

URSIDAE LOCOMOTION: RIGHT DOWN TO THE “BEAR BONES”

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Abstract

The plantigrade posture refers to species that have their entire foot, from heel to toes, on the ground. The Order Carnivora contains terrestrial families of both digitigrade (stand on their toes) and plantigrade species, and includes a wide representation of locomotor behaviours.

Bears (family Ursidae) are the only group of large plantigrade species in Carnivora. This makes ursids a unique family as they are relatively distinct from other mammals. Ursidae morphology is at the extreme plantigrade end of the posture spectrum, therefore representative of plantigrade animals, despite their significantly larger size than other carnivoran species. Within Ursidae there are eight extant bear species; these species range in size, diet, and locomotor behaviour.

There have been many previous studies of the relationship between morphology and locomotor behaviour in Carnivora, all of which have included both digitigrade and plantigrade species. Plantigrade species, particularly bears, are often noted as outliers in these studies. However, it's possible that the morphological differences related to posture are confounding the results.

The aims of this dissertation were to characterise the locomotion of a representative plantigrade carnivoran (grizzly bears; *Ursus arctos horribilis*), and to determine if a model using bone morphology of only plantigrade species could increase accuracy of estimating locomotor behaviour in extinct plantigrade species.

The first chapter of my dissertation is a detailed description of the design, construction, and calibration of a force plate. This force plate was custom built to be used with grizzly bears, although it is suitable for both smaller and larger animals. Chapters 2 and 3 are analyses of grizzly bear locomotion. This includes a description of the gaits used and the ground reaction forces produced by the bears, as well as a more detailed analysis of the forelimb joint dynamics across speed. The fourth chapter of my dissertation is a morphometric analysis of

forelimb bones from 44 extant species of plantigrade carnivorans, plus specimens from two extinct genera.

Overall this dissertation is a comprehensive view of the locomotion of a representative plantigrade species, incorporated into an evolutionary framework by bone shape analysis of several other plantigrade families.

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Dedication

I dedicate this dissertation to my family:

Jim and Jennie Shine, Lizzie and Michael Sanders, and Andy Isaacs.

I cannot express in words how much their love and support has helped me through the last five years, thank you.

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Introduction

Scientists have been studying locomotion for centuries (e.g. Muybridge, 1887; Gray, 1968; Biewener, 1990). Animals must move in order to survive, whether to find food, avoid a predator or search for a mate. Therefore, locomotion and the morphology associated with it are fundamental selection pressures for evolution.

The majority of locomotion studies to date have focused on species that have adapted and specialised for cursoriality (e.g. dogs, horses; Riggs et al., 1993; Robilliard et al., 2007). These species have increased their limb length, and correspondingly decreased their distal limb mass; this increases the speed with which they can move their feet during locomotion. The foot postures associated with this adaptation are digitigrade, in which the animal stand on their toes, and unguligrade, where the animal is standing on the tip of its toes (Figure I.1).

Plantigrady is the ancestral foot posture for mammals (Ginsburg, 1961). This posture refers to species that have their entire foot, from heel to toes, on the ground. The advantages to digitigrady are mentioned above; however, the advantages to plantigrady are rarely discussed. Within mammals the plantigrade posture has been retained by many species. This would suggest that there are evolutionary advantages to retaining this posture, hypotheses include stability during locomotion and increased ability to produce force by the higher distal mass. The Order Carnivora contains terrestrial families of both digitigrade and plantigrade species. Canidae, Felidae, and Hyaenidae are digitigrade Carnivora families; the other ten terrestrial families consist of plantigrade species. There are many osteological characteristics that distinguish plantigrade species from digitigrade species, although posture does form a continuum (Ginsburg, 1961).

There have been few studies of plantigrade locomotion, particularly in Carnivora. One study compared kinkajous, coatis, and raccoons, with reference to locomotion and feeding behaviour (McClearn, 1992). A descriptive study of the locomotion of skunks, specifically gait and footfall patterns, suggest they are representative of the primitive locomotive condition for Carnivora (van de Graaff et al., 1982). In these studies, the plantigrade species

never appeared to use a trot (diagonal couplet gait), despite this being the most common gait at intermediate speeds in previously studied animals.

Bears (family Ursidae) are the only group of large plantigrade species in Carnivora. This makes ursids a unique family as they are relatively distinct from other mammals (Losos and Miles, 1994). Ursidae morphology is at the extreme plantigrade end of the posture spectrum (Ginsburg, 1961). Bears species are therefore representative of plantigrade animals, despite their significantly larger size than other carnivoran species. Within Ursidae there are eight extant bear species; these species range in size, diet, and locomotor behaviour (Brown, 2009). Before I began conducting my research, there had only been one study that solely investigated the locomotion of bears (Renous et al., 1998). However, descriptions of bear locomotion have been included in other studies, and they have been noted to produce an unusual medial wrist rotation during locomotion (Davis, 1949; Gray, 1968; Inuzuka, 1996).

Combining methods for biomechanical analysis with morphometric shape analyses can provide a more inclusive picture of how animals evolved (Fabre et al., 2015). It is important to understand the relationship between morphology and ecology in order to estimate consequences of evolution, particularly for extinct species (Wainwright and Reilly, 1994). Skeletal remains are the only clues we have to the life history of extinct species. It is therefore necessary to use extant species as a comparison to estimate the behaviours of fossil animals.

There have been several morphology studies of locomotor behaviour in Carnivora; however, they have all included both digitigrade and plantigrade species. The inclusion of both postures could cause a confounding effect, which would result in a less successful model when identifying the locomotor behaviour of extinct species.

The aim of my research was to characterise the locomotion of a representative plantigrade carnivoran (grizzly bears; *Ursus arctos horribilis*), and to determine if a model using bone morphology of only plantigrade species could increase accuracy of estimating locomotor behaviour in extinct species.

The first three chapters of my dissertation relate to the investigation of the locomotor patterns of adult grizzly bears (*Ursus arctos horribilis*). Chapter 1 is a detailed description of the design and construction of the force plate used to collect data from the grizzly bears. Due to the size of these bears, it was necessary to build my own force plate for data collection.

Chapter 2 addresses the basics of biomechanics and determines the gaits used by the bears and the associated ground reaction forces that are produced. We found that, similar to previously studied plantigrade carnivorans, grizzly bears do not appear to trot at intermediate speeds (Shine et al., 2015). Additionally, we discovered that grizzly bears produce relatively high medial ground reaction forces (lateral pushing from the animals). These values were more similar to those collected from an alligator (*Alligator mississippiensis*; Willey et al., 2004) than other similarly sized mammals.

The third chapter of my dissertation is a more in depth analysis of the forelimb dynamics produced by the grizzly bears. Overall the results of this study suggest that grizzly bears move similarly to other mammalian quadrupeds in the sagittal plane, despite the differences in size and posture of previously studied species. We also found that the medial ground reaction forces produced by the bears do not relate to a significant amount of joint power produced in the frontal plane. This suggests that the forelimb is acting as a strut in that direction and therefore the force production may be relatively efficient. To date this is the first study of limb dynamics in any bear species and therefore we do not know whether this pattern is similar in all bears or specific to grizzly bears.

Chapter 4 creates a model of Carnivora locomotor behaviour based on plantigrade osteological characteristics. We included 44 extant species of plantigrade carnivoran and analysed bone shape of the forelimb long bones using three dimensional geometric morphometrics. Species were allocated to groups of locomotor behaviour according to previous studies of morphology or observational data. The behavioural groups were: semi-aquatic, arboreal, scansorial, semi-fossorial, and terrestrial. We found significant differences between locomotor behavioural groups in three of the four bones studied (scapula, humerus, and ulna, but not the radius). Interestingly, a pair wise comparison of the groups showed that

different bones produced significant differences between different groups. This highlights the need to include as many morphological characteristics as possible when determining the locomotor behaviour based on osteological materials. We used this model to predict the locomotor behaviour of two extinct bears with mixed results. *Arctodus*, a large North American bear, was estimated to be arboreal, while *Ursus spelaeus*, the European cave bear, was placed into a different behavioural group for each bone analysed. Our study has high error rates for classification of extant species and therefore further analysis is warranted to verify these locomotor behavioural classifications.

Overall this dissertation provides a comprehensive analysis of the locomotor of grizzly bears, while also including an extensive analysis of morphological data in Carnivora. The inclusion of the morphological data with the biomechanical data increases our understanding of locomotion in an evolutionary context. This is particularly important for bears, which represent a relatively unique morphology and, as we have shown, also demonstrate unusual locomotor patterns.

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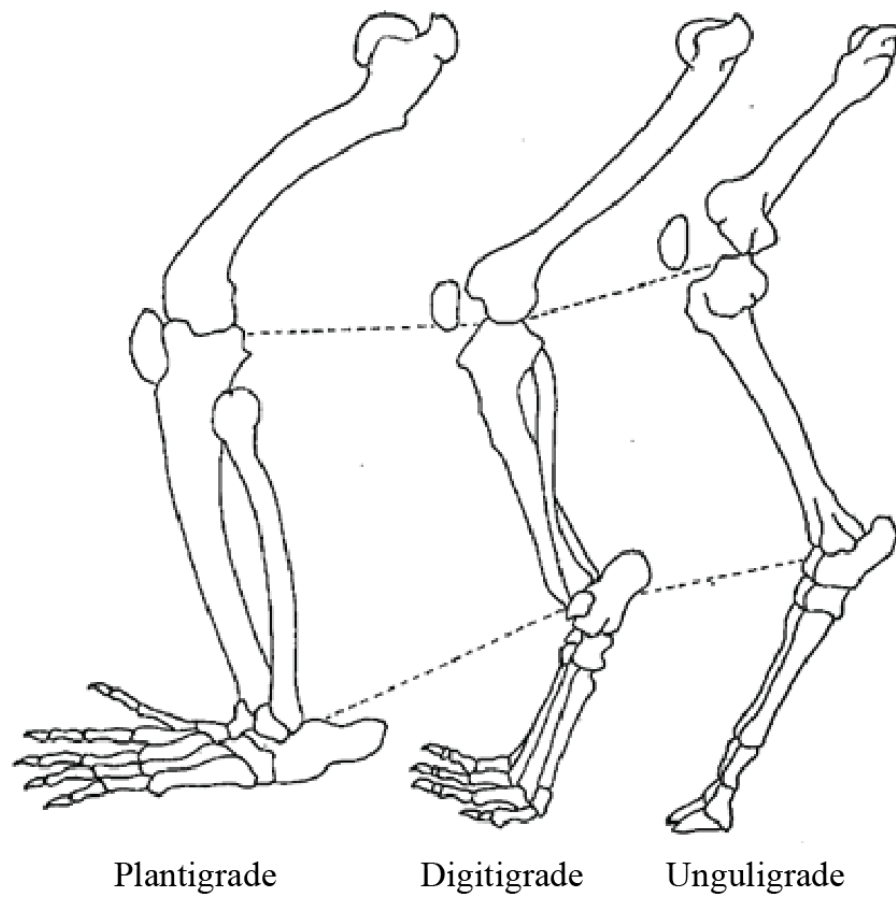


Figure I.1 Foot Postures of Mammals

The plantigrade posture is ancestral for all mammals and is retained in many species (carnivoran examples include: bears, badgers, and weasels). The digitigrade posture is mostly recognised in carnivorans such as: dogs, cats, foxes, and hyenas. The unguligrade posture is not present in Carnivora, but representatives include horses, pigs, and giraffes. Figure adapted from Brown and Yalden (1973).

