

## RESEARCH ARTICLE

# A comparative study of single-leg ground reaction forces in running lizards

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**ABSTRACT**

The role of different limbs in supporting and propelling the body has been studied in many species with animals appearing to have either similarity in limb function or differential limb function. Differential hindlimb versus forelimb function has been proposed as a general feature of running with a sprawling posture and as benefiting sprawled postured animals by enhancing maneuvering and minimizing joint moments. Yet only a few species have been studied and thus the generality of differential limb function in running animals with sprawled postures is unknown. We measured the limb lengths of seven species of lizard and their single-limb three-dimensional ground reaction forces during high-speed running. We found that all species relied on the hindlimb for producing accelerative forces. Braking forces were forelimb dominated in four species and equally distributed between limbs in the other three. Vertical forces were dominated by the hindlimb in three species and equally distributed between the forelimb and hindlimb in the other four. Medial forces were dominated by the hindlimb in four species and equally distributed in the other three, with all Iguanians exhibiting hindlimb-biased medial forces. Relative hindlimb to forelimb length of each species was related to variation in hindlimb versus forelimb medial forces; species with relatively longer hindlimbs compared with forelimbs exhibited medial forces that were more biased towards the hindlimbs. These results suggest that the function of individual limbs in lizards varies across species with only a single general pattern (hindlimb-dominated accelerative force) being present.

**KEY WORDS:** Morphology, Running, Ground reaction force, Lizard, Locomotion

**INTRODUCTION**

Different limbs of multiple-legged animals (e.g. forelimb versus hindlimb in a quadruped) appear to exhibit disparity in morphology and function. For example, many species can be roughly divided into those with hindlimb- versus forelimb-dominated body support (i.e. vertical ground reaction force and impulse) (Rollinson and Martin, 1981; Demes et al., 1994). Additionally, some species seem to rely on hindlimb ‘drive’ wherein the hindlimb produces the majority of the accelerative ground reaction force while the forelimb produces the majority of the braking ground reaction force. However, in other species the forelimb and hindlimb share a more equal role for accelerative-braking ground reaction force (Full et al., 1991; Demes et al., 1994; Witte et al., 2002; Lee et al., 2004; Willey

et al., 2004; Autumn et al., 2006). Finally, mediolateral ground reaction forces are not similar across species or legs. Large erect mammals, primates and small crouched eutherians produce small mediolateral ground reaction forces during steady speed running locomotion (Biewener, 1990); however, semi-erect mammals, alligators, lizards and cockroaches produce greater mediolateral ground reaction forces, with these forces typically being greater in the hindlimbs (Full et al., 1991; Farley and Ko, 1997; Lammers and Biknevičius, 2004; Willey et al., 2004; McElroy and Reilly, 2009).

Chen et al. (Chen et al., 2006) developed a hypothetical framework of how different limbs could function during steady speed locomotion. This framework posits that animals broadly fall into one of two limb functional categories: (1) animals whose forelimbs and hindlimbs both contribute equally to moving the center of mass over the support phase exhibit ‘similarity’ in limb function (see also Alexander and Goldspink, 1977); and (2) animals whose forelimbs and hindlimbs play different roles in moving the center of mass exhibit ‘differential’ limb function (Chen et al., 2006; Deban et al., 2012). Based on data from the house gecko *Hemidactylus garnotii* (Chen et al., 2006) and previous data from the cockroach *Blaberus discoidalis* (Jindrich and Full, 1999), Chen et al. (Chen et al., 2006) argue that there are both maneuvering and mechanical benefits for coupling differential leg function with a sprawling limb posture. Additionally, bipedal running in lizards, which is an extreme form of differential limb function, has been hypothesized to confer enhanced maneuvering and obstacle negotiation (Aerts et al., 2003; Olberding et al., 2012). However, differential limb function is not universal among sprawling animals; single-limb ground reaction forces in iguanas (*Iguana iguana*) suggests similarity of leg function in this species with a sprawling limb posture (Blob and Biewener, 2001). Additionally, American alligators (*Alligator mississippiensis*) use differential limb function but are not maneuverable or efficient; they walk slowly with a semi-erect posture and a massive, dragging tail (Willey et al., 2004). Taken together, these data suggest that a general pattern of limb function for all or most sprawling quadrupedal trotting animals may not exist. To allow any generalities in limb function and its functional benefits in sprawling animals – or even lizards – it would be useful to examine a comparative sample of additional species.

Herein, we present data on seven fast-running lizards that represent a diversity of body forms, limb morphologies and phylogenetic positions among limbed squamates. Using these data we address the two questions: (1) is differential limb function a general characteristic of steady speed running in lizards? We expected differences in limb function across species given the diversity of species in our sample; and (2) does limb function reflect limb morphology? We expected species with more similarly sized forelimbs versus hindlimbs to exhibit greater similarity in limb function and conversely we expected species with hindlimbs that were relatively long compared with the forelimbs to display a greater disparity in the function between the hindlimbs and forelimbs.

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## RESULTS

## Vertical forces and impulses

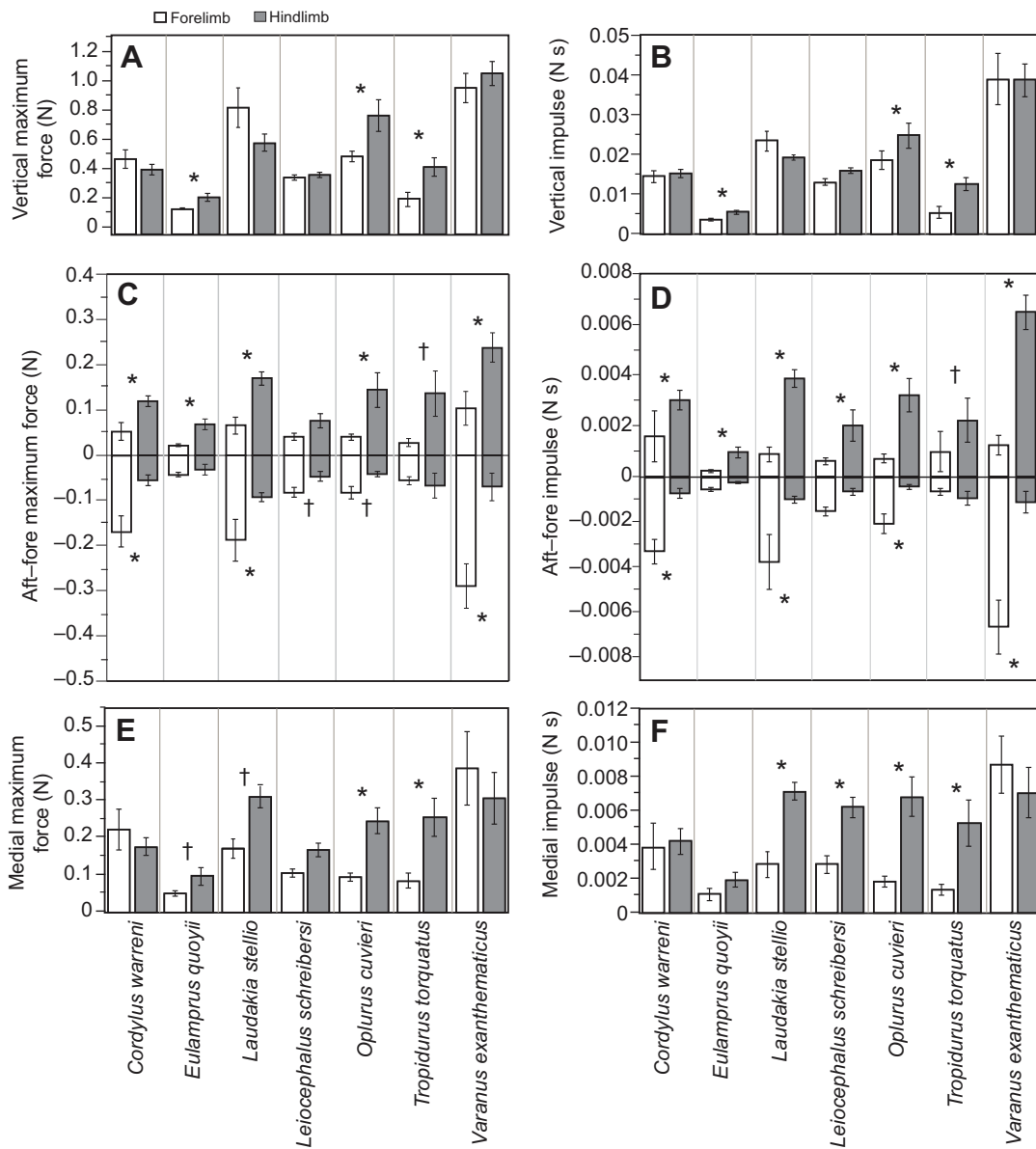
The maximum vertical force was significantly larger in the hindlimb when compared with the forelimb for *Eulamprus quoyii* ( $F_{1,12.3}=9.5$ ,  $P=0.009$ ), *Oplurus cuvieri* ( $F_{1,12.2}=5.1$ ,  $P=0.043$ ) and *Tropidurus torquatus* ( $F_{1,14.4}=10.8$ ,  $P=0.005$ ), whereas the other four species had similar forelimb versus hindlimb maximum vertical forces ( $P>0.10$ , Fig. 1A).

