

RESEARCH ARTICLE

Effects of fore–aft body mass distribution on acceleration in dogs

Rebecca M. Walter^{1,*} and David R. Carrier²

¹National University of Health Sciences, Pinellas Park, FL 33781, USA and ²Biology Department, University of Utah, Salt Lake City, UT 84112, USA

*Author for correspondence (rwalter@nuhs.edu)

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SUMMARY

The ability of a quadruped to apply propulsive ground reaction forces (GRF) during rapid acceleration may be limited by muscle power, foot traction or the ability to counteract the nose-up pitching moment due to acceleration. Because the biomechanics of acceleration change, both throughout the stride cycle and over subsequent strides as velocity increases, the factors limiting propulsive force production may also change. Depending on which factors are limiting during each step, alterations in fore–aft body mass distribution may either increase or decrease the maximum propulsive GRF produced. We analyzed the effects of experimental alterations in the fore–aft body mass distribution of dogs as they performed rapid accelerations. We measured the changes in trunk kinematics and GRF as dogs accelerated while carrying 10% body mass in saddlebags positioned just in front of the shoulder girdle or directly over the pelvic girdle. We found that dogs applied greater propulsive forces in the initial hindlimb push-off and first step by the lead forelimb in both weighted conditions. During these steps dogs appear to have been limited by foot traction. For the trailing forelimb, propulsive forces and impulses were reduced when dogs wore caudally placed weights and increased when dogs wore cranially placed weights. This is consistent with nose-up pitching or avoidance thereof having limited propulsive force production by the trailing forelimb. By the second stride, the hindlimbs appear to have been limited by muscle power in their ability to apply propulsive force. Adding weights decreased the propulsive force they applied most in the beginning of stance, when limb retractor muscles were active in supporting body weight. These results suggest that all three factors: foot traction, pitching of the body, and muscle power play roles in limiting quadrupedal acceleration. Digging in to the substrate with claws or hooves appears to be necessary for maximizing propulsion in the initial hindlimb push-off and first forelimb step. Shifting the center of mass forward, as occurred with the loss of the large and heavy tail in the evolution of mammals, is likely to increase the contribution of the forelimbs to acceleration. Hindlimb muscle power appears to play a greater role in limiting acceleration than does forelimb muscle power. As such, we might expect animals built for rapid acceleration to have an increased ratio of hindlimb to forelimb muscle mass.

Key words: locomotion, acceleration, biomechanics, dogs, ground forces.

INTRODUCTION

Rapid acceleration is crucial to many behaviors that are under strong selection, such as prey capture, predator evasion, and competition for mates, territory and other resources (Brăna, 2003; Huey and Hertz, 1984; Lailvaux et al., 2004). Although all of these activities require high acceleration, the aspects of acceleration that are selected upon in each are likely to differ. For instance, in evading a predator within a closed habitat such as a forest, the distance an animal is able to cover within the first second after recognizing the predator might be most important. In a more open habitat the velocity achieved within 3–4 s, or the ability to change direction rapidly, could be more critical (Djawdan, 1993). Conversely, in fighting interactions, the momentum that can be achieved in a single lunge might determine the outcome. Therefore, two animals that are specialized for rapid acceleration might be built very differently. To predict how various morphological features might influence acceleration performance, it is necessary to understand what determines acceleration rate and what limits maximum acceleration.

The rate of instantaneous acceleration is directly proportional to the sum of the propulsive forces that are being applied to the substrate by all the limbs at that moment ($F=ma$; where m is mass and a is acceleration). This propulsive force could be limited by

several factors: (1) the capacity of the muscles to produce power during limb extension, (2) slippage of the feet on the substrate, (3) head-end up pitching of the body (Alexander, 2002; Williams et al., 2009). Further, the factor or factors posing the greatest limitation to propulsive force production may differ between forelimbs and hindlimbs or between earlier and later phases of acceleration.

Because it requires doing net work, acceleration requires much higher average and instantaneous muscle power than steady-state running. Previous studies on acceleration in turkeys, lizards and humans have recorded much greater power outputs in acceleration than when running at constant maximum speed (Roberts and Scales, 2002; Cavagna et al., 1971; Willems et al., 1995). In fact, measurements of power output from extensor muscles during acceleration in lizards are among the highest seen for vertebrate striated muscle (Curtin et al., 2005; McElroy and McBrayer, 2010; Scales and Butler, 2007). Previous studies have suggested that muscle power limits acceleration capacity in many species of lizards, and limits the later phases of maximum acceleration in greyhounds and ponies (Williams et al., 2009; McElroy and McBrayer, 2010). Based on this hypothesis, the most important morphological adaptations for increasing maximum acceleration would be those that increase the ratio of limb retractor and extensor muscle power

to body weight. In fact, among species of *Anolis* lizards, knee extensor muscle mass is the main morphological predictor of acceleration capacity (Vanhooydonck et al., 2006). Further, sprint acceleration performance in humans is significantly correlated to mass-specific leg muscle power (Sleivert and Taingahue, 2004; Jean-Benoit et al., 2002; Chelly and Denis, 2001).

Although these studies make a compelling argument for extensor muscle power as an important determinant of acceleration performance, results from previous modeling and performance experiments on lizards, dogs and ponies suggest that these animals may not be able to operate their limb extensor muscles at maximal power output during parts of acceleration (Aerts et al., 2003; Williams et al., 2009). According to the force–velocity relationship seen in striated muscle, the maximum force that a muscle can produce decreases with increased contraction velocity (Fenn and Marsh, 1935). Therefore, if acceleration was indeed limited by muscle power, it would be expected that as accelerating quadrupeds retract and extend their limbs more rapidly in each successive step, their maximum propulsive forces would decrease exponentially. Dogs rapidly accelerating on sandpaper-coated flooring, however, apply greater peak propulsive forces with their hindlimbs in the first and second strides than they do in the initial push-off (Walter and Carrier, 2009). This suggests that factors other than muscle strength limit their propulsive force production at the onset of acceleration. Furthermore, if a quadruped was able to achieve its maximal power output during acceleration, one would expect its maximum acceleration rate to be greatly reduced when running uphill, as a result of the additional power required to lift its center of mass against gravity. Yet, the acceleration rate of several species of lizards on 30 or 60 deg inclines does not differ or differs only minimally from that on level surfaces (Huey and Hertz, 1984; Irschick and Jayne, 1998).