Chapter 1: Grizzly Bear (*Ursus arctos horribilis*) Force Plate Design

Catherine L Shine, John EA Bertram, Craig P McGowan

Abstract

Force plates have been used for decades to collect kinetic data from a wide range of animals. Due to the variation in size and mass, there have been several designs of force plate used to collect data across species. We have used a cantilever beam design as a basis for producing a force plate suitable to collect data from adult bears. The plate is strong enough to withstand a 200kg grizzly bear running at speed, yet still sensitive enough to measure the lower magnitude anterior-posterior and mediolateral ground reaction forces produced during locomotion. Our calibrations show there is a linear relationship between force and voltage in vertical and anterior-posterior forces, and a 3rd order curved correlation with mediolateral forces. This force plate produces a high signal to noise ratio, resulting in raw data that requires minimal filtering. One publication has already resulted from the data collected with this force plate.

Introduction

Force plates have been used to collect biomechanical data for decades. These studies have included species ranging in size from rodents to horses (Merkens et al., 1993; Keller et al., 1996; Farley and Ko, 1997; Zumwalt et al., 2006). Results of these studies have shown the similarities of ground reaction forces between different species; for example an M shaped vertical ground reaction force is common in walks of dogs, humans, and horses (Budsberg et al., 1987; Geyer et al., 2006; Robilliard et al., 2007). However, there are significant differences between species, particularly in the horizontal ground reaction forces. This can be related to the upright or sprawled posture of the species (magnitude of lateral forces), as well as the differential use of the forelimbs *versus* hind limbs (Budsberg et al., 1987; Chen et al., 2006).

Force plates are available commercially, and there have been several previous descriptions of force plate designs. Commercial plates are often structured for analysis of human locomotion

and are therefore unsuitable for substantially larger or smaller species of animals. They are also expensive, particularly at larger sizes such as those that would be suitable for bears. Simple force plate designs include cantilever beam structures, with strain gauges attached to thinly cut blades within the beams (Heglund, 1981), and piezoelectric elements sandwiched between two plates (Cross, 1999). Recently there have been more complex designs, including using optical sensors (Hsieh, 2006). Applications of force plates have also developed into being included in treadmills (Kram and Powell, 1989), as well as being designed as load cells that can be adapted to different conditions (Bertram and Chang, 2001; Liu et al., 2010). We are conducting the first study including force plate data from a bear species, and have therefore designed our plate using the cantilever beam structure.

There are several specifications required of any force plate in order for it to be effective during animal locomotion studies. This includes sufficient sensitivity for the data required, while maintaining a high signal to noise ratio (Heglund, 1981). This is accomplished by using a light, stiff top plate, usually a relatively thin plate that has been reinforced. A heavy top plate will decrease the natural frequency of the plate, whereas a flexible plate will not transfer that entire load to the instrumented beams. Natural frequency is the resonance (ringing) of the plate when it is struck. A higher natural frequency is less likely to interfere with recorded signal, and therefore easier to filter out of collected data. This can be increased by altering the ratio of the masses of the top and base plates. For example, securing the force plate to the ground will assist with increasing the natural frequency.

Additional requirements of the force plate may depend on the type of analysis used in a particular study. Many species produce low mediolateral ground reaction forces, therefore most studies of animal locomotion have included only vertical and anterior-posterior forces (e.g. Lee et al., 2004; Dutto et al., 2006). As we were collecting data from a species that had not previously been studied, it was necessary to design a force plate that measures forces in all three directions. Complex analyses such as inverse dynamics require identification of the placement of the force relative to the surface of the plate, known as the centre of pressure. This enables the calculation of the moment arm from the point of application of the force to the distal joint centre.

Bears (Ursidae) are a family of large, plantigrade mammals, and while there are many studies relating to their physiology, there has been very little research on their locomotion. The plantigrade foot posture, in which the entire foot is on the ground, is the ancestral condition for all mammals. This posture has been retained by many species, including rodents and primates. However, bears are the only family of large, quadrupedal, plantigrade mammals. This raises questions about their biomechanics and how they compare to similarly sized species with different foot postures, *versus* smaller plantigrade species.

The force plate design described here fulfils all the above criteria for collection of data from bear species. While it is specifically designed for use with grizzly bears, it is sensitive enough for smaller species or cubs, while also being robust enough to be suitable for data collection from adult male polar bears or other large animals.

Materials and Methods

Overall Design

The plate is a cantilever beam design, made using aluminium stock tubing, with metal foil strain gauges. The dimensions of the completed plate are 0.6x0.4m and 114.3mm in height (Figure 1.1). Due to the orientation of the plate during data collection, the 0.4m dimension of the plate will be referred to as the anterior-posterior beams for the rest of this article. The top of the plate has been covered with a removable adhesive paper, and then coated with a mixture of paint and sand. This mixture prevents the animals slipping on the bare aluminium of the top plate, while also matching the appearance of the force plate to the runway.

Structural Materials

The plate is constructed with a heavy base plate, four instrumented aluminium beams, and a reinforced top plate (Figure 1.1). A heavy base plate is required to anchor the instrumented portion of the plate, and prevent external noise signals being transferred through the strain gauges. We used 12.7mm aluminium. This is sufficient for the above requirements, including increasing the natural frequency, while not being so heavy that the plate becomes difficult to lift and transport. As mentioned above, top plates are required to be light yet stiff. As this plate was designed for large animals, we used 6.35mm aluminium, reinforced with angle iron.

Three sections of angle iron were welded to the top plate along the 0.6m dimension. These pieces were cut to leave 25mm of metal attached to the top plate, with 50mm perpendicular to the top plate.

The instrumented beams are made from aluminium stock tube. The beams are 38.1mm square, with a wall thickness of 4.76mm. The shorter beams are instrumented for both the vertical and anterior-posterior forces, the longer beams are instrumented for the mediolateral forces. This set up is due to the orientation of the plate during data collection from the grizzly bears. However, the plate can be rotated and therefore the two horizontal forces reversed. The beams were cut to leave thin blades in the direction corresponding to the force to be measured (Figure 1.2); this concentrates the strain at a known location, as well as increasing the deformation for a given load. The strain gauges are placed at the edge of the blade in order to increase the potential signal recorded.

Strain gauges (MicroMeasurements, CEA series, 350 Ohms, 3.18mm gauge length) were placed in pairs at each blade, on both the tension and compression sides of the beam. Strain gauges were attached with a heat cured epoxy; additional relief tabs were attached adjacent to the strain gauges to prevent damage to the gauge in the event a wire is caught (Figure 1.2). The top plate is bolted directly to the anterior-posterior beams within the instrumented area. The beams are bolted to each other to ensure the load applied to the top plate is transferred to the lower (mediolateral) beams. The beams are attached to the base plate using specially machined supports outside of the instrumented area (Figure 1.3). This provides a secure attachment while preventing the connection of the beams to the base plate affecting the recorded data.

Electronics

The strain gauges are wired with 30 AWG, silver-coated copper wire, using Wheatstone bridge configurations (Figure 1.3). The vertical force is wired independently at each corner (Figure 1.4), while the two horizontal forces are wired in series across the whole plate (Figures 1.5, 1.6). This results in six channels, each an independent Wheatstone bridge, which combined measure three axes of force. Each vertical channel has four strain gauges, two in

tension and two in compression. The independent wiring of the vertical forces at each corner allows calculation of the centre of pressure. The horizontal forces have eight strain gauges in tension and eight in compression. This provides excellent sensitivity for these forces that are substantially lower than the vertical forces. The wires were passed through the cut portions of the beams; therefore they ran through the hollow beams as much as possible to prevent wires tangling in the centre.

Amplification

The force plate channels are wired into 9 pin D-sub connectors. These connectors are fixed to a metal plate that is bolted to the base plate (Figure 1.1). Cables (24 AWG 10 tinned copper conductor shielded) connect the force plate to the amplifiers (MicroMeasurements, Vishay amplifiers, 2100 and 2200 systems). The level of amplification was a voltage gain of 300 for each channel of the vertical force, and a voltage gain of 2000 for the horizontal forces. Due to the enclosure from which we were collecting data, the cables connecting the plate to the amplifiers were required to be 6.7m long. By using a shielded cable we prevented the introduction of as much electrical noise as possible.

Calibration

The strain gauges output voltages that change in proportion to the strain placed on the beams. In order to interpret this output for locomotor studies, it is necessary to calibrate the plate with a series of known loads and therefore create an equation that can convert the voltage output to the force applied.

Forces were calibrated in each direction independently. The loads applied to the force plate were increased at regular intervals and the voltage output for each load was recorded. In the vertical direction the loads were cumulative; the voltage was measured with each increasing addition, and then again as the loads were removed from the plate. The four vertical channels were summed to produce a total voltage for each applied load. In the horizontal directions, loads were applied to both the positive and negative directions by pulling on the plate with a force transducer. The regression equations from the relationship between force and voltage provide the calibration for future measurements, assuming the same level of amplification.

We also calibrated the force plate for the calculation of centre of pressure. A grid was created on the surface of the plate and a known force applied at each vertex of the grid; therefore a known force was applied at a known distance from each of the four corners. Centre of pressure was calibrated independently for each horizontal direction. The vertical forces from the four corners were paired and a ratio was calculated from each edge of the plate. By using these ratios, the position of any applied force can be calculated.

Results and Discussion

We designed and constructed a force plate suitable for large animals at a significantly lower price than an equivalent commercial plate.