The vertical impulse was significantly larger in the hindlimb when compared with the forelimb for *E. quoyii* ( $F_{1,13.3}=14.6$ ,  $P=0.002$ ), *O. cuvieri* ( $F_{1,12.4}=5.3$ ,  $P=0.039$ ) and *T. torquatus* ( $F_{1,17.1}=17.8$ ,  $P<0.001$ ), whereas the other four species had similar forelimb versus hindlimb vertical impulse ( $P>0.10$ , Fig. 1B).

## Accelerative forces and impulses

Maximum accelerative forces were significantly greater in the hindlimbs compared with the forelimbs for *Cordylus warreni* ( $F_{1,40.4}=6.2$ ,  $P=0.017$ ), *E. quoyii* ( $F_{1,9.3}=7.5$ ,  $P=0.022$ ), *Laudakia stellio* ( $F_{1,10.2}=13.1$ ,  $P=0.005$ ), *O. cuvieri* ( $F_{1,8.5}=10.6$ ,  $P=0.011$ ) and *Varanus exanthematicus* ( $F_{1,13.3}=12.9$ ,  $P=0.003$ ), marginally significantly greater in the hindlimbs for *T. torquatus* ( $F_{1,12.6}=3.9$ ,  $P=0.069$ ), and not significantly different between limbs in *Leiocephalus schreibersi* ( $F_{1,8.8}=2.3$ ,  $P=0.167$ , Fig. 1C).

Accelerative impulses were significantly greater in the hindlimbs compared with the forelimbs for *C. warreni* ( $F_{1,38.1}=5.7$ ,  $P=0.022$ ), *E. quoyii* ( $F_{1,7.7}=7.3$ ,  $P=0.028$ ), *L. stellio* ( $F_{1,8.7}=24.8$ ,  $P<0.001$ ), *L. schreibersi* ( $F_{1,7.2}=8.0$ ,  $P=0.025$ ), *O. cuvieri* ( $F_{1,6.8}=19.9$ ,  $P=0.003$ ) and *V. exanthematicus* ( $F_{1,11.8}=44.2$ ,  $P<0.001$ ) and marginally



**Fig. 1. Forces and impulses for each component of the ground reaction forces for each species.** \*Forelimb had significantly different ground reaction force than hindlimb within a species ( $P < 0.05$ ); †marginal significance ( $0.05 < P < 0.10$ ). Significance was assessed using the linear contrasts within the species $\times$ limb interaction term in the general linear mixed models for component impulse or ground reaction force. Values are means  $\pm$  1 s.e.m. It should be noted that significance tests are for means adjusted for the parameters in the mixed model (see Materials and methods). Panels C and D have two tests each for each species, one for accelerative force and impulse (i.e. comparing forelimb versus hindlimb above zero) and one for braking force and impulse (i.e. comparing forelimb versus hindlimb below zero).

**Table 1. Sample sizes and mean ( $\pm$ s.e.m.) body mass, limb duty factors, accelerative/braking impulses and the braking–propulsion ratio for each species**

Species	Body mass (g)	Limb	N	Duty factor	Accelerative impulse (mN s)	Braking impulse (mN s)	B–P ratio	Time to maximum vertical force (% of step duration)
<i>Cordylus warreni</i> (4, 11)	41 $\pm$ 1.0	Forelimb	4	0.39 $\pm$ 0.01	1.58 $\pm$ 1.01	–3.23 $\pm$ 0.54	2.04	51 $\pm$ 3.2
		Hindlimb	10	0.53 $\pm$ 0.02	3.01 $\pm$ 0.34	–0.70 $\pm$ 0.22	4.30	47 $\pm$ 4.4
<i>Eulamprus quoyii</i> (3, 29)	29 $\pm$ 9.0	Forelimb	18	0.39 $\pm$ 0.01	0.21 $\pm$ 0.04	–0.52 $\pm$ 0.08	2.48	44 $\pm$ 1.9
		Hindlimb	10	0.49 $\pm$ 0.01	0.96 $\pm$ 0.22	–0.20 $\pm$ 0.05	4.80	41 $\pm$ 4.7
<i>Laudakia stellio</i> (2, 33)	49 $\pm$ 2.0	Forelimb	7	0.37 $\pm$ 0.03	0.87 $\pm$ 0.28	–3.75 $\pm$ 1.21	4.31	46 $\pm$ 3.1
		Hindlimb	13	0.48 $\pm$ 0.02	3.86 $\pm$ 0.34	–0.96 $\pm$ 0.15	4.02	54 $\pm$ 3.4
<i>Leiocephalus schreibersi</i> (2, 19)	35 $\pm$ 1.0	Forelimb	14	0.41 $\pm$ 0.02	0.61 $\pm$ 0.14	–1.48 $\pm$ 0.20	2.43	43 $\pm$ 3.2
		Hindlimb	7	0.51 $\pm$ 0.03	2.00 $\pm$ 0.60	–0.61 $\pm$ 0.16	3.29	36 $\pm$ 3.0
<i>Oplurus cuvieri</i> (3, 21)	49 $\pm$ 5.4	Forelimb	19	0.43 $\pm$ 0.01	0.70 $\pm$ 0.17	–2.06 $\pm$ 0.44	2.94	49 $\pm$ 1.8
		Hindlimb	10	0.44 $\pm$ 0.03	3.20 $\pm$ 0.67	–0.40 $\pm$ 0.10	8.00	44 $\pm$ 1.8
<i>Tropidurus torquatus</i> (3, 7)	26 $\pm$ 2.3	Forelimb	5	0.29 $\pm$ 0.03	0.19 $\pm$ 0.06	–0.75 $\pm$ 0.08	3.95	52 $\pm$ 2.5
		Hindlimb	5	0.36 $\pm$ 0.06	2.21 $\pm$ 0.88	–0.92 $\pm$ 0.31	2.40	57 $\pm$ 3.3
<i>Varanus exanthematicus</i> (2, 13)	94 $\pm$ 1.4	Forelimb	8	0.43 $\pm$ 0.02	1.23 $\pm$ 0.39	–6.62 $\pm$ 1.21	5.38	46 $\pm$ 4.4
		Hindlimb	8	0.41 $\pm$ 0.04	6.48 $\pm$ 0.69	–1.09 $\pm$ 0.48	5.94	53 $\pm$ 1.4

Numbers in parentheses after species names are: number of individuals ran, number of individuals for which morphology was measured. B–P ratio, braking–propulsion ratio.

significantly larger in the hindlimbs for *T. torquatus* ( $F_{1,11}=4.4$ ,  $P=0.059$ , Fig. 1D).

