

RESEARCH ARTICLE

Dynamics of horizontal walking and vertical climbing in the Australian green tree frog (*Ranoidea caerulea*)

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ABSTRACT

Despite the high mechanical demands associated with climbing, the ability to ascend vertically has evolved independently in most major animal lineages. However, little is known about the kinetics, mechanical energy profiles or spatiotemporal gait characteristics of this locomotor mode. In this study, we explored the dynamics of horizontal locomotion and vertical climbing on both flat substrates and narrow poles in five Australian green tree frogs (*Ranoidea caerulea*). Vertical climbing is associated with slow, deliberate movements (i.e. reduced speed and stride frequency and increased duty factors) and propulsive fore–aft impulses in both the forelimb and hindlimb. By comparison, horizontal walking was characterized by a braking forelimb and a propulsive hindlimb. In the normal plane, tree frogs mirrored other taxa in exhibiting a net pulling forelimb and a net pushing hindlimb during vertical climbing. In terms of mechanical energy, tree frogs matched theoretical predictions of climbing dynamics (i.e. the total mechanical energetic cost of vertical climbing was predominantly driven by potential energy, with negligible kinetic contributions). Utilizing power as a means of estimating efficiency, we also demonstrate that Australian green tree frogs show total mechanical power costs only slightly above the minimum mechanical power necessary to climb, highlighting their highly effective locomotor mechanics. This study provides new data on climbing dynamics in a slow-moving arboreal tetrapod and raises new testable hypotheses about how natural selection can act upon a locomotor behavior that is notably constrained by external physical forces.

KEY WORDS: Arboreality, Center of mass, Mechanical power, Mechanical energy, Locomotion, Amphibian, Single limb forces

INTRODUCTION

Navigating an arboreal environment requires extreme locomotor flexibility to successfully traverse substrates of varying diameter, compliance, orientation and continuity (e.g. Grand, 1972; Jenkins, 1974; Cartmill, 1985; Preuschoft, 2002). Extensive efforts have been made to describe the biomechanics of arboreal locomotion in

tetrapods, typically focusing on horizontal movement in mammals (e.g. Jenkins, 1974; Larson, 1998; Lemelin and Cartmill, 2010; Lemelin et al., 2003; Schmitt, 1999), squamates (e.g. Higham and Jayne, 2004; Fischer et al., 2010) or birds (e.g. Reader et al., 2022; Young et al., 2022a,b). Less understood are the mechanisms associated with ascending vertically oriented substrates (i.e. vertical climbing; but see Autumn et al., 2006; Granatosky et al., 2019b; Hanna et al., 2017; Wang et al., 2015; Young et al., 2022a). Unlike horizontal movement, in which the animal's body mass is supported by the substrate, vertical climbing necessitates the consistent opposition against gravitational acceleration to prevent falling (Cartmill, 1985; Preuschoft, 2002), resulting in high energetic costs. In spite of this, the ability to climb has evolved independently in numerous lineages of limbed animals (e.g. Cartmill, 1985; Goldman et al., 2006; Labonte and Federle, 2015, 2016).

Mechanics of climbing

Although behavioral modes of climbing have been broadly described across myriad taxa (e.g. Cartmill, 1985; Granatosky et al., 2022; Hill et al., 2018; Hunt et al., 1996; Preuschoft, 2002), quantitative data regarding either the spatiotemporal gait characteristics, kinetics or mechanical energy profiles of climbing are lacking (e.g. Autumn et al., 2006; Bock and Winkler, 1978; Goldman et al., 2006; Theunissen et al., 2014). Broadly, vertical climbing is associated with slow, deliberate movements (i.e. reduced speed and stride frequency and increased stride lengths, contact times, duty factor and overall stride duration; see Granatosky et al., 2019b; Hanna et al., 2022; Herrel et al., 2013; Karantanis et al., 2018; Theunissen et al., 2014). Further, animals are thought to prioritize long strides to regulate speed as a mechanism for decreasing substrate oscillations on thin arboreal supports (Granatosky and McElroy, 2022; Granatosky et al., 2019b; Hanna et al., 2022; Karantanis et al., 2018). These strategies are thought to increase stability and reduce substrate oscillations on thin arboreal substrates (Granatosky and McElroy, 2022; Granatosky et al., 2019b; Hanna et al., 2022; Herrel et al., 2013; Karantanis et al., 2018).

Single limb forces (SLFs) collected during vertical climbing are reported for several primate taxa (Hanna et al., 2017; Hirasaki et al., 1993), parrots (Reader et al., 2022; Young et al., 2022a), geckos (Autumn et al., 2006; Wang et al., 2015) and cockroaches (Clemente and Federle, 2008; Goldman et al., 2006; Watson et al., 2002). It is important to note that owing to the reorientation of the body axis associated with vertical climbing, these forces are not directly comparable to horizontal locomotion (Hanna et al., 2017). Fore–aft forces, which traditionally move an animal forward and backward along a horizontal plane, become upward and downward forces, respectively. Meanwhile, normal forces, which are typically imparted into the ground during horizontal walking, become pushing and pulling forces directed toward and away from the support. These normal forces are of particular importance during

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vertical ascent as climbing inherently creates a gravitational torque pitching the animal away from the support (Norberg, 1986; Preuschoft, 2002; Spring, 1965). Climbing animals are therefore required to generate and balance pulling forces generated by a rostrally positioned limb loaded in tension and pushing forces generated by a caudally positioned limb loaded in compression, such that the sum of the normal forces is zero (Hanna et al., 2017; Norberg, 1986; Preuschoft, 2002; Spring, 1965). Hexapedal insects broadly match the SLF patterns described above (Cruse, 1976; Goldman et al., 2006). Goldman et al. (2006) provided the most in-depth analysis of climbing cockroaches, and determined that all limbs produce propulsive fore–aft forces. Like quadrupedal climbers (Autumn et al., 2006; Hanna et al., 2017; Wang et al., 2015), cockroaches countered pitchback moments due to gravity by using the front-leg normal forces to pull the body toward the substrate while the hindlimbs push away from the substrate. Middle limb-pairs in cockroaches generate small normal forces (Goldman et al., 2006).

Movements of the center of mass (COM) are also altered by climbing. During horizontal locomotion in walking gaits, the limbs act as struts of an inverted pendulum and the COM sways from posterior to the limb at touchdown before assuming an anterior position at lift-off (Ahn et al., 2004; Bertram, 2016; Cavagna et al., 1977; Granatosky et al., 2018; Reilly et al., 2006; Riskin et al., 2016). Through conversion of potential energy to kinetic energy, mechanical energy can be recovered between strides, with the magnitude of energy recovered dependent upon the phasic relationship between potential and kinetic energies (Ahn et al., 2004; Blickhan and Full, 1987; Cavagna et al., 1977; O'Neill and Schmitt, 2012). During climbing, however, this phasic relationship ceases to exist. As animals gain height while climbing, potential energy steadily increases (Autumn et al., 2006; Goldman et al., 2006). While ascent continues, it is therefore impossible for the animal to recover energy within the stride by converting the gained potential energy into kinetic energy. Thus, measurements of mechanical efficiency during climbing are instead derived by comparing total mechanical power with the product of gravity and speed: the theoretical minimum power needed for ascent (Autumn et al., 2006; Goldman et al., 2006). Such patterns appear to hold true regardless of the number of limbs or adhesion mechanism (Autumn et al., 2006; Goldman et al., 2006), and these similarities led Goldman et al. (2006) to propose that the physical constraints of climbing are so great that animals are restricted to a singular global template to effectively ascend vertical surfaces.

