The Company of **Biologists**

RESEARCH ARTICLE

Grizzly bear (*Ursus arctos horribilis*) locomotion: gaits and ground reaction forces

Catherine L. Shine[1,*], Skylar Penberthy[1], Charles T. Robbins[2], O. Lynne Nelson[3] and Craig P. McGowan[1,4]

ABSTRACT

Locomotion of plantigrade generalists has been relatively little studied compared with more specialised postures even though plantigrady is ancestral among quadrupeds. Bears (Ursidae) are a representative family for plantigrade carnivorans, they have the majority of the morphological characteristics identified for plantigrade species, and they have the full range of generalist behaviours. This study compared the locomotion of adult grizzly bears (*Ursus arctos horribilis* Linnaeus 1758), including stride parameters, gaits and analysis of three-dimensional ground reaction forces, with that of previously studied quadrupeds. At slow to moderate speeds, grizzly bears use walks, running walks and canters. Vertical ground reaction forces demonstrated the typical M-shaped curve for walks; however, this was significantly more pronounced in the hindlimb. The rate of force development was also significantly higher for the hindlimbs than for the forelimbs at all speeds. Mediolateral forces were significantly higher than would be expected for a large erect mammal, almost to the extent of a sprawling crocodilian. There may be morphological or energetic explanations for the use of the running walk rather than the trot. The high medial forces (produced from a lateral push by the animal) could be caused by frontal plane movement of the carpus and elbow by bears. Overall, while grizzly bears share some similarities with large cursorial species, their locomotor kinetics have unique characteristics. Additional studies are needed to determine whether these characters are a feature of all bears or plantigrade species.

KEY WORDS: Quadruped, Plantigrade, Mammal, Mediolateral forces

INTRODUCTION

Within terrestrial animals a continuum of foot postures exists, from plantigrade species with their entire foot on the ground, to unguligrade animals that stand on the tips of their toes (Ginsburg, 1961; Carrano, 1997). The plantigrade posture is ancestral for mammals and it is generally agreed that digitigrade and unguligrade postures evolved as adaptations for speed and endurance. Because of this, numerous studies have examined the gait mechanics of digitigrade and unguligrade species (Budsberg et al., 1987; Hutchinson et al., 2006; Robilliard et al., 2007; Hudson et al., 2012). However, relatively few studies have examined the links between the plantigrade posture and locomotor mechanics. Plantigrade species are considered locomotor generalists, and

[1]University of Idaho, Department of Biological Sciences, Life Sciences Building, University Avenue, Moscow, ID 83844, USA. [2]Washington State University, School of the Environment and School of Biological Sciences, Pullman, WA 99164, USA. [3]Washington State University, Department of Veterinary and Clinical Sciences, Pullman, WA 99164, USA. [4]WWAMI Regional Medical Education Program, University of Idaho, Moscow, ID 83844, USA.

*Author for correspondence (shin0453@vandals.uidaho.edu)

because of the lack of cursorial specialisations, their limb movements are less restricted to the sagittal plane (Liem et al., 2001). Within mammals, plantigrade species include raccoons, badgers, weasels, as well as all rodents and primates. All of these animals are small compared with most digitigrade and especially unguligrade species; however, bears also retain the plantigrade stance. The goal of this study was to determine whether the locomotor mechanics of a stereotypical plantigrade quadruped, the grizzly bear (Ginsburg, 1961), differ from those of more extensively studied cursorial quadrupeds.

The selection of gaits used by plantigrade and cursorial species could represent some of the locomotor differences observed between these postures. Analysis of gaits, through footfall patterns, has been applied broadly to a wide range of terrestrial species (e.g. Gray, 1968; Hildebrand, 1976, 1977). Within quadrupedal animals, a lateral walk, in which the placement of the hindfoot is followed by the placement of the ipsilateral forefoot, is the gait used at slow speeds by the majority of species, including bears (Hildebrand, 1976). But, there is variation in terms of intermediate and faster gaits. The most common intermediate gait is the trot, defined by diagonal couplets, as this is seen in digitigrade (e.g. dogs and cats) and unguligrade (e.g. horses) animals, although these animals will also use a pace (ipsilateral couplets; Alexander, 1984). Interestingly, plantigrade carnivorans have not been shown to trot, but there have been a few observations of a pace (McClearn, 1992). Faster gaits include canters and gallops. Canters can be considered a slow gallop; however, they are characterised as being a three beat gait with one diagonal couplet (Hildebrand, 1976). Rotary gallops, as described above for the lateral walk, and transverse gallops, with the leading hindfoot placement being followed by the contralateral forefoot, can both be observed in the same species (Vilensky and Larson, 1989; Walter and Carrier, 2007), although there may be energetic differences between them (Bertram and Gutmann, 2009). Gallops are the fastest gait used by quadrupedal animals and studies have demonstrated that galloping occurs in species representing all three foot postures – unguligrade, digitigrade and bears within plantigrade species (Hildebrand, 1989; Renous et al., 1998; Robilliard et al., 2007; Walter and Carrier, 2007).

Within carnivorans, bears are the most plantigrade along the posture continuum (Ginsburg, 1961). The specific morphological features defining plantigrady include: well-developed digits on both forefeet and hindfeet; different sizes of the metapodials, e.g. metapodials 3 and 4 are rarely the same length in plantigrade species; and a substantial angle produced between the ulna and the humerus during elbow extension (20 deg in bears; Ginsburg, 1961). Ursidae is considered a generalist family; yet, the individual species exhibit substantial differences in diet, habitat and ecology. Grizzly bears have the broadest range of behaviours in Ursidae and are able to climb (particularly as juveniles), swim and have been reported to run as fast as 13.3 m s^{-1} (Garland and Janis, 1993; Brown, 2009).

There has been very limited research into the locomotion and biomechanics of Ursidae (Gambaryan, 1974; Inuzuka, 1996; Renous et al., 1998); however, it is likely that differences in limb morphology and locomotor behaviour may exist within Ursidae (Irschick and Garland, 2001), as well as between bears and other quadrupeds.

Previous studies have shown that locomotion by cursorial animals over a large size range can be described as dynamically similar across all speeds (Farley et al., 1993; Alexander, 2005). Locomotion is considered to be dynamically similar if, at a given dimensionless speed (Froude number), parameters can be made identical by multiplying forces, linear dimensions and time intervals by constant factors (Alexander and Jayes, 1983). In their seminal study, Alexander and Jayes (1983) characterised cursorial animals as those that stand with the humerus and femur closer to vertical than horizontal, which excludes other morphological characteristics that are considered cursorial in other studies (described above).