To the extent that muscle power limits peak propulsive force production, increasing non-muscular body mass would be expected to decrease maximum acceleration rate and initial velocity (acceleration=force/mass). A running animal that attempts to accelerate while carrying an added load mass not only has to apply a greater propulsive force to achieve the same acceleration rate, but also a greater vertical force to support the weight of the mass. If the animal's ground force vectors were directed through its proximal limb joints, then its limbs could act as passive struts and support the added mass without increasing extrinsic limb muscle activity (Gray, 1968). During acceleration, however, the ground force vectors are directed in front of the proximal limb joints for at least the first half of stance (Walter and Carrier, 2009). As such, the extrinsic limb muscles must be active in weight support. As these muscles are responsible for much of the propulsive force production during acceleration, there may be a conflict between supporting an added mass and producing propulsive ground reaction force (GRF) (Williams et al., 2009). This conflict would be greatest at the beginning of stance, when the foot is furthest in front of the proximal limb joint. Here, the weight of the mass would place a protractor moment on the proximal joint of either the forelimb or hindlimb (Fig. 1A,C) (Schilling et al., 2009). An accelerating dog would have to use its limb retractor muscles to counter this protractor moment and increase the vertical GRF the limb produced. If these retractor muscles were already operating at maximum force production, this would be expected to reduce the propulsive component of the GRF that they produced during the first half of stance. In contrast, at the end of stance, the added mass would place a retractor moment on the limb (Fig. 1B,D). Thus, if the maximum propulsive GRF applied was limited by the strength of the retractor muscles, then the added

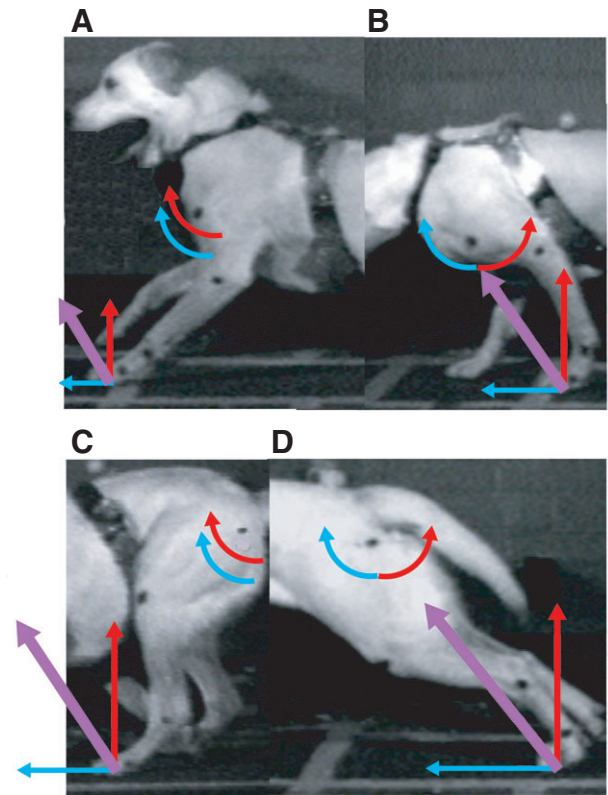


Fig. 1. (A) The initial phase of the stance period of the trailing forelimb in the first stride. Straight arrows represent the vertical (red) and fore–aft (blue) components of the total ground reaction force (GRF; purple) averaged over the first 20% of stance. Curved arrows show the direction of the moments that these GRF components would produce at the shoulder joint if they acted alone. Curved arrows do not represent the magnitude of the moments. (B) The final phase of the stance period of the trailing forelimb in the first stride. Straight arrows show the GRF component averaged over the last 20% of stance. (C,D) The initial and final phases of the stance of the hindlimbs in the first stride. Straight arrows represent GRF components averaged over the first (C) and last (D) 20% of hindlimb stance, and curved arrows represent the moments they would produce at the hip joint acting alone.

mass would not be expected to decrease the propulsive GRF applied at the end of stance.

A second factor that could limit propulsive force production is head-end up pitching of the body or behavioral avoidance thereof (Alexander, 2002; Williams et al., 2009). Head-end up rotation of the trunk could reduce or eliminate the ground contact time available for the forelimbs to apply propulsive forces. It would also decrease the fraction of body weight supported by the forelimbs and thereby intensify the likelihood of forefoot slippage (Lee et al., 1999). A head-end up pitching moment is incurred whenever the net GRF vector is directed in front of the center of mass. Therefore, a rearward shift in the center of mass location would tend to increase head-end up pitching. In models of dynamically bipedal lizards, in which the center of mass is located more caudally than in mammals, the pitching moments incurred during initial acceleration were sufficient to prevent forelimb ground contact (Aerts et al., 2003). In addition, models based on accelerating greyhounds and ponies show that these mammals are also limited by pitch in the early strides (Williams et al., 2009). Propulsive forces produced by the forelimbs in accelerating lizards and greyhounds are often considered to be insignificant (Williams et al., 2009; Aerts

et al., 2003; Curtin et al., 2005). Mixed-breed dogs, however, produce 43% of the total propulsive impulse in the first two strides of rapid acceleration with their forelimbs (Walter and Carrier, 2009). Propulsive force production by a forelimb poses a particular problem with pitch because the ground contact point of the forefoot is in front of the center of mass for most its stance period. When the forelimb is in front of the center of mass, it cannot apply propulsive ground forces without incurring a significant nose-up pitching moment. In fact, dogs' trunks rotate through more than a 30% greater range of pitch angles during the initial acceleration than during steady-state, high-speed galloping (Walter and Carrier, 2009). Although the hindlimbs are better located to produce a propulsive force vector without inducing a nose-up pitching moment, the hindlimb force vector is still directed in front of the center of mass for the first part of stance during rapid acceleration (Walter and Carrier, 2009). Thus mixed-breed dogs might be prevented from applying greater propulsive force with their hindlimbs during the beginning of stance by the excessive nose-up body rotation it would cause. Dogs might also benefit from limiting their propulsive force production at the end of hindlimb stance to produce a more vertically directed GRF vector. A more vertically directed GRF vector at the end of hindlimb stance would produce a nose-down pitching moment, which might be necessary to allow the forelimbs to contact the ground. If nose-up pitching moments limit the acceleration of dogs, they should be able to produce greater propulsive forces when carrying weights in front of their center of mass. In contrast, carrying weights posteriorly should decrease propulsive force production during portions of acceleration that are pitch limited.

