

Adaptive value of ambling gaits in primates and other mammals

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Accepted 22 March 2006

Summary

At speeds between the walk and the gallop, most mammals trot. Primates almost never trot, and it has been claimed that they transition directly from a walk to a gallop without any distinctive mid-speed running gait. If true, this would be another characteristic difference between the locomotion of primates and that of most other quadrupedal mammals. Presently, however, few data exist concerning the actual presence or absence of intermediate-speed gaits (i.e. gaits that are used between a walk and a gallop) in primates. Video records of running in twelve primate species reveal that, unlike most other mammals, all the primates studied almost exclusively adopt an ‘amble’ – an intermediate-speed running gait with no whole-body aerial phase – rather than trot. Ambling is also common in elephants and some horses, raising the

question of why ambling is preferred over trotting in these diverse groups of animals. Mathematical analyses presented here show that ambling ensures continuous contact of the body with the substrate while dramatically reducing vertical oscillations of the center of mass. This may explain why ambling appears to be preferable to trotting for extremely large terrestrial mammals such as elephants and for arboreal mammals like primates that move on unstable branches. These findings allow us to better understand the mechanics of these unusual running gaits and shed new light on primate locomotor evolution.

Key words: primate, ambling, gait, locomotion, running, walking, mammal, evolution.

Introduction

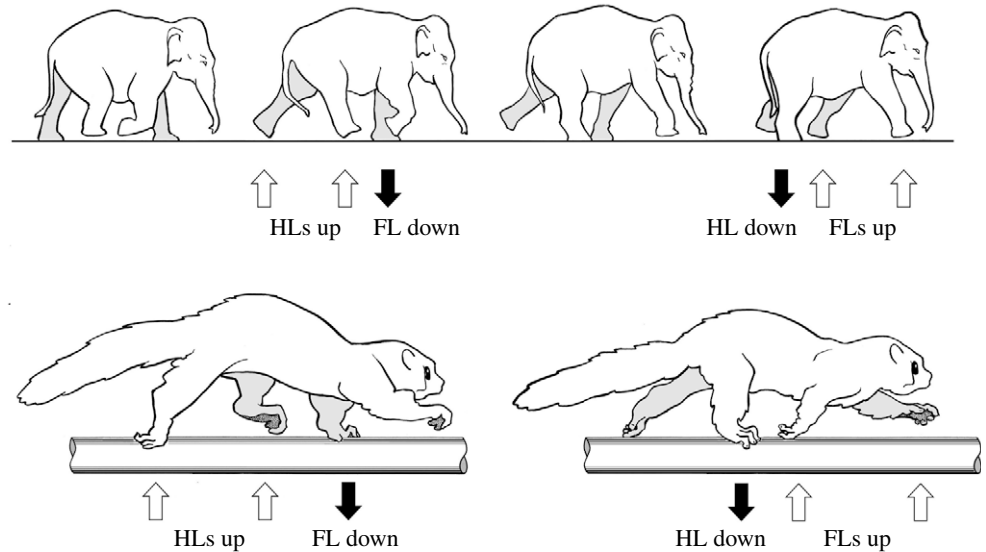
As most quadrupedal mammals increase speed, they shift from a symmetrical walking gait with no aerial phase to a running gait with a whole-body aerial phase (Cartmill et al., 2002; Gambaryan, 1974; Hildebrand, 1976; Hildebrand, 1985; Howell, 1944; Muybridge, 1957). At their fastest speeds, quadrupedal mammals generally use an asymmetrical running gait such as a gallop (Gambaryan, 1974; Hildebrand, 1985; Howell, 1944; Muybridge, 1957). However, at speeds between that of a walk and a gallop, quadrupedal mammals often use symmetrical running gaits that have an aerial phase and in which the feet strike down in diagonal pairs (trot) or unilateral pairs (pace) (Cartmill et al., 2002; Gambaryan, 1974; Hildebrand, 1985; Howell, 1944; Muybridge, 1957). Such symmetrical running gaits are faster than walking gaits but still provide relatively longer periods of bipedal support by both a forelimb and a hindlimb than does galloping (Cartmill et al., 2002). However, trots or paces also produce marked increases in vertical oscillations of the body and high whole-body peak forces compared to either walking or galloping (Biewener and Taylor, 1986; McMahon, 1985; Rubin and Lanyon, 1982).