As described above, the top plate is required to be stiff yet light enough to not affect the natural frequency of the plate. Previous force plate designs have used honeycomb structures to increase the second moment of area, without increasing the material, and therefore mass, of the top plate (Heglund, 1981). In order to accomplish a similar result with animals as large as the grizzly bears, we reinforced the top plate with angle iron. The angle iron was cut asymmetrically to reduce the mass attached to the plate, while substantially increasing the second moment of area, which decreases the bending of the plate. This was a novel solution for such a large species and was successful. The natural frequency of our plate was: vertical = 429Hz, anterior-posterior = 267Hz, and mediolateral = 289Hz. These values are sufficiently high to be easily filtered out of our recorded data.

The results from the calibration showed strong correlations between voltage and force. The relationships are linear for vertical and anterior-posterior forces ($R^2 > 0.99$; Figures 1.7 and 1.8 respectively). Mediolateral forces were calibrated using a curved relationship (3rd order) to increase fit (Figure 1.9); however, the linear relationship still produced an R^2 value above 0.99.

We have used this force plate to collect data from adult grizzly bears (Shine et al., 2015). The force plate has a high natural frequency, and a high signal to noise ratio. The high number of strain gauges used for each channel, plus the shielded cable connecting the force plate to the

amplifiers, assisted in reducing the introduction of electrical noise. We used a low pass moving average filter with a group rate of 10 (Figure 1.10). The results of the study from the grizzly bears show that these animals produce higher medial ground reaction forces than would be expected for a large upright mammal; this may be related to their underlying anatomy (Shine et al., 2015; Shine et al., submitted).

Strain gauges can be affected by temperature, resulting in drift and non-repeatable calibrations. This can be a potential problem when constructing a force plate. Although the excitation voltage to the strain gauges can cause overheating, the effect of temperature is most commonly a problem when recording data in a lab setting with high speed cameras (Hsieh, 2006). Bright lights are required to capture video data above 200 frames per second, and these lights usually produce substantial amounts of heat. As we were collecting data outside for the grizzly bears, we did not have a problem with lighting or temperature and therefore we are confident with our use of strain gauges to collect our data.

This study describes a force plate design suitable for large animals at a much lower cost than a similar commercial plate. The results of studies using data from this force plate demonstrate that it is suitable for detailed complex analyses such as inverse dynamics.

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Figure 1.2 Completed Force Plate

The force plate is composed of a base plate, instrumented aluminium beams, and a reinforced top plate. The surface of the force plate has been coated in a paint and sand mixture to provide traction for the animals. The connectors for the amplification cables are attached to the base plate on one side of the force plate.

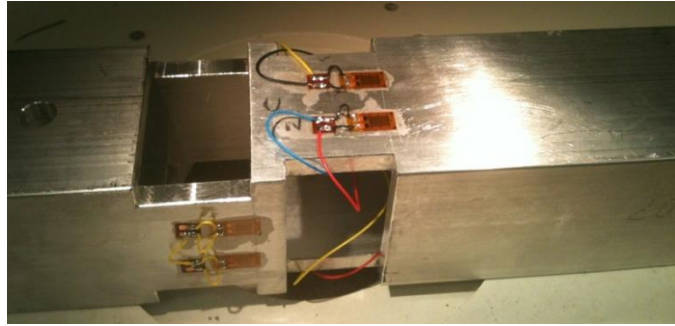


Figure 1.3 Instrumented Beam Design, with Vertical Force Wiring

The aluminium beams were machined leaving a thin blade on each side corresponding to the force being measured. The strain gauges were attached to these blades. The vertical strain gauges were wired as a full Wheatstone bridge on each corner; therefore each strain gauge corresponds to one arm of the bridge. Horizontal forces were wired across the whole plate, with strain gauges wired in pairs at each corner (pictured yellow wiring). Relief tabs were wired to each gauge to prevent damage if a wire was caught or pulled. See figure 1.4 for wiring diagram.

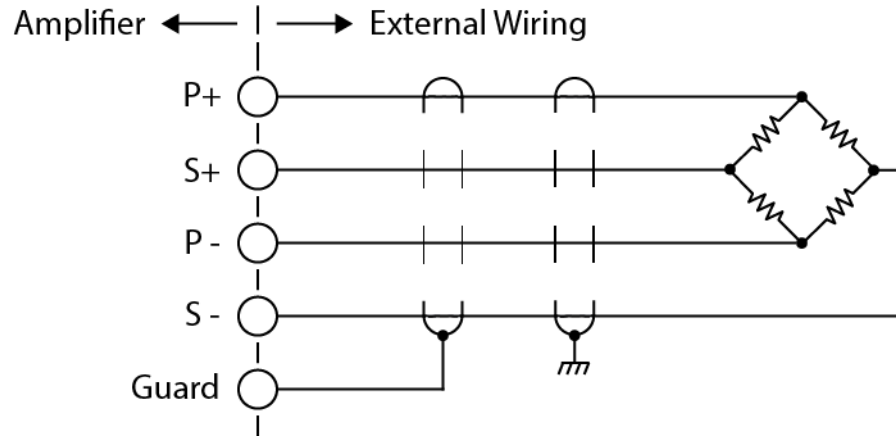


Figure 1.4 Wheatstone Bridge Wiring Diagram

Adapted from Vishay 2200 Systems Instruction Manual 2002. This is the full Wheatstone bridge wiring for the amplifier system we used. The circles represent pins in the plug that connects the force plate cable to the amplifier. Shielding from the cable was wired into the ground (m) at the plate and into the guard at the amplifier. P+ is positive power, P- is negative power, S+ is positive signal, S- is negative signal.

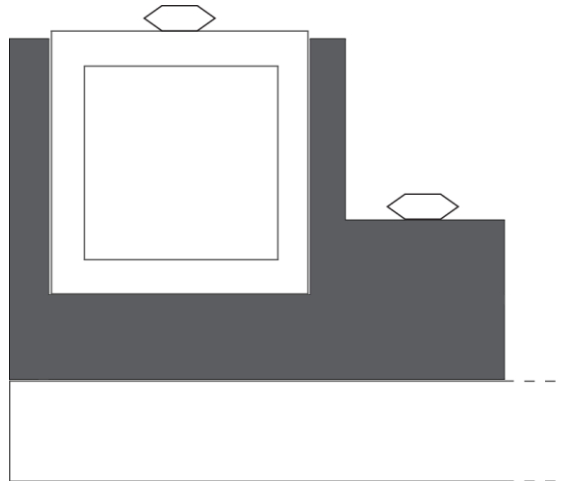


Figure 1.5 Beam Support on Base Plate

The design of this part allows the beams to be secured to the base plate, while preventing this attachment affecting the signal to the strain gauges. The beam is supported, and bolted to a U shaped frame, while an additional flange provides space for a bolt to connect the support to the base plate. This piece is positioned at each of the four corners and allows the beams to bend in the centre.

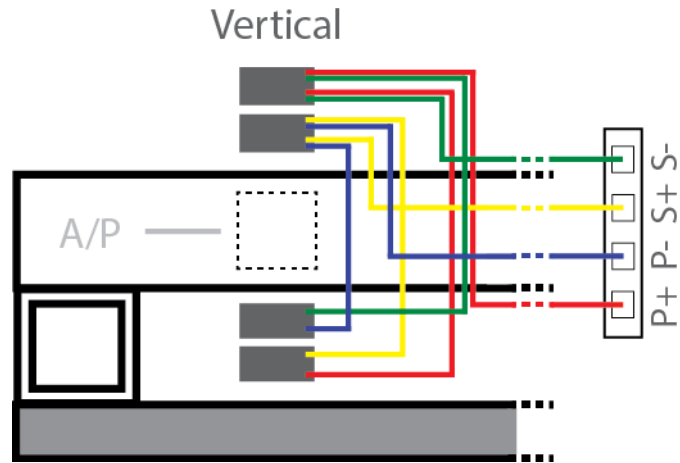


Figure 1.6 Vertical Wiring Map

This is the wiring for the vertical channels at each corner of the plate. When the plate is loaded, the two strain gauges on the top are in compression and the two on the bottom are in tension. This wiring is a full Wheatstone bridge (see figure 1.3).

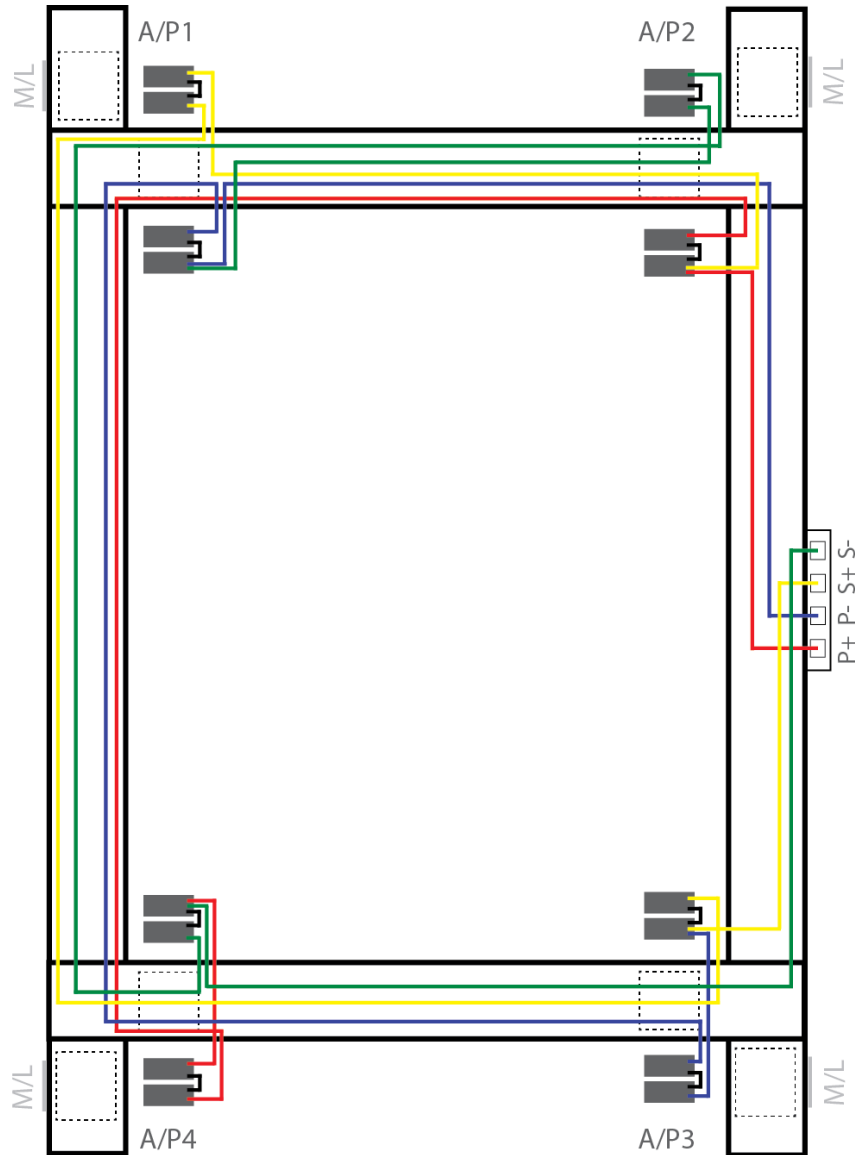


Figure 1.7 Anterior-Posterior Wiring Map

This is the wiring for the anterior-posterior horizontal force. The pairs of strain gauges at the top at each corner are in tension, the pairs on the bottom are in compression, when the animal is applying a braking force. This wiring is a full Wheatstone bridge (see figure 1.3); P+ is positive power, P – is negative power, S+ is positive signal, S – is negative signal.

