Erratum

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There was an error published in *J. Exp. Biol.* **215**, 1728-1739.

In Eqn 8 (p. 1730), the minus sign should be a plus sign. The correct version is given below.

$$s_h = S_{i,h} + \int v_h \, dt \qquad (8)$$

We apologise to the authors and readers for any inconvenience caused.

RESEARCH ARTICLE

The gaits of primates: center of mass mechanics in walking, cantering and galloping ring-tailed lemurs, *Lemur catta*

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SUMMARY

Most primates, including lemurs, have a broad range of locomotor capabilities, yet much of the time, they walk at slow speeds and amble, canter or gallop at intermediate and fast speeds. Although numerous studies have investigated limb function during primate quadrupedalism, how the center of mass (COM) moves is not well understood. Here, we examined COM energy, work and power during walking, cantering and galloping in ring-tailed lemurs, *Lemur catta* (*N*=5), over a broad speed range (0.43–2.91 m s^{-1}). COM energy recoveries were substantial during walking (35–71%) but lower during canters and gallops (10–51%). COM work, power and collisional losses increased with speed. The positive COM works were 0.625 J kg^{-1} m^{-1} for walks and 1.661 J kg^{-1} m^{-1} for canters and gallops, which are in the middle range of published values for terrestrial animals. Although some discontinuities in COM mechanics were evident between walking and cantering, there was no apparent analog to the trot–gallop transition across the intermediate and fast speed range (dimensionless *v*>0.75, *Fr*>0.5). A phenomenological model of a lemur cantering and trotting at the same speed shows that canters ensure continuous contact of the body with the substrate while reducing peak vertical COM forces, COM stiffness and COM collisions. We suggest that cantering, rather than trotting, at intermediate speeds may be tied to the arboreal origins of the Order Primates. These data allow us to better understand the mechanics of primate gaits and shed new light on primate locomotor evolution.

Key words: locomotion, center of mass, collision, gait, mechanical work, quadruped, lemur, *Lemur catta*.

INTRODUCTION

During terrestrial locomotion, the center of mass (COM) moves along a sinusoidal path, oscillating up and down over a stride (Cavagna et al., 1976; Cavagna et al., 1977). This is accomplished through the limbs performing positive and negative mechanical work on the body. Throughout a stride, the limbs collide with the ground, negative work is performed on the COM and mechanical energy is lost. To maintain a steady speed, the lost energy must be replaced through positive work, redirecting the COM upward and into its next arc. The similarities that exist in how terrestrial animals accomplish this task across speeds and gaits are often emphasized using pendular and mass-spring analogies. However, it has also become apparent that important differences exist among species in the details of how they generate mechanical work and power for moving the COM (Ahn et al., 2004; Bertram and Gutmann, 2009; Bishop et al., 2008; Lee et al., 2011; Willey et al., 2004; Zani et al., 2005). Quadrupedal primates offer an opportunity to further investigate the breadth of similarities and differences in locomotor mechanics across mammals.

Most quadrupedal primates, including lemurs, are capable of a wide range of locomotor behaviors. Yet much of the time, they use only a small subset of their range: at slow speeds they prefer to walk, and at intermediate and fast speeds they amble, canter and gallop (Cartmill et al., 2002; Demes et al., 1994; Hildebrand, 1967; Rollinson and Martin, 1981; Schmitt et al., 2006; Vilensky, 1987; Vilensky, 1989). This is distinct from the typical quadruped,

which walks, trots and gallops across its speed range. The amble and canter can be defined, respectively, as a symmetric gait with an aerial phase for forelimb and hindlimb pairs but no whole-body aerial phase, and an asymmetric gait with little to no whole-body aerial phase (Schmitt et al., 2006). The canter has often been referred to simply as a 'slow gallop' (Howell, 1944; Bertram and Gutmann, 2009).

Previous studies have characterized quadrupedal primate gaits through measurements of footfall patterns, single limb forces, joint angles and muscle activation patterns (e.g. Cartmill et al., 2002; Demes et al., 1994; Hanna et al., 2006; Kimura et al., 1979; Larson and Stern, 2008; Patel, 2009; Reynolds, 1985; Schmitt et al., 2006; Vilensky, 1983; see also Schmitt, 2003). This research has provided numerous insights into primate evolution. In particular, several aspects of primate gaits have been identified that are thought to be part of a suite of basal primate adaptations for locomotion and foraging on flexible, terminal branches (e.g. Cartmill et al., 2002; Larson, 1998; Lemelin and Schmitt, 2006; Schmitt, 1999; Schmitt and Lemelin, 2002), including the avoidance of a trot in favor of an ambling or cantering gait at intermediate speeds (Schmitt et al., 2006). However, the fundamental question of how the COM is supported and redirected across gaits and speeds is still poorly understood. This is due in large part to the near-absence of measurements of COM mechanics for primate quadrupedalism (but see Cavagna et al., 1977; Vilesnky, 1979). This is a significant omission, as COM

measurements help to characterize the operation of the musculoskeletal system across multiple organizational levels, from individual muscles to the whole body. The purpose of this study is to begin to fill this critical gap by measuring the COM mechanics of ring-tailed lemurs during level, terrestrial locomotion.

Therefore, the first goal of this study was to determine the COM mechanics of ring-tailed lemurs, *Lemur catta*, across a range of speeds and gaits. We measured the COM energy exchange, as well as the mechanical work and power required for walking, cantering and galloping. In addition to classical calculations (Cavagna, 1975), we used simple point-mass metrics to determine the change in the COM collisional geometry during a stride (Bertram and Gutmann, 2009; Lee et al., 2011; Ruina et al., 2005; Usherwood et al., 2007). Taken together, these data present a more complete characterization of COM mechanics of primate quadrupedalism than has previously been published, and provide a useful baseline for studies of COM mechanics in other primate species.

The second goal of this study was to investigate why ring-tailed lemurs, like other quadrupedal primates, generally avoid trotting at speeds between a walk and a gallop. It has been noted that quadrupedal primates, including other strepsirrhine primates such as dwarf and mouse lemurs, prefer to canter or amble at intermediate speeds (Hildebrand, 1967; Schmitt et al., 2006). However, it is not known how the COM mechanics of their preferred intermediate-speed gait might differ from the trotting gait used by other mammals. Some have argued that quadrupedal primates avoid trotting in order to avert abrupt changes in vertical oscillations of the body and high peak ground forces (Demes et al., 1990; Schmitt, 1999; Schmitt et al., 2006). To test this hypothesis, we generated a simple phenomenological model of a lemur-like quadruped at a trot and canter. This approach allows us to better understand the mechanics of these two gaits and sheds some new light on primate locomotor evolution.

MATERIALS AND METHODS
Animals
Five adult ring-tailed lemurs (*Lemur catta* Linnaeus, 1758; three males, two females; mean ± s.d. body mass=2.52±0.26 kg) were allowed to move along a 9-m-long instrumented runway using a range of speeds and gaits. The animals were selected from a breeding colony maintained by Duke University at the Duke Lemur Center (DLC), Durham, NC. The lemurs are housed in spacious indoor enclosures during winter months and large outdoor, free-range enclosures during the remaining part of the year. The runway for conducting locomotor experiments was constructed in a climate-controlled research room, onsite at the DLC. The Duke University Institutional Animal Care and Use Committee approved all procedures.

Runway and experimental procedures
All locomotor experiments were conducted on a 9.0×2.0×2.3 m runway enclosed by fine-screen mesh strung from wooden posts that were fastened to the floor. The runway was closed at both ends and along the top to completely contain the animal. A canvas blind affixed through the middle of the runway divided it into two 1-m-wide corridors, effectively creating an 18 m roundabout. The floor of the runway was smooth particleboard covered with a coating of polyurethane to seal it and prevent slipping by the animal. A 0.60×0.40 m force plate was fitted with a solid wooden top and set flush with the floor at approximately the midpoint of the runway. The lemurs were placed in the runway area and

encouraged to move through the entire distance of the enclosure using a wide range of speeds. In most cases, walking speeds were self-selected without prompting, whereas cantering and galloping speeds were usually elicited by the presence of a DLC animal technician at the ends of the runway. Among the five ring-tailed lemurs, walking, cantering and galloping strides were obtained from all but one individual, from whom only walking strides were recorded.

Data collection and measurement
Ground reaction forces (GRFs) were measured using a multi-component piezoelectric force plate (model 9281B; Kistler Instruments Corp., Amherst, NY, USA) with an external charge amplifier. Vertical, horizontal (fore–aft) and mediolateral forces were recorded. Force plate output was sampled at 1250 Hz, transferred to a computer and stored by means of a BioWare™ type 2812A1-3 A/D system (DAS1602/16 A/D board) operated using BioWare v.3.2 software (Amherst, NY, USA).