Climbing in tree frogs

Tree frogs have evolved across multiple anuran families (Chan et al., 2018; Peloso et al., 2018; Richards and Moore, 1996; Wiens et al., 2005). As the name implies, these frogs are typically found in trees or other high-growing vegetation and do not normally descend to the ground, except to mate and spawn. Some species eschew even this, instead building foam nests on leaves and thus rarely leaving the trees at all as adults (Granatosky and Krysko, 2011; Kasuya et al., 1996). Tree frogs are typically smaller and more slender than terrestrial frogs, given that their weight must be supported by the branches and twigs in their habitats (Herrel et al., 2013). These small branches are typically traversed via digital grasping, and tree frogs have been shown to generate strong intrinsic grips around thin supports (Herrel et al., 2013; Hill et al., 2018; Manzano et al., 2008). However, larger diameter substrates are typically negotiated via the use of wet adhesion clinging (Federle et al., 2006). Although numerous studies have explored characteristics of arboreal

locomotion in tree frogs (Endlein et al., 2017; Herrel et al., 2013; Hill et al., 2018; Kamada et al., 2017; Manzano et al., 2008), there remains no information about patterns of SLFs or overall movements of the COM. Here, we present impulse data (as derived from single limb force kinetics) from the Australian tree frog across four locomotor conditions (horizontal flat, horizontal pole, vertical flat and vertical pole). We elected to present impulses rather than individual single limb forces, as impulses better reflect the function of the limb during locomotion (Dickinson et al., 2022; Larson and Demes, 2011; Raichlen et al., 2009). We also present data on COM mechanical energy across horizontal flat and vertical flat conditions. Thus, we test the extent to which climbing in tree frogs mirrors patterns seen in other climbing species (Autumn et al., 2006; Goldman et al., 2006; Hanna et al., 2017; Hirasaki et al., 1993; Wang et al., 2015). Specifically, we assess the following three predictions.

Prediction 1

Vertical climbing will be associated with slow, deliberate movements (i.e. reduced speed and stride frequency and increased stride lengths, contact times, duty factor and overall stride duration). Further, animals will increase stride length, as opposed to stride frequency, when increasing speed as a mechanism for decreasing substrate oscillations on thin arboreal supports (Granatosky and McElroy, 2022; Granatosky et al., 2019b; Hanna et al., 2022; Karantanis et al., 2018).

Prediction 2

The functional role of each limb pair (e.g. forelimb versus hindlimb) will change as animals shift from horizontal walking to vertical climbing. Namely, both forelimbs and hindlimbs will adopt propulsive fore–aft roles during climbing, and they will differentiate into a pulling forelimb and pushing hindlimb (Autumn et al., 2006; Goldman et al., 2006; Hanna et al., 2017; Wang et al., 2015). Mediolateral forces will not be altered in response to vertical climbing, but will differ from primarily laterally directed on flat substrates to primarily medially directed on poles (Carlson et al., 2005; Demes et al., 2006; Franz et al., 2005; Schmitt, 2003).

Prediction 3

Total mechanical power will be greater during vertical climbing versus horizontal walking owing to the unavoidable accumulation of height and subsequently potential energy oscillations (Autumn et al., 2006).

MATERIALS AND METHODS

Spatiotemporal gait variables, SLFs and COM movements were collected from five Australian green tree frogs [*Ranoidea caerulea* (White 1790); body mass range 26.5–48.0 g, average body mass=34.1±7.6 g] at the New York Institute of Technology College of Osteopathic Medicine (Old Westbury, NY, USA). All data collection protocols were approved by the Institutional Animal Care and Use Committee (IACUC protocol: MCG-2019-01). Animal subjects were adults and free from any visible gait pathologies.

Spatiotemporal gait data collection and processing

Spatiotemporal variables (i.e. contact time, total stride time, duty factor, stride length and stride frequency) were measured from lateral video footage of locomotor trials. Touchdown, lift-off and subsequent touchdown frames of each stride were recorded and

divided by the recording frame rate to obtain time. Contact time was calculated by taking the difference between initial touchdown and lift-off. Duty factor was calculated by dividing contact time by total stride time. Stride length was calculated by multiplying speed by stride time. Stride frequency is the inverse of stride duration.

SLF data collection and processing

SLFs were collected across four experimental conditions, namely a flat runway and a pole each oriented at either a 0 deg (flat) or 90 deg (vertical) angle relative to the ground. Both the flat and pole runways measured 0.508 m in length, with widths of 0.152 m (flat) and 0.012 m (pole), respectively. Each runway featured a centrally positioned cut-out measuring 0.045 m in length, large enough to accommodate the palm length and sole length of the frog's hand or foot, while limiting the potential for overlapping handfalls or footfalls. These cut-outs were instrumented with a small-load force plate (model HE6X6; Advanced Mechanical Technology, Inc., Watertown, MA, USA) using a 3D printed platform (see Fig. 1). All

trials began by zeroing out the force plate to remove any drift or offsets from previous recordings. In most cases, minimal motivation, such as a gentle tap, was provided to the frogs to encourage movement across both flat and cylindrical platforms. Only trials in which the frogs moved with no visual acceleration or deceleration, and included a clear handfall or footfall, were considered successful. All trials were recorded using two high-speed cameras (XC-2; Xcitex Inc., Woburn, MA, USA) mounted to capture frog movement at 125 Hz from lateral and posterior views. Force data (sampled at 1250 Hz) and video data were synchronized using Procapture (Xcitex). Stride length, stride duration and speed were calculated within ImageJ (Schneider et al., 2012) using the position of the frog's eye and the square-grid background of known distance (0.1 m) to calibrate the space. A stride was defined as forelimb touchdown to subsequent touchdown of the same forelimb.

Single limb forces were processed using a custom-written MATLAB script to correct for direction of travel, orientation and