Relative to cursorial species, bears appear to have substantial movement in the frontal plane during locomotion. For example, bears have an unusual carpal movement, which manifests as a medial rotation during swing (Davis, 1949; Gray, 1968; Inuzuka, 1996). Further, grizzly bears have a medially directed forefoot position during stance, relative to the direction of travel. This differs from most cursorial species, which limit movement to the frontal plane to enhance efficiency and restrict forces to the direction of travel (Liem et al., 2001). Because of this, the mediolateral forces generated by cursorial animals are comparatively small and frequently ignored in the analysis of locomotion (Budsberg et al., 1987). However, some primates walking bipedally and animals with sprawling gaits have been shown to produce mediolateral ground reaction forces equal to or greater than the magnitude of their anterior–posterior forces (Willey et al., 2004). Currently, it is unclear to what extent the forces generated by bears during locomotion are similar to or differ from those of well-studied groups of terrestrial mammals, particularly considering the angle of the forefoot during stance.

In addition to terrestrial locomotion, the forelimbs may be involved in a wide range of other activities, especially in non-predatory carnivorans that may forage for food or exhibit escape behaviours such as climbing. The requirement of predators to chase down vertebrate prey overcomes the need for dexterity upon capture; therefore, forelimb dexterity in carnivores is negatively correlated with vertebrate predation. Bears and other plantigrade carnivores (i.e. generally omnivorous species) have higher dexterity scores than digitigrade carnivorans (Iwaniuk et al., 2000). Contributing to this dexterity is the morphology of the forelimbs, such that the ulna and radius are separate in plantigrade animals, resulting in the ability to supinate and pronate (rotate the forearm to point the palm up or down). In cursorial animals, the ulna and radius are fused to increase stability and therefore speed (Liem et al., 2001). Additionally, pentadactyly is only retained in plantigrade species as loss of digits is characteristic of digitigrade and unguligrade postures; this is associated with the reduction of distal limb mass that, along with elongation of the distal limbs, increases speed in cursorial animals (Garland and Janis, 1993). The difference in forelimb bone anatomy, as well as the differences in ecology, between cursorial and plantigrade species of the Carnivora is likely to have resulted in differences in locomotion.

The overall goal of this study was to determine whether locomotion by grizzly bears differs from that of other large quadrupedal animals, which tend to be digitigrade or unguligrade. We hypothesised that the gaits used by grizzly bears would be similar to those used by smaller plantigrade animals, as opposed to similarly sized cursorial animals, because of the differences in morphology of the distal limb. Further, we predicted that the mediolateral ground reaction forces would be higher in forelimbs of bears, compared with other species, as a result of their medially directed stance. These hypotheses were addressed by examining the footfall patterns and stride parameters of grizzly bears to identify gaits, and characterising the magnitude, time-varying shape and relative distribution of three-dimensional ground reaction forces generated by the forelimbs and hindlimbs over a range of speeds.

RESULTS

Subjects

The results from this study were collected from four adult (10± 1.15 years) female grizzly bears, with an average mass of 168.9± 18.2 kg and leg length of 0.69±0.13 m, measured as the shoulder height at midstance. This length was used to calculate the square root of Froude number ($Fr^{0.5}$; see Materials and methods for details).

Speed and gaits

We collected a continuous range of speeds, approximately 1 to 3.5 m s^{-1} for each bear (overall range: 1.1–3.8 m s^{-1}, $Fr^{0.5}$=0.42–1.46). These speeds are slow to moderate relative to what grizzly bears can achieve in open environments (estimated 13.3 m s^{-1}). Within these speeds we collected a full range of gaits, characterised by footfalls (Hildebrand, 1976), including slow walks, running walks, canters and gallops. However, only two gallops were collected and they were excluded from the analysis because of the small sample size. Canters collected include left and right lead limb trials; however, all force data collected were from non-lead limbs. Only steady speed trials were included in the analysis, with the maximum change in speed less than 20% of the total average forward speed based on kinematics. At the slowest speeds (1.1–2.0 m s^{-1}, $Fr^{0.5}$=0.42–0.77), bears used a lateral sequence walking gait, typical of other quadrupeds (Hildebrand, 1989). As speed increased above the level of a walk (with three overlapping feet on the ground), the most common change of gait was to a running walk (with two overlapping feet on the ground as described by Gray, 1968; Hildebrand, 1989).

ANCOVA results demonstrated no statistical difference between forelimbs and hindlimbs for contact time, stride time or duty factor ($P>0.05$); therefore, limbs were grouped for further analyses.

However, there was a trend for higher duty factor in the forelimbs. Walks were statistically different from running walks and canters for all stride parameters ($P<0.001$); however, running walks and canters were only significantly different for duty factor. This difference is probably due to the small number of canters. Swing time was independent of speed across gaits.

Force plate analyses

The characteristic M-shaped vertical ground reaction force (vGRF) can be seen in both the forelimbs and hindlimbs for the slower speeds/walking gait (Fig. 1A,B), transitioning to approximately a half sine wave at the higher speeds – running walks and canters (Fig. 1C,D). Forelimb vGRF impulse versus speed had a significantly higher intercept than hindlimb vGRF impulse ($P<0.01$), although the slopes were not statistically significant ($P=0.07$). Both forelimb and hindlimb vertical impulse decreased with speed (Fig. 2A). Peak vertical forces were not significantly different between the forelimb and the hindlimb at any speed, and there was a trend for higher peak forces as speed increased (Fig. 3A).
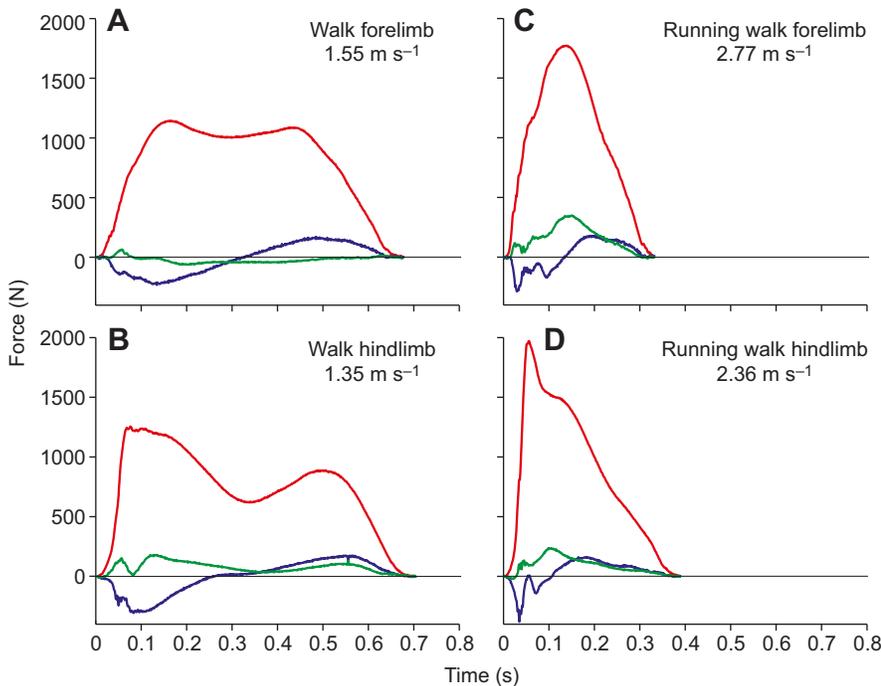
Fig. 1. Representative force traces. Forelimb (A,C) and hindlimb (B,D) force traces from a representative animal during walks (A,B) and running walks (C,D); vertical (red), anterior–posterior (blue) and mediolateral (green) forces are shown. Force traces for canters were similar to those for a running walk.