A third factor that could limit propulsive force production is foot slippage or the risk of foot slippage if greater propulsive forces are applied (Alexander, 2002). If at any point in stance the propulsive GRF exceeds the maximum frictional force, foot slippage will occur. The maximum force of friction between two non-deformable surfaces is linearly dependent on the normal force pressing them together. This relationship occurs because, on the microscopic level, the true area of contact between the surfaces is linearly related to the normal force. When the normal force is low, only high points on the noncompliant surfaces are in contact. However, if one of the surfaces is compliant, such as the footpads of dogs, surface deformations allow for a disproportionately greater amount of true contact area at low normal forces. Whereas true contact area still increases with increased normal force, the relationship is slightly hyperbolic rather than linear (Cartmill, 1974). For the footpads of prosimian primates, the maximum frictional force scales with vertical force to 0.869. If we assume that the compliance of our dogs' footpads is similar to that of prosimian primates, then the maximum propulsive GRF (F_p) that they can apply without foot slippage is equal to the vertical force (F_v) raised to the 0.869 power multiplied by the coefficient of friction (μ_s).

$$F_p \leq F_v^{0.869} \mu_s \quad (1)$$

The coefficient of friction between sanded plywood and the feet of various primates ranges from approximately 0.5 to 2 (Cartmill, 1979). These friction coefficients would allow dogs to apply a force at vector angles of approximately 63 and 27 deg to the horizontal, respectively.

If dogs are limited by friction in their production of propulsive forces, their GRF vector angles should approach those at which slippage would occur. We would expect to see the greatest propulsive forces near the middle of the stance period when vertical forces are greatest. However, dogs should be able to apply GRF at

the smallest vector angles (most propulsive) at the beginning and end of stance when their limbs support the least weight. Increases in vertical GRF necessary to support added mass should be accompanied by increases in propulsive GRF.

In this study, we increased the weight supported by either the forelimbs or hindlimbs by having dogs carry 10% of their body mass positioned either just in front of the shoulder girdle or above the pelvic girdle, and recorded ground forces as they accelerated maximally. The coefficient of friction between the dogs' feet and the sandpaper surface on which they performed accelerations was measured. Finally, we measured pitch angle through which the dogs' backs rotated during the first forelimb and hindlimb stance periods.

MATERIALS AND METHODS

Subjects and equipment

Five adult dogs of various breeds, ranging in morphology from Labrador retrievers to a Shi Tzu, were used in this study. Dogs were selected based on their willingness to chase tennis balls or human runners repeatedly with what appeared to be maximum effort levels while wearing weighted packs. Therefore, the dogs selected were young and highly energetic. Descriptions of subjects have been provided previously [(Walter and Carrier, 2009) dogs: A, C, E, F and G]. Their average mass was 25.3 ± 11.2 kg. They were either privately owned pets or research dogs in training for another study.

The equipment and procedures used have also been described previously (Walter and Carrier, 2007; Walter and Carrier, 2009). A 0.6×0.4 m Kistler 9281B SN force plate mounted flush with a 40 m carpeted runway recorded vertical and fore-aft forces at 500 Hz. Approximately 3.5 m of the runway surrounding the force platform was covered with sandpaper to improve traction over the first strides. Trials were videotaped at 250 Hz with a NAC HSV-500 camera (Tokyo, Japan) positioned perpendicular to the runway. Average velocity over the first 2 m of each trial was measured using laser sensors (Keyence LV-H41; Osaka, Japan) positioned at the approximate starting location for each trial and 2 m from the start. A reflective band wrapped around the thorax of each dog activated the sensors as the dogs passed. A National Instruments (Austin, TX, USA) 6034 A/D board was used to import data from the laser sensors and force plate into the computer where it was analyzed with Labview software.

Procedure

To test the hypotheses of what limits maximum acceleration in quadrupeds, we recorded maximum effort accelerations of dogs that carried additional mass (10% body mass) positioned over the forelimbs or over the hindlimbs. Ground forces and kinematics for the hindlimb push-off and first two accelerating strides were compared for three conditions: front weighted (FW), hind weighted (HW) and no weights (NW). Data recorded for the hindlimb push-off consisted of the vertical and propulsive force impulses applied by the hindlimbs in the initial acceleration and the associated hindlimb kinematics. Stride one consisted of the initial steps that dogs took with the forelimbs during the hindlimb push-off and the first hindlimb flight phase, as well as the first hindlimb stance phase. Stride two consisted of the next forelimb and hindlimb stance periods.

In trials measuring the initial hindlimb push-off, dogs started from a standing position with both hindlimbs on the force platform. For recordings of the first two accelerating strides, subjects started with their forelimb or hindlimbs one or two stride lengths before the force

plate. An experimenter positioned the dog by holding its collar prior to the start of each trial. The subject was released and encouraged to accelerate maximally along the runway by allowing it to chase either a tennis ball or an experimenter running with a hotdog. Trials in which video recordings showed the dog pulling on the collar prior to release were not used for analysis. Trials for each dog were recorded on multiple days. During each recording session, dogs performed trials until their velocity decreased due to fatigue, boredom or a full stomach. Each dog performed at least 20 trials, beginning at each starting location for each condition: FW, HW or NW (a minimum of 240 trials for each dog). In many cases, more trials were required in order to achieve a sufficient number of trials for analysis. For each dog, the five trials for each step with the fastest 2 m velocity that met all the requirements (described below) were used for analysis.

After the completion of each recording session, dogs were weighed on the force plate, both with and without the added weights. Their forelimb–hindlimb mass distribution was determined and checked both with and without added weights by having them stand relaxed with only the forelimbs and then with only the hindlimbs supported by the force platform.

Analysis of ground forces

Trials were acceptable for analysis if they met the following criteria: (1) velocity over the first 2 m was as close as possible to the maximum measured for that dog, (2) the limb or limbs on which forces were analyzed landed fully on the force plate, and (3) they were the only feet on the plate for at least 95% of the stance period. Optimally, trials in which both forelimbs and hindlimbs contacted the plate simultaneously would have been excluded from analysis, as the role of the individual limbs is obscured during this period of overlap. Some dogs, however, consistently exhibited simultaneous ground contact of the lead forefoot and the hindfeet in the first stride. Because these feet were placed very close together, trials without any overlap could not be achieved for all dogs, and trials with minimal overlap (less than 5% of stance) were used for analysis when necessary.

