state of enhanced vigilance (Freymler et al., 2017). Thus, it is possible that body mass would be more tightly correlated with performance if all the animals in this study

were performing closer to their maximal abilities and the variation in jump performance was reduced. This may also explain why there was no relationship between jump height and body mass, the large variation in acceleration scaling exponents (Table 2), and why jump acceleration is maintained without any direct effects on jump distance in the intraspecific comparisons, which does not fit into the framework proposed by Hill (1950).

Kangaroo rat ankle extensor tendons are thicker than those of other bipedal mammals such as kangaroos, suggesting that the primary role of kangaroo rat ankle extensor tendons is likely to transmit the high forces associated with rapid evasive jumping (Biewener et al., 1981; Biewener & Blickhan, 1988). While their tendons are not as stiff as initially assumed and there is likely more elastic return than predicted, desert kangaroo rat tendons are extremely tough and can withstand larger stresses compared with white rat tendons, which supports the hypothesis that their hindlimbs are specially adapted for high levels of locomotor performance (Javidi et al., 2019). Consistent with these findings, the cross-sectional area of the ankle extensor tendons scaled with significant positive allometry (Table 4). Thus, larger kangaroo rat species have disproportionately thicker tendons, presumably to withstand the increase in force production from their disproportionately larger muscles during explosive evasive jumps.

TABLE 3 Constants from muscle scaling equations. Equations are in the form  $y = aM^b$ . Bold values indicate significant difference from isometric exponents (1.0 for mass, 0.67 for area, and 0.33 for length)

	Muscle Mass (g)				Muscle CSA (cm <sup>2</sup> )				Fiber length (mm)			
	a	b	R <sup>2</sup>	±95% CI	a	b	R <sup>2</sup>	±95% CI	a	b	R <sup>2</sup>	±95% CI
<i>Hip extensors</i>	-1.96	<b>1.23</b>	0.91	0.20								
BF	-2.52	<b>1.39</b>	0.81	0.35	-2.55	<b>1.09</b>	0.72	0.35	1.01	0.31	0.86	0.06
ST	-2.78	<b>1.19</b>	0.94	0.15	-2.87	<b>0.90</b>	0.94	0.12	1.07	0.29	0.72	0.10
SM	-2.10	1.01	0.76	0.30	-2.10	0.70	0.63	0.28	0.97	0.31	0.66	0.12
<i>Knee extensors</i>	-2.12	<b>1.20</b>	0.95	0.14								
RF	-2.83	<b>1.32</b>	0.95	0.17	-2.01	0.93	0.81	0.26	0.40	0.24	0.17	0.32
VL	-2.38	<b>1.17</b>	0.96	0.13	-2.24	<b>1.06</b>	0.92	0.17	0.77	<b>0.13</b>	0.16	0.16
VM	-2.74	1.14	0.83	0.27	-2.46	0.99	0.71	0.36	0.62	0.17	0.14	0.24
<i>Ankle extensors</i>	-2.18	<b>1.18</b>	0.97	0.10								
LG	-2.54	1.14	0.94	0.15	-1.85	0.80	0.74	0.26	0.24	0.34	0.38	0.24
MG	-2.54	1.13	0.93	0.16	-1.96	0.91	0.72	0.33	0.32	0.24	0.17	0.30
PL	-3.12	<b>1.33</b>	0.98	0.11	-2.52	<b>1.10</b>	0.84	0.30	0.36	0.21	0.16	0.31

Note: Muscle abbreviations: BF, biceps femoris; ST, semitendinosus; SM, semimembranosus; RF, rectus femoris; VL, vastus lateralis; VM, vastus medialis; PL, plantaris; MG, medial head of gastrocnemius; LG, lateral head of gastrocnemius.

