

RESEARCH ARTICLE

Grizzly bear (*Ursus arctos horribilis*) locomotion: forelimb joint mechanics across speed in the sagittal and frontal planes

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ABSTRACT

The majority of terrestrial locomotion studies have focused on parasagittal motion and paid less attention to forces or movement in the frontal plane. Our previous research has shown that grizzly bears produce higher medial ground reaction forces (lateral pushing from the animal) than would be expected for an upright mammal, suggesting frontal plane movement may be an important aspect of their locomotion. To examine this, we conducted an inverse dynamics analysis in the sagittal and frontal planes, using ground reaction forces and position data from three high-speed cameras of four adult female grizzly bears. Over the speed range collected, the bears used walks, running walks and canters. The scapulohumeral joint, wrist and the limb overall absorb energy (average total net work of the forelimb joints, -0.97 W kg^{-1}). The scapulohumeral joint, elbow and total net work of the forelimb joints have negative relationships with speed, resulting in more energy absorbed by the forelimb at higher speeds (running walks and canters). The net joint moment and power curves maintain similar patterns across speed as in previously studied species, suggesting grizzly bears maintain similar joint dynamics to other mammalian quadrupeds. There is no significant relationship with net work and speed at any joint in the frontal plane. The total net work of the forelimb joints in the frontal plane was not significantly different from zero, suggesting that, despite the high medial ground reaction forces, the forelimb acts as a strut in that plane.

KEY WORDS: Inverse dynamics, Plantigrade, Mammal, Mediolateral, Gait

INTRODUCTION

During locomotion, muscles are required to balance external moments produced by ground reaction forces. Because of the scaling relationship of muscle cross-sectional area compared with body mass, these moments become more difficult to resist as animals become larger (assuming geometric similarity). Large animals have evolved a more erect posture to keep ground reaction forces directed along the limb (Biewener, 1989), which increases the muscle effective mechanical advantage (EMA; ratio of the muscle moment arm to the moment arm of the ground reaction forces) and minimises the external joint moments.

In addition to becoming more upright, many large quadrupeds have evolved a digitigrade or unguligrade posture. While bears are classified as upright animals, they are the only group of large quadrupedal mammals with the palmigrade posture. The increase in the length of the foot in contact with the ground, and the associated shift in the centre of pressure, is likely to affect the joint moments and therefore the amount of mechanical work done by the joints. This relates to the effective mechanical advantage as the limb will not be as fully upright as in unguligrade species. Digitigrade species have also been shown to have lower EMA values than would be predicted for their body size (dogs; Biewener, 1989).

While relatively few studies have examined forelimb joint moments in quadrupeds, a similar trend has been reported despite large differences in size and posture. This includes the production of extensor moments at the scapulohumeral, elbow and wrist joints (Clayton et al., 2000; Witte et al., 2002; Nielsen et al., 2003). Power profiles across the joints of the forelimb do vary across species. The wrist absorbs energy in both horses and dogs (Clayton et al., 1998, 2000; Gregersen et al., 1998). However, the elbow and shoulder have opposite roles in these two species, with the elbow absorbing energy in the dog and the shoulder absorbing energy in horses (Clayton et al., 1998, 2000; Gregersen et al., 1998). This may relate to elastic energy storage at these two joints, as well as morphology differences due to their foot postures.

Both digitigrade and unguligrade species have adaptations for speed and endurance when running, which includes restricting movement of the limbs to parasagittal motion (Liem et al., 2001). This results in negligible mediolateral forces during locomotion in most quadrupeds (Riggs et al., 1993; Nielsen et al., 2003; Parchman et al., 2003; Walter and Carrier, 2007; Corbee et al., 2014). Because of this, the majority of locomotion studies have focused on parasagittal motion and not forces or movement in the frontal plane.

Our previous research has shown that grizzly bears produce higher medial ground reaction forces (lateral pushing from the animal) than would be expected for an upright mammal (Shine et al., 2015). The relative forces produced are closer to values reported for an alligator (*Alligator mississippiensis*; Willey et al., 2004), which have a sprawling posture. These high medial forces could suggest that bears may be producing net work in the frontal plane and therefore may not be efficiently propelling themselves forwards.

The forelimbs have functional roles beyond locomotion in terrestrial animals, particularly in plantigrade and palmigrade species. The morphology of the forelimb in plantigrade species allows for pronation and supination of the manus, which increases dexterity of these animals (Iwaniuk et al., 2000). Palmigrade carnivores use their forelimbs to investigate objects, to grasp food items and also for fighting, particularly in bears (Brown, 2009). In addition to being palmigrade, grizzly bears have a medially deviated forefoot during stance with an associated rotation during swing (Davis, 1949; Gray, 1968; Inuzuka, 1996). The mechanism and

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function of this behaviour is unknown, but it is likely to have an effect on the joint dynamics of the forelimb, particularly in the frontal plane.