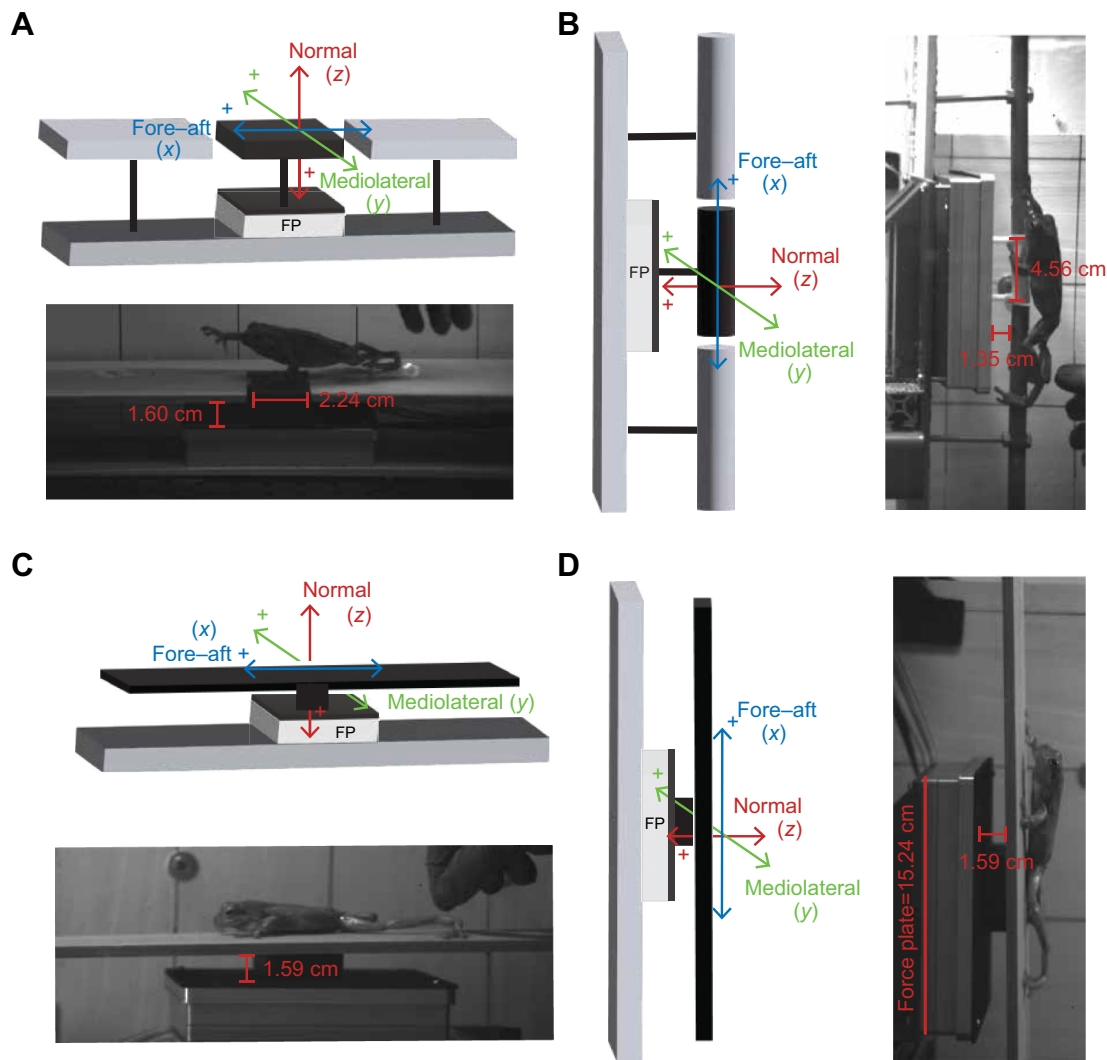


Fig. 1. Experimental setup for single limb force (top) and center of mass (bottom) data collection. Schematic of (A) flat runway oriented horizontally and (B) cylindrical runway oriented vertically instrumented with an AMTI small-load force plate (FP; model HE6X6; load capacity=4 N; Watertown, MA, USA). The majority of the runway is mounted separately from the force plate (grey regions), although small segments (dark regions) are instrumented with force plate. Schematic of flat runway oriented (C) horizontally and (D) vertically instrumented with an AMTI small-load force plate (same as above). The runway is large enough to allow multiple strides. Each panel is accompanied by snapshot of Australian green tree frog (*Ranoidea caerulea*) traversing that experimental setup.

Table 1. Spatiotemporal variables [duty factor, stride time, stride frequency and stride length (means±s.d.)] collected from five Australian tree frogs (*Ranoidea caerulea*) across each of the four experimental setups (flat and pole substrates oriented horizontally and vertically)

Orientation	Substrate	<i>n</i>	Speed (m s ⁻¹)	Duty factor (%)	Stride time (s)	Stride frequency (Hz)	Stride length (m)
Horizontal	Flat	46	0.16±0.05	69.39±7.51	0.53±0.20	2.10±0.67	0.08±0.02
	Pole	38	0.05±0.02	74.66±8.41	1.51±0.83	0.82±0.36	0.04±0.03
Vertical	Flat	30	0.08±0.03	77.50±5.02	1.06±0.38	1.01±0.23	0.07±0.02
	Pole	64	0.06±0.03	79.28±5.84	1.37±0.45	0.80±0.24	0.08±0.03

For individual contributions, see Table S4.

contacting limb (right or left). Forces were standardized such that fore–aft forces were split into negative braking and positive propulsive forces, normal forces were divided into positive pushing and negative pulling forces, and mediolateral forces were divided into negative medially directed forces and positive laterally directed forces. All forces were filtered through a low-pass Fourier filter at 15 Hz (Hanna et al., 2017; Nyakatura et al., 2014; Ogihara et al., 2014) and normalized to a percentage of the animal's body weight (% BW) for peak forces and body weight seconds (% BWS) for impulses to allow statistical comparison between individuals (see below). All net impulses were calculated as the area under the force–time curve in the respective orientation. Although peak force data are reported in Table S1, for ease of readability and to reduce the number of statistical tests, we have elected to only describe single limb force data in terms of net impulse. Net impulse was preferable in the present study as it provides a meaningful summary of the limb's overall role during locomotion (for review, see Demes et al., 1994; Granatosky et al., 2018; Larson and Demes, 2011; Raichlen et al., 2009). For example, a limb's functional braking or propulsive role has been best represented by net fore–aft impulse in numerous studies (e.g. Byron et al., 2017; Demes et al., 1994; Granatosky et al., 2018). Further, weight support distribution between the limbs during horizontal walking has often been analyzed in terms of net normal impulse rather than peaks (Dickinson et al., 2022; Larson and Demes, 2011; Raichlen et al., 2009).

COM dynamics data collection and processing

To collect COM movements, animals walked or climbed across a fully instrumented (HE6X6 force plate as above) flat runway 0.508 m in length and 0.152 m in width. The pole substrate was not used for COM data because the frogs often twisted around the pole, affecting directionality of force readings. Data were

sampled, recorded and synchronized using the same methods as above.

Energy fluctuations of the COM were calculated following previously published methodology (Autumn et al., 2006; Blickhan and Full, 1987; Cavagna et al., 1977; Heglund et al., 1982; Reilly et al., 2006). In summary, COM data were collected as the animal moved across a horizontal and vertical flat instrumented runway long enough to ensure multiple strides (Fig. 1). From the resulting kinetic data, the product of mass and acceleration was subtracted from forces in the plane of gravity (from normal forces in horizontal trials and from fore–aft forces in vertical trials) and subsequently divided by the animal's body mass to arrive at the instantaneous acceleration of the COM. Detrended acceleration (see Bishop et al., 2008; Cole et al., 2014; Gutierrez-Farewik et al., 2006; Ihlen et al., 2013; Walker, 1998) was integrated to calculate instantaneous velocity and secondarily integrated to identify the position of the COM. To obtain constants for integration of velocity (initial fore–aft velocity), we digitized a consistent point on the animal's head over a known distance (see Riskin et al., 2016). Once positional data were acquired, kinetic energy (E_K) in the fore–aft (E_{Kx}), normal (E_{Kz}) and mediolateral (E_{Ky}) planes was calculated as:

$$E_K = \frac{1}{2}mv^2, \quad (1)$$

where m is the mass of the animal and v is the velocity of the COM in each respective axis. Potential energy of the COM (E_P) was calculated using:

$$E_P = mgh, \quad (2)$$

where m is the mass of the animal, g is gravitational force (9.81 m s⁻²) and h is the vertical displacement in each plane COM in each respective axis. Total fore–aft, mediolateral and normal

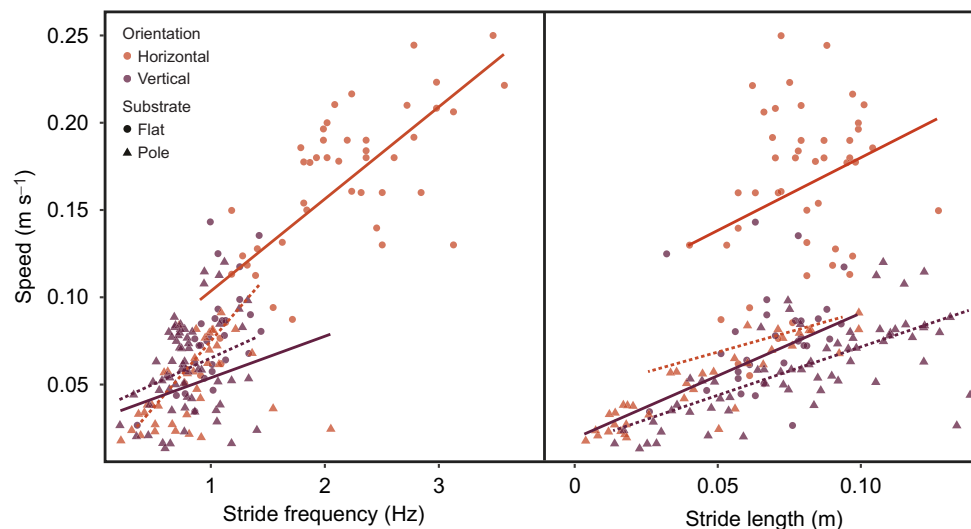


Fig. 2. Bivariate plot demonstrating the relationship between stride frequency and speed (left) and stride length and speed (right). Horizontal (orange) and vertical (purple) orientations are depicted by color. Flat (circle) and pole (triangle) substrates are denoted using different shapes. Dashed and solid lines represent regression lines for the pole and flat substrates, respectively. Regression in stride frequency for horizontal flat: $y=0.05x+0.05$, $R^2=0.56$; horizontal pole: $y=0.02x+0.03$, $R^2=0.14$; vertical flat: $y=0.08x-0$, $R^2=0.37$; vertical pole: $y=0.03x+0.04$, $R^2=0.08$. Regression in stride length for horizontal flat: $y=0.83x+0.09$, $R^2=0.09$; horizontal pole: $y=0.72x+0.02$, $R^2=0.82$; vertical flat: $y=0.46x+0.05$, $R^2=0.07$; vertical pole: $y=0.55x+0.02$, $R^2=0.49$.