The magnitudes of braking and propulsive impulses reduced with speed in both the forelimb and the hindlimb. Our data show no significant difference between the forelimbs and hindlimbs in terms of propulsive force (Fig. 2B), although the braking impulse for the forelimb was greater than the braking impulse for the hindlimb at all speeds. Peak anterior–posterior forces did not differ between forelimbs and hindlimbs across speeds (Fig. 3B). There was no significant difference between the forelimb and the hindlimb for any mediolateral force parameter. Medial impulse (representing the animal pushing laterally/away from the midline) was greater than lateral impulse, which was near zero, at all speeds (Fig. 2C). The hindlimb medial impulse decreased with speed but there was no such relationship with the forelimb. The peak medial forces were approximately equal to the absolute magnitude of the anterior–posterior forces, which represents higher medial forces than seen in most erect quadrupeds.

Force shape analysis

The rate of force development in early stance was significantly correlated with speed for the forelimb (linear regression: $y=4.27x-3.10$, $R^2=0.55$, $P<0.001$) and ranged from ~2 N s^{-1} at the slowest walks to ~15 N s^{-1} at the fastest canters. The rate of force development was independent of speed for the hindlimb and much more variable than for the forelimb. On average, the rate of force development was higher in the hindlimb (11.6 ± 4.8 N s^{-1}) than in the forelimb (6.3 ± 4.0 N s^{-1}) except at the fastest speeds.

DISCUSSION

The overall goal of this study was to determine whether locomotion by grizzly bears differs from that of other large quadrupedal animals. Our results support our hypotheses that bears use similar gaits to smaller plantigrade animals and that they generate substantially higher mediolateral forces than similarly sized cursorial animals. We also found that grizzly bear locomotion was not dynamically similar to that of other quadrupedal species, further indicating differences in locomotor mechanics at equivalent speeds.

Gaits

Researchers have been using gait analysis for over a century to quantify locomotor characteristics of terrestrial animals (e.g. Marey, 1894; Lee et al., 1999; Robilliard et al., 2007). While a number of gaits have been described, most quadrupeds use walks (slow), trots (intermediate), canters and gallops (fast). In our present study of grizzly bears, we were able to record slow, intermediate and fast gaits despite covering a relatively small speed range. Yet, because only two gallops were captured, these data were not included in the analysis. However, this does suggest that a gallop may be the preferred gait at speeds over 4 m s^{-1}, which is the top end of the speed range reported here. It is unclear whether the results found at lower speeds would also be apparent at faster speeds. Within our speed range, the bears used walks at slow speeds (<2.0 m s^{-1}; $Fr^{0.5}<0.77$) and canters at higher speeds (>~3.0 m s^{-1}; $Fr^{0.5}=1.15$, depending on the bear), which is common among quadrupedal animals (Hildebrand, 1989; O'Neill and Schmitt, 2012). However, at intermediate speeds (between 2.0 and 3.0 m s^{-1}; $Fr^{0.5}=0.77$–1.33), bears used a running walk, as opposed to the more common trot. A running walk maintains the footfall sequence of a walk but with a decreased overlap between feet (Hildebrand, 1989). A duty factor below 0.5 and evidence from our force plate analysis (Fig. 1) indicate that this gait is mechanically distinct from walking, despite having a similar footfall pattern. Previous studies have shown that smaller plantigrade carnivorans (e.g. racoons, kinkajous, skunks) also rarely, if ever, use a trot (Van de Graaff et al., 1982; McClearn, 1992). However, opossums (*Didelphis virginiana*) will only trot at speeds above a walk, and do not transition to gallops (White, 1990).

In addition to plantigrade species, there are examples of digitigrade and unguligrade animals that do not trot at any speed. The pace is another intermediate speed bouncing gait, although less common than the trot, and is selected by giraffes and camels (Dagg, 1960; Janis et al., 2002). It has been suggested that this gait limits interference between limbs in animals with long limbs (Dagg, 1973). A study of alpacas found that these animals use lateral sequence walks at slow speeds ($Fr^{0.5}<0.68$) and transverse gallops
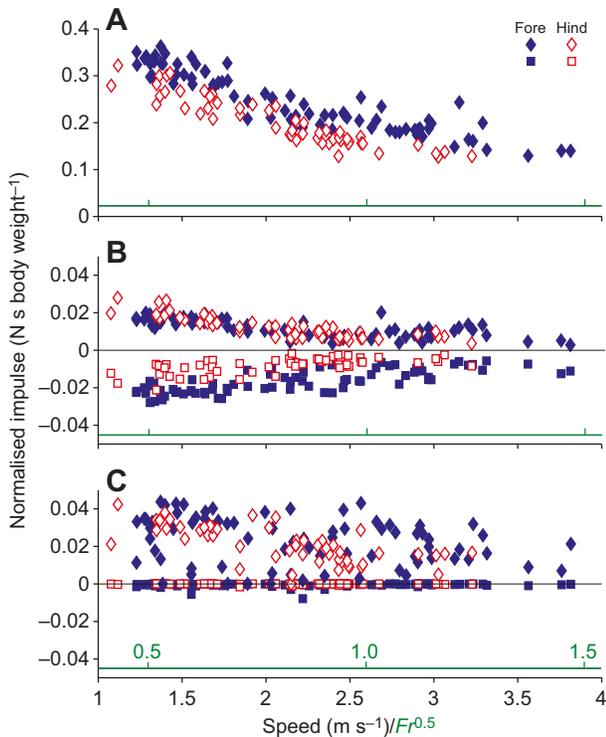
Fig. 2. Vertical, anterior–posterior and mediolateral ground reaction force impulses. Vertical impulses (A) were significantly different between the forelimbs and hindlimbs at all speeds. Anterior–posterior braking impulses (B; negative values, squares) were significantly higher for the forelimb than for the hindlimb, but propulsive impulses (B; positive values, diamonds) are equal between the limbs. Medial impulses (C; positive values, diamonds) were approximately equal to the magnitude of the anterior–posterior impulses. The second x-axis (green) is dimensionless speed (square root of Froude number, $Fr^{0.5}$).