Therefore, in this study we aimed to quantify joint mechanics for grizzly bears across speeds, taking into account both sagittal plane and frontal plane movements, in order to analyse the effects of the high medial ground reaction forces and medially rotated forefoot. We addressed the following questions. (1) Does grizzly bear forelimb motion in the sagittal plane have similarities to that of other large mammals? (2) Do the medial ground reaction forces and forefoot posture result in significant net work and power values in the frontal plane? To our knowledge this is one of few studies to calculate parameters of joint mechanics in the frontal plane in a terrestrial quadruped.

MATERIALS AND METHODS

Animals

The data in this study were collected from four adult female grizzly bears (*Ursus arctos horribilis* Ord 1815; mass 168.9±18.2 kg, age 10±1.15 years, shoulder height at midstance 0.69±0.13 m), born and housed at the Washington State University Bear Center. These animals are involved in various studies, and are therefore trained for research procedures. This research was approved by the Institutional Animal Care and Use Committees at the University of Idaho and Washington State University.

Experimental setup

A 4.26 m runway was placed in a narrow walkway in the bear enclosure with a custom-built force plate (0.6 m×0.4 m) secured in the centre. The force plate measures in three orthogonal axes and data were recorded at 1000 Hz. High-speed cameras (200 Hz, 1248×900; Xcitex Inc., Woburn, MA, USA) were placed with a perpendicular view of the sagittal and frontal planes, and a third camera was placed at 45 deg from the direction of travel. The left scapulohumeral joint, elbow and wrist were shaved on the lateral side and marked, along with the lateral toe, with high-contrast, non-toxic paint. Marker placement was determined by palpation of the joints while the bear was restrained and distracted with food rewards.

Experimental protocol

Bears were called from either end of the walkway and tempted with food rewards. The cameras and force plate (1000 Hz; LabChart 6, version 6.1.1, AD Instruments, Colorado Springs, CO, USA) were synchronised using a trigger. Because of the setup of the cameras, only trials in which the isolated left forelimb landed on the force plate were included in this study. Trials were considered steady speed (and therefore included in the study) if the difference between speeds at the beginning and end of a stride was less than 20% of the average speed.

Speed and gait

Data were processed through custom-written Matlab scripts (The Mathworks, Inc., Natick, MA, USA). Speed was calculated by

digitising (ProAnalyst, Xcitex Inc.) a point on the animal's trunk from at least two camera views for a minimum of one stride as the bear moved over the force plate. This enables a 3D reconstruction of the animal's movement, allowing accurate calculations in both the frontal and sagittal planes. Gaits were determined using footfall patterns and characterised as described in Hildebrand (1976).

Segment properties

Segment inertial properties were modelled using cylinders, with limb segment densities estimated from Winter (1990). Segment dimensions were calculated from a CT scan of a grizzly bear forelimb (4 year old male; 148.8 kg); the scan was divided into upper arm, forearm and manus segments, the volumes of which were calculated using Mimics (Materialise NV, Leuven, Belgium). These values were then scaled to the live animals based on body mass (Table 1). The segment volumes for this study were estimated from a CT scan of a different bear and therefore are potentially inaccurate. A sensitivity analysis was conducted to determine the effect of estimations of segment mass on the results. We varied the segment mass from 75% to 125% from the estimate at 5% increments. This procedure resulted in no more than a 2% difference in peak joint moments with a 25% difference in segment mass. Given this relatively small difference with unrealistically high changes in mass, we are satisfied that our conclusions are not affected by the lack of specifically measured segment properties. Foot segment linear dimensions were measured using the high-speed video footage; the wrist and foot widths were used to correct for the lateral skin markers in the frontal plane. The centre of rotation for the scapulohumeral joint and elbow in the frontal plane was measured from the CT scan, as we were unable to accurately estimate these from the video footage.

Inverse dynamics

Inverse dynamics analyses are based on methods described in Winter (1990). Joint markers were digitised (ProAnalyst, Xcitex Inc.) before, during and after stance. The lateral skin markers were sufficient in the sagittal plane, and we accounted for the distance from the centre of joint rotation in the frontal plane using data from a CT scan of another bear. We assessed the accuracy of this method by also estimating the width of the elbow and wrist from the frontal videos for comparison. The widths of the foot, wrist and elbow were measured, and one half of this distance was subtracted from the marker position on the skin. Joint position and force plate data were imported into Matlab and net joint angle, moment and power were calculated independently for the frontal and sagittal planes. The scapulohumeral joint was calculated relative to horizontal in both planes. The frontal plane wrist angle was calculated relative to the forearm (Fig. 1). Positive sagittal moments were defined as those that are balanced by extensor musculature for the wrist, elbow and scapulohumeral joint. Positive frontal moments are defined as those balanced by abductor musculature for all joints (Fig. 1).