Recently, several studies have reported on the mechanics of

some unusual symmetrical running gaits that do not involve a whole-body aerial phase (Biknevicius et al., 2003; Biknevicius et al., 2004; Hutchinson et al., 2003; Robilliard, 2005). Hutchinson and colleagues (Hutchinson et al., 2003) showed that when elephants increase speed, they shift from a walk to a symmetrical gait in which the forelimbs and hindlimbs undergo separate, non-overlapping aerial phases, with the feet striking the ground independently rather than in pairs (Fig. 1). This pattern of locomotion has previously been reported for elephants (Gambaryan, 1974; Howell, 1944) and horses (Barrey, 2001; Biknevicius et al., 2003; Biknevicius et al., 2004; Nicodemus and Clayton, 2003; Muybridge, 1957; Robilliard, 2005; Zips et al., 2001). These gaits have been called ‘ambles’ (Muybridge, 1957), ‘running walks’ or ‘the single foot’ (Hildebrand, 1967), and ‘tölts’ or ‘toelts’ (Barrey, 2001; Biknevicius et al., 2003; Biknevicius et al., 2004; Nicodemus and Clayton, 2003; Robilliard, 2005; Zips et al., 2001). We here adopt Muybridge’s term ‘amble’.

Ambles do not involve a whole-body aerial phase, thus ensuring that elephants and other large animals using this gait are always supported by at least one foot when increasing speed. These mammals may adopt this odd gait in order to

Fig. 1. Ambling gait cycle in an Asian elephant (*Elephas maximus*) (top) [traced from images in (Gambaryan, 1974)] and a fat-tailed dwarf lemur (*Cheirogaleus medius*) (bottom) (traced from our videotape). Note that during an ambling gait cycle, a single forelimb (FL) or hindlimb (HL) provides support for the entire body while all the other limbs are off the substrate. Mirror-image (R/L) inversions in limb pairs between the two species at corresponding phases of the cycle reflect the difference between the lateral-sequence amble of the elephant and the diagonal-sequence amble of the lemur.



avoid a whole-body aerial phase and associated vertical oscillations of the center of mass during running (Gambaryan, 1974; Hutchinson et al., 2003). This same effect has been noted in connection with the use of the amble (or 'tölt') among certain breeds of horses (Barrey, 2001; Biknevicius et al., 2003; Biknevicius et al., 2004). The classification of ambling as a type of walking or running has been debated since ambling shares characteristics with both symmetrical gait categories. The lack of a whole-body aerial phase suggests that ambles are a type of walk, and whole body mechanics collected by Robilliard support this idea (Robilliard, 2005). Biknevicius et al. argued that horses use similar spring-like limb and body mechanics during ambling and trotting (Biknevicius et al., 2003; Biknevicius et al., 2004). In this paper we refer to the amble as a 'running' gait because of the forelimb or hindlimb aerial phase and the single-peak shape of the ground reaction forces (Biknevicius et al., 2004). This categorization is not intended to imply anything about the exchange of potential and kinetic energy during ambling.

Despite considerable interest in the mechanics of ambling, no clear functional explanation exists as to why these symmetrical running gaits are used by some mammals instead of a trot or pace. This is partly because so few data exist on ambling in mammals.

An examination of locomotion in primates provides a new opportunity to explore the functional correlates of ambling. The quadrupedal locomotion of primates is unusual among mammals in many ways (Cartmill et al., 2002; Cartmill et al., 2006; Demes et al., 1994; Hildebrand, 1967; Kimura et al., 1979; Larson, 1998; Larson et al., 2000; Larson et al., 2001; Lemelin and Schmitt, 2006; Lemelin et al., 2003; Rollinson and Martin, 1981; Schmitt, 1999; Schmitt and Lemelin, 2002; Vilensky, 1989; Vilensky and Larson, 1989). The features that distinguish the walking gaits of primates include the prevalence of diagonal-sequence gaits (in which the contact of each hindfoot is followed by that of the contralateral forefoot), the use of highly protracted arm positions at forelimb

touchdown, and relatively higher vertical peak forces on the hindlimb compared to the forelimb. It has been argued that these features are part of a suite of basal primate adaptations associated with locomotion and foraging on terminal, flexible branches (Cartmill et al., 2002; Cartmill et al., 2006; Larson, 1998; Lemelin and Schmitt, 2006; Lemelin et al., 2003; Schmitt, 1999; Schmitt and Lemelin, 2002).

In addition to those features described, it has also been reported that primates almost never adopt a running trot or pace (Demes et al., 1990; Demes et al., 1994; Hildebrand, 1967; Preuschoft and Gunther, 1994; Rollinson and Martin, 1981; Schmitt, 1995; Vilensky, 1989). Some have argued that primates eschew these gaits in order to avoid abrupt changes in vertical oscillations of the body and high peak ground reaction forces (Demes et al., 1990; Demes et al., 1994; Schmitt, 1999).

