Body mass distribution and gait mechanics in fat-tailed dwarf lemurs (*Cheirogaleus medius*) and patas monkeys (*Erythrocebus patas*)

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Abstract

Most quadrupeds walk with lateral sequence (LS) gaits, where hind limb touchdowns are followed by ipsilateral forelimb touchdowns. Primates, however, typically walk with diagonal sequence (DS) gaits, where hind limb touchdowns are followed by contralateral forelimb touchdowns. Because the use of DS gaits is nearly ubiquitous among primates, understanding gait selection in primates is critical to understanding primate locomotor evolution. The Support Polygon Model [Tomita, M., 1967. A study on the movement pattern of four limbs in walking. J. Anthropol. Soc. Nippon 75, 120−146; Rollinson, J., Martin, R.D., 1981. Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. Symp. Zool. Soc. Lond. 48, 377−427] argues that primates' use of DS gaits stems from a more caudal position of the whole-body center of mass (COM) relative to other mammals. We tested the predictions of the Support Polygon Model by examining the effects of natural and experimental variations in COM position on gait mechanics in two distantly related primates: fat-tailed dwarf lemurs (*Cheirogaleus medius*) and patas monkeys (*Erythrocebus patas*). Dwarf lemur experiments compared individuals with and without a greatly enlarged tail (a feature associated with torpor that can be expected to shift the COM caudally). During patas monkey experiments, we experimentally shifted the COM cranially with the use of a weighted belt (7−12% of body mass) positioned above the scapulae. Examination of limb kinematics revealed changes consistent with systematic deviations in COM position. Nevertheless, footfall patterns changed in a direction contrary to the predictions of the Support Polygon Model in the dwarf lemurs and did not change at all in the patas monkey. These results suggest that body mass distribution is unlikely to be the sole determinant of footfall pattern in primates and other mammals.
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Introduction

Recent research has highlighted several ways in which primate quadrupedalism is kinematically and kinetically distinct from the quadrupedal locomotion of non-primate mammals (e.g., Larson, 1998; Schmitt, 2003a). Differences in preferred footfall patterns during symmetrical gaits (e.g., walking and running) have received particular interest from anthropologists. In a symmetrical gait, the touchdown of each limb in a forelimb or hind limb pair is evenly spaced in time

between the touchdowns of the contralateral limb in the pair (Hildebrand, 1966). Most primates habitually use diagonal sequence (DS) gaits when walking and running (Muybridge, 1887; Hildebrand, 1967; Prost, 1969; Rose, 1973; Rollinson and Martin, 1981; Meldrum, 1991; Cartmill et al., 2002; Schmitt and Lemelin, 2002; but see Prost and Sussman, 1969; Vilensky and Patrick, 1985; Vilensky and Larson, 1989; Vilensky, 1994; Schmitt, 2003b; Stevens, 2006). In a DS gait, hind foot touchdowns are followed by contralateral (i.e., opposite side) forefoot touchdowns. In contrast, most non-primate mammals walk using lateral sequence (LS) gaits, in which hind foot touchdowns are followed by ipsilateral (i.e., same side) forefoot touchdowns. There is a cost associated with the use of DS gaits: because hind limb touchdowns coincide with maximal retraction of

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ipsilateral forelimbs, DS gaits often result in limb interference (Hildebrand, 1968; Larson and Stern, 1987). Nevertheless, the use of DS gaits is nearly ubiquitous among quadrupedal primates and is equally rare among most other quadrupeds. Therefore, understanding the proximate and ultimate selective pressures influencing gait selection in primates is critical to understanding primate locomotor evolution.

Hildebrand (1966) demonstrated that the diversity of gait sequence patterns seen among terrestrial tetrapods could be quantified with limb phase: the duration between hind limb touchdown and the touchdown of the ipsilateral forelimb expressed as a percentage of stride duration—also referred to as "gait number" (Shapiro and Raichlen, 2005) and "diagonality" (Cartmill et al., 2002). Limb phase values of below 6 and above 94 signify paces (in which ipsilateral limbs move in or near synchrony), values of 6–44 indicate LS gaits, values of 44–56 indicate trots (in which contralateral limbs move in or near synchrony), and values of 56–94 indicate DS gaits (Fig. 1). Most quadrupeds walk and run with gaits that fall within a limited range of all possible gaits—primarily those with limb phases between 25 and 75 (Hildebrand, 1966; Prost, 1969; Sukhanov, 1974; Meldrum, 1991; Reilly and Delancy, 1997; Cartmill et al., 2002; Stevens, 2003; Shapiro and Raichlen, 2005). Gaits within this range allow animals to maximize stability by limiting periods of support on only ipsilateral limb pairs.

One model that has been proposed to account for primates' unique use of DS gaits is the Support Polygon Model. Although the conceptual basis of the Support Polygon Model was first developed by Gray (1944), Tomita (1967) and Rollinson and Martin (1981) first proposed the model explicitly as an explanation for primates' use of DS gaits. The Support Polygon Model suggests that gait selection in primates and other mammals is governed by the placement of the center of gravity vector relative to the polygon of support formed by the supporting limbs at any point during the stride cycle. If the center of gravity vector falls outside of the support polygon, an animal might experience a destabilizing torque causing it to pitch forward or roll to one side. Keeping the center of gravity vector inside the support polygon may also allow animals to execute abrupt changes in speed or direction without sacrificing balance (Cartmill et al., 2002).

The Support Polygon Model argues that the relevant parameter controlling gait selection is the position of the center of mass (COM) relative to a line joining contralateral fore- and hind limb pairs. Most animals spend a large portion of each stride supported by such limb pairs (i.e., diagonal couplets: Cartmill et al., 2002). Tomita (1967) and Rollinson and Martin (1981) argued that if an animal's center of mass were positioned cranial to this line, a subsequent forelimb contact would be required to maintain stability, initiating a LS pattern (Fig. 2A). In contrast, if the COM were positioned caudal to this line, a subsequent hind limb contact would best maintain stability, initiating a DS pattern (Fig. 2B). Therefore, primates' habitual use of DS gaits should be associated with a caudal translation of the whole-body COM relative to other mammals. It should be noted that the Support Polygon Model of gait selection only applies to gaits in which the footfalls of each lateral or diagonal couplet are separated in time (i.e., "four-beat gaits"). Gaits in which the footfalls of a couplet occur simultaneously, such as trots and paces, are equivocal with respect to the model. Nevertheless, because pacing necessitates prolonged periods of support upon ipsilateral limb pairs alone, most mammals usually avoid this gait (Hildebrand, 1976; Cartmill et al., 2002). Additionally, because trotting is associated with large vertical displacements of the center of mass—a potential source of instability for animals walking arboreally—primates typically avoid this gait as well, particularly when running (Demes et al., 1990; Preuschoft et al., 1996; Schmitt et al., 2006).

Although the Support Polygon Model was originally developed to explain functional differences *between* LS and DS gaits, there are reasons to suspect that the model may also explain differences in interlimb timing *within* gaits. First, differences in the fore-aft distribution of body mass are often associated with biases in duty factor (i.e., relative contact time), with the limb pair most responsible for the support of body weight showing the greater duty factor (Bertram et al., 2000; Lee et al., 2004). Cartmill et al. (2002) have recently demonstrated that interlimb timing within LS and DS gaits varies as a function of duty factor: limb phase is inversely proportional to forelimb duty factor for an animal using a LS gait, whereas limb phase is directly proportional to hind limb duty factor for an animal using a DS gait. Thus, more cranial
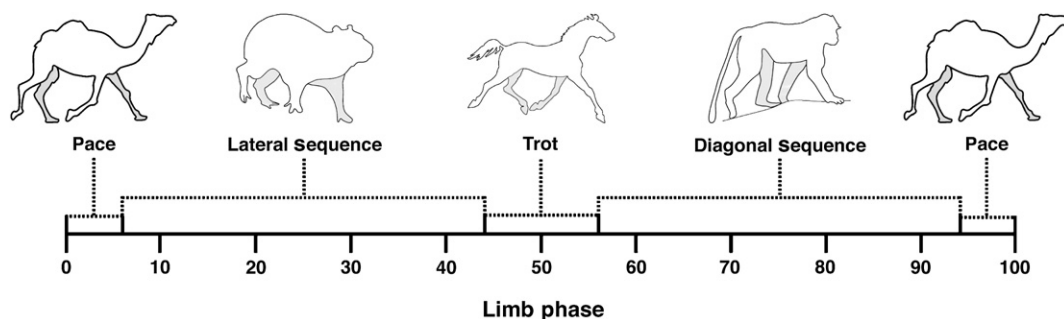