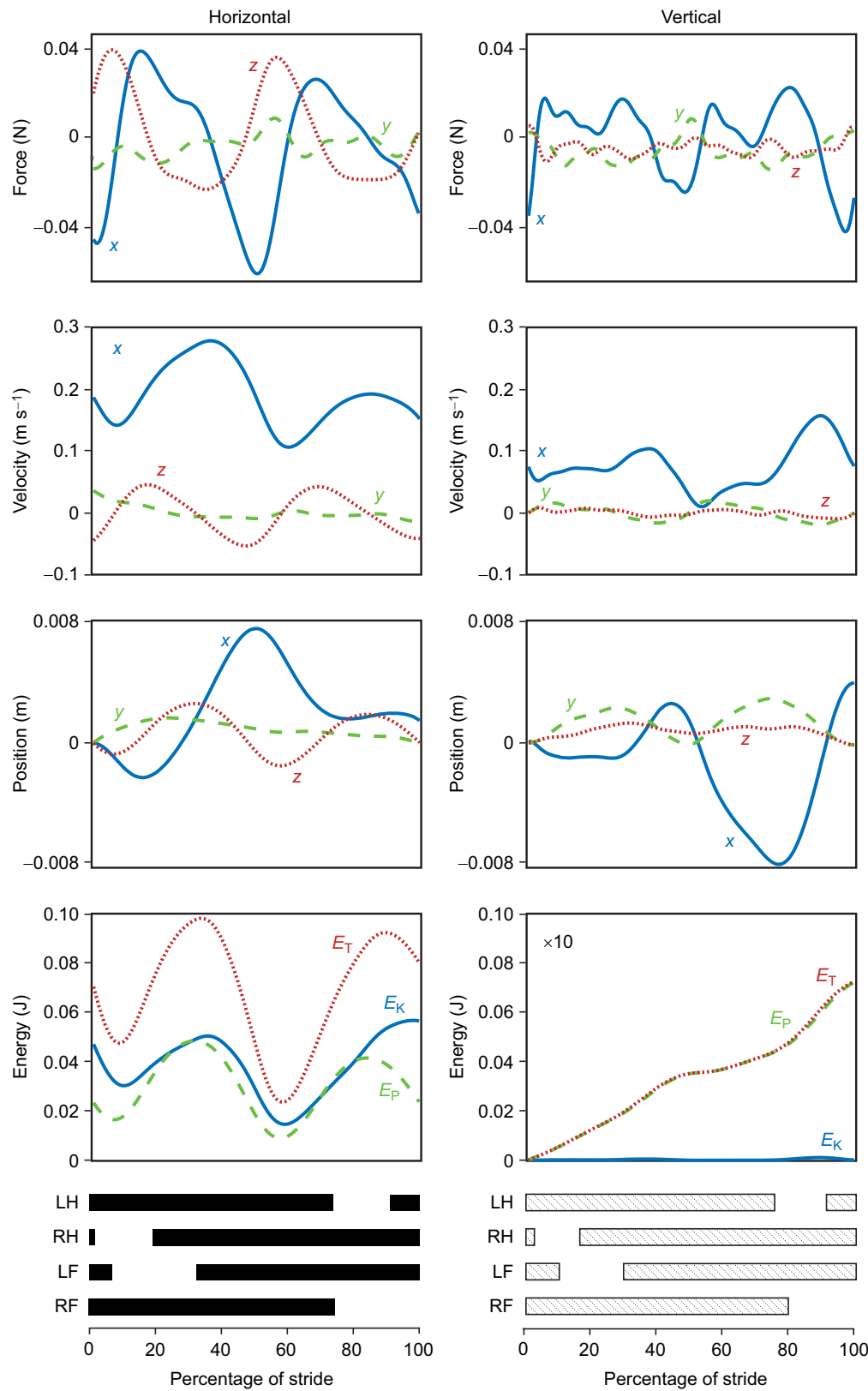


Fig. 3. Average COM force, speed, COM position, energy profiles, and a representative gait sequence during a stride cycle in horizontal walking (left) and vertical climbing (right). A stride was defined from forelimb touchdown to subsequent forelimb touchdown. Solid lines represent the fore–aft direction (braking/propulsive), dashed lines represent mediolateral, and dotted lines represent normal (pulling and pushing in/from substrate) in force and speed traces. Energy components are represented as a solid line for potential energy (E_P), dashed for kinetic energy (E_K) and dotted for total energy (E_T). LH, left hindlimb; RH, right hindlimb; LF, left forelimb; RF, right forelimb.

kinetic (E_K) and potential energies (E_P) were summed during each stride to obtain total energy (E_T) of the COM. The power output of each individual component [power of kinetic energy in each of the fore–aft ($P_{E_{Kx}}$), normal ($P_{E_{Kz}}$) and mediolateral ($P_{E_{Ky}}$)

planes as well as total kinetic energy (P_{E_K}), total potential energy (P_{E_P}) and total energy (P_{E_T})] was determined by summing the positive increments over a stride and dividing by the duration of the stride.

Table 2. Statistical parameters derived from least squares regressions demonstrating the statistical importance of various fixed effects (speed, orientation, limb, substrate) on net impulses in the fore–aft (braking/propulsive), normal (pull/push) and mediolateral axes

Response variable	Fixed effect	Estimate	Standard error	d.f.	<i>t</i>	<i>P</i>
Net fore–aft impulse	Speed	−34.33	65.55	162.96	−0.52	0.601
	Orientation	84.29	3.93	152.95	21.47	<0.001
	Limb	11.95	3.64	161.26	3.29	0.001
	Substrate	8.93	4.16	136.58	2.15	0.033
Net mediolateral impulse	Speed	−113.82	94.72	124.76	−1.20	0.232
	Orientation	−63.59	5.63	132.07	−11.30	<0.001
	Limb	9.10	5.39	160.92	1.69	0.093
	Substrate	−0.16	5.80	59.49	−0.03	0.978
Net tangential impulse	Speed	−89.58	95.91	163.92	−0.93	0.352
	Orientation	−50.74	5.80	159.01	−8.74	<0.001
	Limb	30.84	5.28	160.00	5.84	<0.001
	Substrate	3.67	6.18	154.82	0.59	0.554

Reference in orientation, limb and substrate were to the horizontal condition, forelimb and flat substrate, respectively. Significant *P*-values are in bold.

Statistical analysis

Data on SLFs, mechanical power and spatiotemporal variables (contact time, stride time, duty factor, stride length and stride frequency) were analyzed in R (<https://www.r-project.org/>) using the packages ‘lmerTest’ (Kuznetsova et al., 2017) and ‘lme4’ (Bates et al., 2015). Normality of datasets was assessed with Shapiro–Wilk and Levene’s tests (Sokal and Rohlf, 2012) before rank transforming all data to satisfy assumptions of subsequent statistical analyses (Sokal and Braumann, 1980). Speed, which has been suggested to influence the magnitude of force data (for statistical discussion, see Granatosky et al., 2020), was included in all linear mixed models discussed below. Additionally, individual behavioral idiosyncrasies were accounted for by including individual as a random effect following Winter (2013 preprint) and Bates et al. (2015) in all models.