### Braking forces and impulses

Maximum braking forces were significantly larger in the forelimb when compared with the hindlimb for *C. warreni* ( $F_{1,60.9}=10.6$ ,  $P=0.002$ ), *L. stellio* ( $F_{1,11}=6.5$ ,  $P=0.027$ ) and *V. exanthematicus* ( $F_{1,19.3}=48.1$ ,  $P<0.001$ ), marginally significantly larger in the forelimbs for *O. cuvieri* ( $F_{1,5.3}=5.4$ ,  $P=0.063$ ) and *L. schreibersi* ( $F_{1,7.6}=3.8$ ,  $P=0.089$ ) and not different between limbs in the other two species ( $P>0.10$ , Fig. 1C).

Braking impulses were significantly larger in the forelimb when compared with the hindlimb for *C. warreni* ( $F_{1,47.6}=15.7$ ,  $P<0.001$ ), *L. stellio* ( $F_{1,15.2}=13.3$ ,  $P=0.002$ ), *O. cuvieri* ( $F_{1,14.1}=9.5$ ,  $P=0.008$ ) and *V. exanthematicus* ( $F_{1,18.3}=37.0$ ,  $P<0.001$ ), whereas the other three species had similar forelimb versus hindlimb braking impulses ( $P>0.10$ , Fig. 1D).

### Medial forces and impulses

Maximum medial forces were significantly greater in the hindlimb when compared with the forelimb for *O. cuvieri* ( $F_{1,14.1}=9.5$ ,  $P=0.008$ ) and *T. torquatus* ( $F_{1,14.1}=9.5$ ,  $P=0.008$ ), marginally greater in *E. quoyii* ( $F_{1,11.9}=3.7$ ,  $P=0.079$ ) and *L. stellio* ( $F_{1,12.2}=3.7$ ,  $P=0.076$ ), and did not significantly differ between limbs in the other two species ( $P>0.10$ , Fig. 1E).

Medial impulses were significantly larger in the hindlimb compared with the forelimb for *L. stellio* ( $F_{1,10}=9.4$ ,  $P=0.012$ ), *L. schreibersi* ( $F_{1,8.4}=6.4$ ,  $P=0.034$ ), *O. cuvieri* ( $F_{1,7.9}=12.1$ ,  $P=0.008$ ) and *T. torquatus* ( $F_{1,12.6}=6.02$ ,  $P=0.030$ ), whereas all other species had similar medial impulses when comparing the forelimb with the hindlimb ( $P>0.10$ , Fig. 1F).

### Duty factor, braking–propulsive bias and timing of peak vertical force

Hindlimb duty factor was significantly greater than forelimb duty factor for *C. warreni* ( $F_{1,50}=11.5$ ,  $P=0.001$ ), *E. quoyii* ( $F_{1,7.5}=14.6$ ,  $P=0.006$ ), *L. stellio* ( $F_{1,9.5}=13.7$ ,  $P=0.005$ ) and *L. schreibersi* ( $F_{1,7}=16.6$ ,  $P=0.005$ ), whereas the other species had similar hindlimb and forelimb duty factors ( $P>0.10$ , Table 1).

All species exhibited forelimb-dominated braking and hindlimb-dominated propulsive functionality although there was wide variation (approximate 2–8 $\times$  bias, dependent upon species, Table 1; Fig. 1C,D).

The forelimb was equally biased towards braking as the hindlimb was biased towards propulsion, such that the difference in forelimb versus hindlimb braking–propulsive bias was not significantly different for any species ( $P>0.40$  for all linear contrasts).

Most species had peak vertical ground reaction forces near 50% of support duration; the vertical force profile was nearly symmetrical (Table 1). Only in the hindlimb of *O. cuvieri* and *L. schreibersi* was the upper 95% confidence interval less than 50%, indicating that the vertical force profile of the hindlimb of these species was consistently skewed towards the first half of support duration.

### Morphology–force relationships

Raw residual limb morphology was significantly correlated with raw medial impulse; species with relatively long hindlimbs compared with forelimbs produced greater medial impulses with the hindlimbs compared with the forelimbs (Table 2; Fig. 2A). The independent contrasts for morphology and medial impulse were also significantly correlated, indicating that relatively long hindlimbs and greater hindlimb bias of medial impulse have undergone correlated evolution (Table 2; Fig. 2B). None of the other raw impulses, maximum forces, or their independent contrasts, was significantly correlated with raw vertical, accelerative or braking impulses, or maximum forces (Table 2).

### DISCUSSION

Differential limb function occurs when the forelimb and hindlimb produce different patterns of ground reaction forces (Chen et al., 2006). Our measurements of single-leg ground reaction forces across a diverse sample of lizards indicate a diversity of ground reaction force patterns that exhibit characteristics of both differential and similar limb function.

All species generated more accelerating force and/or impulse with the hindlimb (Fig. 1C,D). This pattern is similar to the house gecko (Autumn et al., 2006; Chen et al., 2006) and thus a general pattern for lizards is that the hindlimb and forelimb function differentially with respect to the production of accelerative forces during steady speed level running. Several previous studies of limb kinematics (e.g. Reilly and DeLancey, 1997; Irschick and Jayne, 1999; McElroy et al., 2012) and limb morphology (e.g. Miles et al., 2007; Herrel et al., 2008; Russell and Bauer, 2008) also suggest that the hindlimb is the dominant propulsor in lizards. In contrast, we found that vertical, braking and medial forces all exhibited species-specific patterns.