Table 1. Segment properties for individual bears

Bear	Body mass (kg)	Upper arm mass (kg)	Forearm mass (kg)	Foot mass (kg)	Wrist width (m)	Foot width (m)
Kio	175	11.55	3.33	1.84	0.114	0.1268
Luna	184/191	11.10/11.52	3.50/3.63	1.93/2.01	0.113	0.1524
Mika	148	8.92	2.81	1.55	0.09	0.1405
Peeka	184	11.10	3.50	1.93	0.1	0.121

Data collected from Luna were from two separate years; segment masses were calculated for each trial according to the body mass at that time.

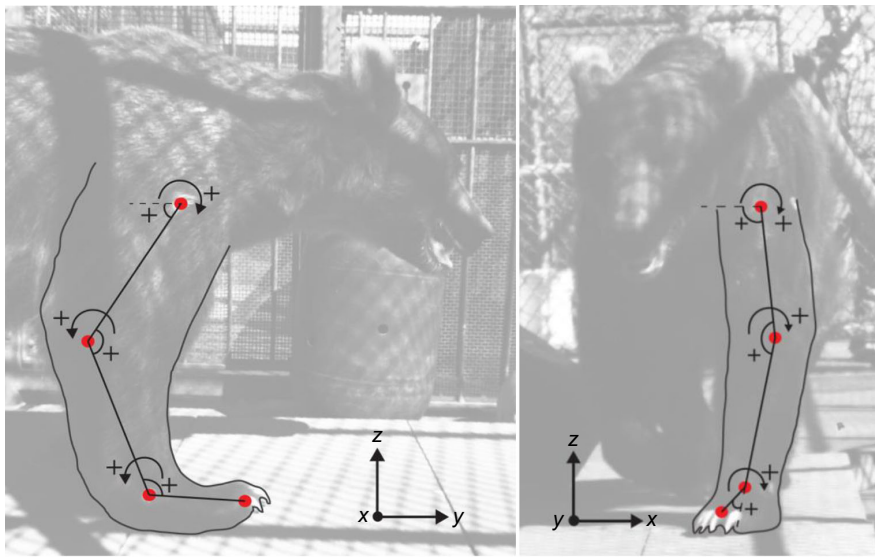


Fig. 1. Schematic diagram of joint angles and moments. (A) Sagittal plane. Scapulothoracic joint angle was calculated relative to the horizontal as we did not have a marker on the scapula. Extensor moments are positive for all joints. Data were collected for the left forelimb; however, analysis was conducted with the y -axis increasing from left to right; therefore, this image has been reflected to demonstrate the moments as calculated in the analysis. (B) Frontal plane. The scapulothoracic joint angle was calculated relative to the horizontal. The wrist angle was calculated as the angle of the foot relative to the forearm. Abductor moments are positive for all joints.

Statistics

Two-tailed ANOVA were conducted to analyse the relationship between speed and net work at each joint. We used t -tests assuming unequal variance to determine differences between variables across gaits.

RESULTS

Trials

We analysed 21 trials for this study, ranging from 1 to 3.5 m s^{-1} , with an approximately equal number of trials from three of the four bears. One bear was only included in one session of data collection and therefore has fewer trials; however, her data are comparable to those of the others and are therefore included in the analysis. Trials included walks, running walks and canters, with gait transitions at approximately 2 and 3 m s^{-1} . Walking trials maintained an M-shaped vertical ground reaction force trace, while the faster gaits produced single peak traces typical of running animals (Fig. 2). Relatively high medial ground reaction forces were present at all speeds (Fig. 2).

Joint angles

The scapulothoracic joint is retracted throughout stance (Fig. 3A). In the frontal plane, the scapulothoracic angle increases in the second half of stance, which is caused by the limb moving laterally as the foot is raised from the ground (Fig. 4A). In the sagittal plane,

the elbow is maintained at a higher angle (closer to full extension) throughout stance at the lowest speeds compared with the higher speeds, although there is some variation at this joint (Fig. 3D). The average frontal elbow angle across all speeds is 155.1 deg. The frontal angle of the foot relative to the forearm (medial deviation) decreases with speed from 31.2 deg at walking speeds to 19.2 deg during cantering, although there is substantial variation, especially at the highest speeds. The frontal wrist angle is maintained for the majority of stance; however, the angles for each gait converge as the wrist is lifted prior to the foot leaving the ground (Fig. 4G).

Moments

Scapulothoracic, elbow and wrist joint moments are all positive during stance, representing extensor moments. The magnitude of scapulothoracic moments is greater than that for moments of the other two joints (elbow, $P=0.016$; wrist, $P<0.001$; Fig. 3B,E,H). Moments produced by both the scapulothoracic joint and elbow are similar in magnitude in the sagittal and frontal planes (Figs 3B,E and 4B,E, respectively), whereas frontal moments are smaller than sagittal moments at the wrist ($P<0.001$; Figs 4H and 3H, respectively). Overall, peak moments increase with speed at all three joints ($P<0.001$). Walks have significantly lower peak moments than the running gaits at all joints ($P<0.001$). Canters have significantly higher moments than running walks at the elbow ($P=0.019$).