Fig. 1. The diversity of gait sequence patterns used by mammals and other tetrapods can be quantified by limb phase—the duration between ipsilateral hind limb and forelimb touchdowns expressed as a percentage of stride duration (Hildebrand, 1966). See text for an explanation of the different gaits. Left limbs are shaded gray.
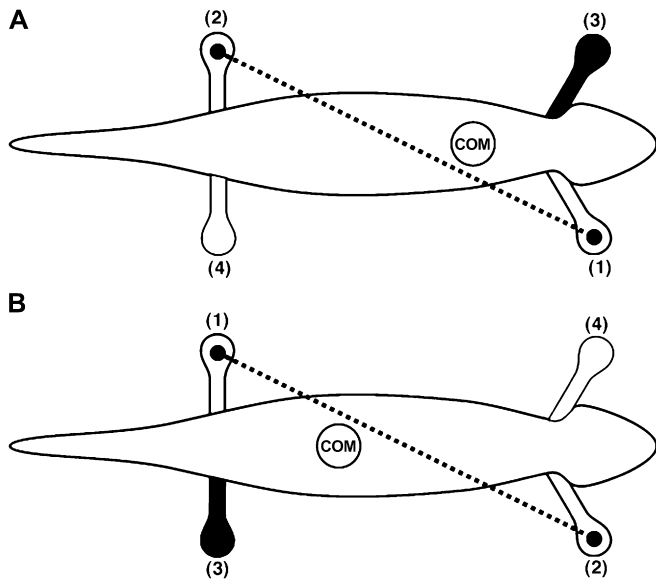
Fig. 2. The Support Polygon Model. (A) If the center of mass (COM) were positioned cranial to a line joining the two limbs in a pair, a subsequent fore-limb contact (in black) would be best able to maintain stability—resulting in a LS gait. (B) If the COM were positioned caudal to a line joining the two limbs in a pair, a subsequent hind limb contact (in black) would be best able to maintain stability—resulting in a DS gait. Numbers above and below limbs indicate the sequence in which footfalls occur in each gait.

positions of the COM, leading to increased forelimb duty factor, should be associated with lower limb phase during LS walking, whereas more caudal positions of the COM, leading to greater hind limb duty factor, should be associated with greater limb phase during DS walking.

Second, when an animal is supported by diagonal couplets, the moment arm of the center of gravity vector and the resulting magnitude of the destabilizing torque will be directly proportional to the perpendicular distance of the COM from the line of support formed by the two contacting limbs. When the destabilizing torque is small, instability could be mitigated by recruitment of proximal limb musculature acting on the trunk (i.e., the limb could act as a supporting lever: Gray, 1944). However, as the distance between the COM and the line of support increases, it would quickly become advantageous for the animal to place another supporting limb on the substrate in order to prevent falling. In other words, the duration between support by diagonal couplets alone and the touchdown of the subsequent fore- or hind limb should be inversely proportional to the perpendicular distance of the COM from the line of support. For an animal using a LS gait, a more cranial position of the COM would be associated with a shorter duration to forelimb contact, thereby decreasing limb phase. Similarly, for an animal using a DS gait, a more caudal position of the COM would be associated with a shorter duration to hind limb contact, thereby increasing limb phase. Taken together, these predictions suggest that limb phase should be directly proportional to the average distance of the COM from the cranial end of the trunk.

The Support Polygon Model has been challenged on theoretical and empirical grounds. First, keeping the center of

gravity vector entirely within the polygon of support during a stride may not always be advantageous (Hildebrand, 1985; Vilensky and Larson, 1989). Allowing the center of gravity vector to fall outside of the support polygon can allow an animal to utilize gravitational potential energy to increase efficiency during forward progression (i.e., "controlled falling"). Second, primates often position their limbs close to the midsagittal plane of the body, perhaps as an adaptation for locomotion on branches (Prost, 1969; Meldrum, 1991; Schmitt, 1994). Any polygons formed with such limb placement should be too narrow to offer substantial support, regardless of the position of the center of gravity vector. Finally, although numerous studies have suggested that primates typically support their body weight more with their hind limbs than their forelimbs during locomotion—e.g., hind limb vertical peak reaction forces are greater than forelimb vertical peak reaction forces (Kimura et al., 1979; Demes et al., 1994; Schmitt and Lemelin, 2002; Hanna et al., 2006), the few studies that have measured primate segmental inertial properties sufficiently to estimate the static position of the whole-body COM have found that, in most cases, it is actually closer to the shoulders than to the hips (Reynolds, 1974; Vilensky, 1979; Grand, 1983; Wells and DeMenthon, 1987; Turnquist and Wells, 1994; Crompton et al., 1996).

Nevertheless, the hypothesis that footfall patterns are determined by body mass distribution has received some support from experimental studies of non-primate mammals. Lee et al. (2004) found that adding weights equal to 10% of body mass to the pectoral or pelvic girdles of domestic dogs shifted walking patterns away from their preferred pattern of trotting. As would be predicted by the Support Polygon Model, cranial translations of COM position shifted interlimb phasing toward LS gaits, whereas caudal translations shifted interlimb phasing toward DS gaits, although limb phase changed by only a few percent in each condition. Tomita (1967) performed a similar study, in which he found that adding weight to the pelvic girdle of dogs occasionally caused them to use DS gaits. Moreover, in a study comparing the body composition and walking kinematics of Labrador retrievers and greyhounds, Bertram et al. (2000) found that Labrador retrievers, in whom the COM was positioned more cranially, tended to use LS gaits with lower average limb phase values than greyhounds.

Studies of primate and non-primate locomotion on oblique supports have provided the clearest support for the Support Polygon Model. When an animal is on a sloped substrate, the position of the center of gravity vector relative to the supporting limbs shifts in proportion with the angle of inclination or declination, provided the animal does not greatly change limb posture (Stevens, 2000, 2001, 2003; Krakauer et al., 2002). Standing or walking on a declined support will shift the center of gravity vector cranially, closer to the forefeet. Conversely, standing or walking on an inclined support will shift the center of gravity vector caudally, closer to the hind feet (Gray, 1944). Therefore, if the Support Polygon Model is valid, animals on declined supports should decrease limb phase and animals on inclined supports should increase limb

phase. In accordance with these predictions, several studies of primates walking on sloped supports have shown an increase in limb phase on inclines and a decrease in limb phase on declines (Prost and Sussman, 1969; Rollinson and Martin, 1981; Vilensky, 1994; Stevens, 2003).

Specific aims and predictions

In spite of the challenges noted above, current evidence does accord with many of the predictions of the Support Polygon Model. Nevertheless, whether the predictions of the Support Polygon Model can explain the use of DS gaits by primates has yet to be tested in a controlled manner. In this study, we examined the effects of natural and experimental variations in body mass distribution on the walking and running kinematics of two distantly related primates, the fat-tailed dwarf lemur (*Cheirogaleus medius*) and the patas monkey (*Erythrocebus patas*). Whereas both dwarf lemurs and patas monkeys use DS gaits preferentially, the two species differ in many aspects of their ecology and evolutionary history. Cheirogaleids represent generalized arboreal quadrupeds that have been suggested to resemble the ancestral primate morphotype (Cartmill, 1972; Gebo and Simons, 1987; Godinot, 1990; Covert, 1995; Fleagle, 1999) and are therefore an ideal model for studying the evolution of primate gait selection. In contrast, cercopithecines are among the most derived primates, with more terrestrial species than any other extant radiation of primates (Jablonski, 2002). Moreover, patas monkeys are among the most terrestrial of the cercopithecines, primarily foraging and traveling in open grasslands (e.g., Isbell et al., 1998). Thus, our choice of animals allowed us to explore the influence of body mass distribution on gait selection across extremes of primate locomotor adaptation.

We exploited natural variation in tail mass in two dwarf lemurs (associated with seasonal torpor) to test the effects of caudal translations in the center of mass on preferred gait sequence pattern. We experimentally varied body mass distribution in a patas monkey by securing a weighted harness equal to 7–12% of body mass above the scapulae, thereby shifting the position of the COM cranially. We predicted that if the Support Polygon Model is valid, caudal shifts in the position of the COM in the dwarf lemurs should increase limb phase, causing changes in interlimb timing within DS gaits. Similarly, cranial shifts in the position of the COM in the patas monkey should decrease limb phase, moving DS gaits toward LS footfall patterns.