**Table 2. Pearson product moment correlations between raw and independent contrasts for residual limb morphology (hindlimb versus forelimb length) and ground reaction forces/impulses**

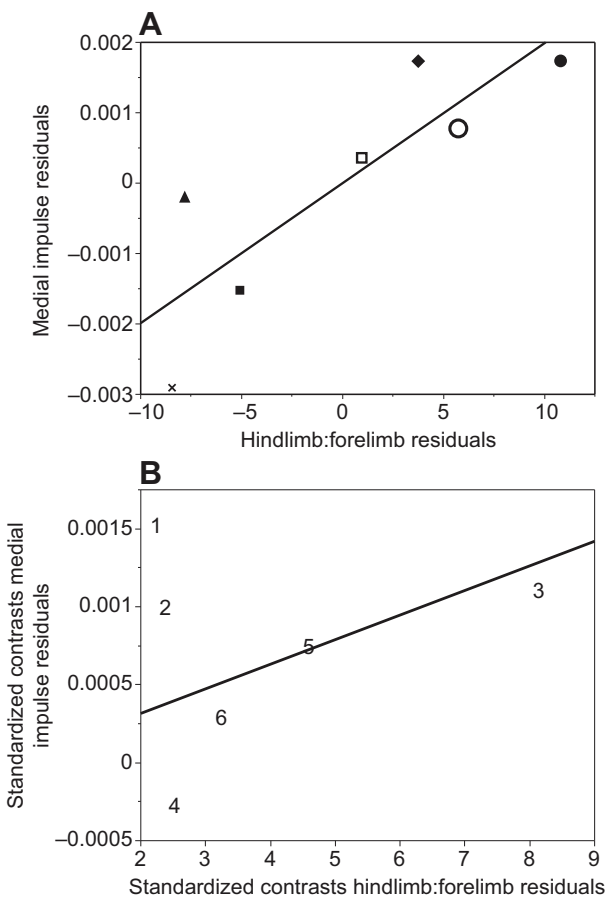
	Raw		Independent contrasts	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Vertical impulse	0.334	0.47	-0.022	0.96
Maximum vertical force	0.170	0.72	-0.122	0.80
Accelerative impulse	-0.005	0.99	-0.394	0.38
Maximum accelerative force	0.243	0.60	-0.076	0.87
Braking impulse	-0.141	0.76	0.302	0.51
Maximum braking force	-0.347	0.45	-0.020	0.97
Medial impulse	0.850	0.02	0.746	0.05
Maximum medial force	0.592	0.16	0.224	0.63

*P*-values are based on *t*-tests with six (raw) or five (independent contrasts) degrees of freedom.

Differential limb function with forelimb-dominated braking forces was evident in four species (*C. warreni*, *L. stellio*, *O. cuvieri* and *V. exanthematicus*) for braking impulse and five species (*C. warreni*, *L. stellio*, *L. schreibersi*, *O. cuvieri* and *V. exanthematicus*) for peak braking forces (Fig. 1C,D). These species apply braking impulses and peak forces like the house gecko (Autumn et al., 2006; Chen et

al., 2006). However, two species do not show any evidence of this pattern (*E. quoyii* and *T. torquatus*); instead their forelimb and hindlimb show similarity of function with respect to the application of braking forces and impulses (Fig. 1C,D). One reason for this discrepancy could be our window of a 20% difference in accelerative versus braking impulse for accepting ‘steady speed’ trials. If one considers that all species show differential limb function with respect to accelerative forces, then it follows that they should show the same pattern for braking forces, because braking and accelerative impulses should be equal during steady speed locomotion. The difference in accelerative versus braking impulses (based on whole body recording from the rest of the trial; Fig. 3) in these species was ~17%; while it was ~11% in the other species. These data support the idea that for *E. quoyii* and *T. torquatus* we may have used trials that were more biased towards ‘accelerating’ than the other species and thus would superficially be expected to have equal forelimb and hindlimb braking forces. This issue is always present when studying ‘steady speed’ because it is quite difficult to obtain steady speed trials and often investigators are forced to use a broad window for accepting ‘steady speed’. This is particularly true in species that do not routinely move at steady speed, which is true of many small sprawling animals (Reilly et al., 2007). For example, studies of ground reaction forces in lizards and other sprawling animals have used changes in speed anywhere from ~5% to 50% as a criteria to define ‘steady speed’ locomotion (Full and Tu, 1991; Full et al., 1991; Farley and Ko, 1997; Ahn et al., 2004; Autumn et al., 2006; Chen et al., 2006; Reilly et al., 2006; McElroy et al., 2008; McElroy and Reilly, 2009). In fact, the study of individual limb forces in the house gecko (Chen et al., 2006) used a speed change of <15%, which was similar to our study. Thus it seems that braking forces may exhibit differential function in the forelimbs versus hindlimbs in all lizards, and the exception in our data may be due to a methodological artifact.

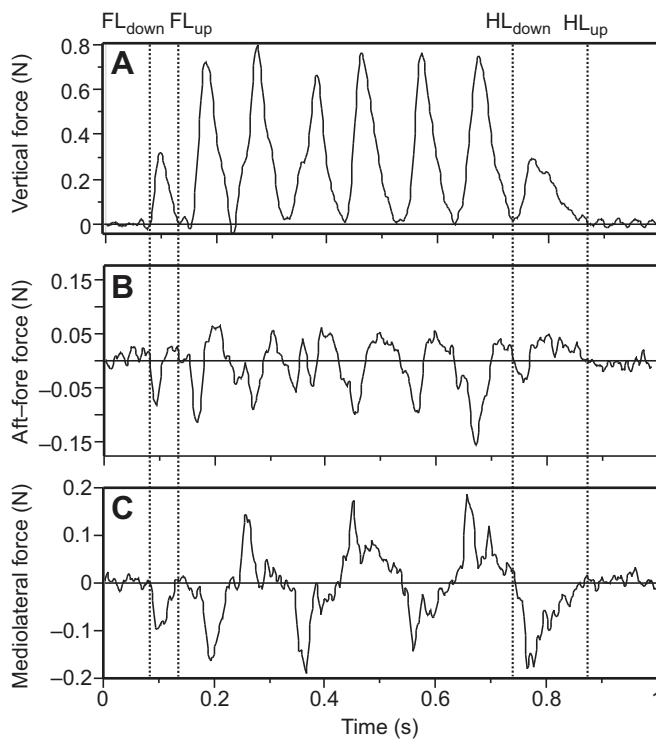
Support of the body’s weight was equally distributed between the forelimb and hindlimb in four species we studied (*C. warreni*, *L. stellio*, *L. schreibersi* and *V. exanthematicus*), much like the house gecko (Chen et al., 2006). However, we found that the hindlimb played a greater role in supporting the body’s weight in *E. quoyii*, *O. cuvieri* and *T. torquatus*, with greater peak vertical ground reaction force and vertical impulses in the hindlimb versus the forelimb (Fig. 1A,B). Such hindlimb-dominated support of the body’s weight could arise via several pathways. First, these three species could have body dimensions that position the centre-of-mass closer to the hindlimb than the other four species. If the centre-of-mass were closer to the hindlimb, then one would expect the hindlimb to bear a greater proportion of body weight and thus exhibit greater ground reaction forces (Aerts et al., 2003; Lee et al.,

**Fig. 2. Bivariate plots of limb morphology and medial impulses.**

(A) Residual hindlimb–forelimb length versus residual (hindlimb versus forelimb) medial impulse. Regression line: intercept= $4.29 \times 10^{-9}$ , slope=0.000199,  $r^2=0.722$ ,  $t_6=3.60$ ,  $P=0.015$ .  $\blacktriangle$ , *Varanus exanthematicus*;  $\bullet$ , *Oplurus cuvieri*;  $\blacklozenge$ , *Laudakia stellio*;  $\times$ , *Eulamprus quoyii*;  $\blacksquare$ , *Cordylus warreni*;  $\square$ , *Tropidurus torquatus*;  $\circ$ , *Leiocephalus schreibersi*.

(B) Phylogenetically independent contrasts for residual hindlimb–forelimb versus residual medial impulse. Regression is forced through the origin: slope=0.000214,  $r^2=0.629$ ,  $t_5=2.91$ ,  $P=0.033$ . Numbers correspond to node numbers from phylogeny in Fig. 5.