RESULTS

Spatiotemporal gait characteristics

Slow walking gaits were used on all substrates (i.e. pole versus flat) and orientations (i.e. vertical versus horizontal). Both substrate and orientation had a significant (all $P < 0.001$; Table 1, Fig. 2, see gait sequence in Fig. 3; prediction 1) influence on locomotor speed, duty factor, stride time, contact time and stride frequency. Stride length was significantly influenced by orientation ($P < 0.001$), but not substrate ($P = 0.136$) (see Fig. 2).

Single limb forces

Speed did not significantly impact impulses in any plane (Table 2) during either horizontal or vertical locomotion (all $P > 0.232$), likely reflecting the limited range of locomotor speeds exhibited by the frogs. Frogs were found to produce significantly greater net fore–aft impulses on flat compared with the pole substrate ($P = 0.033$; Tables 2 and 3, Fig. 4; prediction 2); however, inter-substrate effects were not observed in mediolateral and normal impulses. The hindlimbs of Australian tree frogs were found to produce larger net fore–aft and normal impulses compared with the forelimbs (all $P \leq 0.001$). Net fore–aft impulses were significantly greater during vertical climbing compared with horizontal walking ($P < 0.001$; Tables 2, 3, Fig. 4). Conversely, net mediolateral and net normal impulses were significantly greater during horizontal walking ($P < 0.001$; Tables 2, 3, Fig. 4), but did not differ between pole and flat conditions.

Center of mass dynamics

Compared with horizontal walking, the total mechanical energetic cost of vertical climbing was predominantly driven by potential

energy, with negligible kinetic contributions (Fig. 3). Although phasic relationships between potential and kinetic energy profiles are present in some trials, these are absent during vertical climbing (Fig. 3). Total mechanical power was significantly greater during vertical climbing than during horizontal walking ($P < 0.001$; Tables 4 and 5, Fig. 5A), driven by a major increase in potential power during vertical climbing. Kinetic energy in all planes (fore–aft, mediolateral and normal) was greater during vertical climbing than during horizontal walking (all $P < 0.001$; Tables 4, 5, Fig. 5A).

DISCUSSION

Gait characteristics

The Australian green tree frogs in this study primarily adopted slow, walking (i.e. duty factors above 50%) gaits (Table 5). Consistent with studies of arboreal movement in other taxa (Granatosky et al., 2019b; Hanna et al., 2022; Herrel et al., 2013; Manzano et al., 2008; Nyakatura and Heymann, 2010), horizontal pole and vertical locomotion resulted in a decrease in locomotor speed and an increase in both duty factor and contact time compared with flat horizontal walking. Thus, prediction 1 was supported (Fig. 2).

Fore–aft forces

Fore–aft force profiles for Australian green tree frogs during horizontal locomotion largely match global patterns observed across tetrapods (Bertram, 2016; Granatosky et al., 2018, 2020). These include a braking to propulsive transition, and clear braking and propulsive functional differentiation between the forelimb and the hindlimb (Bertram, 2016; Granatosky et al., 2018), supporting prediction 2 (Fig. 4). Indeed, across all horizontal substrate conditions, Australian green tree frogs demonstrated a tendency for the forelimb to serve a net braking function whereas the hindlimb acts in a primarily propulsive role (Table 3, Fig. 4), a pattern consistent across non-belly-dragging quadrupeds (Nyakatura et al., 2014). Peak fore–aft magnitudes were generally similar in Australian green tree frogs during horizontal locomotion, once corrected for directionality and irrespective of substrate (i.e. flat or pole); however, on flat substrates, forelimb peak braking force was higher than any other fore–aft force magnitude (Table S1). Although not quantified, we noticed a tendency for the forelimb to ‘slap’ the substrate at touchdown, which may explain the higher braking forces. Otherwise, impulse patterns between the forelimbs and hindlimbs are generally similar across substrates. Specifically, the forelimb has relatively larger braking impulses, whereas the hindlimb shows greater propulsive impulses (Table 3, Fig. 4). Accordingly, fore–aft impulse is net braking in the forelimb and net

Table 3. Means±s.d. of impulses (% BWS) in fore–aft (braking/propulsive), normal (pull/push) and mediolateral axes from five Australian green tree frogs (*Ranoidea caerulea*) during horizontal walking and vertical climbing on pole or flat substrates and stratified by forelimb versus hindlimb

Substrate	Orientation	Limb	Variable of interest	<i>n</i>	Impulses (% BWS)
Flat	Horizontal	Forelimb	Braking	8	−12.66±8.28
			Propulsive	8	6.53±5.734
			Net fore–aft	8	−1.46±0.87
			Medial	8	−1.11±1.12
			Lateral	8	1.15±1.08
			Net mediolateral	8	0.04±2.01
			Push	8	21.71±7.76
		Hindlimb	Net tangential	8	21.71±7.76
			Braking	19	−0.75±1.88
			Propulsive	19	2.14±1.66
			Net fore–aft	19	1.40±1.42
			Medial	19	−1.18±1.20
			Lateral	19	1.27±0.94
			Net mediolateral	19	0.09±1.87
	Vertical	Forelimb	Push	19	17.44±11.45
			Net tangential	19	17.44±11.45
			Propulsive	28	31.11±19.97
			Net fore–aft	28	31.11±19.97
			Medial	28	−7.89±4.95
			Lateral	28	1.05±1.72
			Net mediolateral	28	−6.83±5.44
		Hindlimb	Pull	26	−2.68±4.38
			Net tangential	26	−2.68±4.38
			Propulsive	16	20.38±22.04
			Net fore–aft	16	20.38±22.04
			Medial	16	−6.12±4.52
			Lateral	16	2.11±2.13
			Net mediolateral	16	−4.01±4.76
Pole	Horizontal	Forelimb	Pull	8	−0.02±0.02
			Push	16	27.33±23.85
			Net tangential	16	27.32±23.87
			Braking	25	−5.31±4.19
			Propulsive	25	1.39±1.25
			Net fore–aft	25	−3.92±4.46
			Medial	25	−2.05±1.81
		Hindlimb	Lateral	25	1.90±2.27
			Net mediolateral	25	−0.14±3.39
			Push	25	38.33±23.11
			Net tangential	25	38.33±23.11
			Braking	26	−0.88±1.12
			Propulsive	26	4.21±3.34
			Net fore–aft	26	3.33±3.53
Vertical	Forelimb	Medial	26	−1.48±1.52	
		Lateral	26	2.69±2.40	
		Net mediolateral	26	1.21±3.07	
		Push	26	35.32±16.82	
		Net tangential	26	35.32±16.82	
		Propulsive	21	46.52±23.59	
		Net fore–aft	21	46.52±23.59	
	Hindlimb	Medial	21	−6.11±4.00	
		Lateral	21	1.60±1.75	
		Net mediolateral	21	−4.52±4.35	
		Pull	21	−11.35±5.90	
		Net tangential	21	−11.35±5.90	
		Propulsive	23	39.79±16.84	
		Net fore–aft	23	39.79±16.84	
Pole	Vertical	Forelimb	Medial	23	−7.73±5.00
			Lateral	23	0.66±0.83
			Net mediolateral	23	−7.10±5.23
			Pull	12	−0.05±0.07
			Push	20	15.76±19.55
			Net tangential	23	15.76±19.55

Number of total trials given by *n*. For individual contributions, see Table S2.