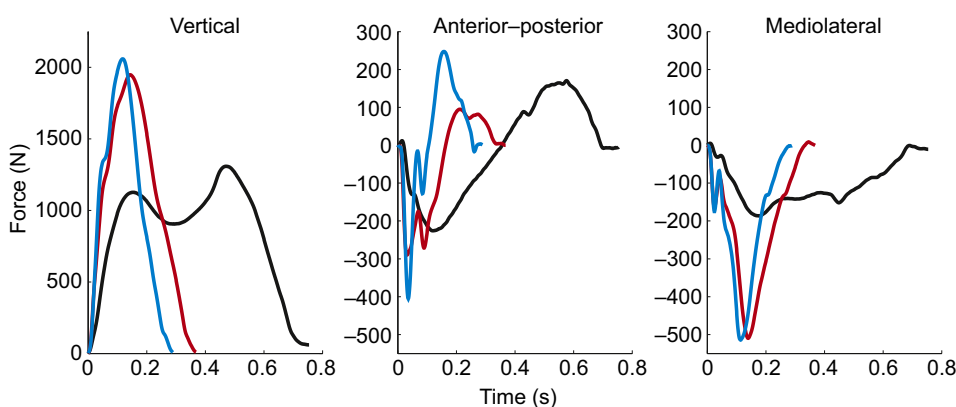


Fig. 2. Representative ground reaction forces. Vertical, anterior–posterior and mediolateral ground reaction force traces from representative trials at a walk (1.4 m s^{-1} ; black), running walk (2.5 m s^{-1} ; red) and canter (3.2 m s^{-1} ; blue). Negative mediolateral force represents a medial ground reaction force, which is produced by the animal pushing laterally. All trials are from the same individual.

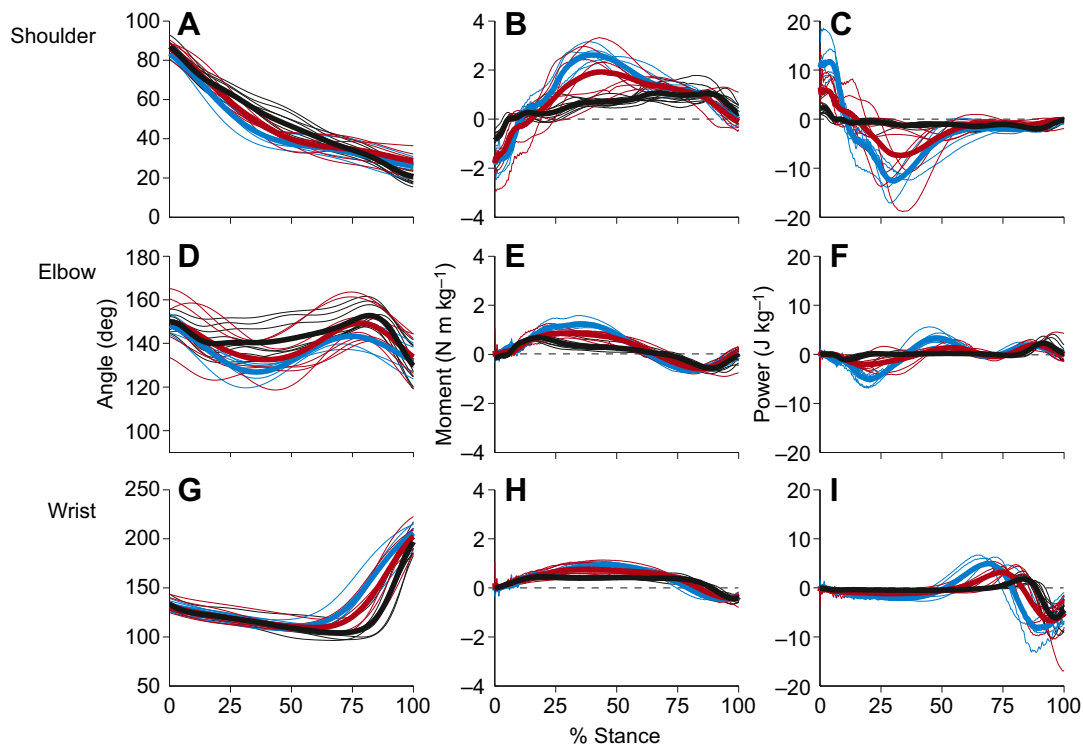


Fig. 3. Angles, moments and power in the sagittal plane. Joint angle, normalised joint moment and normalised joint power for the scapulohumeral joint (A–C), elbow (D–F) and wrist (G–I). Blue represents canterers ($\sim >3 \text{ m s}^{-1}$), red represents running walks ($\sim 2\text{--}3 \text{ m s}^{-1}$) and black represents walks ($\sim <2 \text{ m s}^{-1}$). All trials are plotted using narrow lines, and bold lines are the average for each gait. Zero on the y-axis has been highlighted with a dashed black line for clarity.