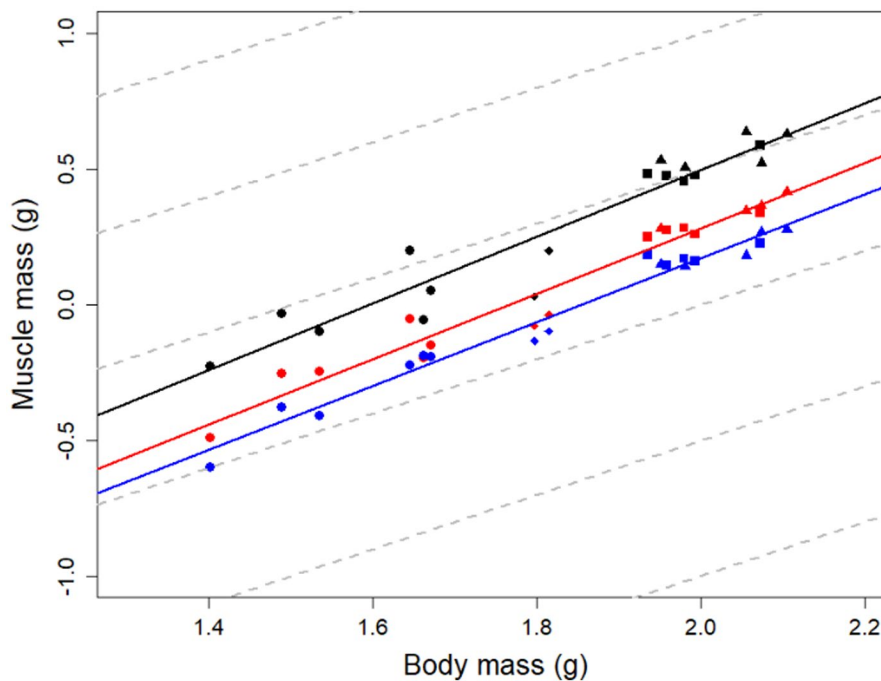


FIGURE 3 Log-log plot of scaling relationships for hindlimb muscle group mass (black = hip extensors, red = knee extensors, and blue = ankle extensors). All functional groups scaled with significant positive allometry. Circles represent DIME, squares represent DIDE, triangles represent DISP, and diamonds represent DISI. Solid lines show regression results and grey dashed lines show expected trend based on isometry ( $b = 1.0$ )

With the exception of the metatarsals, all hindlimb segments scaled isometrically (Table 4). Although the metatarsals scaled with negative allometry (i.e., larger kangaroo rats have disproportionately shorter metatarsals), this difference does not appear to be functionally significant due to the slight positive allometry in the phalanges and slight negative allometry of the calcaneus (Table 4). As a result, the

lever arm ratio about the ankle showed no relationship to body mass, indicating that the mechanical advantage is similar between large and small species. Therefore, mechanical advantage is likely similar across body size regardless of the significant negative allometry in metatarsal length. We would expect larger species to have longer contact times because the absolute length of the distal segments is longer for larger

**TABLE 4** Constants from tendon cross-sectional area and segment length scaling equations. Equations are in the form  $y = aM^b$ . Bold values indicate significant difference from isometric exponents ( $b = 0.33$  for segment length,  $b = 0.67$  for tendon area)

	a	b	R <sup>2</sup>	±95% CI
Femur	0.70	0.36	0.94	0.05
Tibia	0.95	0.35	0.93	0.05
Metatarsals	0.93	<b>0.24</b>	0.90	0.04
Phalanx	0.47	0.37	0.77	0.10
Calcaneus	0.19	0.30	0.66	0.11
Ankle extensor tendon	-3.65	<b>0.95</b>	0.84	0.22

species, yet desert kangaroo rats had a shorter average contact time than the smaller Merriam's kangaroo rats (Table 1). It is possible that kangaroo rats exhibit slight postural shifts as body size changes, which could cause the observed discrepancy between contact time and limb length; a more detailed kinematic analysis examining joint angles at the onset of the jump would be necessary to address this.

Kangaroo rats are one of four extant groups of bipedal rodent, and their bipedal morphology enhances their ability to escape predators (Kotler, 1985; Longland & Price, 1991; Pierce et al., 1992; McGowan & Collins, 2018; Freymiller, 2021). When escaping cursorial predators, bipedal rodents rely on erratic, unpredictable escape paths rather than rapid, powerful jumps (Djawdan, 1993; Djawdan & Garland, 1988; Moore et al., 2017). These predators would therefore place little selective pressure on jump performance. However, when evading single-strike ambush predators such as rattlesnakes and owls, they utilize impressive jump escapes (Freymiller et al., 2019; Higham et al., 2017; Webster, 1962; Whitford et al., 2019). Escaping from such predators requires a quick jump that rapidly moves the body out of the trajectory of the attack; if they are able to dodge the initial strike, the predator cannot immediately launch a fully coordinated second attack, thus giving the kangaroo rat time to escape (Kardong & Bels, 1998; Shifferman & Eilam, 2004). Furthermore, because these attacks occur within relatively small spatial scales compared with attacks from pursuit predators, jump distance and height may be less important. Therefore, predation pressure from single-strike predators likely explains why kangaroo rat morphology favors the ability to quickly displace the body from a predator's attack trajectory by maintaining high acceleration capacity.

## 5 | CONCLUSION

Evolution of large body size (average mass greater than 90 g) has occurred independently at least twice in the *Dipodomys* genus (Alexander, 2003). For rodents, increasing body size can provide advantages in foraging (Muñoz & Bonal, 2008) and interspecific fighting/dominance and territory defense (Bartholomew & Caswell, 1951), but it comes with certain limitations as well (e.g. Kotler et al., 1988). For rodents which rely on jumping to escape predators, and jumping animals in general, a theoretical disadvantage of larger body sizes is a reduction in jump acceleration. This can be circumvented if the morphology of the limbs used to propel the jump

scales with positive allometry. Here we show that, as kangaroo rat species increase in body mass, morphological changes favor rapid jumping rather than jump distance. Hindlimb muscle cross-sectional area, particularly of the proximal muscles, generally scales with positive allometry such that larger species have greater force-producing capacity than expected based on their overall body size. This results in a maintenance of average jump acceleration, which allows larger species to jump away from single-strike predators just as quickly as their smaller counterparts.

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## AUTHOR CONTRIBUTIONS

All authors contributed to the study design, data analysis/interpretation, and revision of the manuscript. GAF, MDW, and MJS contributed to data collection. GAF drafted the manuscript.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.j9kd51cd3>

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