Fig. 3. Peak vertical, anterior–posterior and mediolateral ground reaction forces. There was no significant difference between the forelimbs and hindlimbs for vertical (A), anterior–posterior (B) or mediolateral (C) peak forces. Symbols described in Fig. 2 legend. The second x-axis (green; $Fr^{0.5}$) is dimensionless speed.

at higher speeds ($Fr^{0.5}$>0.68; Pfau et al., 2011), which is similar to the results of our study despite the distinct evolutionary history and morphological differences between bears and alpacas. The trot and the pace require forelimbs and hindlimbs of equal length, with a straight short back (Dagg, 1973); bears are characterised as having a relatively long, sloping back and this may be limiting their use of these gaits. Other animals that use a running walk include elephants, which employ this gait at their fastest speeds (Hutchinson et al., 2003), and most primates, which typically use a running walk as an intermediate between walking and galloping (Schmitt et al., 2006). One of the benefits of the running walk over a trot or a pace is the limited vertical fluctuation in the centre of mass, as well as the ability to maintain contact with the ground with at least one foot throughout the stride (Schmitt et al., 2006). This suggests the apparent lack of a trot by grizzly bears may have implications for energetics as well.

Limb loading
Based on the original dynamic similarity model proposed by Alexander and Jayes (1983), bears do not appear to be dynamically similar to cursorial species. Interestingly, bears have longer relative stride lengths than would be expected for cursorial animals, closer to the relative stride lengths that would be expected for non-cursorial animals (at a Froude number of 1, relative stride lengths: ∼2.5, 1.9 and 2.7 m, respectively; Alexander and Jayes, 1983). A comparison of the duty factors between cursorial animals and bears suggests that bears have lower duty factors than would be expected. For example, at
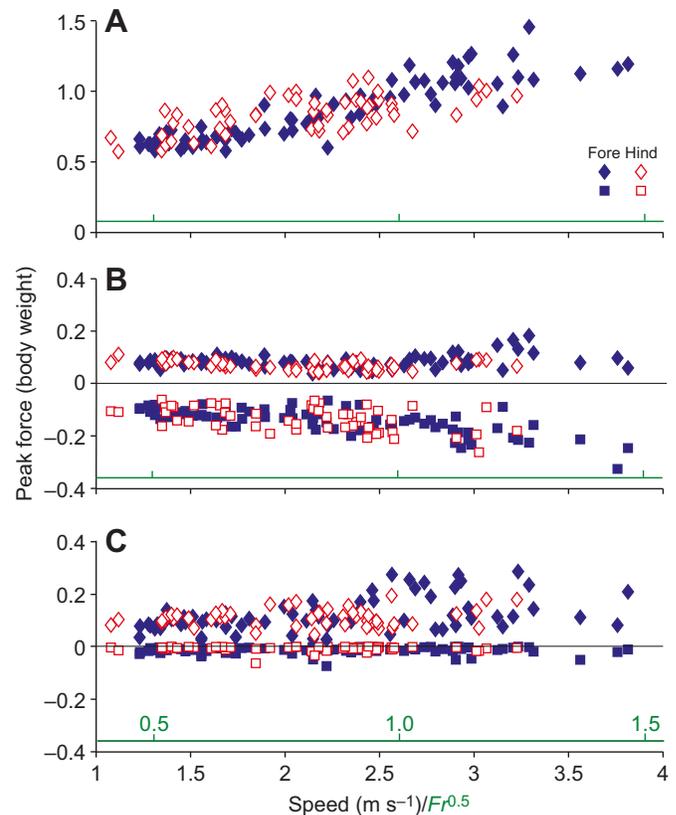
a Froude number of 1 (∼2.6 m s^{-1}), the duty factor for quadrupeds is predicted to be 0.52, compared with a duty factor of 0.47 for bears (Alexander and Jayes, 1983; Fig. 4B), suggesting that bears use a running gait at a relative speed at which other quadrupeds walk. However, several more recent studies have shown that gait transitions, and therefore duty factors below 0.5, occur at lower relative speeds than suggested by Alexander and Jayes (1983). For example, the walk–trot gait transition for horses, ranging in size from miniature to draft, is at an average of $Fr^{0.5}$=0.59 (Griffin et al., 2004), while in elephants the transition from a walk to a running walk occurs at $Fr^{0.5}$=0.25. This suggests that bears transition from a walk to a run at a higher relative speed ($Fr^{0.5}$=0.77) than other quadrupeds.