The following parameters were measured for each trial analyzed and compared between the three conditions (FW, HW and NW): velocity, contact time, mean and maximum vertical and fore–aft forces, vertical and fore–aft impulses, and mean net force vector angle. Contact time was taken as the period over which dogs applied forces greater than or equal to 4% body weight to the force plate. To ascertain whether the risk of foot slippage or muscle power were limiting factors during only a small portion of stance, the stance phase was divided into 20% increments and the three conditions were compared for each increment.

Kinematic measurements

To measure the angle of the upper back, a reflective ball was taped to the back over the last thoracic vertebra as previously described (Walter and Carrier, 2009). The angle made by the base of the neck and the reflective ball with the horizontal was measured. Positive back angles represent a head-end up pitch and negative back angles represent a head-end down pitch. The angular excursion of the upper back was measured during the first stride starting at the onset of stance for the lead forelimb and ending at the end of stance for the hindlimbs.

Measurement of the friction coefficient

The coefficient of friction between the dogs' feet and the sandpaper surface was measured in four additional dogs using the method of Cartmill (Cartmill, 1979). These dogs varied in mass from 15.3 to 25.6 kg. Dogs stood on a board coated with sandpaper, similar to the sandpaper covering the force plate, as the board was gradually tilted upward. Tilting of the board to increase the angle of the surface continued until the dogs' feet began to slide on the sandpaper. The maximum angle at which the dogs could stand without sliding was measured relative to the horizontal, and the tangent of this angle was taken to be the friction coefficient.

Statistics

Ground forces and impulses measured for each dog were normalized by dividing them by the dog's mass without weights. Normalized forces and impulses were compared between the three conditions for each step using ANOVA (Statview, SAS Institute, Cary, NC, USA) as were the different effects of the added mass on different portions of the stance phase.

RESULTS

Overall effects of added mass

Carrying weights above the pelvic girdle (HW condition) significantly reduced the forelimb–hindlimb mass distribution ratio (i.e. shifted the center of mass rearward) when dogs stood at rest, but did not affect the forelimb/hindlimb ratio of vertical forces applied during the trials (Table 1). In contrast, dogs carrying weights placed anteriorly (FW condition) increased the forelimb/hindlimb mass distribution ratio to a greater extent during the trials than when the dogs stood at rest. The average velocities of the dogs over the first 2 m of acceleration were greatest for the NW ($3.7 \pm 0.03 \text{ m s}^{-1}$; mean \pm s.e.m.), followed by the FW ($3.6 \pm 0.07 \text{ m s}^{-1}$) and were lowest for the HW ($3.5 \pm 0.03 \text{ m s}^{-1}$) trials. These differences were significant ($P < 0.05$). The thoracic portion of the dogs' torsos (upper backs) pitched nose-down significantly

Table 1. Effects of added mass on fore–aft body mass distribution and on trunk kinematics: (A) percentage of total weight (body weight plus added mass) supported by the forelimbs in each of the three conditions for dogs standing at rest and accelerating; (B) minimum (most nose-down) and maximum (most nose-up) pitch angles attained by dogs during the first stride, beginning at the onset of the first lead forelimb stance and ending at the end of the first hindlimb stance

	No weights	Hind weighted	Front weighted
A. % Total mass supported by forelimbs			
Standing	63 \pm 3*	59 \pm 2*	68 \pm 2*
Accelerating	43 \pm 2*	43 \pm 2†	50 \pm 3*†
B. Pitch angles (deg)			
Minimum (nose-down)	-16 \pm 2*	-13 \pm 3	-9 \pm 2*
Maximum (nose-up)	15 \pm 3	12 \pm 4	13 \pm 3

Values are means \pm s.e.m.

*†The same symbol indicates significant differences between the conditions at $P < 0.05$ and $N = 5$.

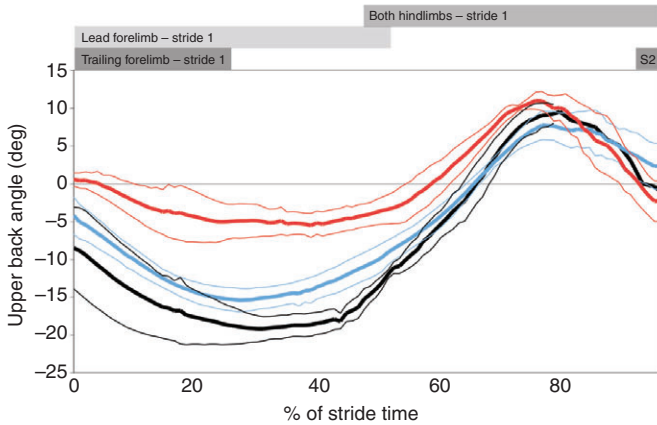


Fig. 2. Pitching movement throughout the first stride for a representative dog (Labrador retriever). Thick lines show the mean angle of the upper back beginning at the onset of the lead forelimb stance (0% stance) and ending at the end of the first hindlimb stance (100% stance). The angle for front weighted (FW) trials is shown in red, that for hind weighted (HW) trials in blue and that for no weights (NW) trials in black. Thin lines represent standard deviations. S2, stride 2.

less in the first stride in the FW compared with the HW and NW conditions (Table 1, Fig. 2). The maximum nose-up pitch angle attained by the dogs' upper backs did not differ significantly between conditions.

Friction coefficient

The mean friction coefficient measured for the dogs' feet on the sandpaper surface that covered the runway was 1.06 ± 0.12 (\pm s.e.m.). This indicates that the dogs should have been able to apply propulsive forces with a minimum force vector angle of 43.5 deg to the horizontal. Because the friction coefficient was only measured in four dogs of relatively similar body mass, the scaling of friction coefficient with body mass was not established.