A thick wooden board (1.3×0.3×0.05 m) was bolted to the top of the plate to collect whole-body forces. The board was firmly affixed such that it hung approximately 0.25 m off either end of the plate to increase measurement area. The board was stiff so that no bending occurred when a lemur walked, cantered or galloped across it.

Trials were filmed in lateral view with a digital high-speed video camera (Redlake Motionscope PCI-500, San Diego, CA, USA) recording at 125 Hz. The camera was positioned approximately 3 m from the runway to reduce the effects of parallax. Video and force-plate data were synchronized *via* a custom-built trigger that simultaneously started video recording and sent a voltage pulse to a separate channel to begin recording from the plate.

Prior to video recording, the forelimbs and hindlimbs of the animals were shaved. Joint centers were located by palpation and then marked using nontoxic white paint. Points marked for the forelimb included the shoulder, wrist and metacarpophalangeal joint (MCP); for the hind limb, the hip, ankle and metatarsophalangeal joint (MTP) were marked. Joint markers, as well as the eye and tail base were digitized in MATLAB (R2008b, The MathWorks, Natick, MA, USA) using DLT Dataviewer (Hedrick, 2008). The coordinate data were filtered using a quintic smoothing spline (Woltring, 1985; Woltring, 1986; Walker, 1998) with a constant error tolerance ('spaps', tolerance=0.005; MATLAB, R2008b). From these data, we calculated horizontal speed, stride duration, duty factor and effective limb length (i.e. shoulder and hip height). Effective limb length was taken as the linear distance from the point of ground contact (i.e. MCP and MTP) to the hip and shoulder markers at approximate mid-stance of a step.

COM classical calculations
Vertical, horizontal and mediolateral instantaneous accelerations of the COM (a_v, a_h and a_l, respectively) were obtained from the measured GRF and body mass (M_b):

$$a_v = \frac{f_v}{M_b} - g \,, \qquad (1)$$

$$a_h = \frac{f_h}{M_b} \,, \qquad (2)$$

$$a_l = \frac{f_l}{M_b} \,, \qquad (3)$$

where g is the vertical acceleration due to gravity (9.81 m s^{-2}). These

expressions can be integrated once with respect to time to provide instantaneous velocities (v):

$$v_v = V_{i,v} + \int a_v dt , \qquad (4)$$

$$v_h = V_{i,h} + \int a_h dt , \qquad (5)$$

$$v_l = V_{i,l} + \int a_l dt , \qquad (6)$$

and with initial velocity conditions ($V_{i,v}$, $V_{i,h}$ and $V_{i,l}$) as integration constants, Eqns 4, 5 and 6 can be integrated again to provide instantaneous positions (s):

$$s_v = S_{i,v} + \int v_v dt , \qquad (7)$$

$$s_h = S_{i,h} - \int v_h dt , \qquad (8)$$

$$s_l = S_{i,l} + \int v_l dt . \qquad (9)$$

Given the initial positions for integration constants ($S_{i,v}$, $S_{i,h}$ and $S_{i,l}$), instantaneous kinetic energy (E_K) and gravitational potential energy (E_P) can be derived from Eqns 4–7 (Cavagna, 1975):

$$E_K = \frac{1}{2} M_b (v_v^2 + v_h^2 + v_l^2) , \qquad (10)$$

$$E_P = M_b g s_v . \qquad (11)$$

The initial velocity conditions ($V_{i,v}$, $V_{i,h}$ and $V_{i,l}$) must be derived from kinematic data obtained from high-speed video, or some other means independent of the force platform. For steady locomotion, we assumed that the average velocities obtained from our kinematic data are close enough to V_i that they could be used as V_i values without causing substantial error (e.g. Cavagna, 1975; Cavagna et al., 1977; Heglund et al., 1982). Consequently, $V_{i,v}$ and $V_{i,l}$ are assumed to equal zero and $V_{i,h}$ is assumed to equal the average horizontal velocity.

The COM mechanical work and power per stride were determined for each trial. The positive COM work was calculated as the sum of the positive incremental changes in the $E_K + E_P$ curve, whereas negative COM work summed the negative increments. The COM power was calculated as the rate of COM work in either the positive or negative direction. The total COM work and power over a stride is taken as the sum of the positive and the absolute of the negative values (Cavagna, 1975; Cavagna et al., 1977; Heglund et al., 1982).

The pendulum-like or spring-like nature of walking was evaluated, in part, by the interchange of E_K and E_P of the COM over a stride. The percent of COM energy recovered (R) throughout a stride is calculated as:

$$R = \frac{\sum E_{K,h} + \sum E_P - \sum(E_K + E_P)}{\sum E_K + E_P} \times 100 , \qquad (12)$$

where the sums refer to the sum of all positive incremental changes over the course of the stride.

To evaluate the relative contributions of COM energy amplitude and phasing to the measured percent COM energy recoveries, we determined the effective limb length (i.e. a proxy for E_P amplitude) and the phase relationship of E_K and E_P. The phase relationship of E_P and E_K was measured as congruity, calculated following Ahn et al. (Ahn et al., 2004):

$$\text{Congruity} = \frac{d}{dt} E_P \times \frac{d}{dt} E_K . \qquad (13)$$

Congruity is positive when E_P and E_K change in the same direction (in phase) and negative when they change in opposite directions (out of phase). As a summary value, we use percent congruity, defined as the percentage of the stride in which congruity is positive. A high percent congruity means that E_P and E_K fluctuate largely in phase, whereas a low percent congruity means that E_P and E_K fluctuate largely out of phase.

COM collisional calculations

Several recent studies have argued that the fundamental reason COM work and power are needed in steady, terrestrial locomotion is to replace the kinetic energy losses that occur when the COM and limbs collide with the ground (Bertram and Gutmann, 2009; Lee et al., 2011; Ruina et al., 2005; Usherwood et al., 2007). Given this, the COM work and power required over a stride should be proportional to the geometry of these collisions (Fig. 1). Following Lee et al. (Lee et al., 2011) and others (Adamcyzk et al., 2006; Adamcyzk and Kuo, 2009), the angle of the COM collision (ϕ) is a function of the angle of the COM velocity vector relative to the GRF resultant vector. Given the COM forces (f_v, f_h and f_l) and velocities (v_v, v_h and v_l), the instantaneous orientation of the COM velocity (λ) relative to the horizontal (fore–aft) and the instantaneous orientation of the resultant GRF (θ) relative to the vertical can be derived (Lee et al., 2011):

$$\lambda = \cos^{-1} \left[\frac{|v_h|}{|\sqrt{v_v^2 + v_h^2 + v_l^2}|} \right] , \qquad (14)$$

$$\theta = \cos^{-1} \left[\frac{|f_v|}{|\sqrt{f_v^2 + f_h^2 + f_l^2}|} \right] . \qquad (15)$$

When the COM velocity and force vectors are orthogonal, the COM energy lost in that instant is zero – as in a rolling wheel (Margaria, 1976; Lee et al., 2011; Ruina et al., 2005) – and (in principle) no mechanical work or power is needed to keep the COM moving. The instantaneous COM collision angle (ϕ) can be calculated as (Lee et al., 2011):

$$\phi = \cos^{-1} \left[\frac{|f_v v_v + f_h v_h + f_l v_l|}{\sqrt{f_v^2 + f_h^2 + f_l^2} \times \sqrt{v_v^2 + v_h^2 + v_l^2}} \right] . \qquad (16)$$

To determine how the COM collisional angles change across gait and speed, we examined the change in λ, θ and ϕ with forward
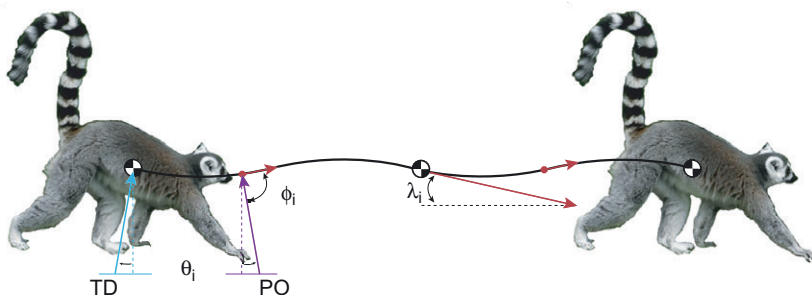

Fig. 1. The whole-body center of mass (COM) motion of a walking ring-tailed lemur. The COM moves in an approximately sinusoidal path over a stride, in which the ground reaction forces (GRFs) from individual limbs support and redirect the COM velocity. The COM velocity (λ) and resultant GRF (θ) change angles at each instant (i) in a stride, such as from touchdown (TD) to push-off (PO) of the same hindlimb. The COM velocity and resultant GRF are separated by some angle, which defines the COM collision angle (ϕ).

velocity. For comparative purposes, the weighted average of each of these parameters over a stride was calculated (see Lee et al., 2011), which are given in the text and figures as λ_{vel}, θ_{GRF} and ϕ_{col}. We then evaluated the equivalence between the COM power (W N^{-1}), work (J N^{-1} m^{-1}), speed (v; m s^{-1}) and average COM collision angle (ϕ_{col}; rad) using least-squares regression:

$$\text{COM power} = C\,(v\phi_{col}) + D\,, \tag{17}$$

$$\text{COM work} = C\,(\phi_{col}) + D\,, \tag{18}$$

where C and D are coefficients (slope and intercept) in the least-squares fits. If the average COM velocity and COM collision angle approximate the mechanical work required per time and per distance, the regression coefficients can be predicted. For Eqns 17 and 18, total COM power and work will be $C=2$, and positive COM power and work will be $C=1$. In both cases, it is expected that $D=0$. Lee et al. (Lee et al., 2011) demonstrated that the average COM work per distance ('mechanical cost of transport'; their eqn 12) scales in direct proportion to ϕ_{col} in dogs and goats. Here, we evaluate this finding against the total and positive COM work per distance (Eqn 18) in ring-tailed lemurs, and extend this expectation to the COM power ('mechanical cost of locomotion'; Eqn 17) to link our classical and collisional COM measurements.