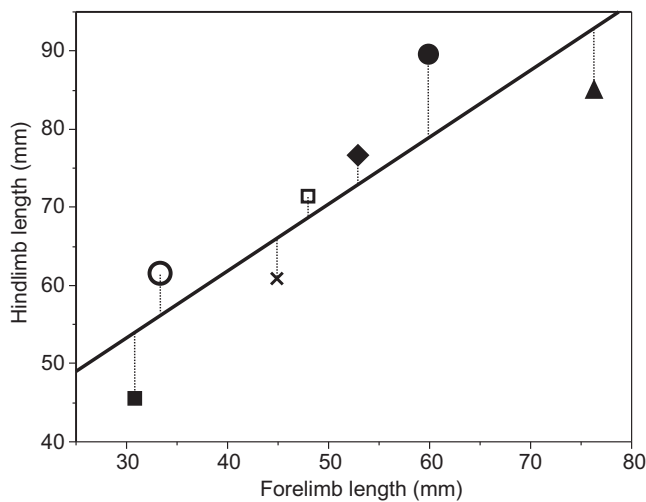
**Fig. 3. Example component force traces for several consecutive steps from *Leiocephalus schreibersi*.** Vertical dotted lines bound isolated forelimb (FL) and hindlimb (HL) support durations ('down' denotes foot contacting substrate, 'up' denotes foot leaving substrate). Force data between these individual limb support durations represent whole body ground reaction forces.

2004). Data on centre-of-mass position and relative weight of different body segments would be needed to test this hypothesis, although these three species do not seem to have body proportions that are different from the other four; in fact both groups have a diversity of body shapes (E.J.M., personal observation). Another possibility is that these species adopt different body postures during high-speed running, such that the forelimbs have reduced contact time with the substrate, resulting in a reduced role in supporting the body (Aerts et al., 2003; Walter and Carrier, 2009). This possibility seems unlikely because patterns in the other aspects of the ground reaction force (propulsive, braking, medial) would be expected to follow body weight support in these species (Aerts et al., 2003), but they do not. In addition, duty factors in the forelimb are only reduced in *E. quoyii*; the other two species have statistically similar forelimb versus hindlimb duty factors (Table 1). A final possibility is that the forelimb maintains contact but the hindlimb still bears more of the weight due to a simple change in body angle. Detailed kinematic data coupled with single-limb ground reaction force over several steps would be required to test these possibilities.

Lee et al. (Lee et al., 2004) suggested that support of the body's weight by the forelimb versus hindlimb would bias the function of the forelimb versus hindlimb in generating accelerative-braking ground reaction forces. Our data show that four species share an equal role of the forelimb and hindlimb in supporting the body and thus these species would be expected to show very small difference in the bias between limbs [i.e. the forelimbs should be as biased towards braking as the hindlimbs are biased towards accelerative force, see fig. 7 in Lee et al. (Lee et al., 2004)]. Indeed these species do not have significantly different forelimb versus hindlimb biases

(Table 1). However, all species had similarity in forelimb versus hindlimb biases, even the three species with hindlimb-dominated body support (Fig. 1). Lee et al. (Lee et al., 2004) predicted that species with hindlimb-dominated body support would show (1) reduced forelimb duty factor and, as a result, (2) reduced forelimb accelerative force (i.e. the forelimb more biased towards a purely braking role). *Eulamprus quoyii*, *O. cuvieri* and *T. torquatus* had hindlimb-dominated body weight support (Fig. 1), but only the duty factor of *E. quoyii* follows the prediction. The duty factor for *O. cuvieri* and *T. torquatus* and the forelimb versus hindlimb bias for all three species were statistically indistinguishable. If we simply examine mean values (Table 1), ignoring the statistical tests, our data show only partial support of Lee's hypothesis: *T. torquatus* does have a larger mean forelimb braking bias and reduced forelimb duty factor, but *E. quoyii* and *O. cuvieri* had the largest difference between forelimb and hindlimb bias with a tendency towards an inflated role of the hindlimb in accelerating, and *O. cuvieri* has essentially no difference in forelimb versus hindlimb duty factor. Perhaps the data from *T. torquatus* lend support to the hypothesis of Lee et al., while *E. quoyii* and *O. cuvieri* suggest a different functional consequence of loading the hindlimb with body weight. Loading the hindlimb with more body weight would allow the hindlimb (and its enlarged musculature and longer bones) to play a more prominent role in generating accelerative forces (Aerts et al., 2003; Walter and Carrier, 2009), which could be occurring in *E. quoyii* and *O. cuvieri*.

Medial ground reaction impulses were biased towards the hindlimb in four of the species we studied (*L. stellio*, *L. schreibersi*, *O. cuvieri* and *T. torquatus*). These species are all members of the suborder Iguania, which suggests that some aspect of Iguanian morphology or physiology may elicit hindlimb-dominated medial impulses. A similar pattern is exhibited by the house gecko (Chen et al., 2006). Three other species show an equal role of the forelimb and hindlimb in generating medial forces/impulses (*C. warreni*, *E. quoyii* and *V. exanthematicus*), suggesting similarity in limb function with respect to medial forces. Two factors may help explain differential versus similar patterns of medial ground reaction forces. First, lizards are known to produce both standing and traveling waveforms along the body axis during running (Ritter, 1992). Ritter (Ritter, 1992) showed that all species shift to a traveling wave during high-speed running, but that the details for the traveling wave were different across species. In two species with elongate limbs (*Dipsosaurus dorsalis* and *Cnemidophorus tigris*) the traveling wave contained a node with less lateral movement, somewhat like a standing-wave pattern (Ritter, 1992). This node was positioned just behind the pectoral girdle, suggesting that the forelimbs experience less of a lateral excursion than the hindlimbs. Interestingly, the four species that showed hindlimb-biased medial impulses (Fig. 1E,F) are those with the longest limbs (McElroy and Reilly, 2009). Additionally, the relative magnitude of medial impulses is correlated with the relative hindlimb versus forelimb length (Table 2; Fig. 2), such that lizard species with relatively longer hindlimb compared with forelimb produce relatively more medial impulse with their hindlimb compared with the forelimb. This pattern coupled with data from Ritter (Ritter, 1992) suggest that species with elongate limbs may use a particular type of traveling wave of lateral bending (with a pectoral 'node') that results in more medial effort in the hindlimb and less in the forelimb. Ritter (Ritter, 1992), suggested that increased medial forces due to standing waves came at a 'cost' to accelerative force production; however, the species in this study all produced substantial accelerative ground reaction forces and were all equally fast. Thus our data imply some other function for



**Fig. 4. Bivariate plot of hindlimb length versus forelimb length.** The continuous black line is ordinary least squares regression (slope=0.856, intercept=27.6); vertical dotted lines represent residuals for each species. ▲, *Varanus exanthematicus*; ●, *Oplurus cuvieri*; ◆, *Laudakia stellio*; ×, *Eulamprus quoyii*; ■, *Cordylus warreni*; □, *Tropidurus torquatus*; ○, *Leioccephalus schreibersi*.

high hindlimb medial forces coupled with low forelimb medial forces. One possibility is that this could relate to maneuvering, as the forelimb must only produce a small change in medial forces whereas the hindlimb must produce larger medial forces to induce a turn (Jindrich and Full, 1999). Another possibility is that the difference in medial forces does not confer a functional advantage, but is a by-product of morphology (Gould and Lewontin, 1979). In fact, the four species with hindlimb-biased medial forces have relatively large hindlimbs compared with their forelimbs (Fig. 4) and the large medially directed forces may be a by-product of the joint excursions experienced during propulsion by a long, sprawling limb (Reilly and DeLancey, 1997; Irschick and Jayne, 1999; Russell and Bels, 2001; Fuller et al., 2011; McElroy et al., 2012; Olberding et al., 2012). Studies that combine forces, kinematics and diverse ways of moving (running, turning, burst locomotion) are needed to tease the relationship between limb length and medial forces in lizards.