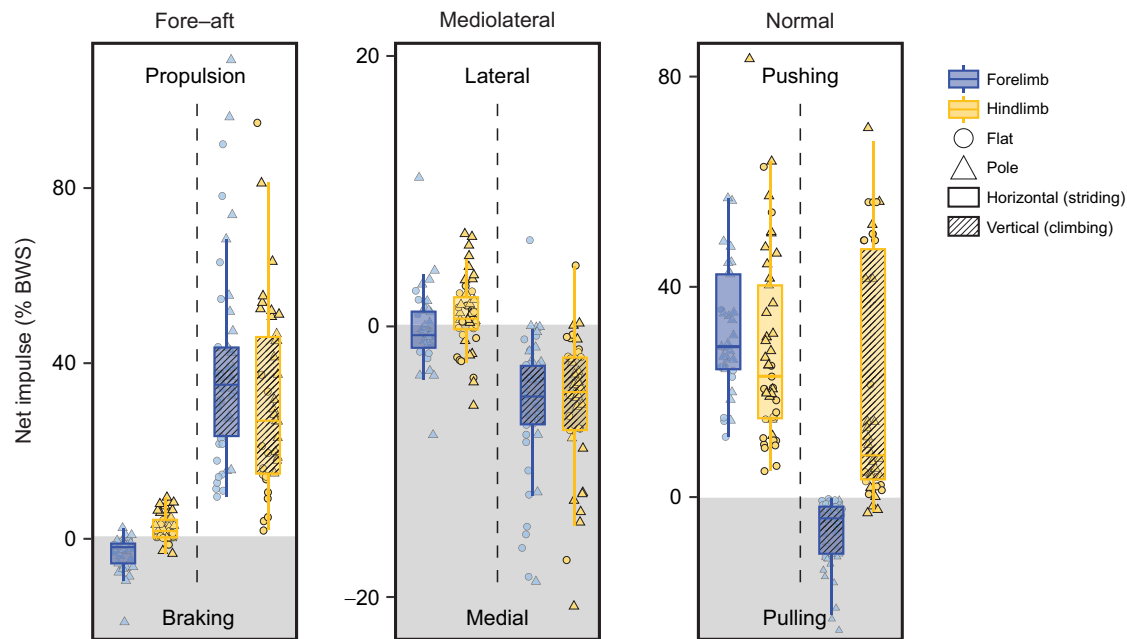


Fig. 4. Impulse (% BWS) differences in the fore–aft (braking and propulsive), mediolateral and normal (pulling and pushing) axes from three Australian green tree frogs (*Ranoidea caerulea*) between horizontal (left of dashed line) and vertical (right of dashed line) experimental conditions. All forelimb impulses are denoted in blue and hindlimb boxes are in yellow. Substrate differences are denoted by circles for flat and triangles for pole.

propulsive in the hindlimb. Fore–aft impulse is generally greater while animals move on the horizontally oriented pole compared with the horizontal flat support (Table 3, Fig. 4). Such a finding can be attributed to the relatively longer contact times and slower velocities observed while Australian green tree frogs moved on simulated arboreal supports (Table 1).

In contrast, during vertical climbing, both the forelimb and hindlimb show exclusively propulsive forces (Table 3, Fig. 4; Table S1), a finding supported across climbing insects and tetrapods (Autumn et al., 2006; Cruse, 1976; Goldman et al., 2006; Wang et al., 2015) and in accordance with prediction 2.

Normal forces

Across tetrapods there is a general trend, with the exception of primates (e.g. Kimura, 1979; Reynolds, 1985) and arboreal opossums (e.g. Schmitt and Lemelin, 2002), to support most of the body weight on the forelimbs (Cieri et al., 2021; Fish et al.,

2021; Gray, 1944). The Australian green tree frog is no exception to this pattern despite the substantial size differentiation between the smaller forelimbs and large hindlimbs. Although there was a tendency for more equal contributions of weight support between the limbs when Australian green tree frogs moved on the horizontally oriented pole (Table 3, Fig. 4), substrate effects in linear mixed-effect models were insignificant.

Australian green tree frogs follow generalized animal patterns of functionally differentiating the cranially positioned limb (pulling) and caudally positioned limb (pushing) (Autumn et al., 2006; Goldman et al., 2006; Hanna et al., 2017) when climbing. This pattern appears to be true irrespective of the clinging mechanism (Autumn et al., 2006; Clemente and Federle, 2008; Cruse, 1976; Hanna et al., 2017; Wang et al., 2015). To our knowledge, no study has yet reported limb-loading patterns during vertical climbing of a claw-clinging species (e.g. squirrels, felines, arboreal varanids, etc.), but data from Young et al. (2022a) showed

Table 4. Statistical parameters derived from least squares regressions demonstrating the statistical importance of various fixed effects on potential, kinetic and total power

Response variable	Fixed effect	Estimate	Standard error	d.f.	<i>t</i>	<i>P</i>
$P_{E_{Kx}}$	Speed	896.81	88.95	85.25	10.08	<0.001
	Orientation	60.72	10.04	83.44	6.05	<0.001
$P_{E_{Ky}}$	Speed	360.34	95.20	128.00	3.79	<0.001
	Orientation	59.34	10.55	128.00	5.62	<0.001
$P_{E_{Kz}}$	Speed	268.05	69.36	69.75	3.87	<0.001
	Orientation	−31.57	7.71	62.27	−4.09	<0.001
P_{E_K}	Speed	932.40	91.90	95.56	10.15	<0.001
	Orientation	67.95	10.37	94.46	6.55	<0.001
P_{E_P}	Speed	411.45	58.01	122.28	7.09	<0.001
	Orientation	108.53	6.55	122.34	16.57	<0.001
P_{E_T}	Speed	479.61	53.73	117.65	8.93	<0.001
	Orientation	113.90	6.07	117.61	18.77	<0.001

Significant *P*-values are in bold. Power of: kinetic energy in the fore–aft direction ($P_{E_{Kx}}$), kinetic energy in the mediolateral direction ($P_{E_{Ky}}$), kinetic energy in the normal direction ($P_{E_{Kz}}$), total kinetic energy (P_{E_K}), total potential energy (P_{E_P}) and total positive mechanical power (P_{E_T}). All orientation effects are referenced to the flat substrate.

Table 5. Sum of positive mechanical power (calculated as the sum of the positive increments of power over a stride divided by the stride duration) represented as means±s.d., collected from three Australian tree frogs (*Ranoidea caerulea*) while navigating horizontally and vertically oriented flat substrates

Orientation	<i>n</i>	Sum of positive mechanical power	Sum of positive mechanical power (W) divided by body mass (kg)
Horizontal	19	$P_{E_{Kx}}$	0.072±0.085
		$P_{E_{Ky}}$	0.024±0.07
		$P_{E_{Kz}}$	0.008±0.005
		P_{E_K}	0.082±0.101
		P_{E_P}	0.081±0.027
		P_{E_T}	0.147±0.102
Vertical	56	$P_{E_{Kx}}$	0.029±0.012
		$P_{E_{Ky}}$	0.005±0.002
		$P_{E_{Kz}}$	0.002±0.001
		P_{E_K}	0.031±0.013
		P_{E_P}	0.753±0.186
		P_{E_T}	0.753±0.186

For individual contributions, see Table S3.

that the claw-clinging hindlimb of parrots follows the same principles described above.

Hanna et al. (2017) reported that during ascent the forelimbs and hindlimbs of primates each experience a pull/push transition, meaning that as the forelimbs and hindlimbs touch down there is an initial pulling normal force subsequently followed by a pushing force at the end of stance phase. Such a pull/push transition during climbing is likely attributable to a limb moving from a cranial to caudal position relative to the COM (Granatosky et al., 2018; Hanna et al., 2017; Norberg, 1986). Although the hindlimb normal force profiles of Australian green tree frogs did indeed demonstrate a pull/push transition (Table 3, Fig. 4; Table S1), we observed no pushing forces in the forelimb. This pattern is consistent with cockroaches (Goldman et al., 2006), geckos (Autumn et al., 2006; Wang et al., 2015) and the beak and hindlimbs of climbing parrots

(Young et al., 2022a). Such a taxonomic difference between primates and other climbing animals requires further investigation and may be attributable to several factors including the tendency for primates to demonstrate large limb excursions (Granatosky et al., 2019a; Larson et al., 2001), overstriding (Cartmill et al., 2020; Demes et al., 1994) or perhaps some unknown phylogenetic differentiation.