We used morphometric, kinematic, and kinetic methods to verify that whole-body COM position shifted in response to variations in body mass distribution. First, we used a recently developed geometric model (Crompton et al., 1996; Raichlen, 2004) to estimate the position of the whole-body COM in each patas monkey experimental condition. Although we were not able to apply the geometric model to the dwarf lemurs, measurements of segment lengths and body mass allowed us to produce a general estimate of the effects of increased tail mass on whole-body COM position. Second, we examined the effects of changes in body mass distribution on forelimb and hind limb duty factor. As discussed above, increases in

the weight-bearing role of a pair of limbs are often concomitant with increases in duty factor (Baudinette and Biewener, 1998; Bertram et al., 2000; Donelan and Kram, 2000; Wickler et al., 2001; Irschick et al., 2003; Lee et al., 2004). Therefore, cranial translations in whole-body COM position in the patas monkey should lead to increases in forelimb duty factor, and caudal translations of COM position in the dwarf lemurs should lead to increases in hind limb duty factor. Third, we examined changes in forelimb and hind limb angular excursion as a function of body mass distribution. Individuals could respond to variation in body mass distribution by adjusting limb excursions to place the less heavily-loaded limb closer to the COM for a greater portion of the stride, thereby redistributing body weight more evenly between the loaded and unloaded limbs. We predicted that the patas monkey should attempt to compensate for cranial shifts in the position of the COM by increasing hind limb protraction. Similarly, caudal shifts in the position of the COM in the dwarf lemurs should be counteracted by increases in forelimb retraction. Finally, we used a force plate to record single-limb vertical impulses during the patas monkey trials. Studies of primate locomotor kinetics have typically only reported peak vertical forces (Kimura et al., 1979; Demes et al., 1994; Schmitt and Lemelin, 2002; Hanna et al., 2006). Impulse, calculated as the area under the force-time curve, quantifies limb contact time as well as force, and is thus a better measure of the contribution of each limb to body weight support (e.g., Bertram et al., 1997). We predicted that cranial translations of COM should increase forelimb vertical impulse while having little to no effect on hind limb vertical impulse.

Methods

Procedures

All procedures were approved by the Stony Brook University and Duke University Institutional Animal Care and Use Committees.

Dwarf lemurs: *Cheirogaleus* individuals routinely exhibit alterations in the fore-aft distribution of body mass due to the storage of fat in the tail in preparation for seasonal torpor (Hladik et al., 1980). For these reasons, a natural experiment was conducted to explore the effects of body mass distribution upon gait sequence patterns and limb kinematics in the fat-tailed dwarf lemur (*Cheirogaleus medius*). Two adult individuals housed at the Duke Lemur Center (DLC) were selected. Both individuals enjoyed regular access to naturalistic supports in their enclosures and were acclimated to study substrates prior to data collection in order to minimize the impact of the experimental setting upon their performance. At the time that animals were brought into the experimental room, limb joint segment lengths and body masses were recorded, a procedure that did not require anesthesia. To facilitate joint identification for later kinematic analysis, reflective tape markers were placed on the shaved skin overlying the shoulder, elbow, wrist, hip, knee, and ankle joints, as well as on the hand and foot. Using two-dimensional kinematic techniques described in Stevens (2003), cameras

were positioned to provide lateral and fore-aft views of the individuals walking, and synchronized with a special effects generator. Cameras were operated at 60 Hz with shutter speeds of 1/1000. Individuals were videotaped walking along simulated branches constructed from 2.4 m sections of 1.25 cm and 5 cm diameter polyvinyl chloride (PVC) pipes. All substrates were coated with a non-slip surface. Vertical marks spaced at 5 cm intervals along the length of the pipes were used to calculate locomotor speed and calibrate distance measurements.

Patas monkey: Artificial manipulations of body mass distribution were used to test the influence of COM position on gait selection and limb kinematics in a patas monkey. An adult female patas monkey (*Erythrocebus patas*), housed at the Stony Brook University Primate Locomotion Laboratory, was used in these experiments (body mass = 7.35 kg). A commercially available dog harness (Dachshund Delights, Garrettsville, OH), custom-tailored to the subject's chest and neck girth, was fitted with lead weights held in place by Velcro fastenings and strapped above the pectoral girdle. Three different harness loads were used in this study, adding weights equal to 0.5 kg (7% body mass), 0.75 kg (10% body mass), and 0.875 kg (12% body mass) to the pectoral girdle. A control condition with no weight was also tested. Because the mass of the harness was negligible (mass = 66.5 g), we were able to assess the influence of weighting independent of any effects induced by wearing the harness. The mean angular excursion of the forelimb during the unweighted control condition (see below) fell within the 99% confidence limits of the mean reported for cercopithecine monkeys by Larson et al. (2000), indicating that the harness did not constrain forelimb movement relative to normal locomotion.

Prior to each experimental session, the subject was anaesthetized with isoflurane gas. While the subject was under anesthesia, the harness was secured and weights were added. Additionally, the skin over the shoulder, elbow, wrist, hip, knee, and ankle joints was shaved and marked with either high-contrast white paint or reflective tape to aid during later kinematic analysis. Because we were unable to apply joint markers prior to testing the animal in the 7% body mass condition, kinematic data are only available for control, 10%, and 12% body mass conditions.

The animal was allowed to awaken from the anesthesia within a large room and become acclimated to the harness prior to the start of data collection. Once acclimated, the animal was moved to the testing apparatus, a 10.5 m by 1.18 m by 0.74 m runway enclosed by clear Lexan. Vertical markers spaced at one-meter intervals along the back wall of the runway were used to calculate locomotor speed and calibrate distance measurements. A Kistler 9281B force plate located in the center of the runway recorded substrate reaction forces in three dimensions during locomotion.

The animal was encouraged with food rewards to move along the runway. Two video cameras (HSC-180NS) were positioned at right angles to the direction of travel in order to videotape the animal's movements throughout the experiment. Cameras were shuttered at rates of 1/2000 and operated at 60 Hz. One of the cameras was adjusted to have a wide field

of view (i.e., "zoomed-out") and used for coding gait sequence data, whereas the other camera was adjusted to have a narrow field of view (i.e., "zoomed-in"), centered on the force plate, and used for coding speed, limb kinematics, and details of contact with the force plate. Video output from each camera was passed through a time-code generator (Gl-250, J. C. Labs) that superimposed a time code onto each video field, allowing for the synchronization of views from different cameras. Further details of the video set-up have been described by Polk (2001).

To record single-limb vertical impulses, analog signals from the force plate were digitally rendered using National Instruments hardware and a LabView virtual instrument. The force traces were sampled at a rate of 2700 Hz and partitioned into four-second long binary files (yielding 10,800 data points per channel per file). Images of the raw ground reaction force components were superimposed over the video from the zoomed-out camera to facilitate the identification of usable strides. Only strides in which a single forelimb or hind limb completely contacted the force plate were included for analysis. Once strides with usable force data had been identified, binary data files representing these strides were imported into Igor Pro software (WaveMetrics, Inc.), smoothed, scaled to body weight, and graphed. Force traces were smoothed using a binomial curve fit algorithm with a window of 400; this corresponds to a low-pass filter where a binomial average mean is taken over a 0.15 second interval and replaces each data point (see Franz et al., 2005). Custom macros were used to calculate vertical impulse over each step for which force data were available.