Despite the widely accepted claim that primates rarely trot or pace, it remains unclear whether primates shift directly from a walk to a gallop as they increase speed or use a previously unidentified gait during this transition. Limited qualitative observations suggest that primates may in fact amble rather than trot (Hildebrand, 1967; Howell, 1944; Rollinson and Martin, 1981; Vilensky and Larson, 1989) (Fig. 1). For example, ambling has been suggested to be the gait used between a walk and a gallop in baboons (Howell, 1944), and it has also been argued that ambling is used by lemurs (Hildebrand, 1967). To date, no quantitative data exist on the distribution and details of this unusual gait in a broad sample of primates.

The fact that ambling appears to be a common, naturally occurring locomotor mode in primates provides an opportunity to explore the biomechanical and adaptive significance of ambling. This project examines the locomotor behavior of 12 primate species to test the hypothesis that primates adopt an amble rather than a trot as their preferred symmetrical running gait. A second hypothesis to be tested, based on the model of Cartmill et al., is that during ambling, primates should time

their footfalls in ways that maximize bipedal support by contralateral limbs (i.e. achieve a diagonality close to the trot) but prevent an aerial phase (Cartmill et al., 2002). In addition to testing these two hypotheses, a model was developed to explore the ways in which ambling influences vertical oscillations of the center of mass. This model was used to develop new ideas about why ambling may be preferred over trotting in some mammals. By studying the frequency and mechanics of ambling in a large phylogenetically and ecologically diverse group of primate species, it will be possible to draw some general conclusions about the adaptive value of this unusual gait pattern in primates and other mammals and better understand the origins of primate locomotor patterns.

Materials and methods

To ascertain the distribution and functional significance of ambling, the locomotor behavior of 12 primate species under laboratory conditions was reviewed and the footfall sequence and timing for all ambles was quantified. All animals were video recorded while walking and running on long runways and raised horizontal poles. Pole diameter varied from 0.625 cm to 11.25 cm (for details, see Lemelin and Schmitt, 2006; Schmitt, 2003a; Schmitt, 2003b; Schmitt and Lemelin, 2004). The species studied included primates that vary widely in body size and substrate preference. Table 1 provides information on species, body masses, numbers of individuals used and the substrates the animals moved on. All locomotor bouts were recorded by at least one lateral-view video camera (60 Hz; shutter at 1/1000 s). Animals were allowed to move

freely within a Plexiglas enclosure (6 m×1 m×1 m) at the Primate Locomotion Laboratory at the State University of New York at Stony Brook or in a Lexan enclosure (6 m×0.66 m×0.66 m) at the Animal Locomotion Laboratory at Duke University and at the Duke University Primate Center. A total of 1800 min of videotape were available for this study.

This study proceeded along four analytical phases. In the first phase, we determined whether gaits fitting the definition of an amble could be found in all the species available for this study. The goal in this phase was to survey the presence of ambles in a sample of primate species. To accomplish this, we searched all video records of all animals on all substrates looking specifically for ambles and counted their occurrence. Ambles were visually identified as symmetrical gaits in which there was an aerial phase for the forelimbs, the hindlimbs, or both, but never for all four limbs at once. Only one stride per locomotor bout (i.e. per traverse of the enclosure) was scored.

The goal of the second phase of this analysis was to determine the relative frequency of ambling and other gaits in the sample. In this phase we scored the frequency of ambling as part of the overall locomotor behavior of the animals under study and ascertained the frequency of other gaits, including trots and paces, using the same video records. To determine the frequency of ambling, an even sampling across videotapes was necessary. Forty steps were analyzed for each species. Steps were analyzed only on the type of substrate commonly used by the animals in the wild. For example, data for patas monkeys (*Erythrocebus patas*) were collected from videos of an animal moving on the ground, whereas data for the fat-tailed dwarf lemur (*Cheirogaleus medius*) were collected from

Table 1. *Sample composition and size*

Species name	Mass (g) ¹	Number of individuals	Substrate ²	Number of ambles ³
<i>Microcebus murinus</i>	61	4	Pole	22
<i>Mirza coquereli</i>	315	3	Pole	88
<i>Cheirogaleus medius</i>	282	4	Pole	73
<i>Loris tardigradus</i>	266	3	Pole	10
<i>Callithrix jacchus</i>	320	2	Pole	56
<i>Saguinus fuscicollis</i>	350	2	Pole	25
<i>Ateles geoffroyi</i>	7500	1	Pole	8
<i>Macaca fascicularis</i>	6546	2	Pole	19
<i>Macaca mulatta</i>	4475	2	Ground	61
<i>Chlorocebus aethiops</i>	3575	2	Ground	21
<i>Erythrocebus patas</i>	8185	1	Ground	18
<i>Papio anubis</i>	19 200	2	Ground	24

All individuals are adult animals.