Mediolateral forces
In studies of quadrupedal mammals, there has been very little focus on mediolateral ground reaction forces generated during locomotion. This is largely because these forces are typically very low, except during turning (Jindrich and Qiao, 2009). Cursorial quadrupeds restrict their movement to the sagittal plane during straight, forward movement and therefore produce minimal medial (generated by a lateral push) and lateral (generated by a medial pull) forces, typically around 5% of the vertical force (Budsberg et al., 1987; Riggs et al., 1993). In this study, we found that grizzly bears produce peak medial forces that averaged nearly 14% of the peak vertical force across speeds and generally exceeded the peak propulsive forces produced. This is consistent with our hypothesis in that the mediolateral forces would be higher than those seen in
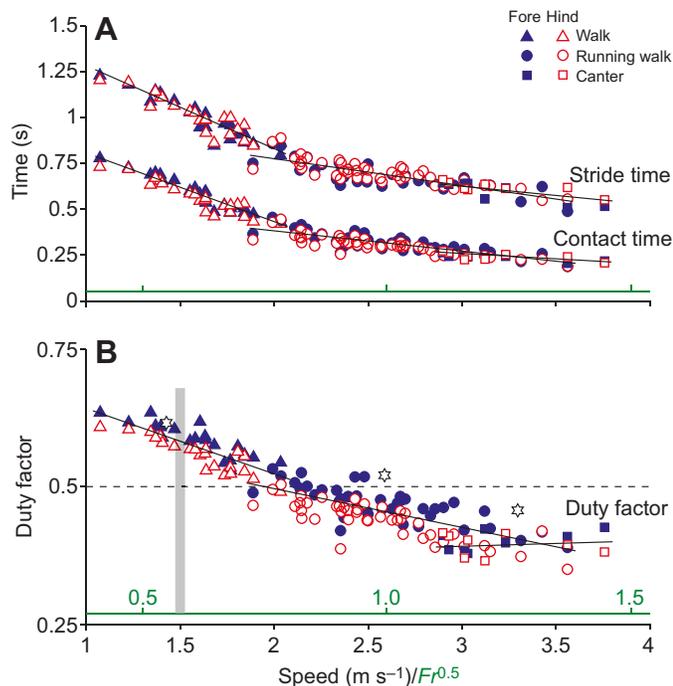
Fig. 4. Stride parameters calculated from video data. (A) Stride and contact time and (B) duty factor across speeds for the forelimbs and hindlimbs. There was a significant relationship with speed for stride and contact time for walks, but no such relationship for running walks or canters. The overlap between speeds of running walks and canters is probably due to variation between individual bears. Estimated forelimb duty factor for bears using dynamic similarity equations for cursorial animals (stars) suggests bears are not dynamically similar to other erect animals. The walk–run transition (duty factor drops below 0.5) occurred at a higher relative speed in bears ($Fr^{0.5}$=0.77) than in horses ($Fr^{0.5}$=0.55–0.61; grey bar). Linear regressions for forelimbs and hindlimbs combined are: walk stride time, $y=-0.45x+1.7$, R^2=0.85, P<0.001; running walk stride time, $y=-0.15x+1.1$, R^2=0.68, P<0.001; canter stride time, $y=-0.13x+1.0$, R^2=0.63, P<0.001; walk contact time, $y=-0.38x+1.2$, R^2=0.89, P<0.001; running walk contact time, $y=-0.12x+0.61$, R^2=0.70, P<0.001; canter contact time, $y=-0.047x+0.39$, R^2=0.54, P=0.001; walk duty factor, $y=-0.12x+0.76$, R^2=0.65, P<0.001; running walk duty factor, $y=-0.07x+0.63$, R^2=0.53, P<0.001; canter duty factor, $y=0.0083x+0.37$, R^2=0.02, P>0.05. The second x-axis (green) is dimensionless speed.

cursorial animals, although the values were still higher than we had anticipated. At fast speeds, the peak medial force occurred coincidently with the transition from braking to propulsive force (Fig. 1C,D), resulting in the horizontal force being perpendicular to the direction of travel. This would suggest that locomotion by bears may be inefficient compared with that in similarly sized cursorial species. The mediolateral forces generated by grizzly bears are approximately between those of cursorial species and the forces produced by animals that use sprawling gaits (with their limbs splayed out to the side rather than directly underneath them). Alligators (*Alligator mississippiensis*), which have a sprawling posture, produce medial forces up to 19% of their peak vertical force (Willey et al., 2004). In these species, large medial forces are generated by lateral foot placement as the limbs are moved in the horizontal as well as the sagittal plane. It has been suggested that for sprawling animals, these forces provide lateral stability, especially in smaller species (Dickinson et al., 2000). For grizzly bears, large medial forces by the forelimbs are probably linked to the medial carpal rotation during swing, which manifests as a medially directed stance. Because of this, forces produced by extension of the carpus and elbow during stance are not in line with the direction of travel.

This has also been suggested for cats as they produce variable mediolateral forces during stance, probably related to pronation and supination at foot down and foot up (Corbee et al., 2014). The magnitudes of medial forces produced by the hindlimbs of grizzly bears are similar to those produced by the forelimbs, but a potential mechanism for this is less clear.

Similar intermediate mediolateral magnitudes have been shown for some primates, such as lemurs (Carlson et al., 2005). Bears, lemurs and alligators, although phylogenetically and morphologically different, are all plantigrade. The higher mediolateral forces in all of these species could be associated with a difference in limb loading specifically due to the plantigrade stance, with variations as a result of the differences in ecology between these groups. It was noted during data collection that the hindquarters of the bears had a substantial amount of long axis rotation resulting in a 'waddle' from side to side. It is possible that this rotation is responsible for producing the large medial hindlimb forces. The potential effect of this waddle on the energetics of bear locomotion is not clear; however, waddling has been shown to be relatively efficient in species such as penguins (Griffin and Kram, 2000). Future studies that measure whole-body centre of mass movements are needed to determine whether the motion produced by the bears' hindlimbs results in similar energy conservation.

Role of the forelimbs versus hindlimbs

Within quadrupeds, forelimbs and hindlimbs may have mechanically different functions during locomotion. In our study, we found that the forelimbs of grizzly bears support between 54% and 60% of body weight, increasing with increasing speed. An approximately 60/40 forelimb/hindlimb ratio is common among quadrupeds, and probably reflects the added mass of the head positioned anterior to the forelimbs (Lee et al., 2004). Deviations from this common pattern have been shown in fast-moving animals (reaching 30/70 in cheetahs; Hudson et al., 2012). Additionally, species that use their forelimbs for extensive object manipulation can use muscle activity to shift their weight onto their hindlimbs (e. g. primates; Vilensky and Larson, 1989). Despite bears using their forelimbs to manipulate objects in their environment, they do not appear to actively support more of their weight on their hindlimbs within the speed range collected in this study.