Steady speed bipedal running in lizards (i.e. extreme differential limb function to the hindlimbs) requires asymmetry of the vertical ground reaction force towards the first half of support duration (Van Wassenbergh and Aerts, 2013). Although the species we studied were not running bipedally during this experiment, the four Iguanian species are capable of bipedal locomotion at high speeds and *E. quoyii* would often have its body pitch up during running as if it could briefly run bipedally (E.J.M., personal observation). Thus one might expect these species to show asymmetry of the vertical force profile. However, we find little evidence of this; only two of the four Iguanian species (*O. cuvieri* and *L. schreibersi*) had peak vertical forces biased towards the beginning of support duration while all other species had symmetrical vertical force profiles (Table 1). The mechanism behind these differences between species is unclear, although it could be due to differences in trunk angle or body kinematics across trials, which we did not measure. Thus while steady speed bipedal running requires vertical force asymmetry to be stable (Van Wassenbergh and Aerts, 2013), steady speed quadrupedal running in lizards does not.

Do all lizards exhibit differential limb function? In short, each species exhibited differential forelimb versus hindlimb function for at least one component of the ground reaction force (i.e. accelerative

force/impulse). However, only one species (*O. cuvieri*) showed differential limb function across all four components (vertical, accelerative, braking, lateral) and most species only showed differential function for two of the four components, but the exact components were species specific (Fig. 1). Additionally, the predication that duty factor and braking-propulsive bias should conform to a lizard body plan (Lee et al., 2004) is only partially upheld by these data. This suggests that differential limb function may not be a general feature of sprawling, quadrupedal trotters. Thus the biomechanics of lizard locomotion seem to be better described by functional diversity that is driven by variation in morphology and physiology across species (see also Vanhooydonck et al., 2006; McElroy and Reilly, 2009). Describing and understanding this diversity is important so that we can begin to build a broader, comparative understanding of the functional morphology and biomechanics of animal locomotion.

## MATERIALS AND METHODS

### Study species

The following lizard species were studied: *Laudakia stellio* Linnaeus 1758, *Leioccephalus schreibersi* Gravenhorst 1837, *Oplurus cuvieri* Gray 1831, *Tropidurus torquatus* Wied-Neuwied 1820, *Eulamprus quoyii* Quoy & Gaimard 1824, *Cordylus warreni* Boulenger 1908 and *Varanus exanthematicus* Bosc 1792. All species were obtained from commercial suppliers (California Zoological Supply, Santa Ana, CA, USA) except *E. quoyii*. *E. quoyii* was wild caught in Brisbane, Australia and released at the point of capture within 36 h. Sample sizes are given in Table 1. All housing and experimental procedures followed approved animal use protocols (Institutional Animal Care and Use Committee U-99-03).

### Data collection

Prior to each trial we measured body mass to the nearest 0.1 g for each individual. Single limb locomotor forces were quantified when lizards travelled down a racetrack towards a dark hide box. We focused on high-speed sprinting locomotion, with lizards induced to sprint down the racetrack by gently pressing on the tail or hindlimb. Each individual was induced to move down the racetrack two to three times in rapid succession. Trials in which signs of fatigue or poor effort were noted (uncoordinated limb movements, dragging belly, or refusal to move after three tail pinches) were immediately discarded. Individuals were allowed to rest and recover for 24 h before subsequent trials. Each individual of each species was chased down the racetrack numerous times to capture a range of the fastest speeds for each species. All species were maintained between 36 and 40°C for the duration of each trial. To achieve these temperatures, lizards were warmed under heat lamps and temperature was checked via an infrared thermal laser directed on the abdomen.

Ground reaction forces were quantified using a custom-made force platform based on a strain gauge, spring-blade design described in Bertram et al. (Bertram et al., 1997). Vertical, fore-aft and mediolateral ground reaction forces were sampled at 500 Hz using National Instruments (Austin, TX, USA) data acquisition hardware and a LabVIEW custom designed virtual data sampling instrument (National Instruments) following Parchman et al. (Parchman et al., 2003). The platform was calibrated such that it produced a linear response over the measurement range and had a minimum resolution of 15 mN in all three directions. The 0.6 m long by 0.2 m wide force platform surface was flush with the racetrack surface and located 3–3.6 m along its 5.2 m length. The entire surface of the racetrack and platform was covered with fine grit sandpaper to prevent foot slippage.

### Analysis of gait parameters and ground reaction forces

Kinematic analyses were conducted using APAS (version 1.0; Ariel Dynamics, Trabuco Canyon, CA, USA). First, we determined speed for each trial by digitizing the tip of the snout as the lizard crossed seven evenly spaced (10 cm apart) lines along the surface of the racetrack. Next, we recorded the timing of touch-down and lift-off for the focal limb and computed support duration as time of lift-off minus time of touch-down, and

stride time as the time of touch-down until the time of the next touch-down of the same limb. Duty factor was defined as support duration divided by stride time.

To record individual limb forces we analyzed only the first limb on (forelimb), and the last limb off (hindlimb), the racetrack (Fig. 3). For each trial, we reviewed high-speed video recordings of sprint sequences (120 or 500 frames  $s^{-1}$ , depending on species) to determine if the isolated forelimb or hindlimb footfalls were 'clean'. A 'clean' footfall was defined as when: (1) the entire foot is in contact with the substrate on the surface of the force platform (trials in which the foot landed on the gap between the racetrack and force platform were discarded), and (2) no other limbs were in contact with the force platform during the entire contact phase (touch-down to lift-off) of the focal limb. These two criteria resulted in isolated individual limb contacts and ground reaction forces for both the forelimbs and hindlimbs for several trials per species (Table 1). It should be noted that forelimb and hindlimb contacts did not always come from the same run. There were no statistical differences in the distributions of speeds or masses in forelimb versus hindlimb data within each species, which shows that our method of choosing contacts from different runs did not bias the analyses. We also note that the mixed model used to analyze the data accounted for the effect of speed and mass on ground reaction forces and impulses (see below).

Individual limb ground reaction forces were numerically integrated over limb contact time to calculate impulse (i.e. the area under the force versus time curve). Impulses were calculated separately for vertical, braking (negative fore-aft), accelerative (positive fore-aft), and medial and lateral directions. Medial and lateral impulses were summed and the resultant impulse was always directed medially. Therefore, we refer to this summed impulse as medial impulse. In addition, peak forces were measured as the maximum force in each direction: peak vertical, braking, accelerative and medial forces.