Center of mass estimates

We used a geometric model, introduced by Crompton et al. (1996) and recently refined by Raichlen (2004), to estimate the influence of weighting condition on the average position of the COM in the patas monkey. In this method, the trunk, tail, arm, forearm, hand, thigh, leg, and foot are modeled as columns with elliptical cross-sections that change dimensions along the length of the column. To derive the parameters required for the model, we used measuring tape to measure segment length and sliding calipers to measure segment diameters at three points along the length of each segment—proximal, mid-segment, and distal. Anatomical landmarks used to identify body segments are described in Table 1. External

Table 1
Anatomical landmarks used to identify body segments

Body segment	Anatomical landmarks
Trunk	Greater trochanter of femur to greater tubercle of humerus
Tail	Spinous process of first caudal vertebra to distal end of the tail
Arm	Greater tubercle to lateral epicondyle of humerus
Forearm	Lateral edge of radial head to radial styloid process
Hand	Radial styloid process to distal end of the third manual ray
Thigh	Greater trochanter to a distal edge of lateral femoral condyle
Leg	Proximal edge of lateral tibial condyle to fibular malleolus
Foot	Calcaneal tuberosity to distal end of the third pedal ray

measurements of the limbs and trunk were used to derive equations expressing how the cross-sectional profile of each segment changes along its length. These equations were then used to estimate segment volumes and centroid locations using formulas provided by Raichlen (2004). Because the density of nearly all terrestrial vertebrates is approximately equal to one (Schmidt-Nielsen, 1975), segment volumes and segment masses are effectively equivalent quantities, as are centroid positions and centers of mass. The head was modeled as an ellipsoid with the COM at the midpoint. Head length was measured from inion to the angle of the mouth, head width as biauricular breadth, and head height from gonion to bregma. Although these measurements exclude the dimensions of the jaw and lower face, this is likely to have little effect on the estimated position of the whole-body COM. To expedite data collection on the anesthetized animal, limbs were measured on the right side only and doubled during later calculations of whole-body COM. Measurements were repeated on three separate occasions in order to quantify error in estimating whole-body COM position.

Whole-body COM position changes with movement of body segments throughout the gait cycle. We attempted to establish an average position of the whole-body COM during locomotion by quantifying changes in posture from video footage of the patas monkey walking in the unweighted control condition. Fifteen steps were randomly selected for analysis: five in which the hind limb closest to the camera was in support phase, five in which the forelimb closest to the camera was in support phase, and five in which both limbs were in swing phase. Using Peak Motus (version 7.1) software, the two-dimensional position of each landmark identified in Table 1, as well as inion and the angle of the mouth, were measured in each frame of each of the fifteen video clips, yielding a total of 102 frames. To simplify calculations, contralateral forelimbs and hind limbs (i.e., limbs facing away from the camera) were modeled as if they were positioned alongside digitized limbs, an assumption that necessarily misrepresents limb positioning in an animal using a symmetrical gait. Nevertheless, because the combined mass of the contralateral limbs was small relative to total body mass (∼15% of unloaded body mass—see below), such errors should have little effect on estimates of the average position of the whole-body COM.

For each of the 102 frames for which positional data were available, the anteroposterior position of the whole-body COM was calculated as the arithmetic mean of all two-dimensional segmental COMs weighted by segment mass (Ozkaya and Nordin, 1999). For the calculation of the whole-body COM position in the weighted trials, the weighted harness was modeled as a point mass over the shoulder blade. The position of the whole-body COM was estimated separately for each replicated set of measurements and each weighting condition, generating a total of 1224 estimates.

Kinematic analyses

Forelimb and hind limb protraction, retraction, and excursion angles were quantified from video clips using Peak Motus

software. For each forelimb and hind limb step in the available dataset the two-dimensional position of each joint marker was quantified at touchdown and lift-off. Protraction and retraction angles were calculated relative to the global x-axis. All angles were measured on the flexor side of the joint. Limb angular excursions were computed as the difference of retraction and protraction angles. Because other limbs or features of the experimental apparatus occasionally obscured joint markers, not all kinematic measures were available for each stride in the total dataset.

Gait analyses

Speed, gait sequence pattern, and duty factors were coded from video clips imported into Peak Motus software. Only symmetrical gaits were analyzed. Following Schmitt et al. (2006), gait symmetry was identified when touchdown of each limb in a forelimb or hind limb pair followed the touchdown of the contralateral limb by $50 \pm 10\%$ of stride time. Speed was measured by counting the number of frames that elapsed as the animals passed the standardized reference markers discussed above. Duty factor and limb phase were calculated by temporally recording limb touchdown (the first frame that a limb made contact with the substrate) and lift-off events (the final frame that a limb was in contact with the substrate). Duty factor was defined as the average proportion of a stride that the limbs were in support phase. Forelimb, hind limb, and mean duty factor were calculated separately for each stride in the dataset. Additionally, as a means of comparing forelimb and hind limb duty factors within each condition, a duty factor ratio was calculated by expressing forelimb duty factor as a percentage of hind limb duty factor. A duty factor ratio of 100 indicates that forelimb and hind limb duty factors are equal, values greater than 100 indicate that forelimb duty factor is greater, and values less than 100 indicate that hind limb duty factor is greater. Gait terminology used to categorize limb phase follows Hildebrand (1966), as described above and illustrated in Fig. 1. Additionally, in order to detect more subtle changes in gait obscured by grouping data categorically, limb phase was examined as a continuous variable.

Statistical methods

Because most samples did not follow a normal distribution, all data were rank transformed prior to analysis. Rank transformations permit analysis of variance without loss of power in data sets that are not normally distributed (Conover and Iman, 1981). Original variates were replaced with ranks, with ties broken by assigning mean ranks to tied cases using SPSS (Version 11.0.4 for Macintosh). As any observed differences in speed may constitute a response to changes in body mass distribution, no attempt was made to constrain speed. Nevertheless, because speed can influence kinematic and kinetic variables independent of other factors (Vilensky and Patrick, 1985; Demes et al., 1990; Polk, 2001), Pearson product-moment correlations were used to test for associations between outcome variables and speed. When the relationship

between speed and outcome variables was constant across all conditions being compared (i.e., regression slopes were not significantly different), analysis of covariance (ANCOVA) was used to test for differences between conditions. When significant relationships with speed were not observed across all conditions, or regression slopes significantly differed among conditions, t-tests or single classification analyses of variance (ANOVA) were used in lieu of ANCOVA. Hochberg's GT2-method was used for pair-wise post hoc analyses (Sokal and Rohlf, 1995) following significant ANOVA results. Non-parametric G-tests of independence were used to test for proportional differences in the frequency of gait sequence use during different experimental conditions. To control for experiment-wise Type I errors, p-values for all t-tests and post hoc analyses were adjusted using the sequential Bonferroni method (Rice, 1988). In this method, p-values from n statistical tests are ranked and compared to alpha values adjusted by n, n−1, n−2…n−(n−1).

Results

Thirty representative walking strides were analyzed for each dwarf lemur (fifteen each on the small and the large diameter supports), yielding a total of 60 strides. For the patas monkey, we analyzed a total of 206 strides across the four loading conditions. Sample sizes for each loading condition, including the number of steps yielding impulses and kinematic data, are detailed in Table 2. Correlation coefficients quantifying the association between all outcome variables and speed are presented in Table 3, grouped by species and condition.

Effects of weighting condition on body mass distribution

Dwarf lemurs. With the exception of a greatly enlarged tail in one individual, the two dwarf lemurs were very similar in overall body size (Table 4). In the dwarf lemur with the heavy tail, tail diameter at the widest point was 46% greater than in the individual with the light tail. Because the two lemurs were virtually identical in all other body dimensions measured, increased tail mass probably accounts for the 33% greater body mass of the individual with the heavier tail. In the simplest

model, in which the COM of the light-tailed individual is placed at the center of the trunk and the tail is modeled as a point mass placed at the caudal end of the trunk, increasing tail mass by 33% of body mass would move the whole-body COM caudally by 12.5% of trunk length. Therefore, although precise estimates of whole-body COM position were not available, it is likely that the COM was positioned relatively more caudally in the animal with the heavier tail. Indeed, previous research with dwarf lemurs has shown that augmented tail mass significantly increases the proportion of body mass supported by the hind limbs during locomotion (Lemelin and Schmitt, 2004), suggesting a caudal translation in the position of the COM when the tail is enlarged.

Patas monkey. Descriptive statistics of segment lengths, estimated segment masses, and estimated segment COM positions are presented in Table 5. In order to assess the precision of our measurements and estimates, coefficients of variation (CV) for all segmental properties were calculated. Whereas CVs for measured segment lengths were generally low (all below 7%), estimated segment masses were more variable. In particular, CVs for estimated forelimb and tail mass were above 20%. Because measured segment lengths were relatively invariable, lower precision for estimated forelimb and tail masses arose from measurement error of external segment diameters. Nevertheless, measurement errors had little effect on the precision of the estimated position of segment COMs (all CV less than 9%). The overall accuracy of estimated segmental properties was assessed by summing predicted segment masses and comparing the result to measured body mass. Mean predicted body mass (7.348 kg) was nearly equal to actual body mass (7.35 kg). Moreover, the coefficient of variation for predictions of body mass was quite low (1.4%), suggesting that overall the model was precise as well as accurate.