Finally, we compared our measured ϕ against the expected values for a 'spring-like' ($\lambda+\theta$) collision, the collisional fraction (Lee et al., 2011). We calculated the collisional fraction as a weighted sum of the instantaneous values, $\Sigma[\phi_i/(\lambda_i+\theta_i)]$, rather than as the fraction of the weighted values $\Sigma\phi/(\Sigma\lambda+\Sigma\theta)]$ described in Lee et al. (Lee et al., 2011). Although the two approaches are highly correlated (slope=0.91, r^2=0.95), the instantaneous calculation used here is more consistent with the instantaneous approach used to determine ϕ, λ and θ over a stride (D. V. Lee, personal communication). In a 'spring-like' collision, the COM velocity and GRF are inversely orthogonal to each other, resulting in high collisional losses and a ratio of measured-to-expected ϕ near 1. In contrast, when the COM velocity and GRF are orthogonal, the measured-to-expected ratio of ϕ is near zero and collisional losses are low. It has recently been shown that quadrupedal trotting gaits, which have often been modeled as mass-spring systems (Farley et al., 1993), tend (as expected) towards collisional fractions near 1 (Lee et al., 2011).

Quadruped model

We performed numerical simulations of a simple phenomenological model of a lemur-like quadruped in order to better understand: (1) the COM energy exchange during walking and (2) the biomechanical differences between a trot and canter at similar speeds.

To evaluate COM energy exchange during walking, we compared the vertical oscillations (i.e. displacements) of the COM of the lemurs with those predicted for a rigid, stiff-limbed walker ['compass-gait model' (Griffin et al., 2004a; Usherwood et al., 2007)]. The amplitudes of the vertical displacements of the COM of the stiffed-limbed walker were based on measurements of limb phase, foot–ground contact time and hip and shoulder height for each lemur. The position of the COM along the length of the trunk (i.e. distance from hip to shoulder) was also input, as vertical displacements of the COM tend to most closely track the movements of the heavier limbs (Griffin et al., 2004a). We set the COM position in lemurs as 63% of trunk length from the shoulder, which we based on the ratio of measured forelimb ($j_{v,f}$) and hindlimb ($j_{v,h}$) vertical ground force impulses [i.e. $j_{v,f}/(j_{v,h}+j_{v,f})$ (Jayes and Alexander, 1978)] for several walking, cantering and galloping steps (O'Neill, 2009). The

ratio of the average vertical amplitude of the measured COM displacement (Eqn 6) and the average amplitude of the predicted COM displacements from the compass-gait model were calculated in order to evaluate how 'strut-like' the limbs of lemurs were across the range of observed walking speeds, as in Usherwood et al. (Usherwood et al., 2007). A value of one means that the COM displacement approximates that of a lemur walking with rigid, strut-like limbs, whereas a value of zero means that the COM travels along a constant, level path.

The COM vertical displacement, vertical stiffness and collisional losses experienced in trotting and cantering at the same speed were compared by mathematically modeling whole-body GRFs, duty factor and limb phases. A model, rather than empirical data, was used in this study because ring-tailed lemurs never trotted, a finding consistent with most other studies of primate gaits (Cartmill et al., 2002; Demes et al., 1994; Hildebrand, 1967; Rollinson and Martin, 1981; Schmitt et al., 2006; Vilensky, 1987; Vilensky, 1989). As a result, it was not feasible to record the appropriate force plate data. GRF patterns for individual limbs were modeled following published methods (Alexander and Jayes, 1980). This required selecting a shape factor for the individual limb force curves that was used to model the force patterns for cantering and trotting. A shape factor value of zero (i.e. one-half a sine wave) was chosen because it approximates the actual vertical force patterns applied to the ground by trotting and cantering mammals (Bobbert et al., 2007; Jayes and Alexander, 1978; Merkens et al., 1993a; Merkens et al., 1993b; Lee et al., 2004; Witte et al., 2004). The horizontal force patterns were modeled as a full sine wave. The lead and nonlead limb forces were biased for braking or propulsion or balanced between braking and propulsion based on published steps from ring-tailed lemurs (Franz et al., 2005; O'Neill, 2009). The phase relationships for the limbs were based on measurements of lemurs cantering at approximately 1.5 m s^{-1}, whereas the phase relationships for trotting were based on the well-known footfall patterns for dogs and other mammals (Cartmill et al., 2002; Lee et al., 1999). The modeled individual limb forces – aligned using known phase relationships – reconstructed whole-body GRF patterns for the contact phase of a trotting and cantering stride in custom-written MATLAB scripts. Together, the resultant whole-body forces were used to calculate the COM velocities and positions.

Using vertical GRFs (f_v) and displacements (s_v), COM vertical stiffness was calculated (Gein et al., 2010; McMahon and Cheng, 1990) and compared between a canter and a trot. In addition, to better understand the effect of gait choice on COM collisional losses, cantering and trotting were compared using the average COM collision angle (ϕ_{col}) and collisional fraction $\phi/(\lambda+\theta)$ (Lee et al., 2011). To evaluate how individual limbs contribute to COM mechanics in a trot or canter, the modeled data were used to calculate the COM work and power for the combined limbs (as in the COM classical calculations) as well as among individual limbs, as in the calculations of Donelan et al. (Donelan et al., 2002).

Statistics

All regressions were computed using a linear mixed model, where individual lemur was set as a random factor (N=5). The goodness-of-fit of the regressions was quantified using a coefficient of determination for mixed models (r^2) (Vonesh and Chinchilli, 1997), which has been shown to perform well in simulation studies (Orelien and Edwards, 2008). Gait-specific effects on COM mechanics were tested using a mixed-model analysis of covariance (ANCOVA), where speed, gait and speed $\times$ gait were set as fixed factors and individual lemur was set as a random factor. All statistical

tests were performed in R (version 2.9 for Mac OS) using the base, 'nlme' and 'lmmfit' libraries (R Development Core Team, 2008). Means are reported ±s.d.

To account for differences in body size among lemurs, analyses were performed with dimensionless variables, using base units of body mass M_b, gravitational acceleration $\boldsymbol{g}$, and average forelimb and hindlimb length L. For the forelimbs and hindlimbs, lengths were measured as the height of the shoulder and hip from the ground during midstance of a walking stride. Velocity was made dimensionless by the divisor $(\boldsymbol{g}L)^{0.5}$ and the Froude number (Fr; $v^2/\boldsymbol{g}L$), the latter of which has been shown to differentiate walking–trotting gaits (at $Fr \sim 0.5$) and trotting–galloping gaits (at $Fr \sim 2.5$) in a range of mammalian quadrupeds (Alexander and Jayes, 1983; Griffin et al., 2004b). Force was made dimensionless by the divisor $M_b\boldsymbol{g}$, displacement by L, work by $M_b\boldsymbol{g}L$ and work rate (power) by $M_b\boldsymbol{g}^{1.5}L^{0.5}$, but SI units are also shown. For example, work and velocity graphs are presented in both dimensionless units and in the more common units of $W\,kg^{-1}$ and $m\,s^{-1}$, respectively. Conversion between the dimensional and dimensionless units can be performed using the mean non-dimensionalizing factors $(\boldsymbol{g}L)^{0.5}=1.42\,m\,s^{-1}$, $\boldsymbol{g}L=2.01\,J\,kg^{-1}$ and $\boldsymbol{g}^{1.5}L^{0.5}=13.93\,W\,kg^{-1}$, although we preferred to show both data sets.