Across the full speed range, the braking impulses produced by the forelimbs were substantially higher than those produced by the hindlimbs, whereas the propulsive impulses were similar (Fig. 2B). This resulted in the forelimbs having a net braking effect at all speeds while the hindlimbs provided net propulsion. These results are consistent with previous studies of cursorial species (Budsberg et al., 1987; Merkens et al., 1993; McLaughlin and Roush, 1994; Rumph et al., 1994). Both braking and propulsive impulses decreased with speed in the forelimbs and hindlimbs, which has also been found in dogs (Riggs et al., 1993). Peak anterior–posterior forces increased with speed for braking but remained approximately constant for propulsive forces across forelimbs and hindlimbs (Fig. 3B). Dogs also demonstrate this pattern (Riggs et al., 1993); however, horses appear to be different. In walking horses, braking forces are positively correlated with speed only in the hindlimbs, whereas during trotting, forelimbs and hindlimbs both demonstrate a positive relationship (McLaughlin et al., 1996). We had anticipated that a differential use of the forelimbs versus the hindlimbs during locomotion may be exacerbated in plantigrade species because of their increased dexterity and ability to pronate and supinate the forearm. However, over the speed range examined in this study, bears were not substantially different from other quadrupeds.

Our analysis of the vGRF patterns showed that there is a significant difference between the forelimbs and hindlimbs in how they support body weight. At walking speeds, the characteristic M-shaped pattern was more pronounced in the hindlimb force (Fig. 1B), having a significantly lower trough (minimum force near midstance). The higher first peak in the hindlimb has been seen in horses, which also have an asymmetrical forelimb vGRF but the second peak is greater (Merkens et al., 1986). In our study, the hindlimb also tended to have a substantially higher rate of force development at all but the fastest speeds, though this measure was quite variable. This result is similar to that found in alligators (see fig. 3A in Willey et al., 2004). Both the rate of force development and the M-shaped pattern of vertical force have been linked to limb stiffness in studies of humans and other animals, as well as modelling studies (e.g. Geyer et al., 2006). A high rate of force development suggests that the limb is stiffer in early stance, whereas a deep trough in the vGRF is characteristic of a compliant limb (Geyer et al., 2006). Both of these features are present in the hindlimb forces of grizzly bears (relative to the forelimbs). This difference in shape between the forelimb and the hindlimb vGRFs is likely to be the cause of the differences between impulses and weight distribution, without a difference in peak force. However, a more detailed analysis of the anatomy and joint loading patterns will be necessary to understand the mechanism underlying this unique force pattern.

Limitations

Working with adult grizzly bears poses several challenges, including gaining access to these animals and the ability to construct a safe research environment. Because of this, our sample size was limited to only four animals. However, there was relatively little inter-individual variation, which suggests that our data are probably representative of the species over the speed range obtained. The ability to record higher speed trials was also limited by the requirements of the enclosure. Further, ground reaction forces in this study were collected with a single force plate, which meant that we could not record forelimb and hindlimb forces simultaneously in one trial. Therefore, our interpretation of forelimb versus hindlimb function was drawn from the compilation of many trials and, in some cases, regression equations fitted to the data. However, all of the trials were at a steady speed (<20% change in forward speed) and we had multiple hits with the forelimbs and hindlimbs at similar speeds.

Conclusions and future directions

To our knowledge, this is the first study to combine a kinematic and kinetic analysis of locomotion by bears of any species. Our results showed that grizzly bears use walks and canters, but they do not appear to trot, which has been shown in other plantigrade quadrupeds. It remains to be seen whether lack of a trot is a characteristic of plantigrade locomotion, as there has been a limited number of species studied to date. The results of our force analysis showed that, while there were some similarities to cursorial quadrupeds, overall locomotion by grizzly bears is not dynamically similar to that in these species. Grizzly bears also generate substantially higher medial ground reaction forces than expected for a large erect mammal. It is possible that these forces are a product of the unusual carpus and elbow movements found in bears, although previously studied plantigrade species also produce high mediolateral forces. High forces perpendicular to the direction of travel would also suggest a higher energetic cost, compared with similarly sized cursorial species. Future work will examine in more detail the mechanisms underlying the unique features of grizzly bear locomotion and may provide valuable insight into the evolution of plantigrade locomotion.
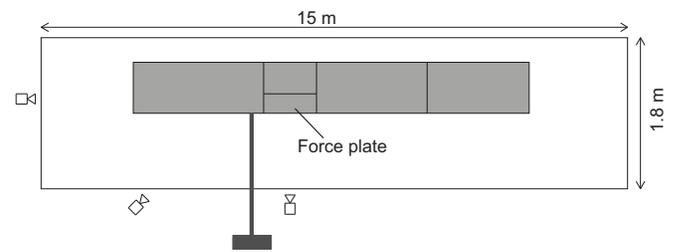

Fig. 5. Schematic diagram of data collection setup. Runway panels are shown in grey with the force plate at the lower centre of the image. The three cameras are shown with approximate angles for data collection. The dark grey box represents the electronic equipment, with a pole carrying cables to the outside of the fence. Trainers were positioned at either end of the enclosure to encourage the bears with food rewards.

MATERIALS AND METHODS
Animals
Four adult female grizzly bears (*Ursus arctos horribilis*; mass 168.9± 18.2 kg, age 10±1.15 years, shoulder height at midstance 0.69±0.13 m) housed at the Washington State University Bear Center were the subjects for this study. These animals were born at the centre and trained for research procedures, including entering a metal crate and allowing access to certain areas of the limb through the bars. All limb joints were shaved and marked with non-toxic high-contrast white paint, while the animals were constrained and distracted with food rewards. This research was approved by the Institutional Animal Care and Use Committee at Washington State University.

Experimental setup
The custom-built force plate (0.6×0.4 m), measuring force in three orthogonal axes, was secured in the centre of a 4.26 m runway within the bear enclosure (Fig. 5) and recorded at 1000 Hz. High-speed cameras (200 Hz, 1248×900 pixels; Xcitex, Inc., Woburn, MA, USA) were placed in the sagittal and frontal planes, as well as an additional camera 45 deg from the direction of travel. Data for this study were collected from bears travelling in both directions.

Calibration
Calibration of the force plate was completed by loading the plate vertically and across all four horizontal directions with gradually increasing loads. These loads were plotted against the voltage output and the resulting relationship (R^2=1.0 for vertical, R^2=0.99 for anterior–posterior, R^2=0.99 for mediolateral) was used to compute the bear data. The natural frequency of the force plate was calculated (vertical=429 Hz, anterior–posterior=267 Hz and mediolateral=289 Hz). The three-dimensional camera volume was calibrated using a calibration frame (Xcitex Inc.), which was placed in view of all three cameras and digitised. The calibration was used to merge the digitised points of the trial data from all three cameras.