Descriptive statistics of the estimated position of the average position whole-body COM and the average range of COM movement within a step are presented in Table 6, grouped by weighting condition. Weighting resulted in a moderate cranial translation of the trunk COM, from 50% of trunk length during control trials to 42% of trunk length in the 12% body mass condition. An 8% difference in the relative position of the trunk COM corresponds to an absolute cranial translation of 2.6 cm. Segmental movement during a step caused the position of the COM to deviate 14–16% of trunk length (4.6–5.3 cm), depending on loading condition. The average position of the whole-body COM differed significantly among loading conditions ($F_{[3,305]} = 43$, $p \ll 0.001$), showing a significant cranial deviation with each increment of added mass (all $p \ll 0.001$). Overall, weighting caused the average position of the whole-body COM to shift from 43% to 40% of trunk length, corresponding to an absolute cranial translation of 1.0 cm.

As another means of assessing the effects of weighting on body mass distribution in the patas monkey, forelimb and hind limb vertical impulses were compared across different harness loading conditions. Neither forelimb nor hind limb vertical impulse was significantly associated with speed in any condition. Means and standard errors of forelimb and

Table 2
Total number of strides, number of strides with impulse data and number of kinematic events by species and condition*

	Total strides	Impulses		FL kinematic events			HL kinematic events		
		FL	HL	TD	MS	LO	TD	MS	LO
Dwarf lemurs									
Light tail	30	–	–	30	30	30	30	30	30
Heavy tail	30	–	–	30	30	30	30	30	30
Patas monkey									
Control	86	10	11	33	30	24	24	27	33
7% BM	26	7	5	–	–	–	–	–	–
10% BM	59	7	11	24	24	24	17	23	17
12% BM	35	6	4	34	31	22	30	31	32

* FL = forelimb, HL = hind limb, TD = touchdown, MS = mid-support, LO = lift-off, BM = body mass.

Table 3

Correlation coefficients (and significance values) of all variables on speed, grouped by species and condition. For abbreviations, see Table 2*

	Dwarf lemurs		Patas monkey			
	Light tail	Heavy tail	Control	7% BM	10% BM	12% BM
Impulse						
FL impulse	–	–	−0.50 (0.14)	0 (1)	0.21 (0.65)	0.19 (0.72)
HL impulse	–	–	−0.40 (0.2)	0.16 (0.8)	0.14 (0.68)	−0.47 (0.53)
Gait variables						
FL duty factor	**−0.44 (0.02)**	**−0.53 (<0.01)**	**−0.55 (<0.01)**	−0.22 (0.29)	**−0.58 (<0.01)**	**−0.67 (<0.01)**
HL duty factor	**−0.54 (<0.01)**	**−0.77 (<0.01)**	**−0.64 (<0.01)**	−0.14 (0.5)	**−0.61 (<0.01)**	**−0.77 (<0.01)**
Mean duty factor	**−0.56 (<0.01)**	**−0.72 (<0.01)**	**−0.61 (<0.01)**	−0.35 (0.08)	**−0.61 (<0.01)**	**−0.76 (<0.01)**
Duty factor ratio	0.15 (0.43)	0.22 (0.24)	0.10 (0.36)	−0.19 (0.38)	0.20 (0.14)	0.24 (0.17)
Limb phase	**0.38 (0.04)**	**0.49 (<0.01)**	0.06 (0.59)	−0.31 (0.14)	**−0.39 (<0.01)**	**−0.76 (<0.01)**
Kinematic variables						
FL protraction	−0.23 (0.22)	−0.15 (0.43)	0.01 (0.95)	–	−0.16 (0.45)	0.11 (0.54)
FL retraction	0.34 (0.07)	−0.10 (0.59)	−0.03 (0.91)	–	−0.30 (0.23)	**−0.62 (<0.01)**
FL excursion	−0.34 (0.07)	−0.06 (0.77)	0.07 (0.78)	–	0.03 (0.9)	0.40 (0.07)
HL protraction	**0.51 (<0.01)**	0.18 (0.36)	0.01 (0.95)	–	0.11 (0.68)	−0.04 (0.85)
HL retraction	0.05 (0.79)	**−0.57 (<0.01)**	−0.31 (0.11)	–	0.01 (0.97)	0.10 (0.58)
HL excursion	**−0.40 (0.03)**	**−0.44 (0.02)**	0.15 (0.55)	–	0.11 (0.69)	−0.11 (0.56)

* Bold values indicate significant correlations.

hind limb vertical impulse in each weighting condition are presented in Table 7. Mean forelimb vertical impulse significantly differed among conditions ($F_{[3,26]} = 4.5$, $p < 0.05$). Relative to the control condition, mean forelimb vertical impulse increased in the 10% body mass condition, although this trend was not significant. In contrast, mean forelimb vertical impulse during the 12% body mass condition actually *decreased* relative to the other three conditions, although the decrease was significant only when compared to the 10% body mass condition. Mean hind limb vertical impulse did not differ among loading conditions ($F_{[3,27]} = 0.5$, $p > 0.05$).

Joint kinematics

Dwarf lemurs. Descriptive statistics of all forelimb (FL) and hind limb (HL) protraction, retraction, and excursion angles for both species are reported in Table 8. Hind limb excursion angle was negatively correlated with speed in both individuals; no other angular variables were significantly associated with speed across both individuals. Forelimb and hind limb excursion angles were significantly greater in the individual with heavier tail (FL: $t_{[58]} = -4.5$, $p \ll 0.001$; HL: $F_{[1,57]} = 23.2$, $p \ll 0.001$). Although the individual with the heavier tail tended to use more protracted forelimb postures and less protracted hind limb postures at touchdown, these differences were not significant following the sequential Bonferroni correction. Therefore, increases in limb excursion were brought about primarily by greater retraction of the limbs at

lift-off (FL: $t_{[58]} = 4.7$, $p \ll 0.001$; HL: $t_{[58]} = -12.5$, $p \ll 0.001$).

Patas monkey. None of the kinematic variables was significantly correlated with speed across all of the three conditions for which kinematic data were available. Although the patas monkey tended to use more protracted forelimb postures in the 10% body mass condition, no significant differences in forelimb or hind limb protraction, retraction, or excursion angles were observed following the Sequential Bonferroni correction.

Duty factor and limb phase

Dwarf lemur. Descriptive statistics of all gait variables in both species are reported in Table 9. The individual with the heavier tail (i.e., greater tail mass) exhibited significantly lower speeds than did the individual with the lighter tail ($t_{[58]} = 6.8$, $p < 0.001$). Forelimb, hind limb, and mean duty factors were negatively correlated with speed in both individuals (Fig. 3A, B). The individual with the heavy tail consistently used gaits with higher duty factors than the individual with the lighter tail, even when differences in speed were controlled for using ANCOVA (FL: $F_{[1,57]} = 19.2$, $p \ll 0.001$; HL: $F_{[1,57]} = 53.5$, $p \ll 0.001$; mean: $F_{[1,57]} = 46$, $p \ll 0.001$). The mean duty factor ratio of the individual with the lighter tail was very close to 100, signifying the forelimb and hind limb duty factors were approximately equal. In contrast, mean duty factor ratio was significantly lower in the individual

Table 4

Dwarf lemur morphology

	Arm length	Forearm length	Hand length	Thigh length	Leg length	Foot length	Tail diameter*	Body mass
Light tail	28 mm	32 mm	5 mm	42 mm	45 mm	7 mm	24 mm	200 g
Heavy tail	27 mm	31 mm	5 mm	44 mm	45 mm	7 mm	35 mm	265 g

* Tail diameters were taken at the widest point (approximately 2 cm from the base of the tail).