RESULTS

A total of 86 strides of constant velocity were obtained over a wide range of gaits and speeds, from 0.43 to 2.91 m s^{-1}. The fastest speed obtained freely was approximately 0.75 m s^{-1} faster than ring-tailed lemurs could be trained to sustain on a treadmill, but not the maximum speed a ring-tailed lemur could gallop (Franz et al., 2005) (M.C.O. and J. B. Hanna, unpublished data). However, the more than sevenfold increase in speed that we sampled represents most of the speed range – and all of the gaits – naturally used by ring-tailed lemurs for sustained overground locomotion.

Three gaits were observed across the speed range (Fig. 2). Most strides were below an Fr of 0.5 (N=69); in all cases, these strides would be classified as walks using traditional kinematic or mechanics-based definitions (Bicknevicius and Reilly, 2006; Cartmill et al., 2002; Hildebrand, 1967). The limb-phase relationship between the reference hindlimb and the ipsilateral forelimb was a mean (±s.d.) of 0.64±0.02, indicating that the ring-tailed lemurs used a diagonal sequence gait. Ten strides fell between Fr=0.5 and 2.5, and in these cases lemurs used a galloping footfall pattern (H_{lead}–$H_{nonlead}$–F_{lead}–$F_{nonlead}$, where H is hindlimb and F is forelimb), with the duration of the whole-body aerial phase ranging from 0 to 15% of stride time, increasing linearly with velocity (Fig. 2B). The remaining strides (N=7) were at $Fr \geq 2.5$, and all were gallops. No trots or ambles were observed.

COM mechanics

The variability of percent COM energy recovered both within and across speed was substantial (Fig. 2). Below 1.0 m s^{-1} (v<0.75, Fr<0.5), the percent recovered was as high as 71%, which is the same as that recorded for more cursorial quadrupeds, such as dogs [~70% (Griffin et al., 2004a; Usherwood et al., 2007)]. Such high values are indicative of an ability to use an effective pendulum-like mechanism during walking. However, the range of COM energy recoveries recorded, from 35 to 71%, is not often noted for other quadrupeds.

Above 1.0 m s^{-1} (v>0.75, Fr>0.5), recoveries ranged from 10 to 51%, decreasing with speed. Low values are consistent with intermediate and high-speed gaits, but are well above the 0% COM energy recoveries predicted for a monopedal mass-spring model. Although the number of trials from cantering and galloping strides
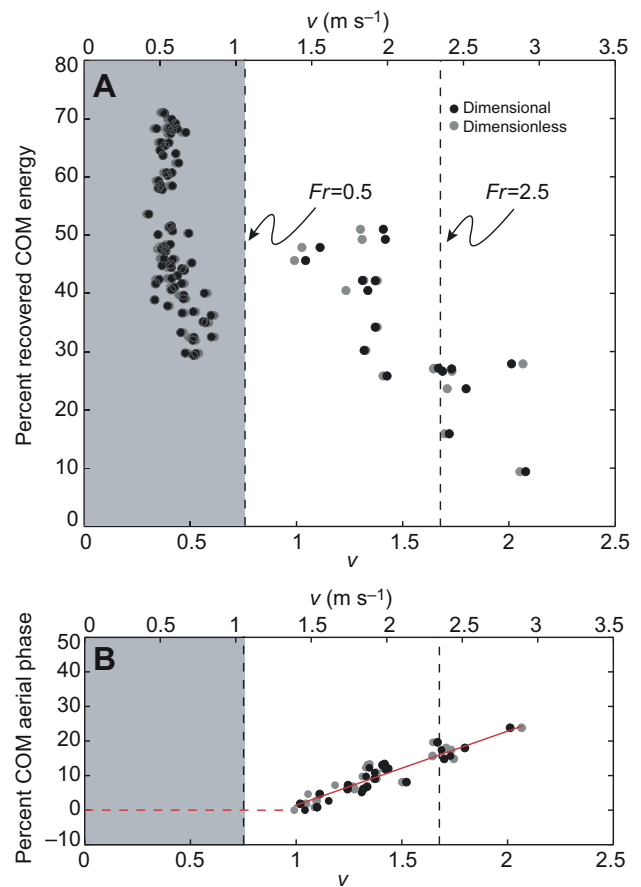

Fig. 2. Percent COM energy recoveries for ring-tailed lemurs *vs* speed. (A) Velocities are shown in dimensionless units (gray circles; bottom axis) and m s^{-1} (black circles; top axis). The percent COM energy recovered per stride generally decreased with gait and speed. The gait transition speeds from a walking gait to an intermediate-speed gait (canter; Fr=0.5), and an intermediate-speed gait to a gallop (Fr=2.5), were predicted using average limb lengths for the five lemurs and the Froude number ($v^2/\boldsymbol{g}L$). Data are for all animals (N=5) walking, cantering and galloping. (B) The percent COM aerial phase *vs* speed. At 1.5 m s^{-1}, ring-tailed lemurs use a galloping footfall pattern, but have no COM aerial phase (i.e. a canter). The duration of the COM aerial phase increases linearly across the speed range, as y=22.32x–20.98, where y is [COM aerial time/stride time]×100 and x is dimensionless velocity (r^2=0.85, N=25), with a slope of 16.50 and an intercept of 22.40 (r^2=0.88) when x is velocity in m s^{-1}. The red dashed line indicates the speed range over which no COM aerial phase is expected for steady, overground locomotion. The shaded areas represent the walking speed range. Data are from a subset of the animals (N=4), and include some additional cantering and galloping trials (N=8) collected as part of these experiments for which the video records were adequate, but GRF data were not.

was small relative to our walking data set, the available data do suggest that there is a general decrease in COM energy exchange from the slow to fast gaits in ring-tailed lemurs (Fig. 2A).

The degree to which kinetic and gravitational potential energies can be effectively exchanged depends on both the phase relationship of E_K and E_P and the relative magnitudes of their fluctuations. Much of the measured variation in percent COM energy recovered is explained by a shift in the phase relationship of E_K and E_P as well as a decrease in effective limb length at intermediate and fast speeds. A multiple regression of congruity and effective limb length accounted for 72% (r^2=0.72) of the variation in the COM energy exchanged across speed.
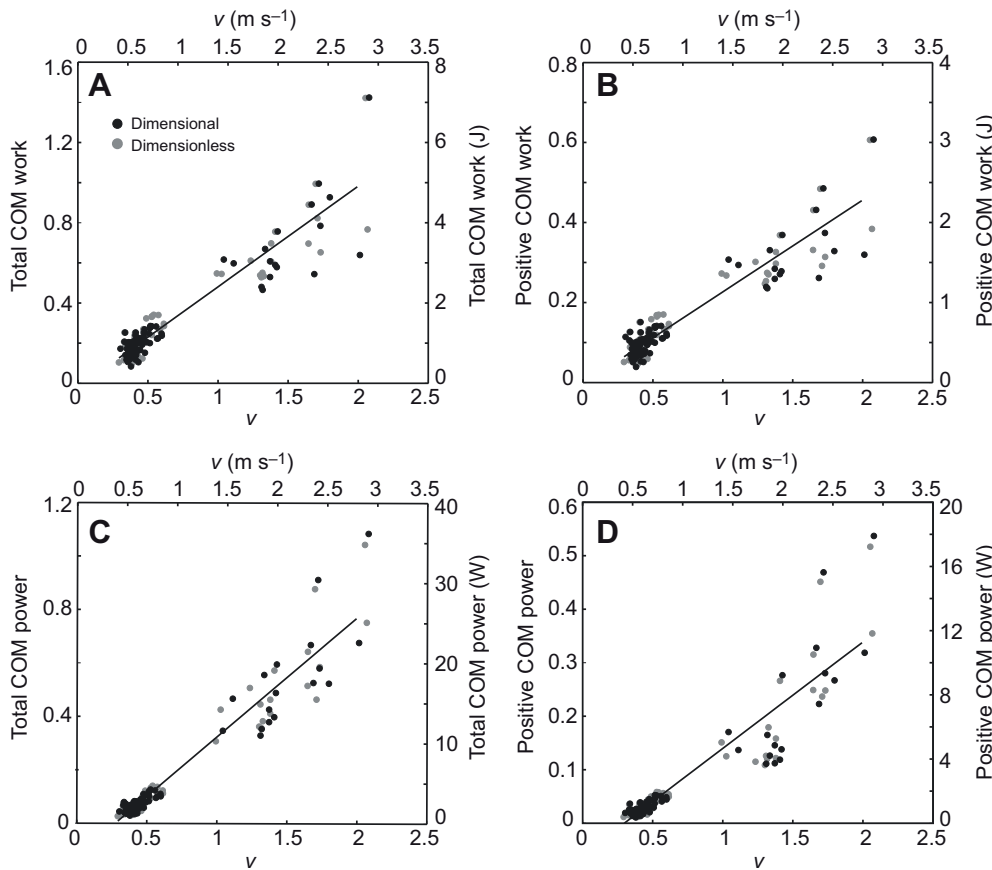
Fig. 3. Total and positive COM work and power *vs* speed in ring-tailed lemurs. The available data show that total and positive COM work (A,B) and power (C,D) increase with locomotor speed and across gaits. Dimensionless data points were fitted with linear regressions (r^2=0.89–0.93; Table 1). COM work, power and velocities are shown in dimensionless units (gray circles; left and bottom axes) as well as in J, W and m s^{-1}, respectively (black circles; right and top axes).