We only analyzed steady speed trials that were defined according to the following criteria. First, we ensured that speed over any 10 cm interval as measured by digitizing the lizard's snout was <20% different than the average speed down the racetrack; by this definition the lizard moved with only small speed fluctuations down the entire surface of the force platform (see also McElroy et al., 2008; McElroy and Reilly, 2009). To further ensure that trials were at steady speed down the length of the force platform, we compared the magnitude of the braking versus accelerative impulse within each trial for the portion of the trial that included whole body forces (Fig. 3). We discarded trials that exhibited greater than 20% difference in digitized speed or impulses. The value of 20% was chosen based on previous studies of lizard locomotion (Farley and Ko, 1997; Chen et al., 2006; McElroy et al., 2008; McElroy and Reilly, 2009). Thus subsequent analyses only included trials that were relatively steady speed as judged by both kinematic and kinetic recordings. We also computed the braking-propulsive bias for the forelimb and hindlimb. For the forelimb we computed this as the ratio of absolute value of braking (numerator) to accelerative (denominator) impulse. For the hindlimb we computed the braking-propulsive bias as the ratio of accelerative (numerator) to the absolute value of braking (denominator) impulse. We computed the ratio differently for forelimb versus hindlimb so that larger values indicated a greater bias towards that limb's predominant type of impulse (forelimb: braking, hindlimb: accelerative).

Finally, we computed the timing of peak vertical ground reaction force as a percentage of support duration.

### Morphology

To quantify morphology we took dorsoventral whole-animal radiographs of multiple individuals per species (Table 1) and measured the total length of the forelimb and the hindlimb by summing the length of their constituent elements: forelimb (humerus, ulna, carpal, third metacarpal, third finger) and hindlimb (femur, tibia, tarsal, fourth metatarsal, fourth toe). Snout-vent length (SVL) was also measured from each radiograph. All specimens were obtained via museum loans.

### Data analysis

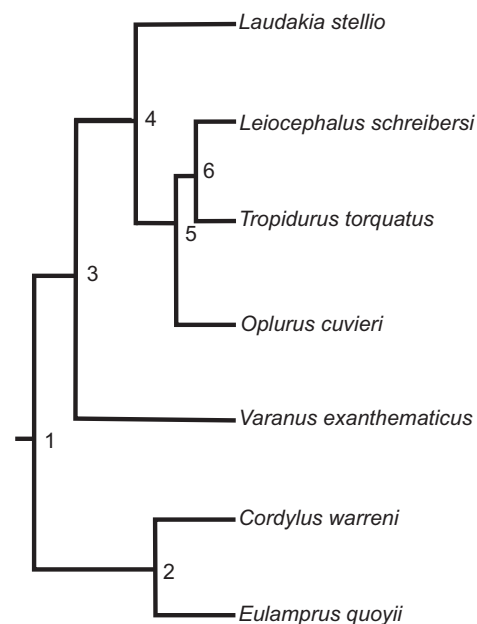
Prior to analyses all data were log transformed. We constructed 10 separate general linear mixed models with component impulses (vertical, braking,

accelerative, medial) or maximum ground reaction forces (vertical, braking, accelerative, medial) or duty factor or the braking-propulsive impulse bias as the response variable in each respective model. For each model, species and limb (hindlimb, forelimb) were entered as main effects, speed and mass were entered as covariates (speed and mass are correlated with ground reaction forces in all species) (see McElroy and Reilly, 2009), species $\times$ limb was entered as an interaction term, and individual was entered as a random effect. Within each species $\times$ limb interaction term, we constructed planned linear contrasts to test the hypotheses that forelimb and hindlimb forces were different within each species (e.g. forelimb versus hindlimb vertical force for *Eulamprus quoyii*). All tests were on means adjusted for the covariates in the model (speed and mass); this effectively removed the effect of these confounding variables. The planned linear contrasts were tested using  $F$ -tests with a significance level of  $P < 0.05$ . We did not control for multiple testing as the linear contrasts were planned prior to analysis (Quinn and Keough, 2003). We note that phylogeny was not taken into account for this analysis because the test of each contrast was within species, not between.

To explore differences in forelimb versus hindlimb morphology we regressed hindlimb length on forelimb lengths. Residuals from this analysis were plotted to compare species differences in forelimb versus hindlimb lengths and were used in the next analysis (Fig. 4).

To examine the relationship between limb morphology and ground reaction forces we computed mean ground reaction forces and impulses for forelimbs and hindlimbs for each species. Then ordinary least squares (OLS) regressions of hindlimb ( $y$ ) on forelimb ( $x$ ) forces and impulses (vertical, accelerative, braking, and medial, separately) were generated. Residuals from each regression were saved for further analyses as a measurement of the relative role of forelimbs versus hindlimbs in contributing to ground reaction forces and impulses. Regression and Pearson product moment correlations were then computed between the residual ground reaction forces/impulses and residual limb morphology.

Species are not independent data points due to their phylogenetic relationships, which violates a fundamental assumption of independence assumed by traditional statistical analyses (Felsenstein, 1985). To account for this non-independence we calculated phylogenetically independent contrasts for residual limb morphology and residual ground reaction force and impulses using the PDAP module in Mesquite (Midford et al., 2002; Maddison and Maddison, 2007). The phylogeny (Fig. 5) was based on Townsend et al. (Townsend et al., 2004) and Bergmann and Irschick



**Fig. 5. Phylogeny for the lizard species in this study.** Nodes are labeled to correspond to the other figures. Branches are not proportional to their lengths; all branch lengths were set at 1 and then the tree was made ultrametric.



(Bergmann and Irschick, 2012); branch lengths were set to 1 and then the tree was made ultrametric. Appropriate standardization was checked by plotting the absolute value of each set of contrasts versus their standard deviations; in all cases no relationship was detected, indicating adequate standardization of the contrasts (Garland et al., 1992). We then recomputed the regression (force through the origin) and Pearson product moment correlations between the independent contrasts for residual limb morphology and the independent contrasts for residual ground reaction forces/impulses.

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#### Competing interests

The authors declare no competing financial interests.

#### Author contributions

E.J.M., A.R.B. and S.M.R. designed the study. All authors played a role in data collection and analysis. E.J.M. wrote the paper and all authors provided input regarding the content of the manuscript and the implications of the main findings.