Mediolateral forces

The analysis and interpretation of single limb mediolateral forces has always been challenging in animal locomotion studies. Accordingly, such data is often not reported (Hanna et al., 2017; Hirasaki et al., 1993; Young et al., 2022a) and overall patterns remain elusive for climbing. Mediolateral forces were significantly ($P<0.001$) influenced by substrate orientation, but not substrate type (i.e. pole versus flat), contrary to prediction 2. During horizontal walking on a flat substrate, net forelimb mediolateral impulses are approximately equally distributed between medial and lateral directions, but, when traversing a vertical flat substrate, forelimb impulses resolved as medially oriented (Fig. 4). A similar pattern is also observed in the hindlimb (Fig. 4). Mediolateral forces were also highly variable and low in magnitude compared with the normal and fore–aft force components. Thus, perhaps it is incorrect to think about mediolateral force patterns as some preordained motor ‘goal’, and such forces should instead be considered as step-to-step adjustments for maintaining balance throughout a stride (Bishop et al., 2018).

Center of mass mechanics

Although COM mechanics during horizontal walking have been widely discussed (Ahn et al., 2004; Blickhan and Full, 1987; Cavagna et al., 1977; Heglund et al., 1982; Reilly et al., 2006; Rubenson et al., 2004), COM mechanics for vertical climbing remain poorly studied (Autumn et al., 2006; Goldman et al., 2006). During horizontal walking, a phasic relationship between kinetic and potential energy drives energy recovery. However, during

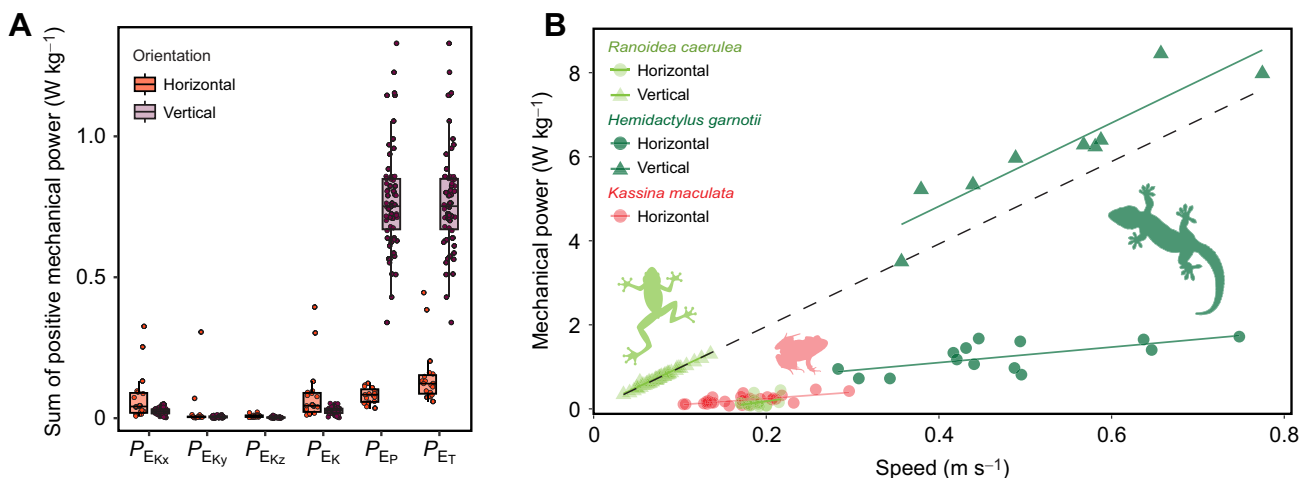


Fig. 5. Costs of horizontal walking and vertical climbing. (A) Mass-specific positive power (as calculated by the summation of positive increments in each component of energy over the stride divided by stride period) between horizontal (orange) and vertical (purple) orientations. Power of: kinetic energy in the fore–aft direction ($P_{E_{Kx}}$), kinetic energy in the mediolateral direction ($P_{E_{Ky}}$), kinetic energy in the normal direction ($P_{E_{Kz}}$), total kinetic energy (P_{E_K}), total potential energy (P_{E_P}) and total positive mechanical power (P_{E_T}). (B) Scatterplot of mechanical power as a function of speed. Orientation is differentiated by shape, with circles representing horizontal walking and triangles depicting vertical climbing. The red-legged running frog (*Kassina maculata*; Ahn et al., 2004) is represented in red, the Australian green tree frog (*Ranoidea caerulea*; present study) in light green and the gecko (*Hemidactylus gamotii*; Autumn et al., 2006; Chen et al., 2006) in dark green. Data from Ahn et al. (2004), Autumn et al. (2006) and Chen et al. (2006) were digitized using WebPlotDigitizer (Drevon et al., 2017; Rohatgi, 2017). The dashed line represents the minimum possible power production necessary to climb, as calculated by speed times gravity ($\sim 9.81 \text{ m s}^{-2}$).

climbing, the phasic relationship between kinetic and potential energy is completely uncoupled owing to the continuous accumulation of potential energy associated with gaining height (prediction 3; Fig. 3). Instead, kinetic components of energy should drive efficiency (Autumn et al., 2006). It can be inferred that efficient climbers should minimize oscillations in their mediolateral and normal axes, thereby reducing total kinetic energetic costs to the bare minimum of fore–aft kinetic energy, lying in their sole axis of travel (Autumn et al., 2006; Goldman et al., 2006; prediction 3). However, this was not observed within our data; instead, both normal and mediolateral kinetic energies were greater during vertical climbing than during horizontal walking (Table 3).

One potential explanation for this trend is that climbing frogs do not utilize particularly efficient locomotion. We can assess climbing efficiency by comparing the total external mechanical power exerted during ascent with the minimum power requirement to lift one's COM against the force of gravity (i.e. the product of gravity and speed; Autumn et al., 2006). Comparing this metric of efficiency between our data and climbing geckos published by Autumn et al. (2006), we observe that frogs are closer to this theoretical minimum of power production than geckos [residual sum of squares (RSS) of frogs=0.023; RSS of geckos=3.22; see Fig. 5]. Therefore, this lack of concordance between our data and theory cannot be ascribed to inefficient climbing.

Instead, we must consider other possible mechanisms to explain efficient climbing. One such explanation is that out-of-plane oscillations of the COM may be less deleterious than originally theorized. In support of this idea, it is noteworthy that mediolateral oscillations of the COM are reported as typical among expert human rock climbers, though no mechanistic explanation has been proposed for these movements (Saul et al., 2019; Zampagni et al., 2011). It is plausible that the pendular nature of left–right swinging in an axis perpendicular to that of the direction of travel may serve as analogous to normal oscillations of the COM during horizontal walking, allowing animals to recover greater energy while climbing. This theory, however, must be further explored through close examination of kinetic energy profiles in future studies.

Finally, we would be remiss to discount the fact that Australian green tree frogs may simply be an inappropriate model to assess mechanical energy between horizontal and vertical locomotion, owing to their small body size and the start–stop nature of their locomotion (Hooper, 2012; Reilly et al., 2007). This is because energy-saving mechanisms associated with greater pendular oscillations of the COM would reduce the relative cost of horizontal walking at large body sizes (Hooper, 2012; Reilly et al., 2007). Such mechanisms are not available during climbing. This disparity between the relative cost of horizontal locomotion and vertical climbing as body size increases has been demonstrated based on metabolic energetic expenditure (Hanna and Schmitt, 2011; Hanna et al., 2008; Taylor et al., 1972). Taken together, we predict that it is at large body sizes that true mechanical energy savings during climbing, most likely driven by modulation of kinetic energy (Autumn et al., 2006), may come into play and provide the necessary variation for natural selection to act upon and drive changes in anatomy and behavior in arboreal species. It is also possible that there is a critical mass at which the relative mechanical costs of climbing no longer represent an energetically feasible form of locomotion (Cant, 1992). However, the presence of climbing behaviors in large-bodied taxa such as bears (Amanat et al., 2020) and gorillas (Remis, 1998) brings such speculation into question. To address these possibilities would require a sample across a broad range of body sizes to assess allometry of climbing mechanical costs.

Conclusions

During horizontal walking, Australian green tree frogs demonstrate the typical quadruped pattern wherein the forelimb serves a net braking function while the hindlimb acts in a primarily propulsive role. Conversely, during vertical climbing both the forelimb and hindlimb show exclusively propulsive forces. In the normal plane, the forelimb serves a net pulling function while the hindlimb is net pushing (Table 2, Fig. 2), in line with observations in other climbing taxa. Finally, mediolateral forces remain enigmatic to interpret and may reflect adaptations towards maintaining stability during a stride (Bishop et al., 2018).