The COM work and power increased significantly across speeds and gaits (Fig. 3). The total and positive COM work patterns were fit well by linear regression (r^2=0.87 and 0.89, respectively), with no gait-specific differences in slopes (Fig. 3A,B, Table 1). Per mass and distance, the average total and positive COM work were 1.503±0.464 and 0.625±0.208 J kg^{-1} m^{-1}, respectively, for walks, and 3.47±0.712 and 1.661±0.387 J kg^{-1} m^{-1} for canters and gallops. The lower average value for walks than for canters and gallops in COM work was significant (ANCOVA, P=0.002 and 0.004, respectively). The total and positive COM powers were also fit well by linear regression, with no significant gait-specific differences in slopes (Fig. 3C,D, Table 1). Across the entire speed range, the maximum positive COM power output was 17.9 W.

The mean COM velocity (λ_{vel}) and GRF angles (θ_{GRF}) over a stride were variable across speed and gait (Fig. 4A,B). The λ_{vel} measured during a walk was 0.113±0.021 rad (6.477±1.182 deg), decreasing slightly to 0.101±0.041 rad (5.769±2.330 deg) for canters and gallops. A linear regression across speed fit the λ_{vel} canters and gallops well, but not the walks (Table 1). The opposite is true of the θ_{GRF}; the θ_{GRF} in walks was moderately well fit by a linear regression, but was uncorrelated with speed in canters and gallops (Table 1). The average COM collisional angle (ϕ_{col}) had almost no correlation with speed within gaits, but a linear fit across speeds was strong (Table 1). The ϕ_{col} was 0.072±0.022 rad (4.129±1.256 deg) in a walk and 0.168±0.028 rad (9.616±1.628 deg) in canters and gallops.

Across all speeds and gaits, the COM power and work increased in direct proportion to COM collisional losses per time (i.e. $v\phi_{col}$) and per distance (i.e. ϕ_{col}), respectively. As predicted, total COM power scaled with a slope of 2.131±0.036 and an intercept –0.001±0.007 (r^2=0.977), and positive COM power with a slope of 1.051±0.018 and intercept –0.009±0.003 (r^2=0.977) against $v\phi_{col}$.

Likewise, total and positive COM works per distance scaled with slope 2.078±0.062 and intercept 0.004±0.006 (r^2=0.932), and slope 1.078±0.032 and intercept –0.015±0.003 (r^2=0.931) against ϕ_{col}, respectively. These values indicate a strong, direct relationship between the measured COM power, work and collisional geometry.

The ratio of the observed ϕ to the potential 'spring-like' collision ($\lambda+\theta$) (the collisional fraction) was, in general, quite low across speed and gaits (Fig. 5). The mean value was 0.404±0.113 for walks, and 0.565±0.060 for canters and gallops. The difference between walks and canters and gallops was significant (ANCOVA, P=0.042), indicating slightly higher collisional losses in canters and gallops. Nevertheless, collisional fraction values well below 1.0 indicate that all the gaits used by ring-tailed lemurs engender only low to moderate COM collisions.

Quadruped model

The compass-gait model predicted much larger vertical displacements of the COM than was observed in walking lemurs. On average, the measured vertical displacements were 0.37±0.12 of the predicted displacement for a rigid-limbed walking stride, indicating that lemurs compress their limbs during periods of body mass support and COM energy exchange. There was no significant correlation between speed and our ratio of observed to predicted displacements.

The results from modeling a 1.5 m s^{-1} canter and a 1.5 m s^{-1} trot are presented in Fig. 6. Empirical data of whole-body force patterns during a canter correspond well to those modeled for a canter (Fig. 6, column 1 *vs* 2). The model results show that the whole-body vertical reaction forces in a canter are reduced from those of a trot at the same speed. The more uniform distribution of the limb forces across a stride reduces the peak force acting on the body (Fig. 6B,C) but results in larger vertical oscillations of the COM (Fig. 6E,F). The

Table 1. Gait-specific center of mass (COM) work, power and collisional angles in ring-tailed lemurs, *Lemur catta*

	Walks			Canters/Gallops				All		
	Intercept	Slope	r^2	Intercept	Slope	r^2	P^a	Intercept	Slope	r^2
Dimensional										
Total COM work (J)	0.379±0.17	0.940±0.32	**0.293**	−0.811±1.03	1.967±0.42	**0.430**	0.912	−0.061±0.12	1.688±0.07	**0.873**
Positive COM work (J)	0.224±0.09	0.405±0.14	**0.223**	0.364±0.43	0.590±0.17	**0.360**	0.800	0.019±0.06	0.762±0.03	**0.872**
Total COM power (W)	−0.501±0.43	4.602±0.66	**0.545**	−2.865±5.58	9.884±2.37	**0.559**	0.074	−4.038±0.53	10.51±0.32	**0.920**
Positive COM power (W)	−0.334±0.20	2.084±0.32	**0.558**	−2.433±3.01	5.198±1.28	**0.532**	0.082	−2.186±0.27	5.175±0.17	**0.906**
λ_{vel} (deg)	7.655±0.90	−1.946±1.36	0.027	15.49±1.80	−4.618±0.81	**0.700**	–	7.221±0.37	−0.988±0.22	**0.119**
θ_{GRF} (deg)	2.039±0.34	2.986±0.54	**0.438**	7.812±1.79	1.619±0.73	0.162	–	1.183±0.22	4.641±0.15	**0.913**
ϕ_{col} (deg)	3.441±0.84	1.050±1.21	0.074	7.290±2.15	1.038±0.94	0.103	–	2.268±0.38	3.252±0.19	**0.756**
Dimensionless										
Total COM work	0.057±0.04	0.313±0.07	**0.396**	−0.095±0.19	0.532±0.11	**0.548**	0.537	−0.015±0.02	0.489±0.02	**0.890**
Positive COM work	−0.028±0.02	0.154±0.04	**0.371**	0.085±0.08	0.169±0.05	**0.488**	0.346	−0.001±0.01	0.222±0.01	**0.893**
Total COM power	−0.020±0.01	0.203±0.03	**0.582**	−0.073±0.16	0.413±0.10	**0.626**	0.077	−0.121±0.01	0.444±0.01	**0.933**
Positive COM power	−0.012±0.01	0.093±0.01	**0.606**	−0.061±0.08	0.213±0.05	**0.590**	0.101	−0.065±0.01	0.218±0.01	**0.920**
λ_{vel} (rad)	0.133±0.02	−0.046±0.03	0.024	0.271±0.03	−0.115±0.02	**0.765**	–	0.127±0.01	−0.025±0.01	**0.134**
θ_{GRF} (rad)	0.036±0.01	0.074±0.01	**0.489**	0.138±0.03	0.039±0.02	0.154	–	0.021±0.00	0.115±0.00	**0.904**
ϕ_{col} (rad)	−0.059±0.01	0.0.28±0.03	0.098	0.132±0.04	0.022±0.02	0.078	–	0.040±0.01	0.080±0.00	**0.751**

λ_{vel}, θ_{GRF} and ϕ_{col}, weighted averages of the instantaneous orientation of COM velocity (λ) relative to the horizontal (fore–aft), the instantaneous orientation of the resultant GRF (θ), and the instantaneous COM collision angle (ϕ), respectively.
Intercepts are the *y*-intercepts of linear regression. Boldface indicates slopes significantly different from zero at α=0.05. Means are presented ±s.e.m.
[a]Mixed-model ANCOVA test for equality of slopes, walks *vs* canters/gallops.

vertical stiffness of the COM also differs substantially between the cantering and trotting models (Fig. 6H,I). For the canter, COM stiffness was –3.6, and for a trot COM stiffness was –14.2. The ϕ_{col} is more than twice as large in a trot (18.5) as in a canter (8.3) (Fig. 6J–L), indicating that the collisional losses are much more substantial in a trot than in a canter of similar speed. For the empirical and modeled canters, the collisional fractions were 0.615 and 0.521, respectively, consistent with the general pattern observed for measured cantering and galloping gaits in ring-tailed lemurs (Fig. 5). This supports the notion that, at intermediate speeds, ring-tailed lemurs use a more 'wheel-like' than 'spring-like' gait, which moderates their COM collisions and associated energy losses. In contrast, the collisional fraction for the modeled trot was 1.031, as expected for a 'spring-like' gait. The plot of ϕ against stride time illustrates that COM collisions remain low throughout a stride in a canter, whereas ϕ is much larger in a trot. In a trotting stride, ϕ only reaches zero at the mid-stance of a step, where the COM velocity is parallel to the ground and the resultant GRF is vertical.