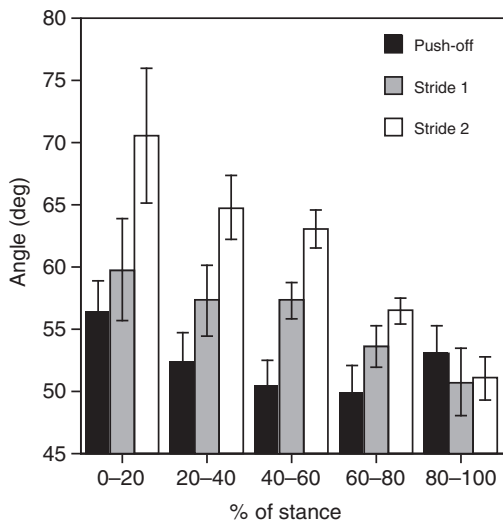


Fig. 3. The net force vector angle relative to the horizontal as it changes over the course of stance for the hindlimbs in the push-off (black), stride 1 (gray) and stride 2 (white) for dogs without added mass. Error bars show standard errors for the five dogs.

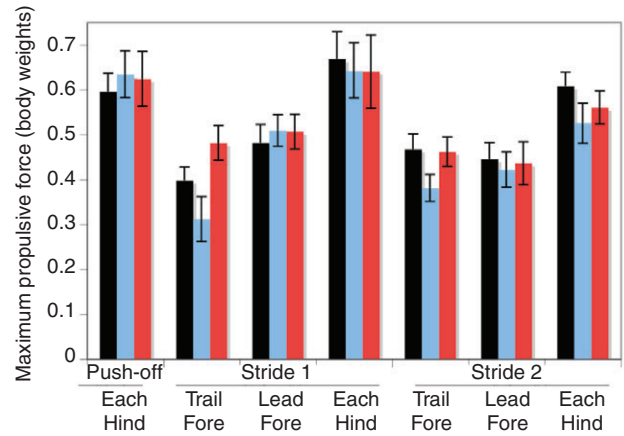


Fig. 4. Maximum propulsive force applied in each step. Maximum force for each hindlimb was determined by dividing the total hindlimb force by two as the hindlimbs acted in synchrony in the first strides. Forces for FW trials are shown in red, those for HW trials in blue and those for NW trials in black. Error bars show standard errors for the five dogs.

Hindlimb push-off

Dogs began accelerating by crouching, and then forcefully propelling themselves forward with both hindlimbs simultaneously (hindlimb push-off) (Walter and Carrier, 2009). The net force vector angle was lowest (most propulsive) from 40 to 80% of stance, where it averaged 50 deg for dogs without added mass (Fig. 3). Maximum propulsive force and propulsive impulse were both greatest in HW trials and lowest in NW trials (Table 2; Figs 4, 5).

Stride 1

During the later part of the hindlimb push-off, dogs stepped forward with one or both forelimbs. When both forelimbs stepped forward, the forelimb that was set down first was the trailing forelimb. The lead forelimb was set down second and placed further forward (Hildebrand, 1977). When only one forelimb stepped forward, it served as the lead forelimb for the first stride and the forelimb that remained planted served as the trailing forelimb. Dogs pitched 10–15 deg nose-down during this stance period, almost appearing to vault over the forelimbs. Compared with the forces applied in NW trials, both forelimbs applied greater propulsive forces in FW trials, whereas in HW trials propulsive forces applied by the trailing forelimb were reduced (Table 2; Figs 4, 5).

As the lead forelimb of the first stride finished its stance phase, the hindlimbs simultaneously began their first stance phase. As in the push-off, the two hindlimbs were synchronized in propelling the dog forward as the back extended. During the first stride, the hindlimbs applied the greatest maximum vertical force and vertical impulse with the hind weights, whereas maximum propulsive force and propulsive impulse did not differ significantly between the three conditions (Table 2; Fig. 5).

Stride 2

As the hindlimbs finished the first stance period, the trailing forelimb for the second stride began its stance. The maximum propulsive force and propulsive impulse produced by the trailing forelimb were similar in the NW and FW trials. In contrast, in the HW trials the maximum propulsive force and propulsive impulse were 21% and 33% lower than in the NW trial (Table 2; Fig. 5).

Table 2. Ground force parameters

	No weights	Hind weighted	Front weighted
Hindlimb pushoff			
Contact time (ms)	270±17*	318±28*	297±26*
Peak fore-aft (BW)	1.19±0.08*†	1.27±0.10*	1.25±0.12†
Fore-aft impulse (BW ms)	198 ±16*	246±17*	231±16*
Mean FV angle (deg)	52 ±1*†	53±1*	53±2†
Minimum FV angle (deg)	44±2*	47±1*	46±1
Stride 1, trailing forelimb (N=4)			
Contact time (ms)	250±9*†	298±46*	274±14†
Peak fore-aft (BW)	0.40±0.03*	0.31±0.05†	0.48±0.04*†
Fore-aft impulse (BW ms)	55±4*	47±7†	71±4*†
Mean FV angle (deg)	56±1*	63±2*†	54±1†
Minimum FV angle (deg)	42±3	48±2*	41±2*
Stride 1, leading forelimb			
Contact time (ms)	178±18	192±32	190±17
Peak fore-aft (BW)	0.48±0.04*†	0.51±0.03*	0.51±0.04†
Fore-aft impulse (BW ms)	46±5*	49±3†	54±4*†
Mean FV angle (deg)	55±1*†	57±1*	58±1†
Minimum FV angle (deg)	37±2	39±2	39±1
Stride 1, both hindlimbs			
Contact time (ms)	159±7*	172±8*†	163±8†
Peak fore-aft (BW)	1.34±0.12	1.29±0.12	1.28±0.16
Fore-aft impulse (BW ms)	130±10	128±9	125±10
Mean FV angle (deg)	56±2*	61±4*†	58±4†
Minimum FV angle (deg)	42±2	45±2	44±2
Stride 2, trailing forelimb (N=4)			
Contact time (ms)	120±16*	109±8*†	122±12†
Peak fore-aft (BW)	0.47±0.03*	0.38±0.03*†	0.46±0.03†
Fore-aft impulse (BW ms)	32±3*	21±2*†	28±4†
Mean FV angle (deg)	61±2*†	71±3*	69±4†
Minimum FV angle (deg)	38±3*†	51±3*	47±2†
Stride 2, leading forelimb			
Contact time (ms)	111±11	119±12	118±12
Peak fore-aft (BW)	0.45±0.04	0.42±0.04	0.44±0.05
Fore-aft impulse (BW ms)	30±1	28±1	29±2
Mean FV angle (deg)	59±2*†	68±2*	69±3†
Minimum FV angle (deg)	39±3*†	50±3*	47±1†
Stride 2, both hindlimbs			
Contact time (ms)	127±14	146±18	142±17
Peak fore-aft (BW)	1.22±0.06*	1.05±0.09*	1.12±0.07*
Fore-aft impulse (BW ms)	90±6*	79±7*†	88±5†
Mean FV angle (deg)	62±2*	70±3*†	64±3†
Minimum FV angle (deg)	44±2	47±4	46±3

Peak force (BW) values were normalized by dividing data from force recordings by each dog's body weight without added mass; impulse is the average force normalized by body weight multiplied by the duration of contact. Mean FV angle and Min FV angle are the mean and minimum angles of the net force vector from the horizontal over the stance period.