¹Average species body mass for males and females combined (Fleagle, 1999).

²'Substrate' refers to the specific substrate considered for each primate species during the second phase of this study (see text for details). During the first phase, data were collected on a variety of pole sizes (for details, see Schmitt, 2003a; Schmitt, 2003b; Schmitt and Lemelin, 2002; Schmitt and Lemelin, 2004; Lemelin and Schmitt, 2004) and the ground – with the exception of the slender loris (*Loris tardigradus*), which never walked on the ground.

³The absolute number of ambles observed during the first phase of this study involving a search of 1800 min of video in which only ambles were noted. These values are recorded and presented to examine whether ambles are common in all primates. The relative frequency of ambles and other gaits is displayed in Table 2.

videos of subjects moving on a horizontal pole. To sample without bias, the total time of available videotape for a species (e.g. 120 min) was divided evenly to allow for collection of 40 strides (e.g. 3 min sample intervals). At each time interval, the gait being used by the animal was recorded. This approach provided a conservative estimate of the frequency of ambling in primates and as such it may have underestimated its frequency in species adopting the amble less commonly (i.e. ambling events may not be evenly distributed).

In the third analytical phase, we calculated the timing of the footfalls following a published method (Cartmill et al., 2002), which allows the calculation of the timing of contact and lift-off for each limb for an entire stride. These values were used to calculate duty factor (i.e. foot-ground contact time divided by stride time) for any limb and diagonality (i.e. the percent phase difference between ipsilateral fore- and hindlimb cycles). Data were then plotted on a bivariate graph. To evaluate the symmetry of a gait cycle, we followed Cartmill et al.'s convention (Cartmill et al., 2002). If the time from the first hind footfall to the next (contralateral) hind footfall was greater than 60% or less than 40% of the total stride period ($\pm 10\%$ deviation from symmetry), the gait cycle was considered asymmetrical and rejected from further analysis. Symmetrical gaits with a limb duty factor less than 50% were identified as running gaits. Those with a diagonality value of $50\pm 5\%$ were identified as trots. Those with a diagonality value of $100\pm 5\%$ were identified as paces. Ambles were those symmetrical gaits with a duty factor less than 50% in at least one limb and diagonality between 55% and 95% or 5% and 45% such that no whole-body aerial phase occurred during the stride. The model (Cartmill et al., 2002) suggested that adjustments in footfall patterns as speed increased during walking were governed in part by the value of maintaining relatively long periods of bipedal support in which the body is supported by a forelimb and hindlimb. A similar model was applied to the ambling data.

The goal of the fourth and last phase of the analysis was to model the way in which ambling gaits may influence vertical oscillations of the center of mass compared to trotting. A model, rather than empirical data, was used in this study because our primates trotted so rarely and on the few occasions that they did so we were unable to record force plate data. Ideally, we would have liked to compare substrate reaction forces and movements of the center of mass during trotting and ambling in the animals themselves, but we were unable to do so for this study.

The theoretical foundations of the model are as follows. During trotting, diagonal limb pairs strike the ground simultaneously, thus generating peak forces twice that of a single limb acting on the whole body. In contrast, ambling animals should generate much lower peak forces acting on the whole body because the periods of simultaneous forelimb and hindlimb support are brief, thereby distributing the peak limb forces more evenly throughout the stride. Lower whole-body peak forces would be expected to reduce the vertical oscillation of the center of mass.

Vertical oscillations of the center of mass for ambling and trotting gaits were compared by mathematically modeling whole-body vertical ground reaction force patterns. In order to make this model operational, we specified values for the individual limb vertical ground reaction force, duty factor and diagonality. Vertical ground reaction force patterns for individual limbs were modeled following published methods (McNeill Alexander and Jayes, 1978). This requires selecting a shape factor for the force curves that will be used for modeling the vertical force pattern for trotting and ambling. A shape factor value of 0.0 (i.e. one-half sine wave) was chosen because it approximates the actual force patterns applied to the ground by trotting mammals and ambling primates. It is also consistent with the shape of single-limb peak force curves recorded by Biknevicius et al. for ambling horses (Biknevicius et al., 2004). We determined this relationship through data found in the literature and from our laboratory. The actual empirical value for this shape factor is -0.03 ± 0.06 (mean \pm s.d.), based on a sample of representative steps from three dogs (McNeill Alexander and Jayes, 1978), one horse (McGuigan and Wilson, 2003), three Old World monkeys and two prosimians (unpublished primate data from our laboratory). The data from our laboratory were collected from several single footfalls for five individuals. The method for force plate data collection is described in detail elsewhere (Schmitt, 1999; Schmitt, 2003a). All data were collected as the animal crossed an isolated section of the force-plate. Force-plate output was processed with Motus 2000 software and filtered with a Butterworth 30 Hz filter. The shape factor was then calculated following the mathematical model used (McNeill Alexander and Jayes, 1978). These values were used to set the parameters for the model. In addition, the empirical values for a single ambling step with both forelimb and hindlimb contacts for one primate were used to compare the output of the model with actual values.