Net work and power – sagittal plane

Average net work produced by the forelimb (summed across joints) is -0.97 W kg^{-1} , decreasing with speed ($P < 0.01$; Fig. 5). Positive work for all three joints is approximately 0.2 W kg^{-1} at all speeds; however, negative work varies for each joint and with speed. The scapulohumeral joint absorbs energy (i.e. net negative work) for the majority of stance (Fig. 3C). The magnitude of the energy absorbed by the scapulohumeral joint is greater than that of the wrist and elbow, and decreases with increasing speed ($P = 0.016$). The power produced by the elbow remains low throughout stance and across speeds (Fig. 3F). Net work at the elbow has a negative relationship with speed ($P < 0.001$), beginning with positive net work during walks, but becoming negative in running walks and canterers (Fig. 6). The wrist produces low power values for the first 75% of stance; this increases towards the end of stance as the foot is preparing to leave the ground (Fig. 3I). There is no significant relationship between net work and gait at the wrist.

Net work and power – frontal plane

Joint power in the frontal plane fluctuates around zero for all three joints, with the highest magnitude and most variation at the scapulohumeral joint. Overall, the power produced in the frontal plane is low across all speeds. The scapulohumeral joint produces positive net work across all speeds, whereas the elbow produces negative net work at all speeds (Fig. 6). Positive work for the scapulohumeral joint, averaged across speeds, is 0.19 W kg^{-1} , and average negative work at the elbow is -0.16 W kg^{-1} . For both joints, average net work values are significantly different from zero ($P < 0.05$) but still low compared with values from the sagittal plane. There is no relationship between net work and speed in the frontal plane at the wrist, and the magnitudes are low. Absolute values for both positive and negative work are less than 0.05 W kg^{-1} at all

speeds. The total limb net work is not significantly different from zero and does not change with speed (Fig. 5).

DISCUSSION

The goal of this study was to investigate forelimb joint dynamics across speeds by grizzly bears, in the sagittal and frontal planes. We aimed to determine whether forelimb motion in grizzly bears was similar to that of other large mammals, and also whether net work was produced in the frontal plane, which could be related to the medial ground reaction force produced by the grizzly bears. Bears are relatively distinct from other mammals. They are the only family of large, palmigrade species in the Carnivora order, which probably influences their locomotor mechanics. However, despite the differences in size and posture, we found substantial similarities between grizzly bears and other quadrupeds in joint dynamics in the sagittal plane. Further, we found that the relatively high medial ground reaction forces do not result in significant mechanical work being done in the frontal plane.

Sagittal plane joint mechanics

In general, the sagittal plane joint mechanics of grizzly bears are similar to those of other quadrupeds, including digitigrade, unguligrade and plantigrade species. A previous study compared data from several mammalian species over a wide size range, and also found similar patterns in the relative timing of joint dynamics despite the differences in size and posture (Witte et al., 2002).

Shoulder dynamics are relatively consistent across species, even with differences in posture. However, differences in how shoulder angle is calculated are common in the literature and caution should be used when comparing across species and studies. The scapulohumeral angle in our study was calculated relative to the horizontal as we were unable to place a marker on the scapula.