Table 5
Means, standard deviations (SD), and coefficients of variation (CV) for patas monkey segment lengths, estimated segment masses, and estimated segment centers of mass*

	Segment length			Segment mass			Segment center of mass		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Head	56 cm	0.5 cm	1.0%	1767 g	110 g	6%	50.0%	–	–
Trunk	33 cm	0.3 cm	2.1%	3236 g	228 g	7%	51.4%	0.3%	0.7%
Arm	18 cm	0.5 cm	2.7%	267 g	69 g	26%	58.0%	0.4%	0.6%
Forearm	17 cm	1.0 cm	6.1%	82 g	17 g	21%	59.5%	2.0%	3.4%
Hand	9 cm	0.1 cm	0.6%	28 g	7 g	25%	56.9%	1.6%	2.9%
Thigh	17 cm	0.2 cm	1.0%	517 g	28 g	5%	58.9%	1.6%	2.8%
Leg	16 cm	0.2 cm	1.3%	166 g	13 g	8%	60.0%	1.5%	2.5%
Foot	5 cm	0.2 cm	3.4%	46 g	4 g	9%	54.8%	4.6%	8.4%
Tail	33 cm	0.0 cm	0.0%	133 g	32 g	24%	69.8%	2.8%	4.0%
Total body mass	–	–	–	7.348 g	85 g	1%	–	–	–

* Segment centers of mass are expressed as a percentage of segment length from to the proximal to the distal end (see Table 1).

with the heavy tail ($t_{[58]} = 4.0$, $p \ll 0.001$), suggesting that augmented tail mass disproportionately increased hind limb duty factor relative to forelimb duty factor.

Limb phase values partitioned into discrete gait sequence categories revealed that the individual with the heavier tail also utilized significantly fewer DS gaits and more trots, with only half of the trials exhibiting limb phase values greater than or equal to 56 ($G_{[2]} = 29.5$, $p < 0.001$; Table 9). In contrast, the individual with the lighter tail utilized DS gaits in nearly all trials, with limb phase values falling below 56 only once. When examined as a continuous variable, limb phase was positively correlated with speed in both individuals (Fig. 3C). Limb phase values were significantly lower in the individual with the heavier tail ($F_{[1,57]} = 10.8$, $p < 0.01$), even when differences in speed were taken into account (Fig. 3C, D). Moreover, if the dataset is restricted to only those portions where the speeds sampled from two lemurs overlap, all differences in limb phase and duty factor remain significant (forelimb duty factor: $F_{[1,30]} = 9.6$, $p < 0.01$; hind limb duty factor: $F_{[1,30]} = 47.9$, $p \ll 0.001$; mean duty factor: $F_{[1,30]} = 30.1$, $p \ll 0.001$; duty factor ratio: $t_{[57]} = 3.2$, $p < 0.01$; limb phase: $F_{[1,30]} = 7.4$, $p < 0.05$).

Patas monkey. Speed varied significantly among conditions ($F_{[3,187]} = 7.6$, $p \ll 0.001$), although this variation can be explained entirely by the low average speed during the 10% body mass trials. Forelimb, hind limb, and mean duty factors were negatively correlated with speed in the control, 10% body mass and 12% body mass conditions (Fig. 4A,B). All duty factors tended to increase with weighting. However, after

adjusting alpha levels for multiple comparisons, this trend was only significant for the 12% body mass condition (FL: $F_{[1,186]} = 25.1$, $p \ll 0.001$; HL: $F_{[1,186]} = 12$, $p \ll 0.001$; mean: $F_{[1,186]} = 20.6$, $p \ll 0.001$). Duty factor ratios tended to be greater in the three weighted conditions than in the unloaded control condition, suggesting that forelimb duty factor increased slightly more than hind limb duty factor. Nevertheless, differences in duty factor ratio were not significant ($F_{[3,202]} = 2.8$, $p > 0.05$).

Limb phase was negatively correlated with speed in some, but not all, experimental conditions (Fig. 4C). When limb phase was partitioned into discrete gait sequence categories, no significant differences in the frequencies of different footfall patterns used in the four loading conditions were observed ($G_{[3]} = 5$, $p > 0.05$). DS gaits predominated in all conditions, always representing more than 98% of the strides sampled (Fig. 4D). Although a small number of strides in two of the three weighted conditions qualified as trots, this variation was not significant. When limb phase was examined as a continuous variable, no significant differences were found among loading conditions ($F_{[3,202]} = 1.6$, $p > 0.05$).

Discussion

This study represents the first experimental test of the Support Polygon Model of gait selection in primates. Before discussing the results and their implications, it must be noted that these results should be treated with some caution. For example, the dwarf lemur data were collected from separate individuals. We cannot rule out the possibility that the individual with the heavier tail simply 'preferred' to use a greater proportion of trots than the individual with the lighter tail. While primates as a group are uniquely characterized by the habitual use of

Table 6
Estimated position of the center of mass (COM) in each patas monkey loading condition. Data are presented as means ± standard error. Ranges are shown in parentheses*

	Trunk COM	Whole-body COM
Control	50 ± 0.04% (< 1%)	43 ± 0.01% (35−51%)
7% BM	45 ± 0.13% (< 1%)	42 ± 0.01% (34−49%)
10% BM	43 ± 0.16% (43−44%)	41 ± 0.01% (34−48%)
12% BM	42 ± 0.17% (42−43%)	40 ± 0.01% (33−47%)

* Center of mass positions are expressed as a percentage of trunk length from the shoulder to the hip.

Table 7
Forelimb and hind limb impulse (bw/s) in the patas monkey. Data are presented as arithmetic means. Standard errors are shown in parentheses

	Control	7% BM	10% BM	12% BM
FL impulse	0.09 (0.006)	0.09 (0.005)	0.11 (0.004)	0.08 (0.006)
HL impulse	0.10 (0.007)	0.10 (0.010)	0.11 (0.007)	0.11 (0.020)

Table 8
Joint kinematics by species and condition. Continuous variables correlated with speed are presented as estimated marginal means (evaluated at the grand mean of speed across groups). All other continuous variables are presented as arithmetic means. Standard errors are shown in parentheses. Asterisks indicate the significance of comparisons against the light-tailed individual (dwarf lemurs) or the control condition (patas monkey): * = $p < 0.05$, *** = $p < 0.001$. Bold shading indicates a significant difference after the sequential Bonferroni correction

	Dwarf lemurs		Patas monkey			
	Light tail	Heavy tail	Control	7% BM	10% BM	12% BM
Forelimb						
Protraction	135.5 (1.0)	139.0* (1.0)	106.0 (0.94)	–	110.2* (1.2)	108.1 (1.1)
Retraction	47.9 (0.9)	**42.4*** (0.7)**	43.5 (0.72)	–	45.1 (0.7)	48.4 (2.0)
Excursion	87.6 (1.4)	**96.7*** (1.5)**	62.7 (1.3)	–	64.6 (1.6)	59.7 (2.3)
Hind limb						
Protraction	64.0 (1.3)	60.4* (0.7)	76.0 (1.5)	–	73.5 (1.6)	72.4 (1.3)
Retraction	128.6 (0.7)	**139.0*** (0.5)**	129.1 (0.5)	–	126.1 (1.0)	128.9 (0.7)
Excursion	67.2 (1.3)	**75.9*** (1.3)**	53.5 (1.5)	–	52.2 (1.1)	56.4 (1.2)

DS gaits, gait selection between individuals, or even within a single individual across several strides, can be quite variable (Vilensky and Larson, 1989; Vilensky and Moore, 1992; Shapiro and Raichlen, 2005). Our sample was necessarily limited by the availability of fat-tailed dwarf lemurs in captivity. Moreover, captive cheirogaleids are seldom allowed to go into torpor, limiting the opportunity for researchers to study the locomotor effects of natural variations in body mass distribution. Ideally, future tests of the Support Polygon Model might attempt to examine the relationship over time between gait selection and natural variations in tail mass within individual dwarf lemurs.

Comparisons of gait mechanics in the dwarf lemur sample were also complicated by differences in preferred speed, with the individual with the heavier tail exhibiting significantly lower speeds than the light-tailed individual. While it is possible that observed differences in the gait mechanics used by the two dwarf lemurs resulted from divergent speeds, all differences remained significant after the effects of speed were factored out using ANCOVA. Moreover, the speeds sampled from the lemurs overlapped for a substantial portion of their range (45% and 63% of the range for the light-tailed and heavy-tailed individuals, respectively). Finally, all differences remained significant when the dataset was truncated to only those portions where the speeds sampled from the two lemurs overlapped.