The ϕ_{col} for a trot and canter predict significant differences in the COM mechanics, as ϕ_{col} is strongly correlated with the average COM power and work (as above) (see also Lee et al., 2011). Indeed, the total and positive COM works were 3.020 and 1.588 J, respectively, for a canter, and 6.037 and 3.191 J for a trot when estimated using classical COM calculations. However, using an individual-limb-based approach, this difference mostly disappears: the canter requires 5.620 J of total COM work and 2.888 J of positive COM work. Thus, based on our simple model, it is evident that the classical COM calculations [or 'combined-limbs approach' (Donelan et al., 2002)] underestimate the total and positive limb work in a canter by 82–86%.

DISCUSSION
COM energy, work and power
The percentage COM energy recoveries generally decreased with speed and gait (Fig. 2). This represents a useful baseline for evaluating patterns of percentage energy recovery across speed and gait in other quadrupedal primates. The highest value in a walking stride (71%) is near the maximum values reported for other quadrupeds (Gein et al., 2010; Griffin et al., 2004a; Usherwood et

al., 2007), suggesting that lemurs are capable of using effective pendular-like mechanics at walking speeds; however, the departure of the limbs from a compass-gait-like stride must be considered. The percentage recoveries in cantering and galloping strides were lower (10–51%), consistent with values for these gaits in other quadrupeds (Heglund et al., 1982; Minetti et al., 1999). Considered together, much of the variation in percentage recoveries is accounted for by shifts in the phase relationship of E_P and E_K, as predicted from simple quadruped models (Griffin et al., 2004a) and noted in other terrestrial mammals (Bishop et al., 2008). A decrease in effective limb length from slow to faster speeds accounted for an additional, but much smaller portion of the COM energy recovered. The COM vertical displacements of 0.015 m at a walk was similar to previous measures of trunk displacement in ring-tailed lemurs (measured using a lumbar marker) [mean: 0.019 m, range: 0.009 to 0.031 m (Franz et al., 2005)]; however, the mean COM displacements of 0.035 m measured at a canter or gallop did not include the whole-body aerial phase of a stride and were therefore much lower than trunk marker estimates [mean: 0.087 m, range: 0.027 to 0.143 m (Franz et al., 2005)].

The COM energy recoveries have been used to differentiate walking, trotting and galloping gaits in some terrestrial animals (Cavagna et al., 1977; Minetti et al., 1999). However, these mechanics-based differences do not necessarily correspond to other parameters, such as the presence of a whole-body aerial phase or spring-like limb kinematics (Bicknevicius and Reilly, 2006; Hutchinson et al., 2003). Our ring-tailed lemurs never trotted and there were no discontinuities in the COM energy recoveries or other mechanical parameters from a canter to a gallop. As such, we found no analog to the trot–gallop transition seen in other quadrupeds, the absence of which confounds the use of this point of 'physiological equivalence' (Heglund and Taylor, 1988) for interspecific comparisons that include ring-tailed lemurs. The absence of a trot–gallop transition has been noted before in other primates, with those studies attempting to estimate an equivalent trot–gallop transition speed from limb kinematics (Reynolds, 1987; Vilensky, 1980; Vilensky, 1983). It was also observed that ring-tailed lemurs only began to use a whole-body aerial phase at a dimensionless *v*

of ~1.0, consistent with theoretical expectations (Alexander, 1989; Usherwood, 2005), but well after their expected transition from a walk to a canter at Fr=0.5. It should be noted that our own data from ring-tailed lemurs walking and cantering on a treadmill indicate that the Fr=0.5 prediction is quite close to the actual gait transition speed (O'Neill, 2009).

Both theoretical (Alexander, 1977) and empirical (Heglund et al., 1982; Full et al., 1989) data indicate that the COM work per mass and distance varies independent of mass, with most terrestrial animals (including insects) fluctuating around $1\,\mathrm{J\,kg^{-1}\,m^{-1}}$. Previous studies have reported values between approximately 0.1 and $2.0\,\mathrm{J\,kg^{-1}\,m^{-1}}$ (Cavagna et al., 1977; Gein et al., 2010; Heglund et al., 1982), based on the equations of Cavagna (Cavagna, 1975). Ring-tailed lemurs used $0.625\,\mathrm{J\,kg^{-1}\,m^{-1}}$ to walk and $1.661\,\mathrm{J\,kg^{-1}\,m^{-1}}$ to canter or gallop, falling in the middle of the previously measured range. This walking value is similar to the 0.466 and $0.561\,\mathrm{J\,kg^{-1}\,m^{-1}}$ of positive COM work estimates for the two juvenile macaques (Cavagna et al., 1977).

The COM work can also be characterized in terms of the total extensor muscle mass of the hindlimbs and forelimbs, which is approximately 8% of body mass (~0.3 kg) in an adult ring-tailed lemur (O'Neill, 2009). Assuming that all the COM work is generated by the extensor musculature of the limbs, we estimated the COM work rate required during high-speed locomotion. The highest positive COM power output (~18 W) in the fastest gallop recorded herein (~$3.0\,\mathrm{m\,s^{-1}}$; Fig. 3) would require approximately $60\,\mathrm{W\,kg^{-1}}$ of extensor limb muscle mass. This is well below the maximum power-generating capacity for vertebrate skeletal muscle [~$250\text{--}400\,\mathrm{W\,kg^{-1}}$ (Lutz and Rome, 1994; Weis-Fogh and Alexander, 1977)]. However, as shown here and elsewhere (Donelan et al., 2002; Ren et al., 2010), COM measurements can underestimate total limb extensor power production when individual limb forces overlap. Nevertheless, even if the value for total limb power production is underestimated by two to three times, 120 to $180\,\mathrm{W\,kg^{-1}}$ is still substantially lower than COM power estimates from some other behaviors, such as vertical jumping (Aerts, 1998; Scholz et al., 2006) in primates. For this reason, we suggest that steady, level locomotion may place only modest demands on the potential power-generating capabilities of the lemur musculoskeletal system as a whole. Indeed, ring-tailed lemurs regularly engage in
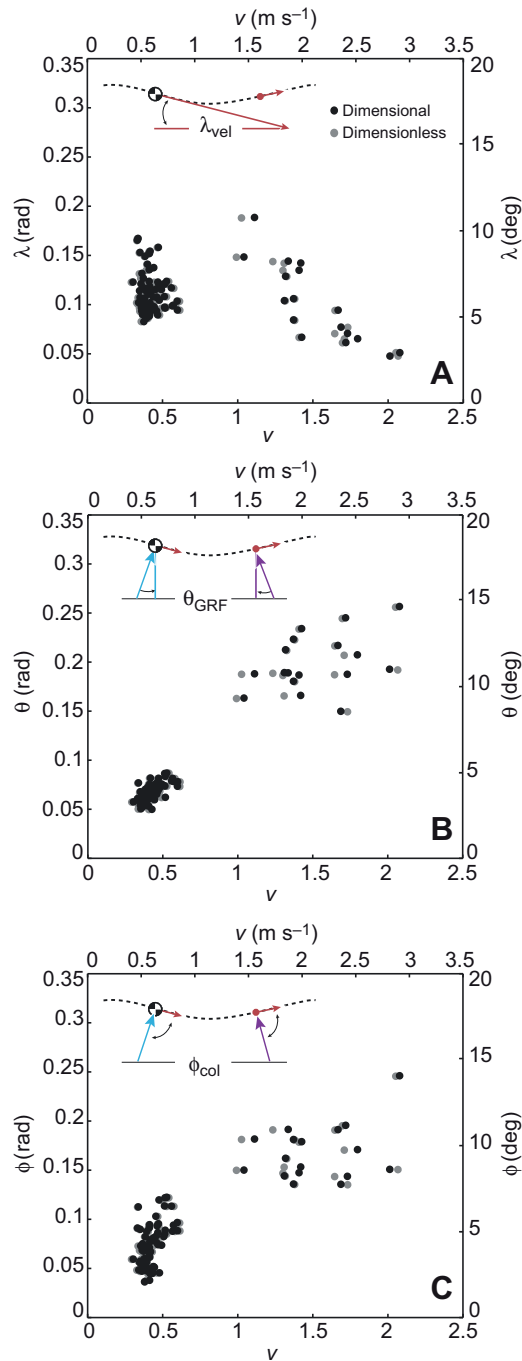