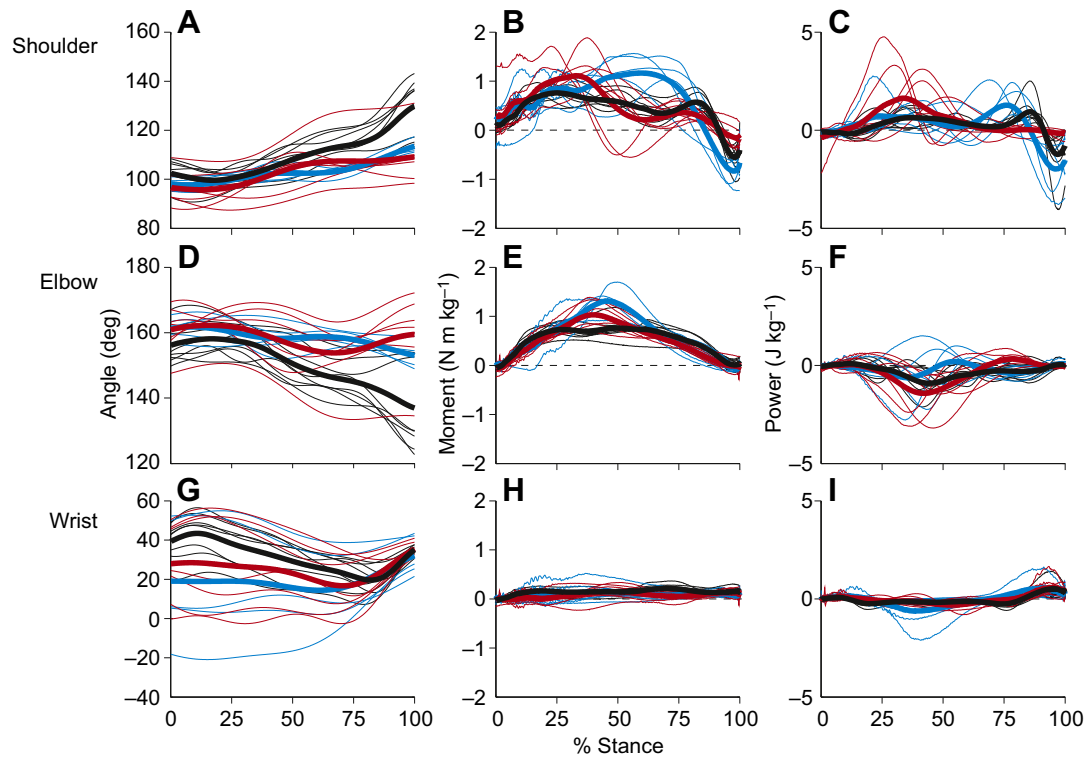


Fig. 4. Angles, moments and power in the frontal plane. Joint angle, normalised joint moment and normalised joint power for the scapulohumeral joint (A–C), elbow (D–F) and wrist (G–I). Blue represent canters ($\sim 3 \text{ m s}^{-1}$), red represents running walks ($\sim 2\text{--}3 \text{ m s}^{-1}$) and black represents walks ($\sim <2 \text{ m s}^{-1}$). All trials are plotted using narrow lines, and bold lines are the average for each gait. Zero on the y-axis has been highlighted with a dashed black line for clarity.

Based on this analysis, the scapulohumeral angle in the sagittal plane is close to 90 deg when the foot touches the ground and retracts (i.e. flexes) under an extensor moment throughout stance, which results in energy absorption. A similar result has been shown for small mammals, as well as dogs and pigs (Witte et al., 2002; Nielsen et al., 2003; Thorup et al., 2008). Horses also produce an extensor moment at the shoulder, which results in energy absorption during walking (Clayton et al., 2000).

The functional role of the elbow also appears to be consistent across body size and limb posture. During stance, bears produce extensor moments at the elbow, which mainly act to prevent collapse of the limb under the acceleration due to gravity. This is consistent across mammalian quadrupeds, including small and large species and all three postures (horses, Clayton et al., 2000; small mammals, Witte et al., 2002; dogs, Nielsen et al., 2003; pigs, Thorup et al., 2008). The net work done by the elbow joint in grizzly bears has a negative relationship with speed. This pattern may also

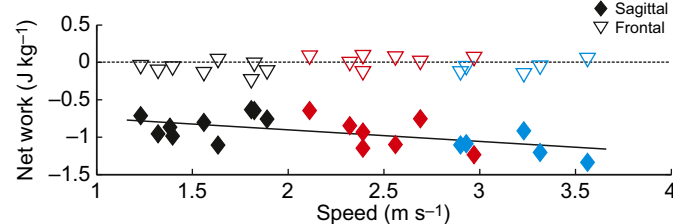


Fig. 5. Limb net work across speeds. The net work for joints was summed to produce total limb net work in the sagittal (diamonds) and frontal (triangles) planes. Frontal net work is not statistically different from zero. The forelimb absorbs energy (i.e. negative work) in the sagittal plane, increasing with increasing speed ($P < 0.01$). Each data point represents an individual trial; gaits are coloured as described in Fig. 3.

been seen in horses, which produce positive power at the elbow during walking, but approximately equal energy absorption and generation during trotting (Clayton et al., 1998, 2000).

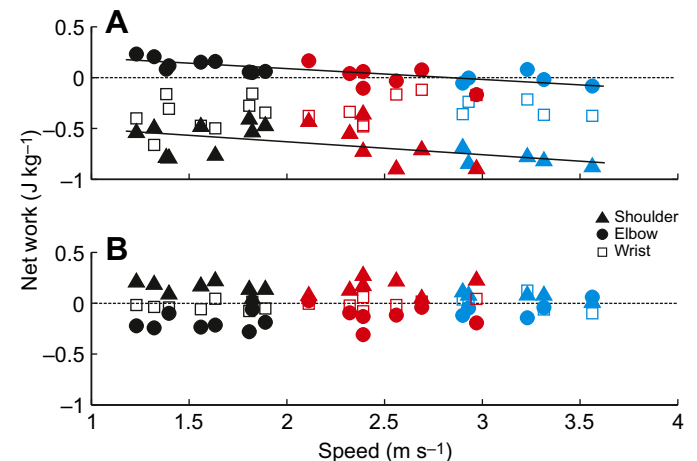


Fig. 6. Joint net work across speeds. (A) Sagittal plane. The wrist absorbs energy at all speeds, although with low magnitude, and there is no significant relationship with speed (squares). The net work produced by the elbow has a significant negative relationship with speed ($P < 0.001$; circles), beginning with positive net work at a walk, and becoming more negative during the running gaits. The scapulohumeral joint absorbs energy at all speeds, and this increases with increasing speed ($P < 0.05$; triangles). (B) Frontal plane. The scapulohumeral joint produces positive net work at all speeds (triangles). The elbow has a significant positive relationship with speed ($P < 0.05$; circles). The net work produced by the wrist was not significantly different from zero (squares). Each data point represents an individual trial; gaits are coloured as described in Fig. 3.