This study is one of the few (Autumn et al., 2006; Goldman et al., 2006) to report COM movements and energy profiles during non-human climbing. Overall, Australian green tree frogs match theoretical predictions of climbing dynamics (i.e. total energetic requirements are primarily driven by the accumulation of potential energy as the animal ascends; Autumn et al., 2006; Goldman et al., 2006). We suggest that attention should be directed towards fluctuations in kinetic energy, the only means by which natural selection can act to reduce overall mechanical costs. Utilizing power as a means for estimating efficiency, we observed that Australian green tree frogs are highly mechanically efficient, barely exceeding the minimum mechanical power necessary to climb at a certain speed (Fig. 5). Although it is often assumed that gaits maximizing stability are in direct conflict with speed-related decreases in overall cost of transport (Heglund and Taylor, 1988; Heglund et al., 1982; O'Neill, 2012), it would appear that Australian green tree frogs move both slowly and efficiently. Indeed, a tendency for careful movement during vertical climbing seems to be a broad pattern observed across climbing species (Goldman et al., 2006; Granatosky et al., 2019b; Hanna et al., 2022; Herrel et al., 2013; Karantanis et al., 2018), and may represent a viable means to achieve both stability and mechanical efficiency. All climbing species are not slow, however, and assessing how such species balance stability and energetic considerations would be of great interest. The findings in this study raise exciting considerations about what makes a good climber from a mechanical perspective, and future work is required to quantify variation in climbing efficiency across species of differing anatomical configurations and body sizes.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.W.Y., N.D.F., E.D., M.C.G.; Methodology: M.W.Y., N.D.F., J.R.Y., A.R., N.G., M.C.G.; Software: M.W.Y., N.D.F., M.C.G.; Validation: M.W.Y., N.D.F., J.R.Y., E.D., M.C.G.; Formal analysis: M.W.Y., N.D.F., J.R.Y., A.R., N.G., M.C.G.; Investigation: M.W.Y., N.D.F., J.R.Y., A.R., N.G., E.D., M.C.G.; Resources: M.C.G.; Data curation: M.W.Y., J.R.Y., A.R., N.G., E.D., M.C.G.; Writing - original draft: M.W.Y., J.R.Y., A.R., N.G., E.D., M.C.G.; Writing - review & editing: M.W.Y., J.R.Y., A.R., N.G., E.D., M.C.G.; Visualization: M.W.Y., N.D.F., E.D., M.C.G.; Supervision: M.C.G.; Project administration: M.W.Y., M.C.G.; Funding acquisition: M.C.G.

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Data availability

All data used for statistical analysis within this study are available from GitHub: <https://github.com/melodyoungg/TreeFrogs>

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Table S1. Peak forces as mean \pm standard deviations in fore-aft (braking/propulsive), normal (pull/push), and mediolateral axes divided by limb (forelimb/hindlimb), orientation (horizontal/vertical), and substrate (flat/pole).

Substrate	Orientation	Limb	Variable	n	Peak
Flat	Horizontal	Forelimb	Braking	8	-12.66 \pm 8.28
			Propulsive	8	6.53 \pm 5.75
			Medial	8	-7.85 \pm 4.59
			Lateral	8	8.01 \pm 6.26
			Push	8	61.73 \pm 9.16
		Hindlimb	Braking	19	-11.71 \pm 6.24
			Propulsive	19	13.37 \pm 11.73
			Medial	19	-9.29 \pm 7.66
			Lateral	19	9.36 \pm 5.28
			Push	19	53.66 \pm 19.53
	Vertical	Forelimb	Propulsive	28	57.29 \pm 23.80
			Medial	28	-21.56 \pm 9.52
			Lateral	28	6.13 \pm 5.55
			Pull	27	-9.79 \pm 5.92
		Hindlimb	Propulsive	16	30.89 \pm 14.12
			Medial	16	-17.96 \pm 7.08
			Lateral	16	11.04 \pm 6.08
			Push	16	16.72 \pm 11.69
Pole	Horizontal	Forelimb	Braking	25	-14.67 \pm 7.43
			Propulsive	25	19.10 \pm 7.33
			Medial	25	-10.54 \pm 5.72
			Lateral	25	11.06 \pm 4.63
			Push	25	69.51 \pm 6.31
		Hindlimb	Braking	26	-12.56 \pm 6.09
			Propulsive	26	9.73 \pm 6.28
			Medial	26	-8.35 \pm 4.76
			Lateral	26	10.58 \pm 4.96
			Push	26	53.55 \pm 14.24
	Vertical	Forelimb	Propulsive	21	64.98 \pm 12.17
			Medial	21	-15.87 \pm 5.27

		Lateral	21	7.95 ± 5.70
		Pull	21	-21.85 ± 6.35
	Hindlimb	Propulsive	23	64.89 ± 11.31
		Medial	23	-15.44 ± 6.25
		Lateral	22	5.65 ± 4.40
		Pull	9	-16.29 ± 6.66
		Push	23	17.51 ± 4.87

Table S2. Contributions of each animal to single limb force data, separated per experimental condition/orientation.

Orientation	Substrate	Individual	Mass (Kg)	Limb	Trials Contributed
Upright	Flat	Fuji	0.030366	Fore	1
				Hind	1
		Gala	0.02963	Hind	4
				Grannysmith	0.047958
		Hind	2		
		HoneyCrisp	0.035837	Fore	3
	Hind			5	
	PinkLady	0.026446	Fore	1	
			Hind	7	
	Pole	Grannysmith	0.047958	Fore	1
				Hind	1
		HoneyCrisp	0.035837	Fore	10
				Hind	9
		PinkLady	0.026446	Fore	1
Hind				1	
Fuji	0.030366	Fore	12		
		Hind	14		
Gala	0.02963	Fore	1		
		Hind	1		
Vertical	Flat	Fuji	0.030366	Fore	11
				Hind	5
		Gala	0.02963	Fore	5
				Hind	6
		Grannysmith	0.047958	Fore	4
				Hind	1
	HoneyCrisp	0.035837	Fore	2	
			PinkLady	0.026446	Fore
	Hind	4			
	Pole	PinkLady	0.026446	Fore	4
				Hind	3
		Gala	0.02963	Fore	1
Hind				2	
HoneyCrisp		0.035837	Fore	16	
			Hind	18	

Table S3. Contributions of each animal to center of mass data, separated per experimental condition/orientation.

Orientation	Individual	Mass (Kg)	Trials Contributed
Upright	Fuji	0.030366	7
	PinkLady	0.026446	12
Vertical	Fuji	0.030366	30
	HoneyCrisp	0.035837	1
	PinkLady	0.026446	25

Table S4. Contributions of each animal to spatiotemporal data, separated per experimental condition/orientation.

Orientation	Substrate	Individual	Mass (Kg)	Trials Contributed
Upright	Flat	Fuji	0.030366	12
		Grannysmith	0.047958	10
		HoneyCrisp	0.035837	2
		PinkLady	0.026446	22
	Pole	HoneyCrisp	0.035837	12
		PinkLady	0.026446	4
		Fuji	0.030366	21
	Gala	0.02963	1	
Vertical	Flat	Fuji	0.030366	12
		Gala	0.02963	6
		HoneyCrisp	0.035837	3
		PinkLady	0.026446	9
	Pole	Fuji	0.030366	12
		Gala	0.02963	11
		Grannysmith	0.047958	6
		HoneyCrisp	0.035837	25
		PinkLady	0.026446	10



Movie 1. Triaxial [Fore/aft (top); Normal (center); and Mediolateral (bottom)] single limb forces collected from the forelimb (blue) and hindlimb (yellow) collected during vertical climbing in Australian green tree frogs (*Ranoidea caerulea*). All data presented as a proportion of body weight (% BW).