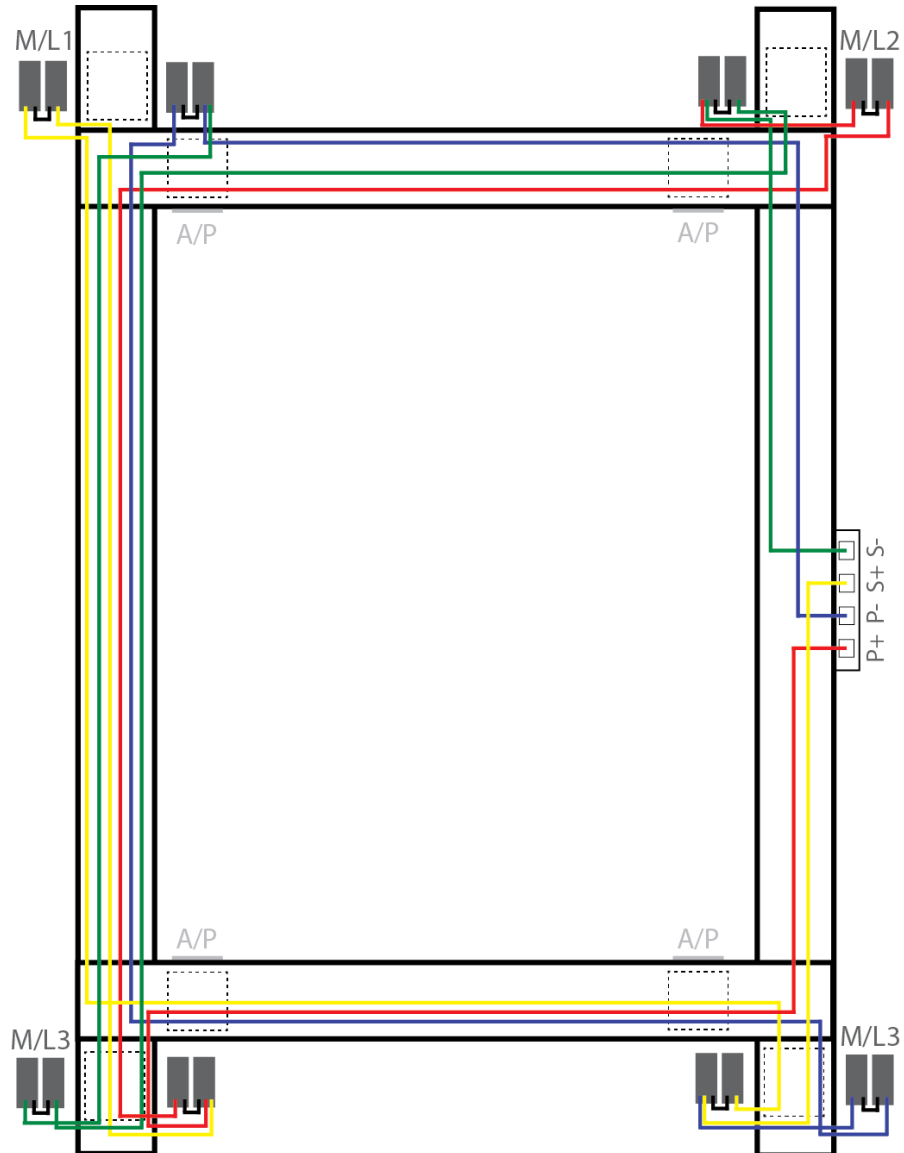


Figure 1.8 Mediolateral Wiring Map

This is the wiring for the mediolateral horizontal force. The pairs of strain gauges on the left at each corner are in tension, the pairs on the bottom are in compression, when the animal is producing a lateral force (with the left forelimb) This wiring is a full Wheatstone bridge (see figure 1.3); P+ is positive power, P- is negative power, S+ is positive signal, S- is negative signal.

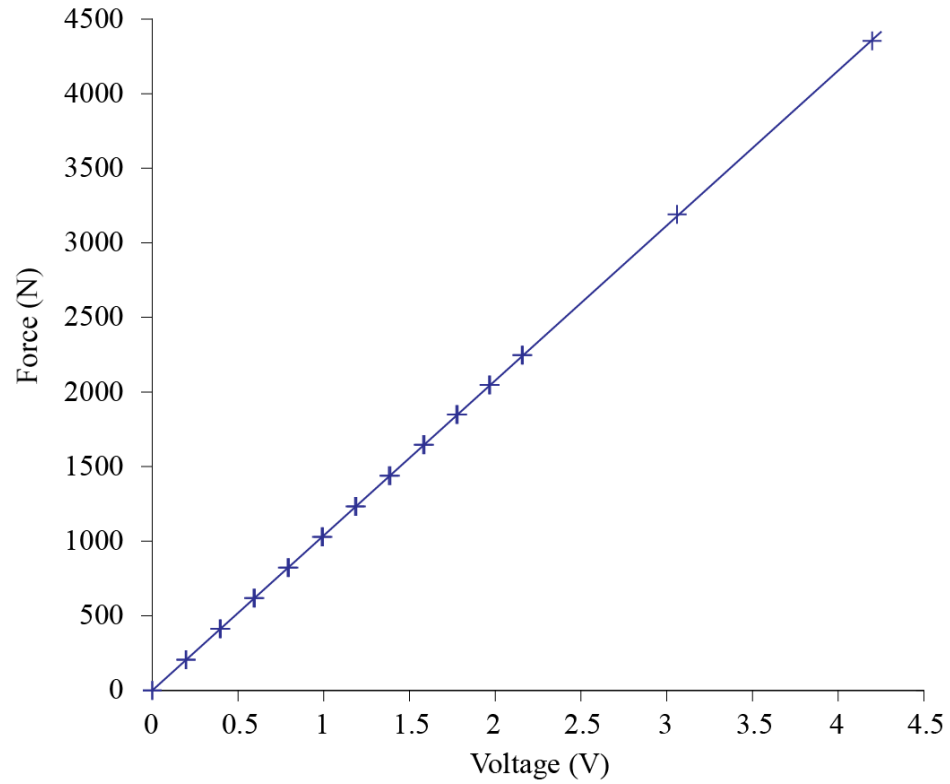


Figure 1.9 Vertical Force Calibration

Voltage output was measured for the four vertical corners and summed together. Known loads were applied to the plate, and then removed in turn. Points are plotted for both increasing and decreasing loads. Regression line equation: $y = 1039.5x + 0.15506$. $R^2 = 1$.

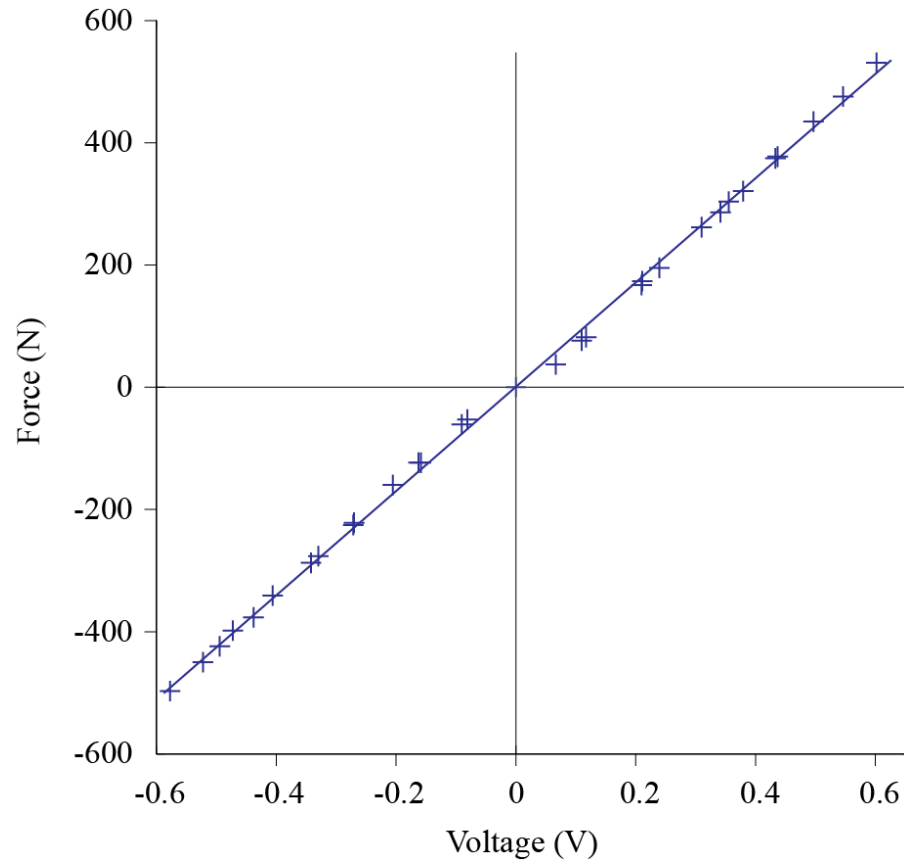


Figure 1.10 Anterior-Posterior Force Calibration

Loads were applied by pulling on the force plate in both positive and negative directions. The regression was plotted using a linear relationship as there was very little improvement in fit using a quadratic or cubic equation. Regression equation: $y=852.14x + 1.6706$; $R^2 = 0.99$.