We would expect the most likely differences between plantigrade species and those with other postures to be in the moments at the wrist. In plantigrade and palmigrade species, the entire foot is in contact with the ground, and therefore has a greater moment arm to the ground reaction force due to the position of the centre of pressure under the middle of the foot. In digitigrade and unguligrade species, the wrist is off the ground and more in line with the ground reaction force. Additionally, the wrist joint plays a different role in horses, being involved in their ability to sleep while standing; the extensor moment enables this joint to be passively ‘locked’ into position during weight bearing (Hildebrand, 1987). Despite these differences in morphology, palmigrade, digitigrade and unguligrade species produce extensor moments and absorb energy at the wrist (horses, Clayton et al., 2000; bears, this study; small mammals, Witte et al., 2002; dogs, Nielsen et al., 2003; pigs, Thorup et al., 2008).

Large animals with more upright limb positions have lower joint moments due to an increased EMA (Biewener, 1989). However, although EMA calculations have included a wide size range of species, foot posture has not been taken into account. The majority of large species included in previous studies have been unguligrade (Biewener, 1989, 2005). Ground reaction force moments arms about the joints are shorter in unguligrade species than in similarly sized digitigrade species (Lee et al., 2014). The greater moment arm at the wrist in plantigrade species is likely to affect the overall limb EMA, particularly for larger animals, which generally have an overall more upright posture. We estimated EMA for the grizzly bear forelimb, using the ratio of ground reaction force impulse to muscle force impulse from a subset of trials (Biewener, 2005). The average EMA across speeds was 0.62, which is lower than the predicted value of 0.85, based on the equation from Biewener (1989). This suggests that they do not benefit from reduced moments due to an upright posture as much as would be predicted. However, as mentioned above, many of the species included were unguligrade, particularly of a similar size to bears, which will affect the average EMA calculation.

While aspects of forelimb joint dynamics appear to be conserved across mammalian quadrupeds, there may be substantial differences in the capacity for elastic energy storage at the joints. We did not calculate elastic energy storage; however, the joint power produced by the wrist suggests that the bears lack the capacity for elastic energy storage in this joint within the speed range included in this study (Fig. 3I). For elastic energy storage to occur, the wrist would need to absorb energy, negative power, before the production of positive work. Our data show that the wrist produces the opposite pattern and therefore this joint is not behaving in a spring-like manner. The wrist is the functional spring in the locomotion of dogs (Gregersen et al., 1998; Lee, 2005). However, in unguligrade species, the most spring-like joint is the metacarpophalangeal joint (goats; Lee, 2005; Lee et al., 2008). This suggests that as the limb elongates, as a result of the morphological differences between digitigrade and unguligrade species, the more distal joint acts as the functional spring.

The lack of spring-like behaviour at the wrist may relate to gait choice in grizzly bears. For example, bears do not use a trot at intermediate speeds, instead using a running walk (Shine et al., 2015). Trotting is defined by a diagonal couplet footfall pattern, and is a bouncing gait that benefits from elastic energy storage in the tendons. This gait is used by many digitigrade and unguligrade species. A running walk maintains the same footfall pattern as a walk, but with a shorter overlap between steps, and is therefore less affected by the need for elastic energy storage.

The similarities in sagittal limb dynamics between bears and other species suggest that mammalian quadrupeds move in a similar manner, despite their differences in morphology due to the palmigrade, digitigrade and unguligrade postures. However, differences in limb orientation and capacity for elastic energy storage may result in locomotor differences that are not accounted for in this study.

Frontal plane joint mechanics

To our knowledge this is one of only a few studies to examine joint dynamics in the frontal plane of a quadrupedal animal. The frontal elbow angle demonstrates a deviation from a fully erect posture, which would not be expected for a large mammal. This more flexed elbow position results in greater moments in the frontal plane; however, this does not translate into power produced because of the minimal angle change during stance, especially at the higher speeds. A more flexed joint position during locomotion is energetically more expensive as it requires muscular force to maintain this position and resist gravitational force. The flexed posture could be a result of underlying morphology. Previous research has demonstrated that bears are outliers when their morphology is compared with that of other carnivorous species (Van Valkenburgh, 1987); they also appear to have a passive coupling mechanism between elbow and wrist flexion.