Volumetric estimates and impulse data indicate that the weighted harness used in the patas monkey experiments may not have greatly changed the position of the center of mass. Volumetric estimates indicated that although weighting significantly affected body mass distribution, whole-body COM position moved cranially by 1 cm, or 3% of trunk length. It is possible that a 1 cm deviation is insufficient to impact locomotor behavior. Nevertheless, augmenting body mass by 10% has been shown to affect body mass distribution and gait in other animals (Lee et al., 2004). Future studies might better test the predictions of the Support Polygon Model by documenting the instantaneous position of the whole-body COM during the portions of the stride when the animal is supported by diagonal couplets alone, as this is the critical period of the stride according to the model.

Impulse data demonstrate that although forelimb vertical impulses tended to increase in the 10% body mass condition, weighting did not significantly increase impulse magnitude in any of the experimental conditions. More significant differences between conditions might have been observed with larger sample sizes. However, because primates frequently

Table 9
Gait variables by species and condition. Continuous variables correlated with speed are presented as estimated marginal means (evaluated at the grand mean of speed across groups). All other continuous variables are presented as arithmetic means. Standard errors are shown in parentheses. Asterisks indicate the significance of comparisons against the light-tailed individual (dwarf lemurs) or the control condition (patas monkey): * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Bold shading indicates a significant difference after the sequential Bonferroni correction

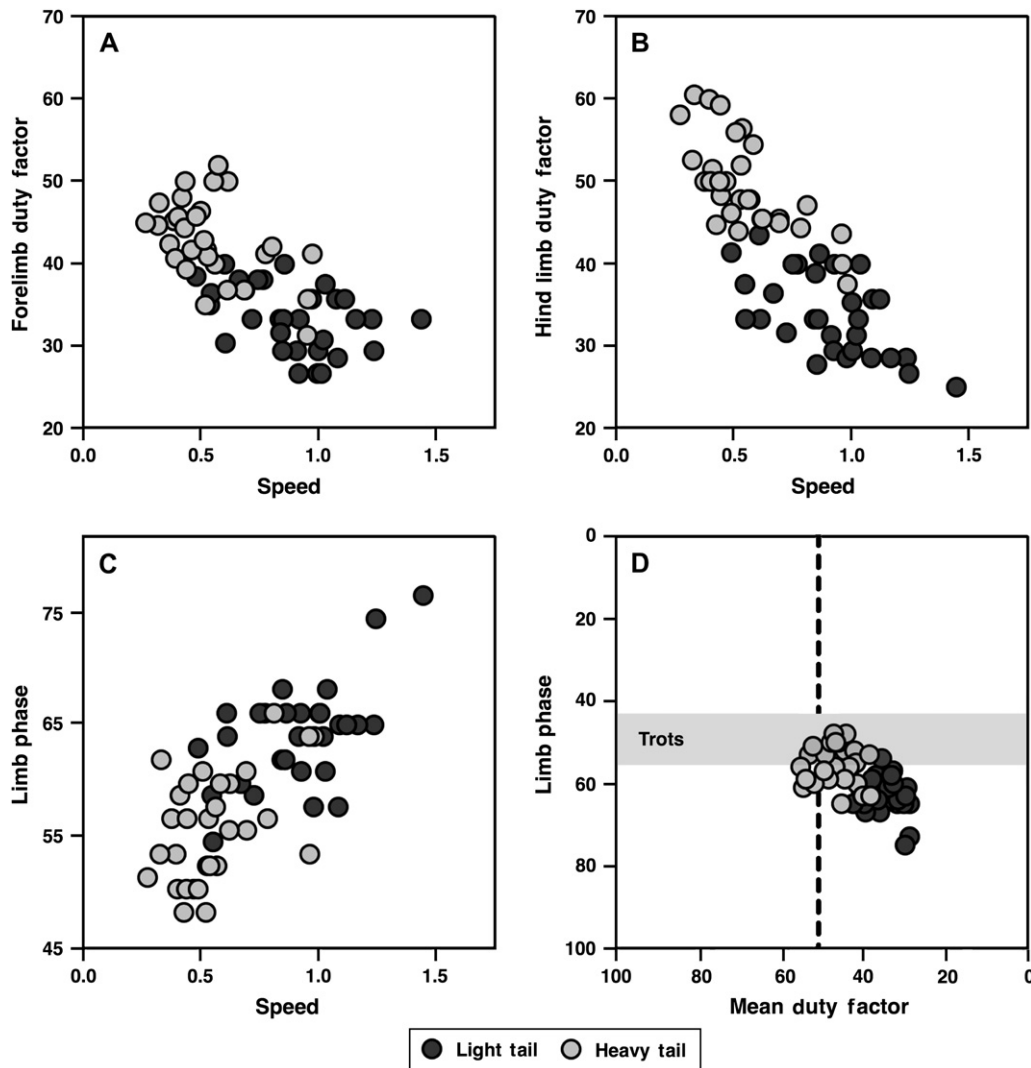|	Dwarf lemurs		Patas monkey			
	Light tail	Heavy tail	Control	7% BM	10% BM	12% BM
Speed (ms^{-1})	0.90 (0.04)	**0.54*** (0.03)**	3.58 (0.07)	3.74 (0.08)	**3.24** (0.08)**	3.47 (0.08)
Duty factor						
FL	35.0 (0.9)	**41.0*** (0.9)**	29.5 (0.5)	31.8* (0.9)	31.0* (0.6)	**33.1*** (0.7)**
HL	36.9 (0.9)	**46.4*** (0.9)**	30.4 (0.5)	31.4 (1.0)	31.2 (0.6)	**32.7** (0.7)**
Mean	36.0 (0.7)	**43.7*** (0.7)**	30.0 (0.5)	31.8* (0.9)	31.0 (0.6)	**32.6** (0.7)**
Duty factor ratio	99.5 (2.5)	**87.1*** (2.0)**	96.9 (0.9)	100.5 (1.8)	98.5 (1.2)	101.7* (1.2)
Limb phase	61.1 (0.8)	**57.3** (0.8)**	66.6 (0.5)	64.8 (1.0)	67.0 (0.5)	65.2 (0.8)
DS gaits	96.7%	**36.7%***	100%	96.2%	100%	97.1%
Trots	3.3%	**63.3%***	0%	3.8%	0%	2.9%

Fig. 3. Gait distinctions between the light-tailed and heavy-tailed dwarf lemurs. (A) Association between forelimb duty factor and speed. (B) Association between hind limb duty factor and speed. (C) Association between limb phase and speed. (D) A "gait graph" (sensu Hildebrand, 1966) of limb phase versus mean duty factor. Limb phase and duty factor are both plotted on reversed axes. Lateral sequence gaits fall on the top portion of the graph, trots in the middle (indicated by the shaded box) and diagonal sequence gaits on the bottom. Walks (strides with duty factors greater than 50) fall on the left side of the graph and runs (strides with duty factors less than 50) fall on the right side. A duty factor of 50 is indicated by the dashed vertical line.

overstride (i.e., place a hind limb contact very near to, or even in front of, the ipsilateral forelimb) obtaining single-limb impulses for an entire step is often difficult. Finally, we were only able to record impulses from a single limb during a given stride. A more complete characterization of body mass distribution between forelimbs and hind limbs requires simultaneous impulse data from all four limbs over the entire stride (Bertram et al., 1997). This could be accomplished in future studies with the use of multiple force platforms.

Caveats aside, kinematic data suggested that variations in body mass distribution were sufficient to affect some locomotor behaviors in the animals examined in this study. Both species significantly increased forelimb and hind limb duty factors in response to weighting. Previous studies of humans (Donelan and Kram, 2000), domestic dogs (Lee et al., 2004), horses (Wickler et al., 2001), wallabies (Baudinette and Biewener, 1998), and geckos (Irschick et al., 2003) have

also observed systematic changes in duty factor in conjunction with increases or decreases in body weight. In both the dwarf lemurs and the patas monkey, increases in duty factor were slightly greater in the loaded pair of limbs. Significantly lower duty factor ratios in the dwarf lemur with the heavier tail indicated that increases in hind limb duty factor outpaced increases in forelimb duty factor. Although duty factor ratios did not vary significantly among the patas monkey conditions, duty factor ratios tended to increase with weighting, suggesting that increases in forelimb duty factor slightly outpaced increases in hind limb duty factor. Overall, these results suggest that weighting redistributed body weight and whole-body COM position towards the loaded pair of limbs.