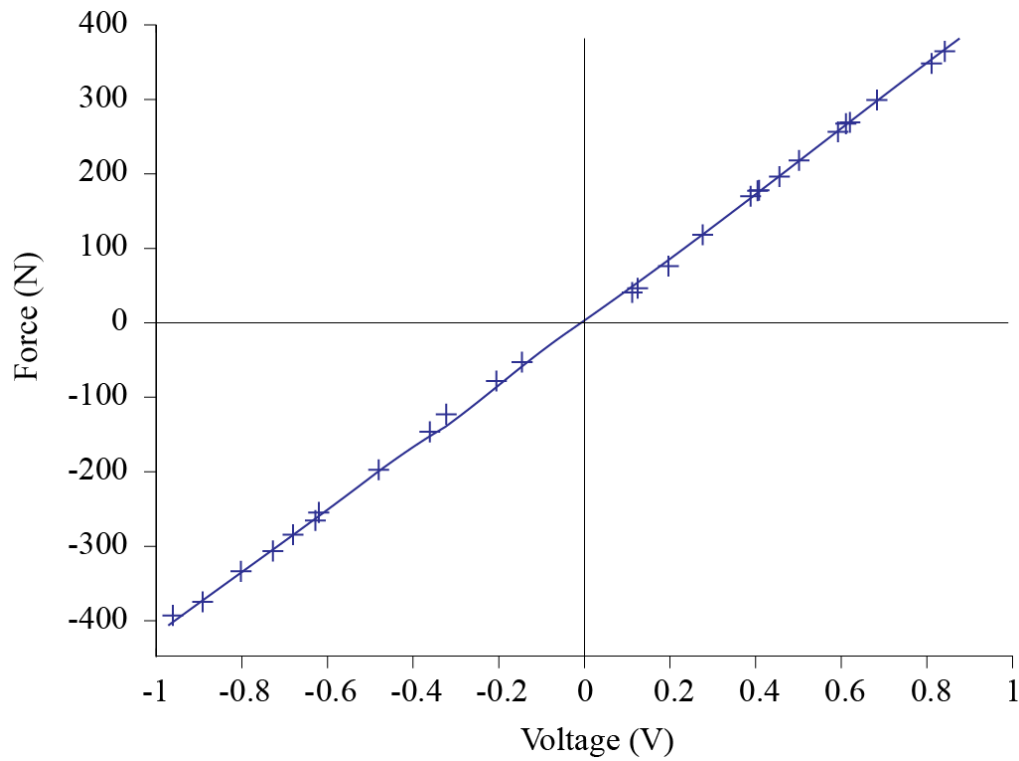


Figure 1.11 Mediolateral Force Calibration

Loads were applied by pulling on the force plate in both positive and negative directions. The regression was fitted using a cubic relationship as this improved fit compared to a linear regression, although the linear fit still produced an R^2 of 0.99. Regression equation: $y = 6.809x^3 + 8.234x^2 + 420.1x + 2.501$.

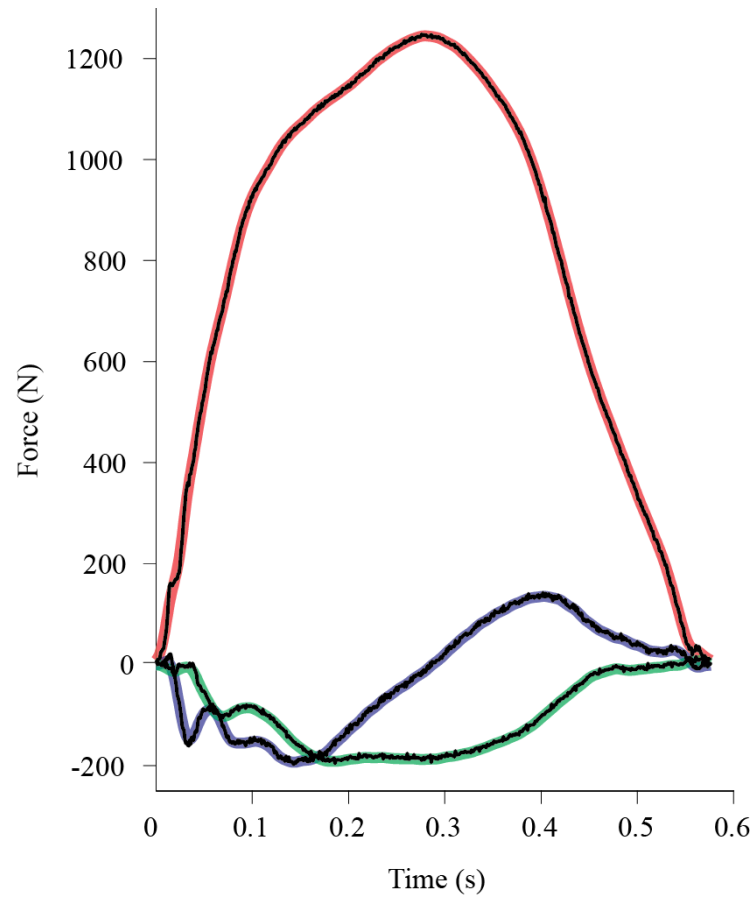


Figure 1.12 Representative Force Data

Vertical (red), anterior-posterior (blue), and mediolateral (green) forces for a representative trial from a grizzly bear. Data were recorded at 1000Hz. Black lines are unfiltered data. The data were filtered using a low pass filter (see text for details).

Chapter 2: Grizzly Bear (*Ursus arctos horribilis*) Locomotion: Gaits and Ground Reaction Forces

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Abstract

Locomotion of plantigrade generalists has been relatively little studied compared to 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 compares the locomotion of adult grizzly bears (*Ursus arctos horribilis* Linnaeus 1758), including stride parameters, gaits and analysis of three dimensional ground reaction forces, to 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 hind limb. The rate of force development was also significantly higher for the hind than 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 crocodylian. 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 if these characters are a feature of all bears or plantigrade species.

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 due to 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 to most digitigrade and especially unguligrade species; however, bears also retain the plantigrade stance. The goal of this study is to determine if the locomotor mechanics of a stereotypical plantigrade quadruped, grizzly bears (Ginsburg, 1961), differ from 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; Hildebrand, 1977). Within quadrupedal animals, a lateral walk, in which the placement of the hind foot is followed by the placement of the ipsilateral fore foot, 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, leading hind foot placement being followed by the contralateral fore foot, 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 this 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 fore and hind feet; different sizes between 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 degrees 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 meters per second (ms^{-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 Jr, 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) characterized 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 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 if locomotion by grizzly bears differs from other large quadrupedal animals, which tend to be digitigrade or unguligrade. We hypothesized that the gaits used by grizzly bears would be similar to smaller plantigrade animals, as opposed to similarly-sized cursorial animals, due to 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 to other species, due to their medially directed stance. These hypotheses were addressed by examining the footfall patterns and stride parameters to identify gaits, and characterising the magnitude, time varying shape, and relative distribution of three dimensional ground reaction forces generated by the fore and hind limbs over a range of speeds.

Results

Subjects

The results from this study are 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 Methods for details).

Speed and Gaits

We collected a continuous range of speeds, approximately 1 ms^{-1} to 3.5 ms^{-1} for each bear (overall range: $1.1\text{-}3.8 \text{ ms}^{-1}$, $Fr^{0.5} = 0.42\text{-}1.46$). These speeds are slow to moderate relative to what grizzly bears can achieve in open environments (estimated 13.3 ms^{-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 have been excluded from the analysis due to 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 ($1.1\text{-}2.0 \text{ ms}^{-1}$; $Fr^{0.5} 0.42\text{-}0.77$) 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 hind limbs 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 likely 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 fore and hind limbs for the slower speeds/walking gait (Figure 2.1A, B), transitioning to approximately a half sine wave at the higher speeds - running walks and canters (Figure 2.1C, D). Forelimb vGRF impulse vs. speed had a significantly higher intercept than hind limb vGRF impulse ($p < 0.01$), although the slopes were not statistically significant ($p = 0.07$). Both forelimb and hind limb vertical impulse decrease with speed (Figure 2.2A).

Peak vertical forces were not significantly different between the forelimb and the hind limb at any speed, and there was a trend for higher peak forces as speed increased (Figure 2.3A). The magnitudes of braking and propulsive impulses reduce with speed in both the forelimb and the hind limb. Our data show no significant difference between fore and hind limbs in terms of propulsive force (Figure 2.2B), although the braking impulse for the forelimb is greater than the braking impulse for the hind limb at all speeds.

Peak anterior-posterior (A/P) forces do not differ between fore and hind limbs across speeds (Figure 2.3B). There is no significant difference between the forelimb and the hind limb for any mediolateral (M/L) 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 (Figure 2.2C). The hind limb medial impulse decreases with speed but there is no such relationship with the forelimb. The peak medial forces are approximately equal to the absolute magnitude of the A/P forces, which represents higher medial forces than seen in most erect quadrupeds.

Force Shape Analysis

The rate for 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 $\sim 2 \text{ N s}^{-1}$ at the slowest walks to $\sim 15 \text{ N s}^{-1}$ at the fastest canters. The rate of force development was independent of speed for the hind limb and much more variable than the forelimb. On average, the rate of force development was higher in the hind limb ($11.6\pm 4.8 \text{ N s}^{-1}$) than the forelimb ($6.3\pm 4.0 \text{ N s}^{-1}$) except at the fastest speeds.

Discussion

The overall goal of this study was to determine if locomotion by grizzly bears differs from 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 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 ms^{-1} , which is the top end of the speed range reported here. It is unclear if the results found at lower speeds would also be apparent at faster speeds. Within our speed range, the bears used walks at slow speeds ($< 2.0 \text{ ms}^{-1}$; $Fr^{0.5}<0.77$) and canters at higher speeds ($> \sim 3.0 \text{ ms}^{-1}$; $Fr^{0.5} 1.15$, 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 ms^{-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 (Figure 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 (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 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 fore and hind limbs 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 for 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, but closer to relative stride lengths that would be expected for non-cursorial animals (at a Froude number of 1, relative stride lengths: ~2.5 m, 1.9 m, 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 ($\sim 2.6 \text{ ms}^{-1}$) the duty factor for quadrupeds is predicted to be 0.52, compared to a duty factor of 0.47 for bears (Alexander and Jayes, 1983; Figure 2.4B), suggesting that bears use a running gait at a relative speed in 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 $\text{Fr}^{0.5} 0.59$ (Griffin et al., 2004); while in elephants the transition from a walk to a running walk occurs at $\text{Fr}^{0.5} 0.25$. This suggests bears transition from a walk to a run at a higher relative speed ($\text{Fr}^{0.5} 0.77$) than other quadrupeds.

Mediolateral Forces

In studies of quadrupedal mammals, there has been substantially less focus on mediolateral ground reaction forces generated during locomotion. This is largely due to the fact that 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 cursorial animals, although the values were still higher than we had anticipated.