Holding everything else equal, these modeled individual-limb forces were used to reconstruct whole-body ground reaction force patterns for the complete range of possible trotting and diagonal-sequence ambling combinations using a custom-written program with LabVIEW software (v 4.0.1, National Instruments, Austin, TX, USA). To do so, whole-body ground reaction force traces were created for 36 diagonality–duty factor combinations, where diagonality varied from 0.5 to 0.75 and duty factor varied from 0.25 to 0.5. These reconstructed, whole-body ground reaction forces were used in turn to calculate the vertical oscillations (i.e. displacements) of the center of mass, using Cavagna's methods (Cavagna, 1975).

Results

Table 1 includes the results of the first analytical phase, in which all ambles observed for the entire sample were recorded. These data provide information on how many ambles were observed in this phase of the study and are relevant to answering the question of whether or not ambling is common in primates. Four hundred and twenty-five gait cycles were

Table 2. Frequency of all gait types observed and relative frequency of ambles and canters in 12 primate species

	Walk	Amble	Trot	Canter	Gallop	Half-bound	Relative frequency (%)		
							Ambles overall	Ambles of symmetrical runs	Canter of asymmetrical runs
<i>Microcebus murinus</i>	22	18	0	0	0	0	45	100	–
<i>Mirza coquereli</i>	25	13	0	2	0	0	33	100	100
<i>Cheirogaleus medius</i>	10	17	1	10	2	0	43	94	83
<i>Loris tardigradus</i>	39	1	0	0	0	0	3	100	–
<i>Callithrix jacchus</i>	4	3	4	22	3	4	8	43	76
<i>Saguinus fuscicollis</i>	0	2	0	32	6	0	5	100	84
<i>Ateles geoffroyi</i>	38	2	0	0	0	0	5	100	–
<i>Macaca fascicularis</i>	40	0	0	0	0	0	0	–	–
<i>Macaca mulatta</i>	23	12	0	5	0	0	30	100	100
<i>Chlorocebus aethiops</i>	14	4	0	12	10	0	10	100	55
<i>Erythrocebus patas</i>	39	1	0	0	0	0	3	100	–
<i>Papio anubis</i>	27	6	0	6	1	0	15	100	86
Totals	281	79	5	89	22	4	17	94	73

For each species, a total of 40 observations were made at evenly spaced time intervals throughout the video records.

visually identified as ambles. Ambling was documented in all 12 species, although this gait was more common in running quadrupeds like the Coquerel's dwarf lemur (*Mirza coquereli*) and rhesus macaque (*Macaca mulatta*) than in more deliberate quadrupeds like the slender loris (*Loris tardigradus*) or the highly suspensory spider monkey (*Ateles geoffroyi*).

Table 2 shows the absolute number of each gait type observed from a random sample of 40 steps for each species. It also includes the percentage of symmetrical running gaits that are ambles and the percentage of asymmetrical running gaits that are canters. These results show that ambling was considerably more common than trotting in primates (17% vs 1% of all gaits observed). Ambling represents 94% of all symmetrical running gaits observed (Table 2). The canter, an asymmetrical gait with no whole-body aerial phase (Howell, 1944), was preferred to galloping (18% vs 5% of all gaits observed). Canters represent 73% of all asymmetrical running gaits observed (Table 2). The amble and the canter both are gaits that allow animals to maintain at least one foot in contact with the substrate during a stride. As mentioned above, the sampling method for this phase of the analysis may have underestimated the frequency of ambling gaits relative to other gaits. Although several ambles were found for the crab-eating macaque (*Macaca fascicularis*) in the first video analysis phase (Table 1), the systematic sampling yielded no ambles at all (Table 2).