Analyses of joint kinematics also indicated that weighting had a significant effect on locomotor behavior in the dwarf lemurs. Forelimb and hind limb retraction and excursion angles were significantly greater in the individual with the heavier
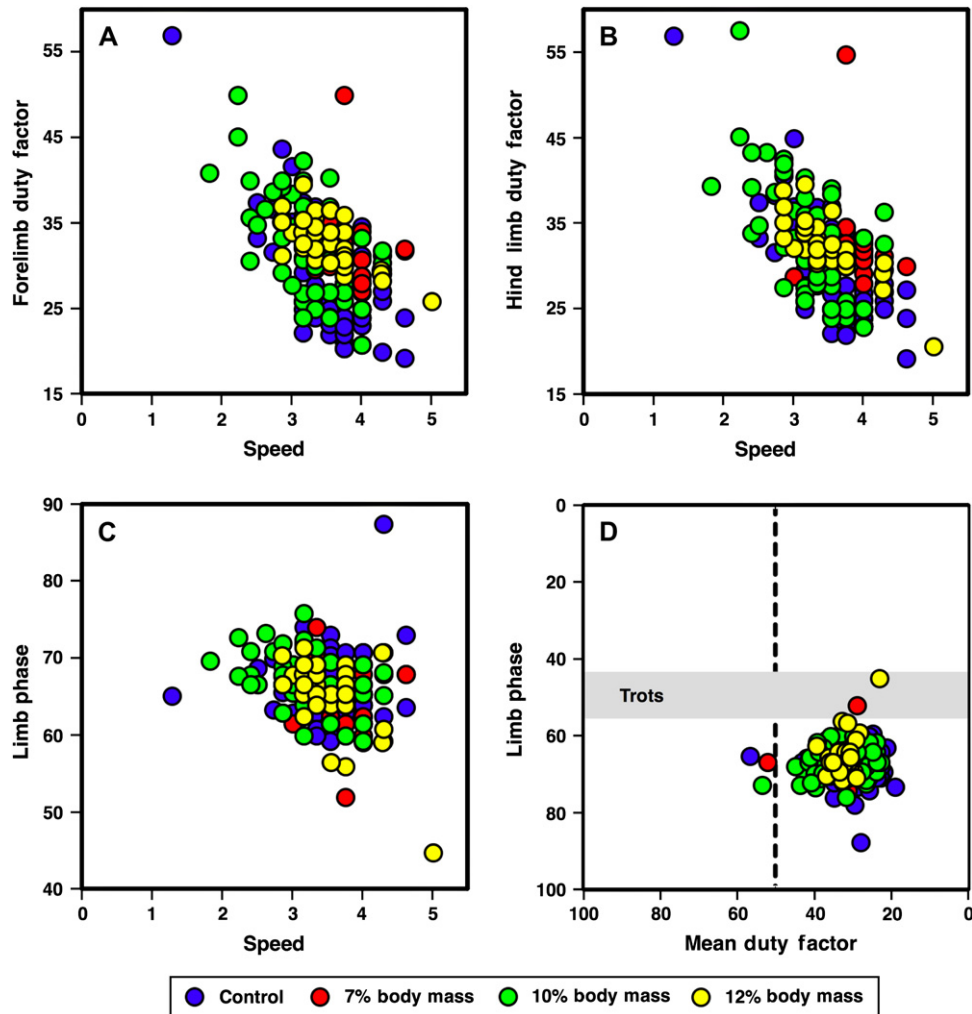
Fig. 4. Gait distinctions between the patas monkey loading conditions. (A) Association between forelimb duty factor and speed. (B) Association between hind limb duty factor and speed. (C) Association between limb phase and speed. (D) A "gait graph" of limb phase versus mean duty factor. See Fig. 3 legend for clarification.

tail. Increases in forelimb retraction angle may have allowed the heavier-tailed dwarf lemur to compensate for increased tail mass by placing the hand closer to the COM for a greater proportion of the stride, thereby redistributing body weight more evenly between the forelimbs and hind limbs. Moreover, activation of forelimb protractor musculature while the forelimb was retracted could be used to apply a pitching moment to the trunk, thereby decreasing the amount of body weight supported by the hind limbs and further compensating for changes in body mass distribution (Reynolds, 1985). It is also possible that increased retraction and excursion angles might reflect adaptations to increase stability on arboreal substrates. Greater angular excursions would allow for longer strides without altering stride frequency, thereby permitting the dwarf lemur with the heavier tail to maintain speed while mitigating increases in branch sway that might have been caused by higher weight-related substrate forces (Demes et al., 1990). Moreover, because contact time is a function of stride length and speed, increases in angular excursion may partially account for observed speed-independent increases in forelimb and hind limb duty factor. Contradicting

our predictions, weighting had no effect on patas monkey limb kinematics, indicating that the animal made no attempt to compensate kinematically for experimentally induced variations in body mass distribution.

Overall, limb phase results did not provide strong endorsement for the Support Polygon Model. The model would predict that caudal shifts in the position of the COM should increase both limb phase and the relative frequency of DS footfall patterns, whereas cranial shifts in the position of the COM should decrease limb phase and increase relative frequency of trots and LS footfall patterns. In contrast, a posterior weight shift in the lemur with the heavier tail was associated with significantly lower limb phases and significantly more trots than observed in the dwarf lemur with the smaller tail mass. Moreover, a cranial shift in the position of the patas monkey's whole-body COM had little effect on preferred footfall patterns, although experimental deviations of COM position were admittedly slight. Nevertheless, the Support Polygon Model predicts that an animal with the whole-body COM positioned cranial to the midpoint of the trunk should experience periods of instability when attempting to use DS

gaits. Yet we found that the patas monkey used DS gaits in 99% of all of the strides analyzed, despite having an unloaded COM located at 43% of trunk length.

Future studies may find verification of the Support Polygon Model in different contexts. For example, studies of locomotor development may offer a "model system" in which to probe the factors influencing gait selection in primates (Shapiro and Raichlen, 2005, 2006). Prior research has demonstrated that the hallmark characteristics of primate quadrupedal locomotion are not present during initial locomotor efforts by infants, but rather develop slowly over the course of postnatal ontogeny. In particular, young primates show great variability in gait selection, frequently using LS gaits and functional trots in addition to DS gaits (Rollinson and Martin, 1981; Hurov, 1982; Kimura, 1987; Vilensky and Gankiewicz, 1989; Shapiro and Raichlen, 2005, 2006). Moreover, an ontogenetic decrease in relative head mass and increase in relative hind limb mass shift the whole-body COM caudally as animals grow (Grand, 1983; Turnquist and Wells, 1994; Johnson, 1998). As such, ontogeny may offer a "natural experiment" (German and Meyers, 1989; Hurov, 1991) with which to test hypothetical form-function relationships influencing footfall sequence in primates and other mammals.

If future studies with larger sample sizes and greater manipulations of COM position continue to suggest that gait selection is not governed by the differences in body mass distribution, what other factors might lead to primates' habitual use of DS gaits? Some researchers have argued that DS gaits facilitate arboreal locomotion, helping primates to limit destabilization by gripping branches with contralateral fore- and hind limbs simultaneously, allowing them to exert opposing torques that could counteract any mediolateral balance disruptions (Prost, 1969; Meldrum, 1991; Crompton et al., 2000; Schmidt, 2005; but see Stevens, 2006) or facilitate the exploration of upcoming untested supports (Cartmill et al, 2002; Schmitt and Lemelin, 2002; but see Shapiro and Raichlen, 2005). Others have suggested that the use of DS gaits is predicated on primates' having greater cortical control over limb movements, allowing them to utilize more flexible patterns of interlimb coordination than would be possible for other mammals (Vilensky and Larson, 1989; Stevens, 2006). Certainly, future experimental studies should examine these and other explanations for primates' rather unique use of DS gaits.

Overall, this study provisionally supports the idea that quadrupedal primates should not be modeled as "static tabletops" (Vilensky and Larson, 1989), as implicitly assumed under the Support Polygon Model. Instead, dynamic equilibrium and inertial forces play a more important role in maintaining stability during regular locomotion (Tardieu, 1991; Full et al., 2002). Indeed, both species examined in this study predominantly used running gaits, in which inertial forces and dynamic stability would be expected to become rather important. Additionally, it is possible that the natural and experimental shifts in body mass distribution are insufficient to disrupt stability on horizontal, level substrates. Perhaps the predictions of the Support Polygon Model are only realized when balance is challenged more substantially, such as when animals are walking on sloped substrates (Prost and Sussman, 1969; Rollinson and Martin, 1981; Vilensky, 1994; Stevens, 2003).

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