At fast speeds, the peak medial force occurred coincidentally with the transition from braking to propulsive force (Figure 2.1C, D) resulting in the horizontal force being perpendicular to the direction of travel. This would suggest that locomotion by bears may be inefficient compared to 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 likely 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 in cats as they produce variable mediolateral forces during stance, likely related to pronation and supination at foot down and foot up (Corbee et al., 2014). The magnitudes of medial forces produced by the hind limbs 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 hind quarters 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 hind limb 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 if the motion produced by the bears hind limbs results in similar energy conservation.

Role of the fore vs. hind limbs

Within quadrupeds, fore and hind limbs may have mechanically different functions during locomotion. In our study, we found that the forelimbs of grizzly bears support between 54 - 60% of body weight, increasing with increasing speed. An approximately 60/40 forelimb/hind limb ratio is common among quadrupeds, and likely 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 hind limbs (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 hind limbs; whereas the propulsive impulses were similar (Figure 1). This resulted in the forelimbs having a net braking effect at all speeds while the hind limbs provided net propulsion. These results are consistent with previous studies of cursorial species (Budsberg et al., 1987; Merkens et al., 1993; McLaughlin Jr and Roush, 1994; Rumph et al., 1994). Both braking and propulsive impulses decreased with speed in the fore and hind limbs, 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 fore and hind limbs. Dogs also demonstrate this pattern (Riggs et al., 1993); however horses appear to be different. In walking horses, braking forces were positively correlated with speed only in the hind limbs, whereas during trotting fore and hind limbs both demonstrated a positive relationship (McLaughlin Jr et al., 1996). We had anticipated that a differential use of the forelimbs vs. the hind limbs during locomotion may be exacerbated in plantigrade species due to 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 vertical ground reaction force patterns showed that there is a significant difference between the fore and hind limbs in how they support body weight. At walking speeds, the characteristic M-shaped pattern was more pronounced in the hind limb force (Figure 2B), having a significantly lower trough (minimum force near midstance). The higher first peak in the hind limb has been seen in horses, which also have an asymmetrical forelimb vertical ground reaction force but the second peak is greater (Merkens et al., 1986). In our

study the hind limb also tended to have a substantially higher rate of force development at all but the fastest speeds, though this measure was quite variable for the hind limb. This result is similar to that found in alligators (see figure 3A in Willey et al., 2004). Both the rate of force development and the M-shape pattern of vertical force have been linked to the 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 vertical ground reaction force is characteristic of a compliant limb (Geyer et al., 2006). Both of these features are present in the hind limb forces of grizzly bears (relative to the forelimbs). This difference in shape between the fore and the hind limb vertical ground reactions forces 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 likely 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 fore and hind limb forces simultaneously in one trial. Therefore, our interpretation of fore vs. hind limb function was drawn from the compilation of many trials and, in some cases, regression equations fit 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 fore and hind limbs 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 if a lack of a trot is a characteristic of plantigrade locomotion, as there have 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 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 to 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.

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 Centre 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 area 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 m x 0.4 m), measuring force in three orthogonal axes, was secured in the centre of a 4.26 m runway within the bear enclosure (Figure 2.5) and recorded at 1000 Hz. High speed cameras (200 Hz, 1248x900; Xcitex, Inc., Woburn, MA, USA) were placed in the sagittal and frontal planes, as well as an additional camera 45° from the direction of travel. Data for this study were collected from the 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, 0.99 for AP, 0.99 for ML) was used to compute the bear data. Natural frequency of plate was calculated (Vertical = 429 Hz, Anterior-Posterior = 267 Hz, and Medial-Lateral = 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 two seconds pre-trigger and one second 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 if the trials were 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 to 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 digitized (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 hind limbs. Speeds were converted to square root of Froude number ($Fr^{0.5} = v/(gh)^{0.5}$; where v = speed, g = gravitational acceleration, h = 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 are only comparing 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 metres per second and plotted with the rest of our data (Figure 3B).

Peak ground reaction forces and impulses were calculated for vertical, anterior-posterior and mediolateral directions. Because fore and hind limb data were not available for the same trials fore vs. hind limb 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 fore and hind limbs at a fixed set of speeds (1, 2, 3, and 4 ms^{-1}). These impulses were then used to calculate the forelimb/hind limb 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 analyzes were conducted using the Matlab Statistical Toolbox. An analysis of covariance (ANCOVA) was carried out to identify differences between forelimbs and hind limbs, and between gaits, using speed as the covariate. Linear regressions were calculated on an average of forelimb and hind limb values for each stride parameter (Figure 3), and ANCOVAs were calculated to identify differences between walk, running walk and canter slopes and intercepts. Vertical impulse curves (Figure 1A) were log transformed to provide a linear relationship for an ANCOVA.

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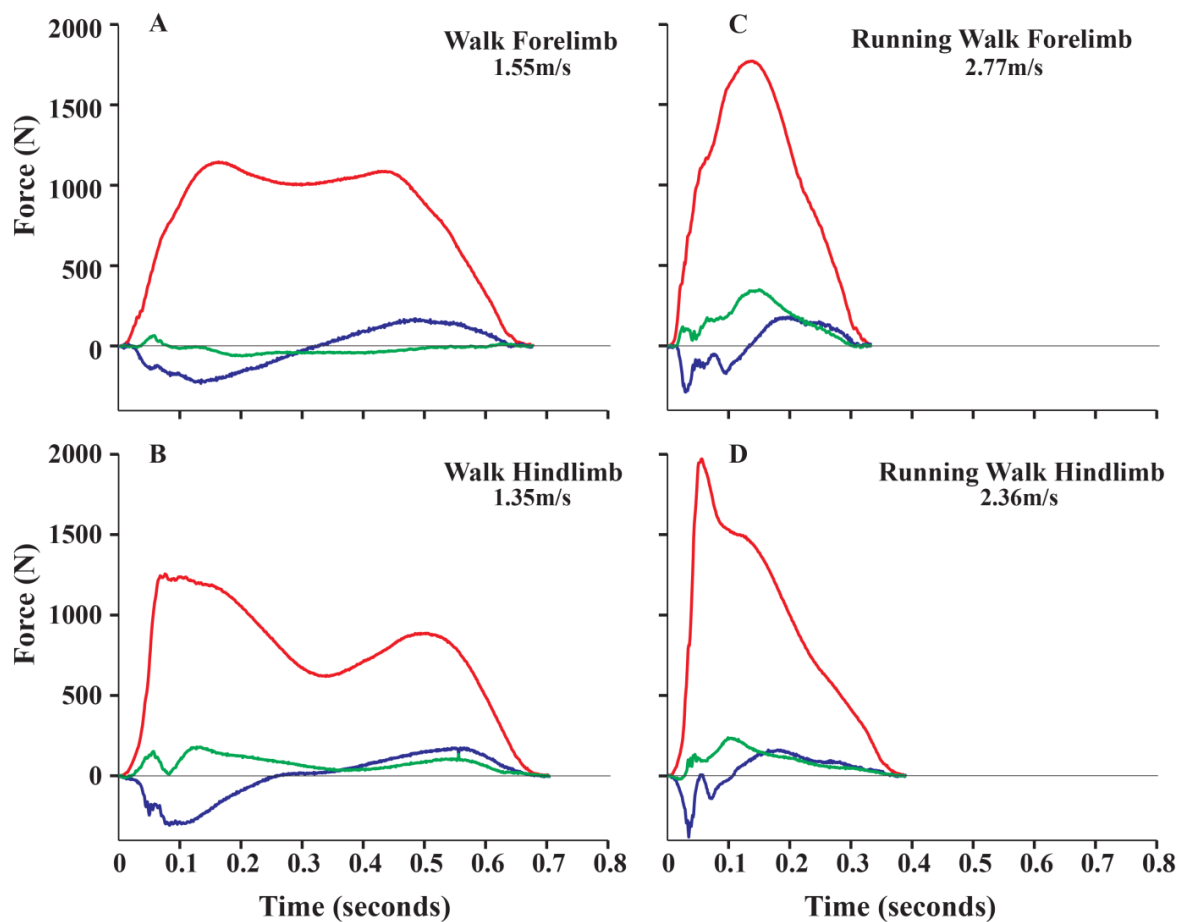


Figure 2.13 Representative Force Traces

Forelimb and hind limb force traces from a representative animal during walks (A, B respectively) and running walks (C, D respectively); vertical (red), anterior-posterior (blue), and mediolateral (green) forces are shown. Force traces for canters are similar to running walk.