The results of the analysis of footfall timing are displayed in Fig. 2. Footfall timing of only 295 of the original 425 gait cycles was calculated. Some steps were rejected because of asymmetry and others were not used because of incomplete video sequences due to narrow camera zoom. A bivariate graph of forelimb duty factor (S_f ; percent of the stride interval during which the forelimb contacts the substrate) vs diagonality (phase difference between ipsilateral fore- and hindlimb touchdowns) (Fig. 2) reveals that ambles cluster around a line on the graph

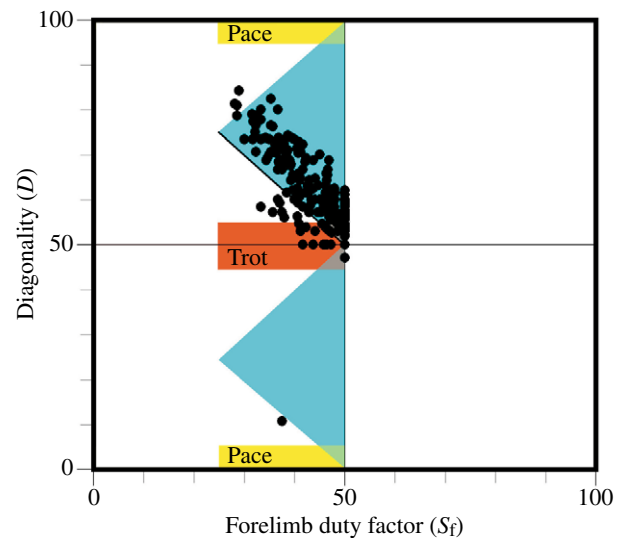
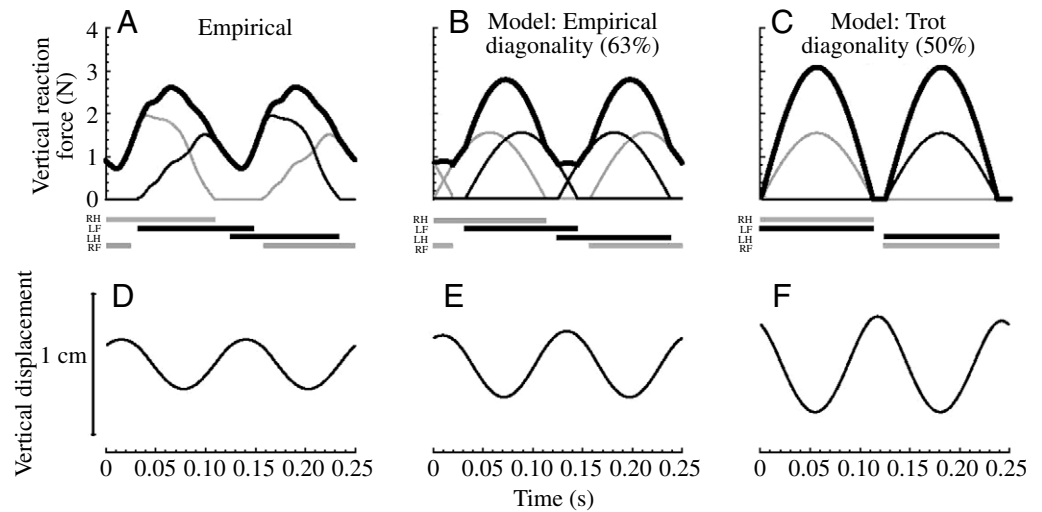


Fig. 2. Modified Hildebrand diagram showing distribution of the 295 gait cycles for which diagonality (D) and duty factor (S_f) were calculated (i.e. in which deviations from symmetry were 10% or less for both forelimbs and hindlimbs). Gait cycles plotted within the blue triangles lack a whole-body aerial phase. In the upper blue triangle (diagonality $>50\%$), animals are using diagonal-sequence ambles. In the lower blue triangle (diagonality $<50\%$), animals are using lateral-sequence ambles. Rectangular bands indicate running trots (in red) (diagonality equal to or near 50%) and paces (in yellow) (diagonality equal to or near 100% or 0%). The diagonal black line represents the equation diagonality = 100 – forelimb S_f [forelimb duty factor is the relevant duty factor in this case, based on the mathematical model used (Cartmill et al., 2002)]. Those gait cycles plotting directly on that line have maximal duration of bipedal support periods. Primate ambling strides plot above but close to the line, thus eliminating the whole-body aerial phase while preserving near-maximal periods of bipedal support. Note that some of the data represent running trots (mostly for *Callithrix jacchus*).