Values are means ± s.e.m., N=5, except where indicated.

Part way through the trailing forelimb's stance, the lead forelimb was set down. For the lead forelimb neither the maximum propulsive force nor the propulsive impulse differed significantly between the three conditions.

Dogs continued to use a half-bound in the second stride such that the two hindlimbs acted in synchrony. The maximum propulsive force was greatest in NW trials and lowest in HW trials (Table 2; Fig. 5). The difference in propulsive GRF between the HW and NW trials was greatest at the beginning stance (Table 3).

DISCUSSION

Friction limits initial acceleration

During the initial push-off, the dogs produced both the greatest impulses and the highest peak vertical and propulsive forces with their hindlimbs in the HW trials. This suggests that they did not limit their propulsive force production to avoid producing an excessive nose-up pitching moment. In fact, at the end of hindlimb

stance the force vector passed behind the center of mass producing a nose-down pitching moment (Figs 1–3) (Walter and Carrier, 2009). The peak propulsive force applied by the hindlimbs in the push-off was lower than that applied in the first step when the hindlimbs were retracted and extended more rapidly (Table 2). Based on the force-velocity relationship of muscle (Fenn and Marsh, 1935), this implies that muscle strength did not limit the propulsive force produced. The minimum force vector angle of 44 deg approached the limit of 43.5 deg predicted based on the friction coefficient. This suggests the dogs limited the propulsive forces they applied in the hindlimb push-off to avoid slippage.

The lead forelimb in the first stride applied greater propulsive force in both weighted conditions, when vertical force was increased (Table 2; Figs 4, 5). This positive correlation between the applied vertical and the propulsive forces is consistent with friction having limited the maximum propulsive force in this step (Eqn 1). The force vector angle was lowest (closest to horizontal) at the onset of stance,

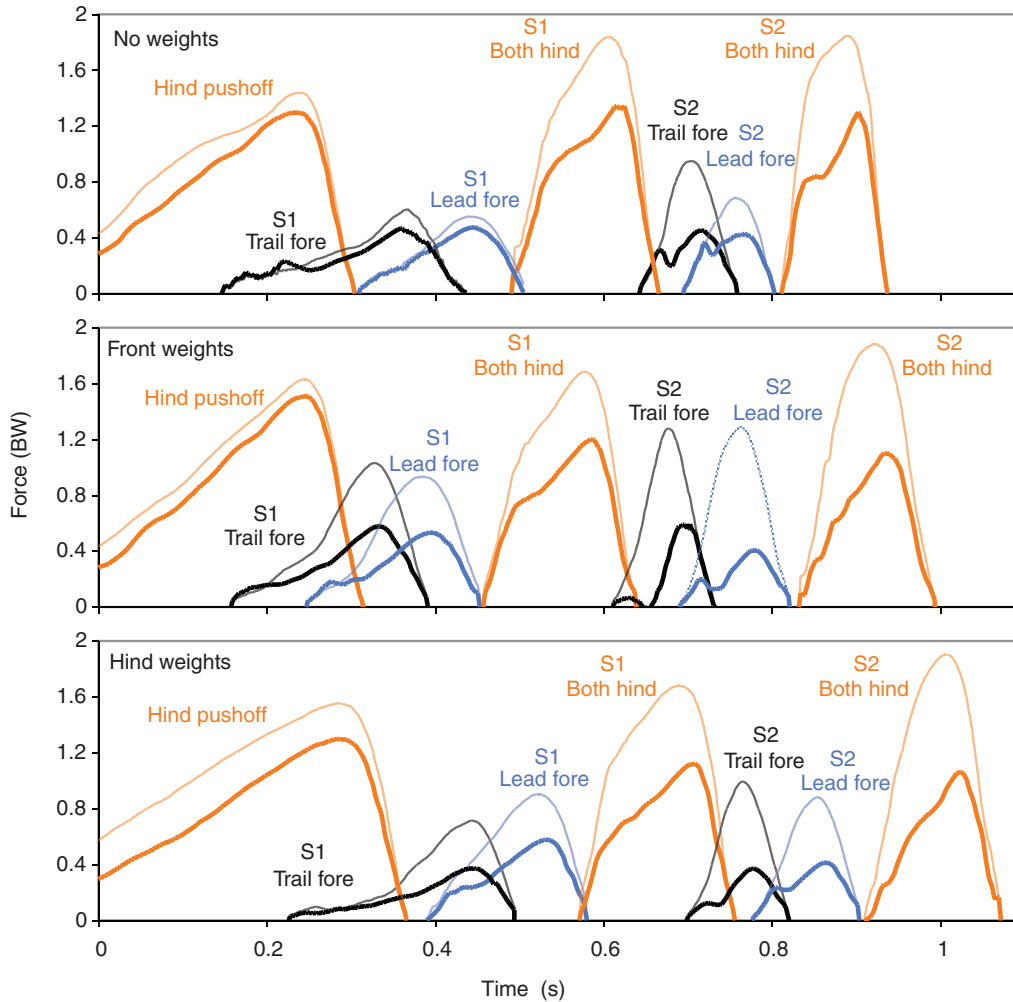


Fig. 5. Ground reaction forces plotted over time for the hindlimb push-off, and first two strides for a representative dog (Labrador retriever). Dark lines show propulsive forces and light lines show vertical forces. Lines shown are the means from five trials unless otherwise indicated. Steps in which fewer than five trials could be obtained from this dog include: the trailing forelimb from the first stride under all conditions, the lead forelimb from the first stride under the unweighted condition, and the trailing forelimb from the second stride under the frontally weighted condition. Forces for both hindlimbs are shown in orange, those for the trailing forelimb in black and those for the lead forelimb in blue. S1, stride 1; S2, stride 2. (A) Without weights [taken from Walter and Carrier (Walter and Carrier, 2009)], (B) with weights placed anteriorly and (C) with weights placed posteriorly.

where a small amount of foot slippage sometimes occurred. This slippage rapidly ended as the lead forelimb began to support a significant portion of the body weight.