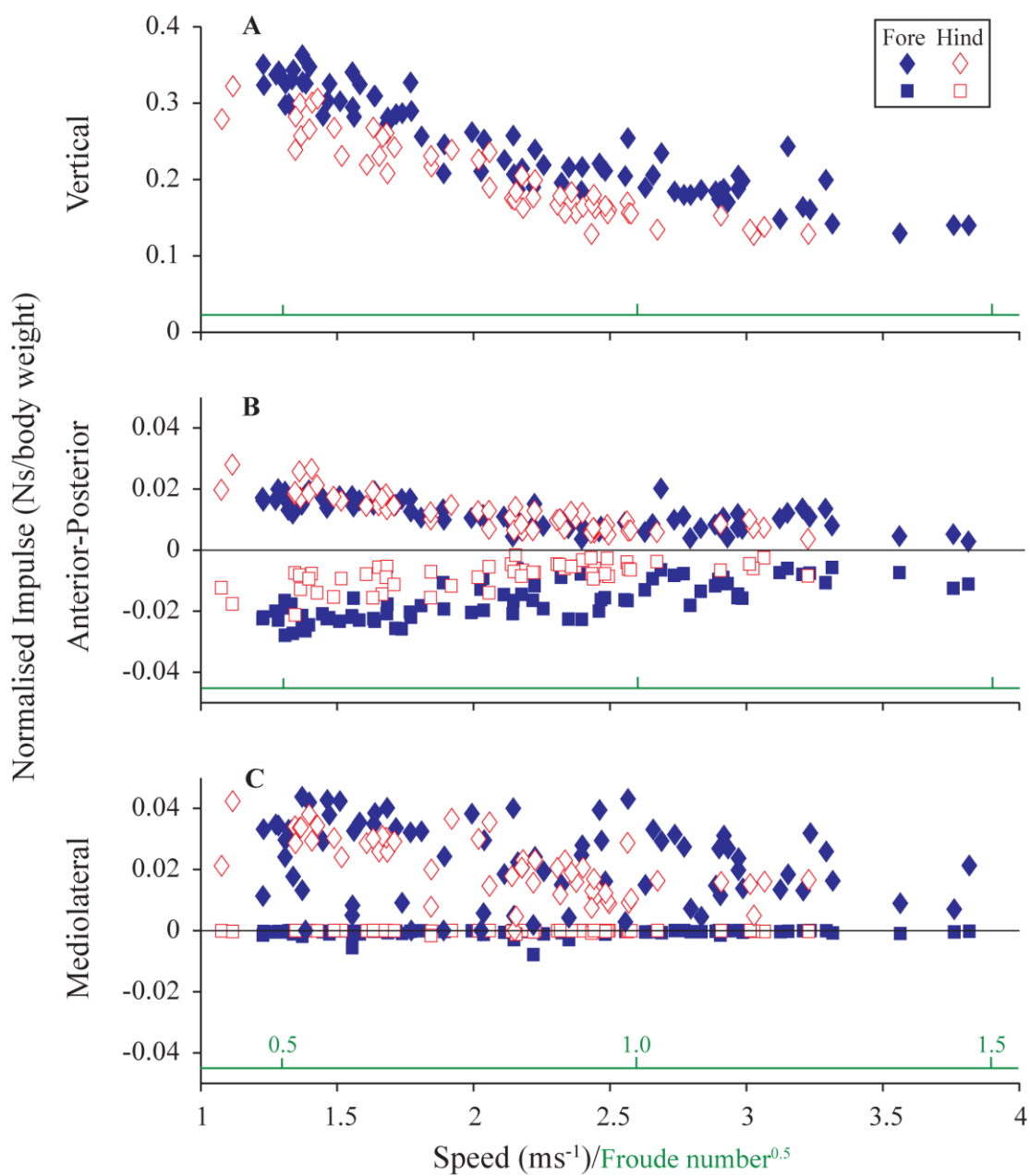


Figure 2.14 Vertical, Anterior-Posterior, and Mediolateral Ground Reaction Force Impulses
 Vertical impulses (A) are significantly different between the fore and hind limbs at all speeds. Braking impulses (B, negative, squares) are significantly higher for the forelimb than the hind limb, but propulsive impulses (B, positive, diamonds) are equal between the limbs. Medial impulses (C, positive, diamonds) are approximately equal to the magnitude of the anterior-posterior impulses. Second x-axis (green) is dimensionless speed.

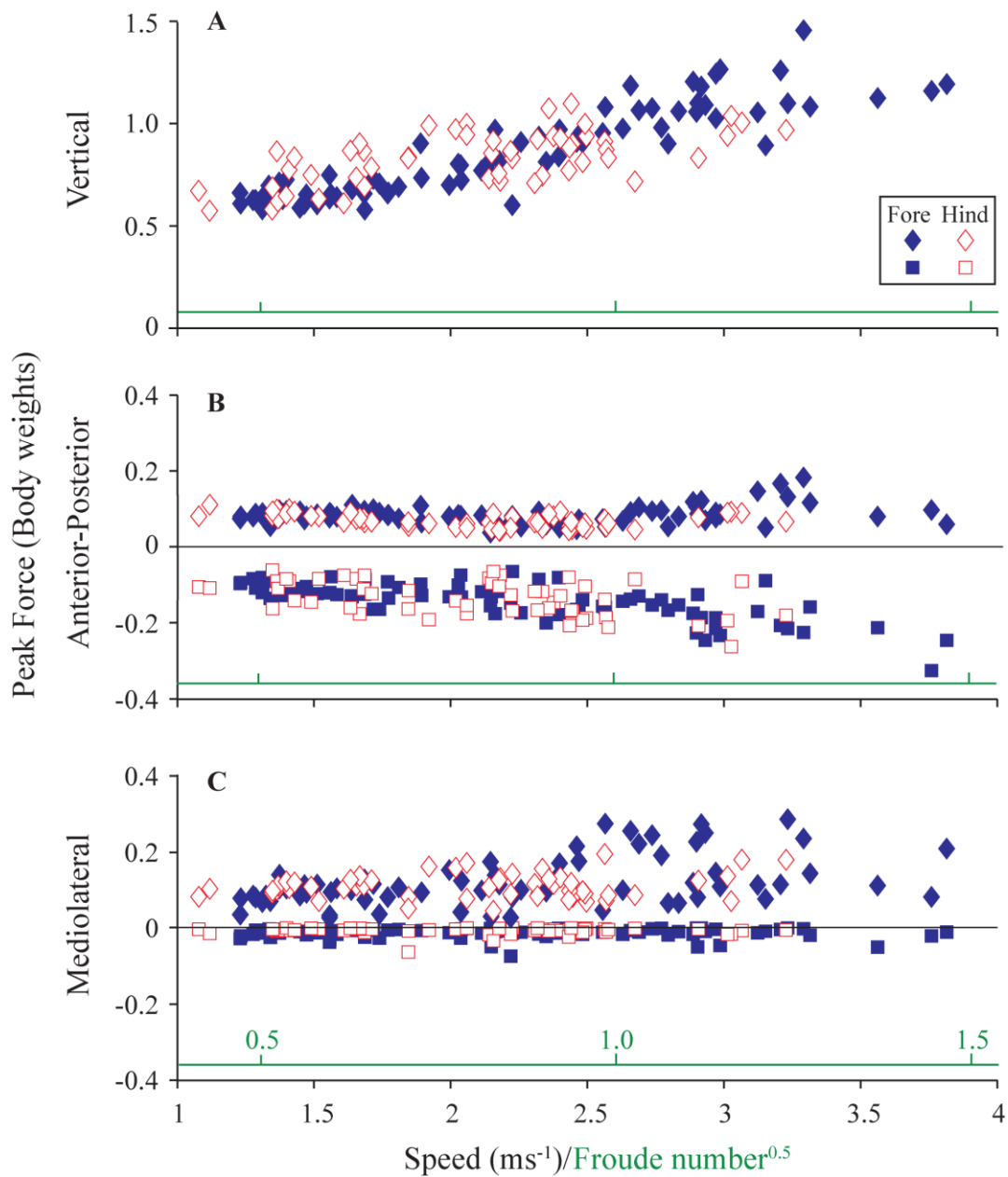


Figure 2.15 Peak Vertical, Anterior-Posterior and Mediolateral Ground Reaction Forces

There was no significant difference between the forelimbs and hind limbs for vertical (A), anterior-posterior (B), or mediolateral (C) peak forces. Symbols described in Fig. 1 legend. Second x-axis (green) is dimensionless speed.

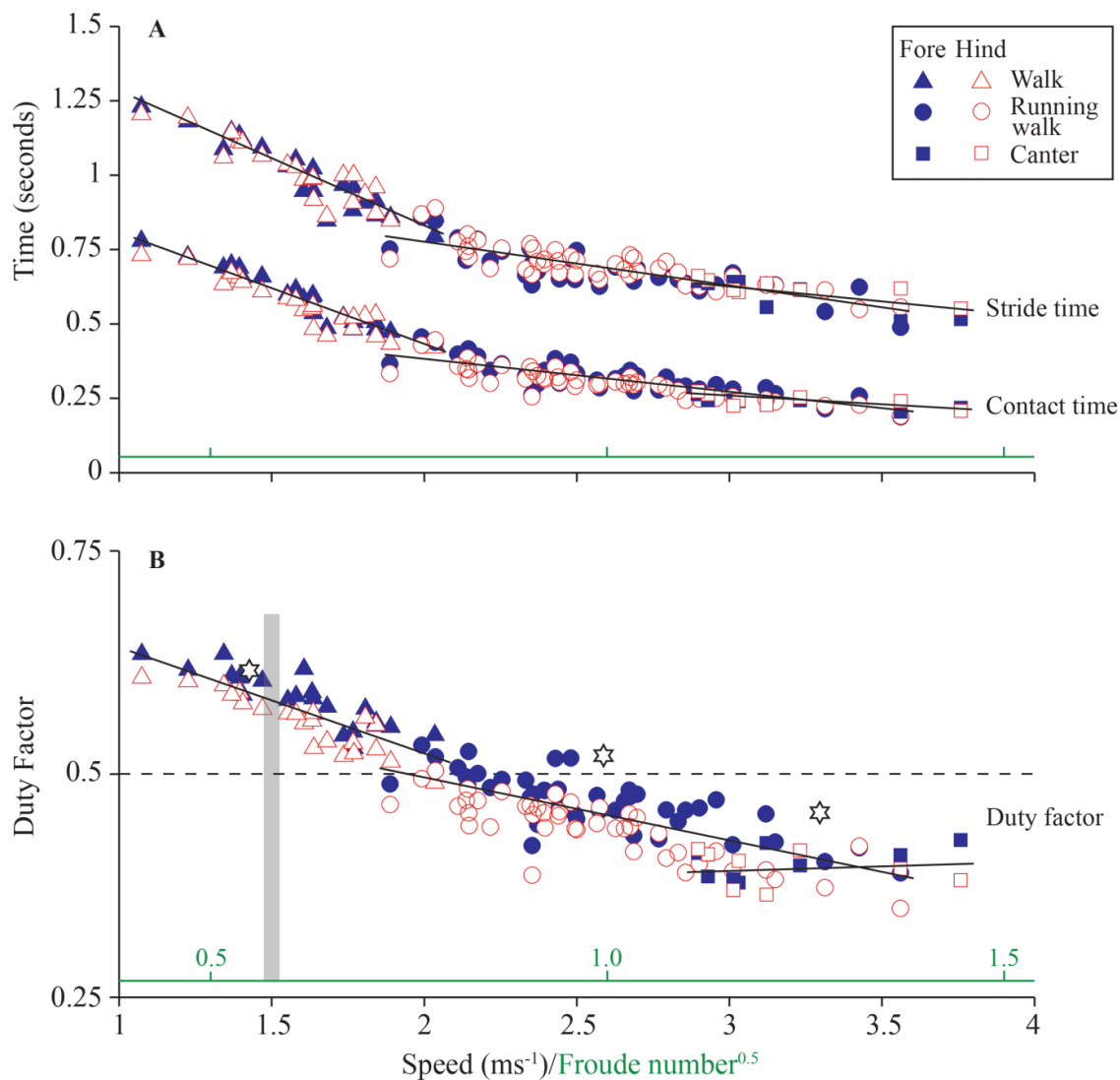


Figure 2.16 Stride Parameters Calculated from Video Data

(A) Stride and contact time and (B) duty factor across speeds for the fore (blue) and hind limbs (red). There is 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 likely due to variation between individual bears. Estimated forelimb duty factor for bears using dynamic similarity equations for cursorial animals (black stars) suggest bears are not dynamically similar to other erect animals. Walk-run transition (duty factor drops below 0.5) occurs at a higher relative speed in bears ($\text{Fr}^{0.5}$ 0.77) than horses ($\text{Fr}^{0.5}$ 0.55-0.61; grey bar). Linear regressions for fore and hind limbs 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, $y = 0.0083x + 0.37$, $R^2 = 0.02$, $P > 0.05$. Second x-axis (green) is dimensionless speed.