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#### References

- Aerts, P., Van Damme, R., D'Août, K. and Vanhooydonck, B. (2003). Bipedalism in lizards. Whole-body modeling reveals a possible spandrel. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **358**, 1525-1533.
- Ahn, A. N., Furrow, E. and Biewener, A. A. (2004). Walking and running in the legged running frog, *Kassina maculata*. *J. Exp. Biol.* **207**, 399-410.
- Alexander, R. M. and Goldspink, G. (1977). *Mechanics and Energetics of Animal Locomotion*. London: Chapman and Hall.
- Autumn, K., Hsieh, S. T., Dudek, D. M., Chen, J., Chitaphan, C. and Full, R. J. (2006). Dynamics of geckos running vertically. *J. Exp. Biol.* **209**, 260-272.
- Bergmann, P. J. and Irschick, D. J. (2012). Vertebral evolution and the diversification of squamate reptiles. *Evolution* **66**, 1044-1058.
- Bertram, J. E. A., Lee, D. V., Todhunter, R. J., Foels, W. S., Williams, A. J. and Lust, G. (1997). Multiple force platform analysis of the canine trot: a new approach to assessing basic characteristics of locomotion. *Vet. Comp. Orthop. Traumatol.* **3**, 44-53.
- Biewener, A. A. (1990). Biomechanics of mammalian terrestrial locomotion. *Science* **250**, 1097-1103.
- Blob, R. W. and Biewener, A. A. (2001). Mechanics of limb bone loading during terrestrial locomotion in the green iguana (*Iguana iguana*) and American alligator (*Alligator mississippiensis*). *J. Exp. Biol.* **204**, 1099-1122.
- Chen, J. J., Peattie, A. M., Autumn, K. and Full, R. J. (2006). Differential leg function in a sprawled-posture quadrupedal trotter. *J. Exp. Biol.* **209**, 249-259.
- Deban, S. M., Schilling, N. and Carrier, D. R. (2012). Activity of extrinsic limb muscles in dogs at walk, trot and gallop. *J. Exp. Biol.* **215**, 287-300.
- Demes, B., Larson, S. G., Stern, J. T., Jr, Jungers, W. L., Biknevicius, A. R. and Schmitt, D. (1994). The kinetics of primate quadrupedalism: 'hindlimb drive' reconsidered. *J. Hum. Evol.* **26**, 353-374.
- Farley, C. T. and Ko, T. C. (1997). Mechanics of locomotion in lizards. *J. Exp. Biol.* **200**, 2177-2188.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1-15.
- Full, R. J. and Tu, M. S. (1991). Mechanics of a rapid running insect: two-, four- and six-legged locomotion. *J. Exp. Biol.* **156**, 215-231.
- Full, R. J., Blickhan, R. and Ting, L. H. (1991). Leg design in hexapedal runners. *J. Exp. Biol.* **158**, 369-390.
- Fuller, P. O., Higham, T. E. and Clark, A. J. (2011). Posture, speed, and habitat structure: three-dimensional hindlimb kinematics of two species of padless geckos. *Zoology* **114**, 104-112.
- Garland, T., Jr, Harvey, P. H. and Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18-32.
- Gould, S. J. and Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. B* **205**, 581-598.
- Herrel, A., Vanhooydonck, B., Porck, J. and Irschick, D. J. (2008). Anatomical basis of differences in locomotor behavior in Anolis lizards: a comparison between two ecomorphs. *Bull. Mus. Comp. Zool.* **159**, 213-238.
- Irschick, D. J. and Jayne, B. C. (1999). Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *J. Exp. Biol.* **202**, 1047-1065.
- Jindrich, D. L. and Full, R. J. (1999). Many-legged maneuverability: dynamics of turning in hexapods. *J. Exp. Biol.* **202**, 1603-1623.
- Lammers, A. R. and Biknevicius, A. R. (2004). The biodynamics of arboreal locomotion: the effects of substrate diameter on locomotor kinetics in the gray short-tailed opossum (*Monodelphis domestica*). *J. Exp. Biol.* **207**, 4325-4336.
- Lee, D. V., Stakebake, E. F., Walter, R. M. and Carrier, D. R. (2004). Effects of mass distribution on the mechanics of level trotting in dogs. *J. Exp. Biol.* **207**, 1715-1728.
- McElroy, E. J. and Reilly, S. M. (2009). The relationship between limb morphology, kinematics, and force during running: the evolution of locomotor dynamics in lizards. *Biol. J. Linn. Soc. Lond.* **97**, 634-651.
- McElroy, E. J., Hickey, K. L. and Reilly, S. M. (2008). The correlated evolution of biomechanics, gait and foraging mode in lizards. *J. Exp. Biol.* **211**, 1029-1040.
- McElroy, E. J., Archambeau, K. L. and McBrayer, L. D. (2012). The correlation between locomotor performance and hindlimb kinematics during burst locomotion in the Florida scrub lizard, *Sceloporus woodi*. *J. Exp. Biol.* **215**, 442-453.
- Maddison, W. P. and Maddison, D. R. (2007). *Mesquite: A Modular System For Evolutionary Analysis*. Version 2.0. <http://mesquiteproject.org>
- Midford, P. E., Garland, T., Jr and Maddison, W. (2002). *PDAP:PDTree Package For Mesquite*. Version 1.00. [http://mesquiteproject.org/pdap\\_mesquite/](http://mesquiteproject.org/pdap_mesquite/)
- Miles, D. B., Losos, J. B. and Irschick, D. J. (2007). Morphology, performance, and foraging mode. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode* (ed. S. M. Reilly, L. B. McBrayer and D. B. Miles), pp. 49-93. Cambridge, UK: Cambridge University Press.
- Olberding, J. P., McBrayer, L. D. and Higham, T. E. (2012). Performance and three-dimensional kinematics of bipedal lizards during obstacle negotiation. *J. Exp. Biol.* **215**, 247-255.
- Parchman, A. J., Reilly, S. M. and Biknevicius, A. R. (2003). Whole-body mechanics and gaits in the gray short-tailed opossum *Monodelphis domestica*: integrating patterns of locomotion in a semi-erect mammal. *J. Exp. Biol.* **206**, 1379-1388.
- Quinn, G. P. and Keough, M. J. (2003). *Experimental Design and Data Analysis for Biologists*. Cambridge, UK: Cambridge University Press.
- Reilly, S. M. and DeLancey, M. L. (1997). Sprawling locomotion in the lizard *Sceloporus clarkii*: the effects of speed on gait, hindlimb kinematics, and axial bending during walking. *J. Zool. (Lond.)* **243**, 417-433.
- Reilly, S. M., McElroy, E. J., Andrew Odum, R. and Hornyak, V. A. (2006). Tuataras and salamanders show that walking and running mechanics are ancient features of tetrapod locomotion. *Proc. Biol. Sci.* **273**, 1563-1568.
- Reilly, S. M., McElroy, E. J. and Biknevicius, A. R. (2007). Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. *Zoology* **110**, 271-289.
- Ritter, D. (1992). Lateral bending during lizard locomotion. *J. Exp. Biol.* **173**, 1-10.
- Rollinson, J. and Martin, R. D. (1981). Comparative aspects of primate locomotion, with special reference to arboreal Cercopithecines. *Symp. Zool. Soc. London* **48**, 377-427.
- Russell, A. P. and Bels, V. (2001). Biomechanics and kinematics of limb-based locomotion in lizards: review, synthesis and prospectus. *Comp. Biochem. Physiol.* **131A**, 89-112.
- Russell, A. P. and Bauer, A. M. (2008). The appendicular locomotor apparatus of Sphenodon and normal limbed squamates. In *Biology of the Reptilia*, Vol. 21 (ed. C. Gans, A. Gaunt and K. K. Adler), pp. 1-466. Ithaca, NY: Society for the Study of Amphibians and Reptiles.
- Townsend, T., Larson, A., Louis, E. and Macey, J. R. (2004). Molecular phylogenetics of squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Syst. Biol.* **53**, 735-757.
- Van Wassenbergh, S. and Aerts, P. (2013). In search of the pitching momentum that enables some lizards to sustain bipedal running at constant speeds. *J. R. Soc. Interface* **10**, 20130241.
- Vanhooydonck, B., Herrel, A., Van Damme, R. and Irschick, D. J. (2006). The quick and the fast: the evolution of acceleration capacity in Anolis lizards. *Evolution* **60**, 2137-2147.
- Walter, R. M. and Carrier, D. R. (2009). Rapid acceleration in dogs: ground forces and body posture dynamics. *J. Exp. Biol.* **212**, 1930-1939.
- Willey, J. S., Biknevicius, A. R., Reilly, S. M. and Earls, K. D. (2004). The tale of the tail: limb function and locomotor mechanics in *Alligator mississippiensis*. *J. Exp. Biol.* **207**, 553-563.
- Witte, H., Biltzinger, J., Hackert, R., Schilling, N., Schmidt, M., Reich, C. and Fischer, M. S. (2002). Torque patterns of the limbs of small therian mammals during locomotion on flat ground. *J. Exp. Biol.* **205**, 1339-1353.