These results suggest that the hindlimbs in the push-off and the lead forelimb in the first stride were limited in their propulsive force production by foot slippage or the risk of foot slippage if greater propulsive forces were applied. Based on the measured friction coefficient of 1.06 between the dogs' feet and the sandpaper, dogs should be able to apply propulsive forces at 43.5 deg to the horizontal, which is lower than the average force vector seen in these strides (Table 2). This measurement of friction, however, was taken with the dogs standing at rest. During the hindlimb push-off dogs applied peak vertical forces that were more than 3.5 times greater than the weight supported by the hindlimbs in dogs standing at rest. Because the footpads of dogs are elastically deformable, similar to the volar pads of primates, the friction coefficient is likely to decrease slightly with increased vertical force as it does in prosimian primates (Cartmill, 1979). This would also explain the dogs' abilities to produce propulsive forces at force vector angles of 39 ± 2 deg at the beginning of forelimb stance. During this period

Table 3. Difference in the mean propulsive force between trials in which dogs did not carry weights and trials in which they did

	First 40% (% difference)	Last 40% (% difference)
Front weighted vs no weights		
Step 1 trailing forelimb	8±26*	65±11*
Step 1 lead forelimb	5±6	9±8
Step 2 trailing forelimb	-14±27	18±18
Step 2 lead forelimb	-14±14	8±9
Hind weighted vs no weights		
Hindlimb pushoff	10±9	10±7
Step 1 both hindlimbs	-9±7	-2±4
Step 2 both hindlimbs	-41±7*	-18±4*

Negative values indicate that the mean propulsive force applied was lower when dogs carried weights, and positive values indicate that dogs produced greater forces when carrying weights.

*A significant difference in the effect of weights between the first and last 40% of stance.

Values are means ± s.e.m., $N=5$.

of forelimb stance, when dogs were attempting to pull backward on the sandpaper, the vertical forces applied by the forelimbs were lower than those for a standing dog. We would, therefore, expect minimum force vector angles to be somewhat lower than 43 deg if friction was limiting. Although we attempted to avoid using trials showing foot slippage for analysis, there were trials in which it occurred. The 36-grade sandpaper used to coat the force plate and beginning of the runway is relatively coarse and is likely to have as much friction as many hard surfaces found in nature.

One major difference between our runway and most natural surfaces is that our runway had a tile or metal surface beneath the sandpaper making it impenetrable to the dogs' claws. In many of our trials, dogs left scratch marks on the runway from their attempts to dig into the runway with the claws of their forefeet at the onset of stance. This is consistent with a previous study in which greyhounds accelerating on carpeted laboratory flooring were suggested to have been limited by their inability to dig their claws into the substrate (Williams et al., 2009). This increase in acceleration performance through digging into the surface is not limited to dogs. Humans can accelerate more rapidly with spikes or cleats, whereas the toe fringes of sand dwelling lizards significantly improve their capacity to accelerate on sand (Carothers, 1986). These results suggest that in nature dogs and other running animals must be able to dig their claws, hooves or other foot specializations into the surface in order to apply their maximum propulsive forces in the initial hindlimb push-off and first forelimb steps. Many natural surfaces, however, cannot be penetrated by hooves or claws. Animals accelerating rapidly from a standstill on these surfaces are likely to initially be limited by traction in the propulsive GRF they produce.

Muscle power limits hindlimb force production after the first stride

In contrast to the hindlimb push-off, the propulsive forces that the hindlimbs applied in the first and second strides were not greater in HW trials. During the first stride, neither maximum propulsive force nor propulsive impulse differed between the three conditions, whereas in the second stride, both were greatest in the NW trials (Table 2). In the second hindlimb stance phase, the propulsive force produced under weighted conditions was much further below that produced by unweighted dogs at the beginning of stance than at the end of stance (Table 3). This is consistent with the hindlimbs being limited by the muscle power of the hip retractor muscles during this stride. At the beginning of stance, when the hindlimbs were angled forward, the weight of the added mass placed a protractor moment on the hindlimbs. This required the hip muscles to generate a counteracting retractor moment to support the weights in addition to the retractor moment required to produce the propulsive ground force (Fig. 1). In contrast, at the end of stance, the weight of the added mass put a retractor moment on the hindlimbs and is unlikely to have increased the muscle power required for a given level of propulsive force production. This differential effect of added mass on muscle power requirement throughout the stride is demonstrated in trotting dogs, where carrying added mass has been found to increase the electromyography (EMG) activity of the hip retractor muscles at the beginning of stance but to have no effect on retractor muscle activity at the end of stance (Schilling et al., 2009). The reduced propulsive GRF at the beginning of the second hindlimb step in HW trials suggests that at this point, the activity of the hip retractor muscle could not be further increased, and that force production was limited by muscle power. For the forelimbs, in contrast, carrying weights did not cause more of a decrease in

propulsive force at the beginning of stance than at the end of stance. Furthermore, the reduced propulsive force produced by the trailing forelimb in the first and second strides of HW trials, when dogs moved most slowly, is not consistent with muscle power limiting propulsive force production.

Hindlimb muscle power played an important role in limiting maximum acceleration after the first stance phase. In fact, hindlimb muscle power may be a major factor limiting acceleration in most quadrupeds, as well as in humans (Sleivert and Taingahue, 2004; Jean-Benoit et al., 2002; Chelly and Denis, 2001; Vanhooydonck et al., 2006; Curtin et al., 2005). In contrast, muscle power played a much smaller role in limiting propulsive forces applied by the forelimbs. Thus, we would expect that animals built for acceleration might have a higher ratio of hindlimb to forelimb muscle mass distribution. However, dogs running at high speed apply similar propulsive impulses with the forelimbs and hindlimbs, whereas the forelimbs exert much greater vertical and decelerating impulses (Walter and Carrier, 2007). Thus, we would expect mammalian quadrupeds built for sustained high-speed running to have a more even forelimb to hindlimb mass distribution than those built for rapid acceleration. An example of this dichotomy occurs in racehorses where the short-distance American quarter horses appear from visual examination to have a much greater hindlimb to forelimb muscle mass ratio than the longer-distance thoroughbreds. A similar example can be found in the suni and the gazelles. Suni, which have a greater hindlimb to forelimb muscle mass ratio than the gazelles and live in more densely vegetative areas, generally make short dashes for cover or zig-zag when pursued, whereas gazelles, which live in more open areas, run greater distances when pursued (Kingdon, 1982).