Fig. 3. Empirical and modeled vertical ground reaction forces and displacements of the center of mass. (A) Empirical vertical ground reaction force data for *Cheirogaleus medius* (body mass=180 g) while ambling at 1.2 m s^{-1} along a 28 mm diameter pole. Thin lines correspond to the individual limb forces and the thick line is the total (i.e. summed) force. The black thin line represents the left fore- and hindlimb forces obtained from sequential, overlapping footfalls on a pole segment connected to a force platform. The left limb forces were replicated a half-cycle out of phase to obtain right limb forces (gray lines). Individual limb forces were modeled following the mathematical model used (McNeill Alexander and Jayes, 1978) using empirical values for body mass and duty factor. (B) Model forces reconstructed for a whole stride for a diagonality of 63% (i.e. the diagonality used by *C. medius* in A). (C) Model forces reconstructed for a diagonality of 50% (i.e. a running trot). Horizontal bars below the reaction forces represent the footfall patterns (RH=right hindlimb, LF=left forelimb, LH=left hindlimb, and RF=right forelimb). The vertical displacements of the center of mass corresponding to the vertical force data in A–C are shown in D–F, respectively. Displacement data were calculated following published methods (Cavagna, 1975).



representing the following linear equation: $\text{diagonality} = 100 - S_f$. [Forelimb duty factor is the relevant duty factor in this case for the same sort of mathematical reasons that make hindlimb duty factor solely relevant in computing optimal diagonalities for diagonal sequence walks, in which hindfoot contact is followed by that of the contralateral forefoot (Cartmill et al., 2002), p. 408]. Those gaits that plot directly on this line will maximize the duration of bipedal support phases in the cycle without introducing a whole-body aerial phase. Gaits that plot below the line approach more closely to the trot, with diagonally opposite limbs moving in near-synchrony, thereby providing longer periods of bipedal support by a contralateral forelimb and hindlimb but also introducing a whole-body aerial phase. For gaits that plot above the line, bipedal support periods are reduced but there is no whole-body aerial phase. Most of the sampled primate gaits fall above the line, but close to it (Fig. 2).

The results of the final part of the analysis, which involved mathematically modeling ambling and trotting whole-body ground reaction force patterns for a range of possible diagonality–duty factor combinations, are displayed in Figs 3 and 4. Empirical data of forces and vertical displacements of the center of mass during ambling correspond closely to those we modeled for a running gait with a duty factor of 45% and a diagonality of 63% (i.e. amble) (Fig. 3). They also show that ambling greatly reduces the whole-body vertical reaction forces and displacement fluctuations compared to running gaits with a diagonality of 50% (i.e. trot) (Fig. 3). On the basis of the results of our model for a range of duty factor and

diagonality values, it was concluded that reductions in vertical displacements of the center of mass are greatest as duty factor decreases and diagonality approaches 75% (Fig. 4), which is where the majority of our primate data cluster at the lowest

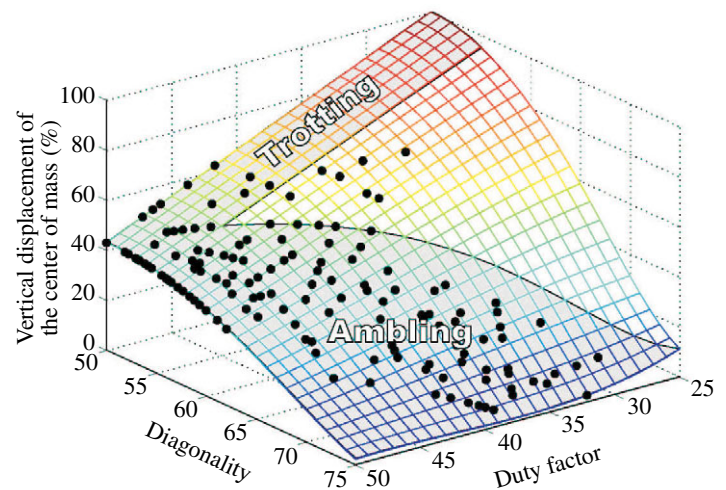


Fig. 4. Vertical displacement of the center of mass across a range of different diagonality and duty factor combinations, computed from a mathematical model of the vertical component of the force exerted by the foot on the ground (McNeill Alexander and Jayes, 1978). Vertical-displacement data are presented for diagonalities of 50–75% and duty factors of 50–25%. Empirical data (black dots) are plotted at the actual diagonality: duty factor combinations used by the primates in our sample. Ambling results in smaller vertical oscillations of the center of mass because the individual limb forces are more uniformly distributed throughout the stride, which reduces the peak force acting on the body.

observed duty factors (Fig. 2). For a duty factor value of 35%, the predicted vertical displacement of the center of mass during trotting (i.e. diagonality of 50%) is more than 50 times greater than during ambling with a diagonality of 75% (Fig. 4).

Discussion

This study of a diverse sample of primate species found that at speeds between the trot and a fast gallop, primates prefer the amble or the canter. Both gaits allow animals to maintain contact with the substrate with at least one limb at all times. These data support our hypothesis that primates adopt an amble rather than a trot as their preferred symmetrical running gait.