Although the forelimbs produce high lateral forces during locomotion, they produce little net work in the frontal plane. It is therefore likely that this force production is relatively efficient, as the limb is acting as a strut in this direction. This is in contrast to animals with a sprawling gait, such as lizards, that also produce high lateral forces but as a result of differences in anatomy are also required to produce power away from the direction of travel (Blob and Biewener, 2001; Chen et al., 2006). Lizards and crocodilians use lateral bending of the spine to increase stride length; this sideways movement results in lateral power production (Baier and Gatesy, 2013).

Effects of speed and gait

Grizzly bears use the running walk as their intermediate speed gait, as opposed to the more common trot (Shine et al., 2015). This may produce different results in horses and bears at intermediate speeds, as well as across the gait transition. In walking horses, energy absorption at the shoulder increases with speed, specifically at the end of stance (Khumsap et al., 2002); this suggests that the forelimb may increase energy absorption with increasing speed at that gait. However, in trotting horses, the shoulder provides propulsion towards the end of stance, resulting in the production of positive work (Clayton et al., 1998; Dutto et al., 2006). This pattern was not seen in the bears; the scapulohumeral joint increased energy absorption as speed increased, regardless of the gait used.

Net work is also continuous across speed in grizzly bears; there is no distinct change associated with gait transitions. This is true of the individual joints, and the total net work of the forelimb joints. Although walks and running walks are mechanically different gaits, they maintain the same footfall pattern. The order and relative timing of the foot placement remain consistent between these gaits, but there is reduced overlap between footfalls, and the vertical ground reaction force displays a different pattern (Fig. 2). The transition from a walk to a trot requires a more dramatic change in mechanics because of the transition from a four-beat to a two-beat gait. This is likely to result in a less distinct change in joint mechanics at a walk–running walk transition than at a walk–trot transition. At steady speed locomotion, the net work produced by an

animal must be essentially zero; as our results show an increase in energy absorption by the forelimbs with speed, we can assume that the hindlimbs of the grizzly bears are producing more positive work to maintain a steady speed. However, we cannot be sure of the role of the scapula in the forelimb during locomotion, which may affect the overall work done by the limb.

Scapula motion

The scapula has been shown to play a role in the protraction and retraction of the forelimb during locomotion (e.g. Gray, 1968; Fischer et al., 2002; Carrier et al., 2006). The scapula acts as an additional segment, with the vertebral edge of the scapula being the fulcrum for the rotation of the entire limb (Jenkins and Weijs, 1979; Carrier et al., 2006). The scapula is not fixed to the torso by a bony structure in mammals, and is therefore only loosely held in place using muscular attachments. This allows the scapula to slide back and forth across the rib cage, which will also affect the moments of the scapulohumeral joint, and the forelimb overall (Payne et al., 2005; Dutto et al., 2006). We were unable to include a marker on the scapula of the bears; this means we are unable to include results from the rotation or translation of this segment. Additionally, the scapula may be able to act as a lever in the frontal plane; however, as the scapulohumeral angle was calculated relative to the horizontal, movement of the scapula relative to the body will have been encompassed in our calculations to some extent.

Limitations

There are several challenges when working with large, non-model organisms, as well as inherent limitations of the analysis used; however, we have addressed these where possible. We acknowledge that we have a small sample size. This sample was sufficient for statistical significance in our previous study (Shine et al., 2015), and for the results of this study. Therefore, we are confident that these animals are representative of the species as a whole. Inverse dynamics analysis has inherent limitations; this analysis produces net results for each joint and cannot take biarticular or antagonistic muscle actions into account. Therefore, we cannot estimate individual muscle mechanics or account for energy transferred between segments.

Conclusions

Although there are significant differences in anatomy between palmigrade, digitigrade and unguligrade animals, sagittal plane joint mechanics appear to be relatively conserved. The results of this study show that there are similarities between grizzly bears and other mammals in the sagittal plane. This also appears to be the case between large and small species. However, effective mechanical advantage from distal limb orientation may be less effective in palmigrade species as a result of the extended foot contact area and therefore greater moment arm at the wrist. The proximal joints may be straightened to increase the effective mechanical advantage, therefore counteracting the increase in moment arm at the wrist. Additionally, more significant differences may be present in the capacity to store elastic energy, which may also have a bearing on the gait choice at intermediate speeds in digitigrade and unguligrade species compared with plantigrade species.

The results of this study also show that the high medial ground reaction force is not related to joint work in the frontal plane of grizzly bears. Instead, it appears that the forelimb is acting as a strut in the frontal plane. Dissection of a grizzly bear forelimb has shown that the medially directed wrist rotation seen during locomotion is passively coupled to flexion of the elbow. This anatomy, along with

the results of the inverse dynamics analysis in the frontal plane, suggests that the lateral pushing during stance is probably not energetically costly.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Experimental design: C.L.S., C.T.R., O.L.N. and C.P.M. Data collection: C.L.S., C.T.R., O.L.N. and C.P.M. Data analysis: C.L.S. and C.P.M. Manuscript preparation: C.L.S., C.T.R., O.L.N. and C.P.M.

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