Effects of fore-aft body mass distribution and the role of pitch as a limiting factor

During forelimb stance in the first stride, dogs pitched nose-down 30–40% less when they carried the weights anteriorly compared with the caudally weighted or unweighted control conditions (Table 1, Fig. 2). This result seems counter-intuitive as moving the center of mass forward relative to the net force vector would increase nose-down pitching moment (or decrease the nose-up pitching moment) if the net force vector remained the same. In FW trials, dogs modified the ground forces that they applied in first forelimb steps in a manner that overcompensated for the weights. Whereas the pack weights increased the dogs' mass by only 10%, dogs applied more than 30% greater propulsive and vertical forces with their trailing forelimb when they carried the weights anteriorly compared with the HW and NW conditions (Table 2; Figs 4, 5). Dogs may have limited their nose-down pitching when they carried the weights on their front ends to avoid the greater risk of capsizing or to avoid the greater force that would be required to rotate back nose-up. Alternatively, dogs carrying weights anteriorly may have applied greater vertical and propulsive forces with their trailing forelimbs and pitched nose-down less because they anticipated having less of a problem with nose-up rotation during the following hindlimb stance. As such, these results would be consistent with, but not necessarily indicative of pitching of the torso being the primary limiting factor on the production of propulsive force by the trailing forelimb in the first strides. This finding would be similar to the findings of Williams and colleagues on accelerating greyhounds, where the trailing forelimb failed to contact the ground on the third stride (Williams et al., 2009).

The GRF vector passes in front of the center of mass for approximately the first half of hindlimb stance in acceleration

(Walter and Carrier, 2009). Despite this, results of this study suggest that dogs do not limit the propulsive forces they produce with their hindlimbs to reduce nose-up pitching. This differs from greyhounds, for which pitch limits propulsive force production by the hindlimbs for the first several strides (Williams et al., 2009). In greyhounds, the center of mass is located much more caudally, such that greyhounds standing at rest support only 56% of their body mass with their forelimbs (Lee et al., 1999). Thus, even when the dogs in this study carried weights caudally, their centers' of mass were still more anteriorly located than those of greyhounds (Table 1). We were unable to move the center of mass more caudally because it was not possible to motivate dogs to accelerate maximally when they carried packs weighing more than 10% of their body mass over their hind ends. Greyhounds also differ from mixed-breed dogs in that they have a much greater ratio of hindlimb extensor muscle mass to body mass (Williams et al., 2008). As such it seems that greyhounds would be more likely to be pitch limited in initial acceleration whereas other dogs would be more likely to be limited by the power of their hindlimb extensor muscles.

Our results do suggest that pitch may limit the propulsive force dogs apply with their trailing forelimbs in both the first and second steps. This possibility has implications for the acceleration performance of species differing in anteroposterior body mass distribution. More frontally weighted quadrupeds, such as lions and buffalo, might have an advantage, at least in the first forelimb steps of acceleration, over more caudally weighted animals, such as cheetahs and gazelles. More anteriorly weighted mammals such as lions, buffalo, wildebeests and other artiodactyls with heavy antlers or horns might benefit from an increased ability of their forelimbs to apply propulsive forces in the short distance charges seen during male–male aggression. In the first strides, mixed-breed dogs apply 43% of the propulsive forces with their forelimbs (Walter and Carrier, 2009). In contrast, in the much more caudally weighted greyhounds, the forelimbs barely touch down in the first strides and make very little contribution to initial acceleration (Williams et al., 2009). Whereas in greyhounds there is strong selection to accelerate to 60 km per hour as rapidly as possible over many strides, fighting animals, such as pit bulls, are likely to face greater selection for maximum acceleration in a single lunge. In a one- or two-stride acceleration, the more anterior center of mass of a pit bull might be advantageous. Whereas moving the center of mass anteriorly in mammals is likely to reduce the ratio of hindlimb extensor muscle mass to body weight, this reduction might be more than counteracted by the increased propulsive force production by the forelimbs. Anteroposterior body mass distribution has only been measured in approximately 20 species (Rollinson and Martin, 1981; Lee et al., 2004), where it ranges from the forelimbs supporting 52–66% of the body weight in most mammals to the forelimbs supporting less than 50% of the body weight in lizards, alligator and primates. Compared with modern mammals, basal synapsids such as *Ophiacodon* and *Cotylorhynchus* have very long and heavy tails. The loss of this long and heavy tail in the evolution of mammals may have led to improved acceleration capabilities by moving the center of mass forward. This would have increased the propulsive forces that they could have applied without becoming bipedal (Aerts et al., 2003), and would have also allowed them to produce greater propulsive forces with their forelimbs.

CONCLUSIONS

Results from this study suggest that all three factors – foot traction, pitching moment and muscle power – play roles in limiting

acceleration at different points in acceleration from a standstill. On many surfaces, both natural and artificial, foot traction plays an important role in limiting the propulsive force applied in the initial hindlimb push-off and first forelimb step. In sports, humans avoid this limitation by wearing shoes with spikes, cleats, toe grabs or studs, whereas in nature animals may dig into the substrate with claws or hooves. Unlike greyhounds, which have a more caudally located center of mass, mixed-breed dogs appear not to limit the propulsive forces they apply with their hindlimbs in the first strides to avoid nose-up pitching. They may, however, be limited by nose-up pitching in the propulsive force they produce with their trailing forelimb. Shifting the center of mass forward, as occurred through the loss of the large and heavy tail in the evolution of mammals, is likely to allow the forelimbs to play a greater role in acceleration. By the second stride, it appears that muscle power limits the propulsive force applied by the hindlimbs. To improve their capacity for rapid acceleration, quadrupeds could increase their hindlimb musculature (Vanhooydonck et al., 2006; Williams et al., 2008). As such, we would expect animals built for rapid acceleration to have a higher ratio of hindlimb to forelimb muscle mass than those built for sustained high-speed running.

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