Cartmill et al. argued that during walking, footfall timing is governed by the value of maintaining relatively long periods of support on maximized support polygons (Cartmill et al., 2002). Trotting maintains long periods of bipedal support by contralateral forelimbs and hindlimbs, but also introduces a whole-body aerial phase. In contrast, ambling eliminates the whole-body aerial phase, thus allowing an animal to maintain continuous contact with the substrate, but can also reduce the duration of bipedal support by contralateral limbs. The primates we observed in this study generally fall above the line that represents a maximized duration for contralateral bipedal support phases without introducing a whole-body aerial phase (Fig. 2). This pattern suggests that eliminating the aerial phase takes precedence over the maintenance of relatively long periods of bipedal support. However, the data on the primates follow the trend of the line in Fig. 2, suggesting that maximizing bipedal support is still an important secondary goal.

Diagonal-sequence walking gaits (i.e. contact of the right hindfoot followed by that of the left forefoot) are typical for walking primates (Cartmill et al., 2002; Hildebrand, 1967; Muybridge, 1957; Vilensky, 1989; Vilensky and Larson, 1989). All ambles we observed in our primate sample (except for one cycle) were diagonal-sequence as well (Fig. 2). This suggests that a diagonal sequence footfall pattern typifies both the walking and running gaits of primates. In contrast, ambles observed in elephants (Fig. 1) and horses are uniformly lateral-sequence (i.e. contact of the right hindfoot followed by that of the right forefoot) (Biknevicius et al., 2004; Hutchinson et al., 2003).

Diagonal-sequence walking gaits may provide a biomechanical advantage in terms of stability and safety while foraging on terminal branches (Cartmill et al., 2002; Cartmill et al., 2006; Larson, 1998; Lemelin et al., 2003; Lemelin and Schmitt, 2006; Rollinson and Martin, 1981; Schmitt and Lemelin, 2002; Vilensky and Larson, 1989). It has been argued that this arboreal milieu (i.e. thin and flexible branches) was critical to the early evolution of primates (Cartmill, 1974) and that diagonal-sequence gaits, and other unique aspects of primate locomotion, are part of an adaptive complex associated with this milieu (Cartmill et al., 2002; Cartmill et al., 2006; Larson, 1998; Lemelin et al., 2003; Lemelin and Schmitt, 2006; Schmitt and Lemelin, 2002). We hypothesize that ambling represents another characteristic part of this complex

of locomotor traits that evolved very early in primate history to facilitate movement on thin branches.

Why is ambling preferable to trotting in a fine-branch arboreal environment? Our mathematical models show that adopting an amble rather than a trot allows animals to maintain a flatter trajectory of the center of mass, as suggested for elephants (Hutchinson et al., 2003). By excluding a true aerial phase, maintaining contact with the substrate with at least one limb at all times, and avoiding the simultaneous contact of limb pairs (as in a trot), the amble allows animals to avoid relatively high whole-body oscillations and to moderate whole-body peak forces when increasing locomotor speed. This could be important to animals that forage on flexible and unstable terminal branches and that may want to avoid being seen or oscillating the support when moving fast. Biknevicius et al. reported that peak single-limb forces are lower in horses during ambling compared to trotting, possibly due to changes in duty factor or limb mechanics (Biknevicius et al., 2004). They found no abrupt peak force transition when horses shift from a walk to an amble, a finding that is also consistent with preliminary force data collected in primates walking and ambling (Hanna et al., 2003).

The conclusions of this study apply to primates and primate evolution but also provide a better understanding of the use of ambling by nonprimate mammals. Although primates and elephants may have developed ambling in different contexts and for different functional reasons, the biomechanical advantages of ambling gaits appear to be the same for both, namely, continuous contact with the substrate and reduced whole-body forces and vertical oscillations of the center of mass.

We are grateful for the extensive help and support of Susan Larson and Jack Stern at the Primate Locomotion Laboratory at the State University of New York at Stony Brook, Julie Ives, Stephanie Combes, Bill Hess and Bill Hylander at the Duke University Primate Center, and Ann Zumwalt and Anita Pai in the Animal Locomotion Laboratory at Duke University. We are grateful to John Hutchinson, Jim Usherwood, and Alan Wilson for insightful discussions. We also thank Rodger Kram, John Hutchinson, Chris Wall and two anonymous reviewers for helpful comments on this project and on early drafts of this manuscript. This work was supported by NSF SBR-9209004 (D.S.), NSF BCS-9904401 (D.S., P.L.), NSF BCS-0137930 (M.C., D.S., P.L.), NRSA NIH AR051672 (T.G.) and an NSF GRF (J.H.).

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