Experimental protocol
The bears were encouraged to move along the runway with food rewards; faster trials were achieved by withholding food on the morning of data collection. A trigger was used to synchronise the force plate (LabChart 6, version 6.1.1, AD Instruments, Colorado Springs, CO, USA) and the cameras (ProCapture, Xcitex Inc.); data were saved for 2 s pre-trigger and 1 s post-trigger, to capture the entire length of time the animal was on the runway. A total of 444 trials were recorded over the data collection period; 176 of these were analysed independently for gait and force. Gait trials (total=76) were selected based on speed and visibility of full strides for all limbs, and did not necessarily include contact with the force plate. Trials were considered suitable for force analysis if there was an isolated footfall on the force plate (total=137). An approximately equal number of trials from each of the four bears were included in the analyses. To determine whether the trials were at steady speed, forward speeds of a trunk point at the beginning and end of a stride (foot strike to subsequent same foot strike) were compared with the mean forward speed over the whole trial. Trials

were rejected if the difference between the beginning and the end was greater than 20% of the average.

Analysis

All data were processed through custom-written Matlab (Mathworks Inc., Natick, MA, USA) routines. Speeds were calculated by differentiating a digitised (ProAnalyst, Xcitex Inc.) point on the animal's trunk for at least one stride while the bear was on the runway. This point was digitised in two different cameras to ensure no errors due to parallax or the position of the camera. Gait was determined by footfall times for one stride, and stride time, contact time and duty factor were calculated for each limb. There was no difference between left and right limbs, and therefore these parameters were averaged for the forelimbs and the hindlimbs. Speeds were converted to square root of Froude number [$Fr^{0.5}=v/(gh)^{0.5}$; where v is speed, g is gravitational acceleration and h is characteristic length] to normalise for body size, which allows comparison between bears and other species. Shoulder height was used for the length metric (h), and therefore we only compared dynamic similarity data for the forelimb. Predicted stride parameters were calculated using dynamic similarity equations (Alexander and Jayes, 1983) at average speeds for each gait. These values were converted to m s^{-1} and plotted with the rest of our data (Fig. 4B).

Peak ground reaction forces and impulses were calculated for vertical, anterior–posterior and mediolateral directions. Because forelimb and hindlimb data were not available for the same trials, forelimb versus hindlimb force distribution was calculated based on a regression of impulse against speed. Specifically, we used the quadratic equation from the regressions against speed to calculate the impulse for the forelimbs and hindlimbs at a fixed set of speeds (1, 2, 3 and 4 m s^{-1}). These impulses were then used to calculate the forelimb/hindlimb impulse ratio. All force data outputs were normalised by body weight. Positive mediolateral forces are lateral pushing by the animal on the ground.

Statistics

Statistical analyses were conducted using the Matlab Statistical Toolbox. An analysis of covariance (ANCOVA) was carried out to identify differences between forelimbs and hindlimbs, and between gaits, using speed as the covariate. Linear regressions were calculated on an average of forelimb and hindlimb values for each stride parameter (Fig. 4), and ANCOVA were calculated to identify differences between walk, running walk and canter slopes and intercepts. Vertical impulse curves (Fig. 2A) were log transformed to provide a linear relationship for an ANCOVA.

References

Alexander, R. M. (1984). The gaits of bipedal and quadrupedal animals. *Int. J. Robot. Res.* **3**, 49-59.

Alexander, R. M. (2005). Models and the scaling of energy costs for locomotion. *J. Exp. Biol.* **208**, 1645-1652.

Alexander, R. M. and Jayes, A. S. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool.* **201**, 135-152.

Bertram, J. E. A. and Gutmann, A. (2009). Motions of the running horse and cheetah revisited: fundamental mechanics of the transverse and rotary gallop. *J. R. Soc. Interface* **6**, 549-559.

Brown, G. (2009). *The Bear Almanac.* Guilford, CT, USA: The Lyons Press.

Budsberg, S. C., Verstraete, M. C. and Soutas-Little, R. W. (1987). Force plate analysis of the walking gait in healthy dogs. *Am. J. Vet. Res.* **48**, 915-918.

Carlson, K. J., Demes, B. and Franz, T. M. (2005). Mediolateral forces associated with quadrupedal gaits of lemurids. *J. Zool.* **266**, 261-273.

Carrano, M. T. (1997). Morphological indicators of foot posture in mammals: a statistical and biomechanical analysis. *Zool. J. Linn. Soc.* **121**, 77-104.

Corbee, R. J., Maas, H., Doornenbal, A. and Hazewinkel, H. A. W. (2014). Forelimb and hindlimb ground reaction forces of walking cats: assessment and comparison with walking dogs. *Vet. J.* **202**, 116-127.

Dagg, A. I. (1960). Gaits of the giraffe and okapi. *J. Mammal.* **41**, 282.

Dagg, A. I. (1973). Gaits in mammals. *Mammal Rev.* **3**, 135-154.

Davis, D. D. (1949). *The Shoulder Architecture of Bears and Other Carnivores.* Chicago: Chicago Natural History Museum.

Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R. and Lehman, S. (2000). How animals move: an integrative view. *Science* **288**, 100-106.

Farley, C. T., Glasheen, J. and McMahon, T. A. (1993). Running springs: speed and animal size. *J. Exp. Biol.* **185**, 71-86.

Gambaryan, P. (1974). *How Mammals Run: Anatomical Adaptations.* New York: Wiley.

Garland, T. and Janis, C. M. (1993). Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *J. Zool.* **229**, 133-151.

Geyer, H., Seyfarth, A. and Blickhan, R. (2006). Compliant leg behaviour explains basic dynamics of walking and running. *Proc. R. Soc. B Biol. Sci.* **273**, 2861-2867.

Ginsburg, L. (1961). Plantigradie et digitigradie chez les carnivores fissipedes. *Mammalia* **25**, 1-21.

Gray, J. (1968). *Animal Locomotion.* New York: Weidenfeld & Nicolson.

Griffin, T. M. and Kram, R. (2000). Biomechanics: penguin waddling is not wasteful. *Nature* **408**, 929-929.

Griffin, T. M., Kram, R., Wickler, S. J. and Hoyt, D. F. (2004). Biomechanical and energetic determinants of the walk–trot transition in horses. *J. Exp. Biol.* **207**, 4215-4223.

Hildebrand, M. (1976). Analysis of tetrapod gaits: general considerations and symmetrical gaits. *Neural Control Locomotion* **18**, 203-236.