Fig. 4. COM collisional mechanics across gait and speed for ring-tailed lemurs. Angles and velocities are shown in radians and dimensionless units (gray circles; left and bottom axes), as well as degrees and $\mathrm{m\,s^{-1}}$ (black circles; right and top axes). The mean (A) COM velocity (λ_{vel}), (B) resultant GRF (θ_{GRF}) and (C) COM collisional (ϕ_{col}) angles are shown as functions of speed. Data are for all animals (N=5) walking, cantering and galloping. Insets show definitions for λ_{vel}, θ_{GRF} and ϕ_{col}. Red, blue and purple arrows correspond to approximate touchdown and push-off points (see Fig. 1).
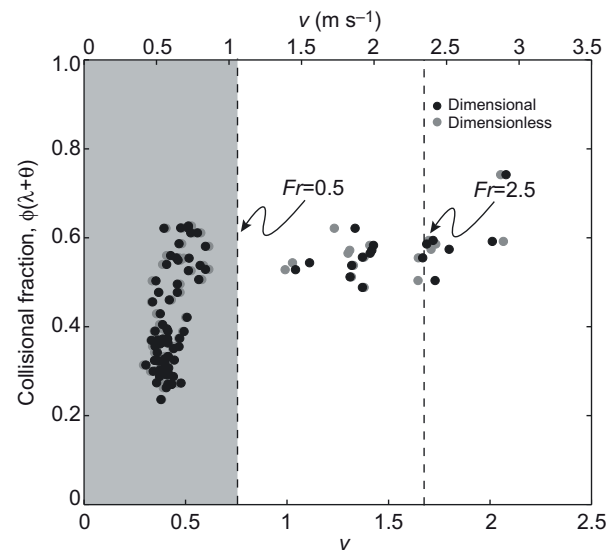

Fig. 5. COM collisional fraction, $\phi/(\lambda+\theta)$, across speed and gait for ring-tailed lemurs. Velocities are shown in dimensionless units (bottom) and $\mathrm{m\,s^{-1}}$ (top). The mean (±s.d.) COM collisional fraction for walking was 0.404±0.113, and for canters and gallops was 0.565±0.060 (mixed-model ANCOVA, walking vs cantering/galloping, P=0.042). The consistently low values (<1) indicate that ring-tailed lemurs select gaits that reduce their COM collisional losses across all speeds.
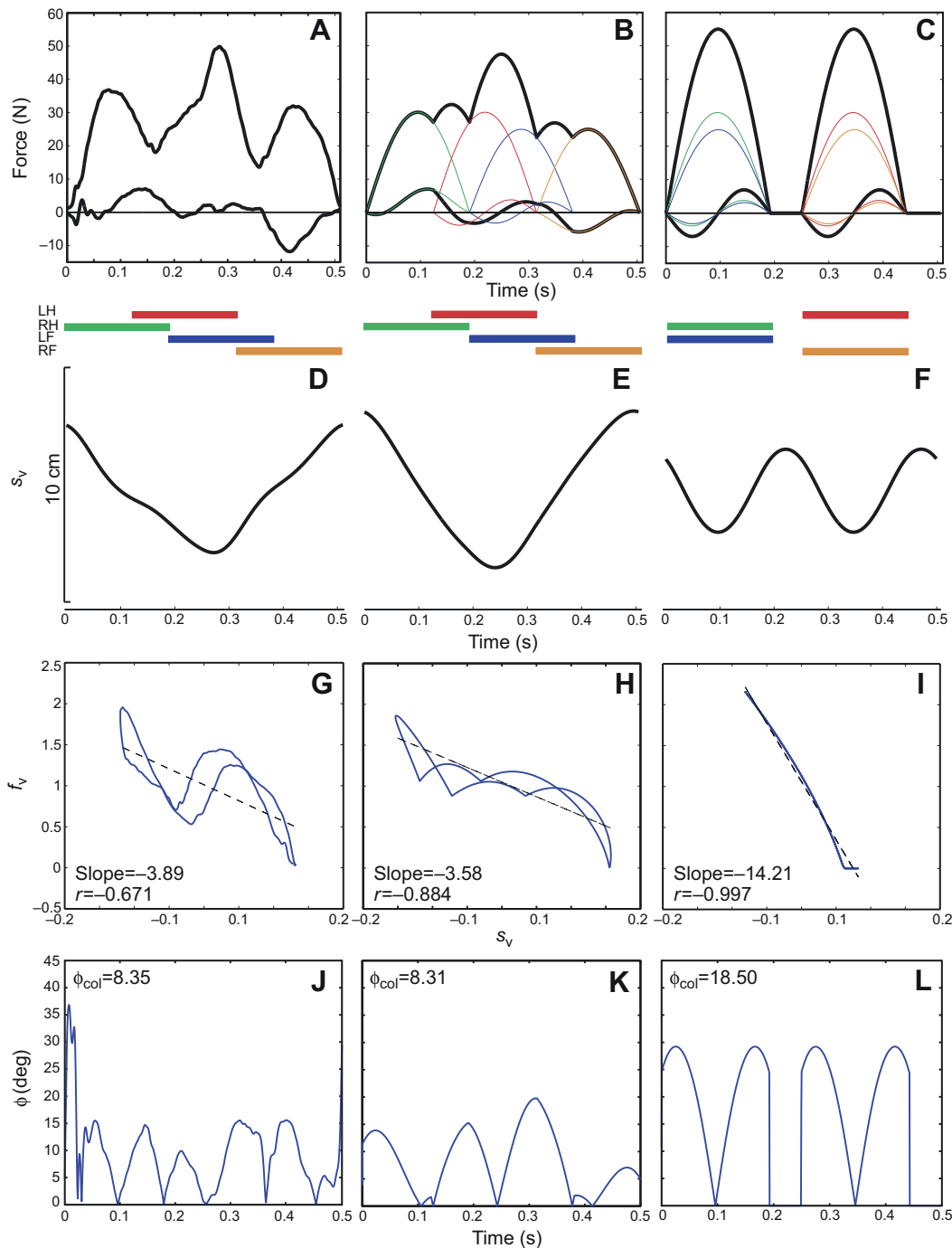
Fig. 6. Actual (column 1) and modeled (columns 2 and 3) GRF, displacement, stiffness and collisional mechanics of the COM in ring-tailed lemurs. (A–C) Empirical force measurements, model forces reconstructed for a 1.5 m s^{-1} canter and model forces reconstructed for a 1.5 m s^{-1} trot. Horizontal bars below the reaction forces represent the footfall patterns (LH=left hindlimb, RH=right hindlimb, LF=left forelimb, RF=right forelimb). (D–F) Vertical displacements (s_v) of the COM corresponding to the force data in A–C, respectively. Vertical displacements were calculated following the equations given in the Materials and methods. (G–I) Calculation of COM vertical stiffness as force (f_v) vs displacement (s_v). The slope of the linear least-squares regression through the data is an estimate of the COM vertical stiffness during ground contact. (J–L) Plots of instantaneous collision angle (ϕ) over a stride for the empirical and modeling data. In a canter, the ϕ remains low over a stride, whereas in a trot the ϕ is generally higher. The collisional fraction, $\phi/(\lambda+\theta)$, is 0.62 and 0.51 for an empirical and modeled canter, respectively, and 1.03 for a trot at the same speed. A value near 1 indicates that the COM mechanics of a trot are well characterized by a monopedal mass-spring model, whereas those of a canter are not.

leaping and vertical climbing (Gebo, 1987), and these behaviors may be more important in setting the limits of their musculoskeletal design. More studies quantifying the work and power production of individual joints and muscle–tendon units across locomotor modes is needed to better understand the limits of limb function.

Consistent with our measures of COM work and power across speed and gait, significant changes in λ_{vel}, θ_{GRF} and ϕ_{col} with forward velocity were found. As predicted by simple point-mass models of walking and galloping (Adamcyzk and Kuo, 2009; Bertram and Gutmann, 2009; Lee et al., 2011; Ruina et al., 2005), there was a strong and direct correlation between COM collision angle and our measured COM power and work. The average ϕ_{col} found in walking, cantering and galloping lemurs is nearly the same as the values for walking and galloping gaits in goats and dogs (Lee et al., 2011).

The primary difference between lemurs and these other taxa occurred at intermediate speeds (Fr=0.5–2.5), where the collision ratio for lemurs was approximately half the value for trotting goats and dogs. This suggests that ring-tailed lemurs – and possibly primates in general – select gaits that minimize collisions in their intermediate speed range, whereas goats, dogs and other trotting mammals maximize them. Of course, large COM collisional losses may be useful if the associated negative work can be stored and recovered *via* passive elastic mechanisms.