Hildebrand, M. (1977). Analysis of asymmetrical gaits. *J. Mammal.* **58**, 131-156.

Hildebrand, M. (1989). The quadrupedal gaits of vertebrates. *BioScience* **39**, 766-775.

Hudson, P. E., Corr, S. A. and Wilson, A. M. (2012). High speed galloping in the cheetah (Acinonyx jubatus) and the racing greyhound (Canis familiaris): spatio-temporal and kinetic characteristics. *J. Exp. Biol.* **215**, 2425-2434.

Hutchinson, J. R., Famini, D., Lair, R. and Kram, R. (2003). Biomechanics: are fast-moving elephants really running? *Nature* **422**, 493-494.

Hutchinson, J. R., Schwerda, D., Famini, D. J., Dale, R. H. I., Fischer, M. S. and Kram, R. (2006). The locomotor kinematics of Asian and African elephants: changes with speed and size. *J. Exp. Biol.* **209**, 3812-3827.

Inuzuka, N. (1996). Preliminary study on kinematic gait analysis in mammals. *Mammal Study* **21**, 43-57.

Irschick, D. J. and Garland, T., Jr. (2001). Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Systemat.* **32**, 367-396.

Iwaniuk, A. N., Pellis, S. M. and Whishaw, I. Q. (2000). The relative importance of body size, phylogeny, locomotion, and diet in the evolution of forelimb dexterity in fissiped carnivores (Carnivora). *Can. J. Zool. Rev. Can. Zool.* **78**, 1110-1125.

Janis, C. M., Theodor, J. M. and Boisvert, B. (2002). Locomotor evolution in camels revisited: a quantitative analysis of pedal anatomy and the acquisition of the pacing gait. *J. Vertebr. Paleontol.* **22**, 110-121.

Jindrich, D. L. and Qiao, M. (2009). Maneuvers during legged locomotion. *Chaos* **19**, 026105.

Lee, D. V., Bertram, J. E. A. and Todhunter, R. J. (1999). Acceleration and balance in trotting dogs. *J. Exp. Biol.* **202**, 3565-3573.

Lee, D. V., Stakebake, E. F., Walter, R. M. and Carrier, D. R. (2004). Effects of mass distribution on the mechanics of level trotting in dogs. *J. Exp. Biol.* **207**, 1715-1728.

Liem, K. F., Walker, W. F., Bemis, W. E. Grande, L. (2001). *Functional Anatomy of the Vertebrates: An Evolutionary Perspective.* Philadelphia: Harcourt College Publishers.

Marey, E.-J. (1894). *Le Mouvement.* Paris: Masson.

McClearn, D. (1992). Locomotion, posture, and feeding behavior of kinkajous, coatis, and raccoons. *J. Mammal.* **73**, 245-261.

McLaughlin, R. M., Jr. and Roush, J. (1994). Effects of subject stance time and velocity on ground reaction forces in clinically normal greyhounds at the trot. *Am. J. Vet. Res.* **55**, 1666-1671.

McLaughlin, R., Jr., Gaughan, E., Roush, J. and Skaggs, C. (1996). Effects of subject velocity on ground reaction force measurements and stance times in clinically normal horses at the walk and trot. *Am. J. Vet. Res.* **57**, 7-11.

Merkens, H. W., Schamhardt, H. C., Hartman, W. and Kersjes, A. W. (1986). Ground reaction force patterns of Dutch Warmblood horses at normal walk. *Equine Vet. J.* **18**, 207-214.

Merkens, H. W., Schamhardt, H. C., Osch, G. J. V. M. and Van Den Bogert, A. (1993). Ground reaction force patterns of Dutch Warmblood horses at normal trot. *Equine Vet. J.* **25**, 134-137.

O'Neill, M. C. and Schmitt, D. (2012). The gaits of primates: center of mass mechanics in walking, cantering and galloping ring-tailed lemurs, *Lemur catta*. *J. Exp. Biol.* **215**, 1728-1739.

Pfau, T., Hinton, E., Whitehead, C., Wiktorowicz-Conroy, A. and Hutchinson, J. R. (2011). Temporal gait parameters in the alpaca and the evolution of pacing and trotting locomotion in the Camelidae. *J. Zool.* **283**, 193-202.

Renous, S., Gasc, J.-P. and Abourachid, A. (1998). Kinematic analysis of the locomotion of the polar bear (*Ursus maritimus*, Phipps, 1774) in natural and experimental conditions. *Neth. J Zool.* **48**, 145-167.

Riggs, C., DeCamp, C., Soutas-Little, R., Braden, T. and Richter, M. (1993). Effects of subject velocity on force plate-measured ground reaction forces in healthy greyhounds at the trot. *Am. J. Vet. Res.* **54**, 1523-1526.

Robilliard, J. J., Pfau, T. and Wilson, A. M. (2007). Gait characterisation and classification in horses. *J. Exp. Biol.* **210**, 187-197.

Rumph, P., Lander, J., Kincaid, S., Baird, D., Kammermann, J. and Visco, D. (1994). Ground reaction force profiles from force platform gait analyses of clinically normal mesomorphic dogs at the trot. *Am. J. Vet. Res.* **55**, 756-761.

Schmitt, D., Cartmill, M., Griffin, T. M., Hanna, J. B. and Lemelin, P. (2006). Adaptive value of ambling gaits in primates and other mammals. *J. Exp. Biol.* **209**, 2042-2049.

Van De Graaff, K. M., Harper, J. and Goslow, G. E. Jr. (1982). Analysis of posture and gait selection during locomotion in the striped skunk (*Mephitis mephitis*). *J. Mammal.* **63**, 582-590.

Vilensky, J. A. and Larson, S. G. (1989). Primate locomotion: utilization and control of symmetrical gaits. *Ann. Rev. Anthropol.* **18**, 17-35.

Walter, R. M. and Carrier, D. R. (2007). Ground forces applied by galloping dogs. *J. Exp. Biol.* **210**, 208-216.

White, T. D. (1990). Gait selection in the brush-tail possum (*Trichosurus vulpecula*), the northern quoll (*Dasyurus hallucatus*), and the Virginia opossum (*Didelphis virginiana*). *J. Mammal.* **71**, 79-84.

Willey, J. S., Biknevicius, A. R., Reilly, S. M. and Earls, K. D. (2004). The tale of the tail: limb function and locomotor mechanics in *Alligator mississippiensis*. *J. Exp. Biol.* **207**, 553-563.