Although the material properties of the limb tendons of lemurs are unknown, it has been observed that the free tendons of quadrupedal primates in general tend to be short and thick (Rauwerdink, 1993; Thorpe et al., 1999), and this tendon design provides limited capacity for strain energy storage (Bennett et al.,

1986; Pollock and Shadwick, 1994). It should be noted, however, that series elastic structures involved in the storage and recovery of COM work are not limited to free tendons, but can also include ligaments and aponeuroses (Alexander, 1988; Azizi et al., 2009) in the limbs and trunk. Careful accounting of potential stores of elastic strain energy in lemurs and other small mammals is needed to better understand the role of passive, spring-like biological materials in minimizing active muscle contributions to COM work and, by extension, the cost of muscle-powered movements.

These issues raise the question of how to characterize the intermediate- and high-speed gaits of ring-tailed lemurs, and possibly other quadrupedal primates. The monopedal mass-spring model has provided important insights into several aspects of intermediate- and high-speed locomotion, as it can accurately predict fluctuations in COM energy, as well as the compression and extension of the support limbs (Blickhan, 1989; McMahon and Cheng, 1990). Given this, the mass-spring analogy has been used to describe a number of bouncing gaits, including running, trotting and hopping, for a range of terrestrial animals (Cavagna et al., 1977; Farley et al., 1993). However, as demonstrated here for ring-tailed lemurs, and noted elsewhere based on theoretical grounds (Ruina et al., 2005; Bertram and Gutmann, 2009), the COM mechanics of canters and gallops are not well characterized by a monopedal mass spring. This is evident in the COM energy exchange as well as the interaction of the COM velocity and resultant GRF, where different limbs operate as brakes, motors and springs within a stride in order to redirect the COM from down to up. In a monopedal mass spring, COM energy exchange is zero and all limbs are equally spring-like with a single stiffness. Our results suggest that as a predictive tool, a simple monopedal mass-spring model is inadequate for characterizing the COM mechanics of quadrupedal primates that canter and gallop across their intermediate- and high-speed range. Rather, a point-mass model that experiences a series of sequenced limb–ground collisions may be more useful in predicting the interaction the COM mechanics across gait and speed in ring-tailed lemurs and other quadrupedal primates.

This is not to say that no individual limb will behave in a spring-like manner in a canter or gallop. Geyer et al. (Geyer et al., 2006) have shown that a mass-spring model that represents individual limbs as springs of equal stiffness can characterize the COM energy exchange and individual limb forces of a bipedal walking stride with reasonable accuracy. As such, it may be possible to add features to a mass-spring model (or spring-loaded inverted pendulum) to better predict the COM mechanics of canters and gallops, such as multiple limbs of variable stiffness. McMahon (McMahon, 1985) developed a simple model of galloping in which the mass spring is affixed to a rolling wheel with some successes, but included some unrealistic assumptions regarding the distribution of foot contacts. More recently, Herr et al. (Herr et al., 2002) developed a much more complex quadruped model that can trot and gallop using individual limb-springs of constant stiffness. The horizontal COM forces in a cantering or galloping ring-tailed lemur – both in our experimental data and in our simple model – raise the possibility that the nonlead hindlimb and the lead forelimb have some spring-like behavior. However, this is less apparent for the first (lead hindlimb) and last (nonlead forelimb) limbs in a stride, which mostly accelerate and decelerate the COM, respectively.

Why not use trotting gaits?

It is well known that quadrupedal primates generally avoid trotting gaits (Cartmill et al., 2002; Demes et al., 1994; Hildebrand, 1967; Rollinson and Martin, 1981; Schmitt et al., 2006; Vilensky, 1987; Vilensky, 1989), and instead use 'grounded-running' gaits such as the canter or amble. Previous authors have suggested that primates do not trot to minimize branch oscillations during arboreal foraging (Demes et al., 1990; Schmitt, 1999; Schmitt et al., 2006), and instead use an ambling gait to reduce COM movements and maintain a secure handhold during locomotion (Schmitt et al., 2006). We were interested in the differences that exist between the COM mechanics of the canter and the trot in order to better understand why lemurs and other primates adopt the canter more frequently than the trot at intermediate speeds.

Because trots could not be recorded, we relied on a mathematical model that indicates that canters have lower whole-body stiffness and peak forces but engender larger vertical oscillations of the COM than trots at the same speed. This is consistent with the predictions of McMahon (McMahon, 1985), who suggested that a canter is a much more compliant gait than a trot at the same speed. Our model indicates that the COM vertical stiffness of a lemur trot would be more than twice as large as that of a canter. This is due to the lower COM forces experienced when using a cantering footfall pattern. The COM displacement findings are also in line with the experimental data of Cavagna et al. (Cavagna et al., 1977) and Minetti et al. (Minetti et al., 1999). In both studies, vertical displacements of the COM are much larger in 'slow gallops' than in 'trots' of similar speed in monkeys, rams, dogs and horses. These data also reinforce the point that by adjusting footfall patterns alone – rather than force impulses – terrestrial animals can negotiate a substrate using a high (e.g. trot) or low (e.g. canter) COM vertical stiffness. The average COM collisional angle (ϕ_{col}) indicates that the mechanical energy losses due to limb–ground collisions are much lower in cantering than in trotting at the same speed. Collisional losses are reduced in a canter through the more orthogonal orientation of the COM velocity and resultant GRF vectors, as in a rolling wheel.

Overall, adopting a canter rather than a trot allows animals to maintain contact with the substrate with at least one limb (little or no aerial phase) and avoid higher whole-body peak forces when increasing locomotor speed. This is consistent with the predictions of simple mathematical models of mammalian 'running' gaits (McMahon, 1985; Ruina et al., 2005). These factors may be important for movement on unstable supports, where stability and stealth during foraging may drive locomotor performance (Demes et al., 1990; Schmitt et al., 1999; Schmitt et al., 2006). In line with this view, cantering was found to be the gait most commonly used during simulated arboreal locomotion in marmosets and squirrel monkeys (Young, 2009). However, more data on the ecological scenarios in which ambles and canters are used by primates are needed to further understand the adaptive value of these two intermediate-speed gaits.

CONCLUSIONS

The mechanics of terrestrial locomotion in quadrupedal primates has been the focus of extensive research, although most of this research has focused only on walking. Two previous studies investigated whole-body mechanics across gaits in quadrupedal primates (Cavagna et al., 1977; Vilensky, 1979), but these data are limited. Here, we present an analysis of COM energy, work, power and collisions in ring-tailed lemur walking, cantering and galloping in order to provide a more detailed characterization of COM mechanics across a wider range of gaits and speeds.

Ring-tailed lemurs have substantial COM energy exchanges during walking, although there is significant variability in these values between strides and individuals. At no speed or gait did the COM energy ever decrease to zero, as predicted for a monopedal

mass-spring model, but values recorded were relatively low for canters and gallops as compared with walks. COM work increased significantly with speed, and per mass and distance, increased significantly from a walk to a canter or gallop. COM power also increased with speed. The maximum COM power output at the fastest speeds we measured ($2.91\,\mathrm{m\,s^{-1}}$) was approximately $18\,\mathrm{W\,kg^{-1}}$ of body mass or $60\,\mathrm{W\,kg^{-1}}$ of limb extensor mass. Both of these values are well below the maximum power-producing capabilities of vertebrate skeletal muscle, as well as similar COM measurements during vertical jumping in other primates. We measured the change in the COM collisional geometry, using λ_{vel}, θ_{GRF} and ϕ_{col}, as well as the collisional fraction. These data suggest that COM collision losses increase across speed and gait, but never approach those of a monopedal mass-spring system, and are strongly correlated with COM power and work production.

We found that ring-tailed lemurs do not trot at intermediate speeds and do not exhibit a clear analog to the trot–gallop transition of most other terrestrial animals, as has been noted previously (Reynolds, 1987; Vilensky, 1980; Vilensky, 1983). Using a simple phenomenological model of a lemur-like quadruped, we found that cantering increases ground contact time as well as reduces the whole-body peak vertical force, vertical stiffness and COM collisional losses when compared with a trot. These factors may be important during movement on unstable supports, making quadrupedal primate locomotion stealthier during foraging.

LIST OF SYMBOLS AND ABBREVIATIONS

a_{v}, a_{h}, a_{l}	vertical, horizontal and mediolateral acceleration
COM	center of mass
E_{K}	kinetic energy
E_{P}	gravitational potential energy
Fr	Froude number
f_{v}, f_{h}, f_{l}	vertical, horizontal and mediolateral ground reaction force
$\boldsymbol{g}$	gravitational acceleration
GRF	ground reaction force
$j_{\mathrm{v,f}}$, $j_{\mathrm{v,h}}$	forelimb and hindlimb vertical force impulse
L	limb length
M_{b}	body mass
s_{v}, s_{h}, s_{l}	vertical, horizontal and mediolateral position
v_{v}, v_{h}, v_{l}	vertical, horizontal and mediolateral velocity
λ	COM velocity angle
θ	resultant GRF angle
ϕ	COM collision angle

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