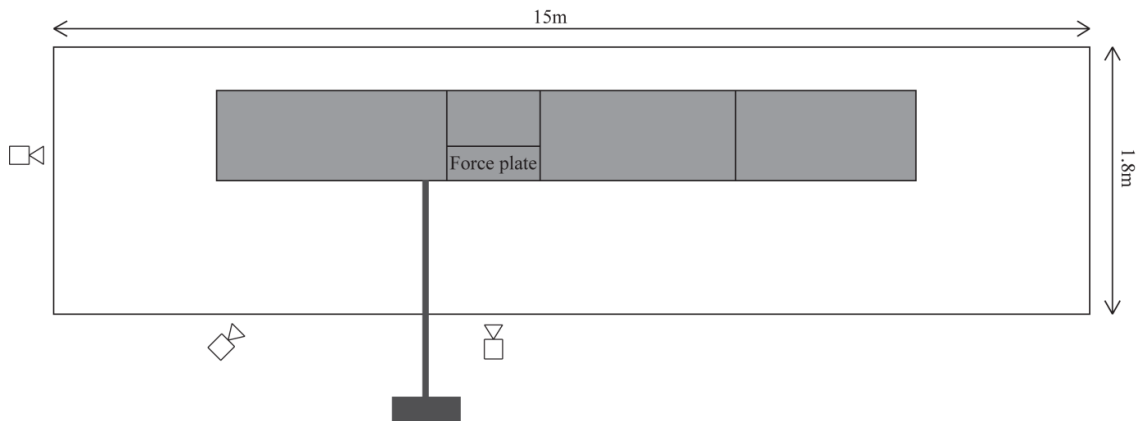


Figure 2.17 Schematic of Data Collection Setup

Runway panels are shown in grey with the force plate at the lower center of the image. The three cameras are shown with approximate angles for data collections. The dark grey 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.

Chapter 3: 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 sagittal and frontal planes, using ground reaction forces and position data from three high speed cameras of four adult female grizzly bears. The shoulder, wrist, and the limb overall absorb energy (summed limb average = -0.97 Wkg^{-1}). The shoulder, elbow, and summed limb net work have negative relationships with speed, resulting in more energy absorbed by the forelimb at higher speeds. The net joint moment and power curves maintain similar patterns across speed as 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 summed net work in the frontal plane is not significantly different from zero, suggesting that, despite the high medial ground reaction forces, the forelimb is acting as a strut in that plane.

Introduction

During locomotion, muscles are required to balance external moments produced by ground reaction forces. Due to the scaling relationship of muscle cross-sectional area compared to 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 (ratio of the muscle moment arm to the moment arm of the

ground reaction forces) and minimises the external joint moments. Despite these differences in posture, horses, dogs, and small therian mammals all maintain similar joint loading patterns over time in the forelimb (Clayton et al., 2000; Witte et al., 2002; Nielsen et al., 2003). These similarities include producing extensor moments at the shoulder and elbow, with the shoulder producing the highest magnitude of work.

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 plantigrade 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.

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 forces produced were closer to values reported for an alligator (*Alligator mississippiensis* (Willey et al., 2004), which have a sprawling posture. These high forces could suggest that bears are producing net work in the frontal plane and therefore, may not be as efficiently propelling themselves forwards.

The forelimbs have functional roles beyond locomotion in terrestrial animals, particularly in plantigrade 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). Plantigrade carnivorans use their forelimbs to investigate objects, to grasp food items and also for fighting, particularly in bears (Brown, 2009). In addition to being

plantigrade, grizzly bears have a medially deviated forefoot during stance with an associated rotation during swing (Davis, 1949; Gray, 1968; Inuzuka, 1996). The mechanism and function of this behaviour is unknown, but it is likely to have an effect on the joint loading of the forelimb, particularly in the frontal plane.

Therefore, in this study we aim to identify 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 lateral ground reaction forces and medially placed forefoot. We address the following questions: 1) Is grizzly bear locomotion in the sagittal plane similar to previously studied large mammals? 2) Do the lateral ground reaction forces and forefoot posture result in high 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*; 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. These animals were born at the centre, are involved in various studies, and 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 4.26m runway was placed in a narrow walkway in the bear enclosure with a custom built force plate (0.6 m x 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, 1248x900; 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° from the direction of travel. The left shoulder, 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. Due to 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 (Mathworks, Inc., Natick, MA, USA) scripts. 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 (Four 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). 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. Centre of rotation for the shoulder and elbow in the frontal plane were 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. Frontal plane joint centres were estimated from the CT scan and the videos to compare accuracy, with the exception of the shoulder, which was calculated from the CT scan. 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 angles, moments, and powers were calculated independently for the frontal and sagittal planes. The shoulder is calculated relative to horizontal in both planes. The frontal plane wrist angle is calculated relative to the forearm (Figure 3.1). Positive sagittal moments are defined by those that are balanced by extensor musculature for the wrist, elbow, and shoulder. Positive frontal moments are defined as those balanced by abductor musculature for all joints (Figure 3.1).

Statistics

Two-tailed ANOVAs 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 m s^{-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 the others and are therefore included in the analysis. Trials included walks, running walks, and canters, with gait transitions at approximately 2 m s^{-1} 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 (Figure 3.2). Relatively high medial ground reaction forces were present at all speeds (Figure 3.2).

Joint Angles

The shoulder is retracted throughout stance (Figure 3.3A). In the frontal plane the shoulder angle increases in the second half of stance, which is caused by the limb moving laterally as the foot is raised from the ground (Figure 3.4A). In the sagittal plane, the elbow is maintained at a higher angle (closer to full extension) throughout stance at the lowest speeds compared to the higher speeds, although there is some variation at this joint (Figure 3.3D). The average frontal elbow angle across all speeds is 155.1°. The frontal angle of the foot relative to the forearm (medial deviation) decreases with speed from 31.2° at walking speeds to 19.2° 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 (Figure 3.4G).

Moments

Shoulder, elbow, and wrist joint moments are all positive during stance, representing extensor moments. The magnitudes of shoulder moments are greater than the other two joints (elbow, $p=0.016$; wrist, $p<0.001$; Figure 3.3B,E,H). Moments produced by the shoulder and elbow are similar magnitudes in the sagittal and frontal planes (Figures 3.3B,E and 3.4B,E, respectively), whereas frontal moments are smaller than sagittal moments at the wrist ($p<0.001$; Figures 3.4H and 3.3H, 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 ($p<0.001$). Peak moments at a canter are significantly higher than running walks at the elbow ($p=0.019$).

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 ($p<0.01$; Figure 3.5). The shoulder absorbs energy (i.e. negative work) for the majority of stance (Figure 3.3C). The magnitude of the energy absorbed by the shoulder 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 (Figure 3.3F). 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

canter (Figure 3.6). 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 3.3I). 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 shoulder. Overall, the power produced in the frontal plane is low across all speeds. The shoulder produces positive net work across all speeds, whereas the elbow produces negative net work at all speeds (Figure 3.6). For both joints, these values are significantly different from zero ($p < 0.05$) but still low compared to 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. The total limb net work is not significantly different from zero and does not change with speed (Figure 3.5).

Discussion

The goal of this study was to investigate forelimb joint dynamics across speeds in grizzly bears, in the frontal and sagittal planes. Bears are relatively distinct from other mammals. They are the only family of large, plantigrade species in the Carnivora order, which likely 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 other quadrupeds, including digitigrade, similarly sized unguligrade, and small plantigrade species. In order to compare species of a similar size, for which data have been reported, we have compared bears to horses. Bears and horses produce similar peak moments at all three joints when normalised for body mass (Dutto et al., 2006); however, these values are substantially greater than for other species, including dogs (Nielsen et al., 2003), pigs (Thorup et al., 2008), and small

mammals (Witte et al., 2002). Horses and bears are closer in body mass and substantially larger than any of the other species discussed which may be the cause of this difference.

Shoulder dynamics are relatively consistent across species, even with differences in posture. However, differences in how shoulder angle is calculated makes comparisons across species difficult. The shoulder angle in our study was calculated relative to the horizontal as we were unable to place a marker on the scapula. Based on this analysis the shoulder angle in the sagittal plane is close to 90° when the foot touches the ground and retracts under an extensor moment throughout stance, which results in energy absorption. A similar result has been shown for small mammals, 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). However, during trotting power values fluctuate around zero and result in net positive work (Dutto et al., 2006).

All species described in this discussion, including bears, produce extensor moments at the elbow. The extensor moments are mainly acting to prevent collapse of the limb under the acceleration due to gravity, and this is therefore expected to remain consistent across species.

We would expect the most likely difference between plantigrade species and the other postures to be in the moments at the wrist. Plantigrade species produce extensor moments (bears, this study; small mammals, Witte et al., 2002), whereas small digitigrade and unguligrade species produce flexor moments (dogs and pigs, respectively; Nielsen et al., 2003; Thorup et al., 2008). In plantigrade 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. However, horses are unguligrade species that produce extensor moments (trotting and walking, Clayton et al., 1998; Clayton et al., 2000). There may be a scaling argument that is independent of posture that results in a large unguligrade species producing extensor moments similar to plantigrade species. This could relate to the direction of the ground reaction force vector resulting from support of the head and neck.

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 plantigrade, digitigrade, and unguligrade postures.

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 the 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 due to the minimal angle change during stance, especially at the higher speeds. This posture could be a result of underlying morphology, previous research has demonstrated that bears have an unusual elbow joint compared to other carnivoran species (Van Valkenburgh, 1987).

Although the forelimb produces 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 due to the differences in anatomy are also required to produce power away from the direction of travel (Blob and Biewener, 2001; Chen et al., 2006).

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 production of positive work (Clayton et al., 1998; Dutto et al., 2006). This pattern was not seen in the bears; the shoulder increased energy absorption as speed increased, regardless of the gait used.

Net work is also continuous across speed. There is no distinct change associated with gait transitions. This is true of the individual joints, and the total summed limb net work. Although walks and running walks are mechanically different gaits, they maintain the same footfall pattern. The order and relative timing of the foot placement remains consistent between these gaits, but there is reduced overlap between footfalls and the vertical ground reaction force displays a different pattern (Figure 3.2). The transition from a walk to a trot requires a more dramatic change in mechanics due to 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 that of 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 compensate.

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. These animals are representative of the species as a whole. 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 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 75-125% 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. Inverse dynamics analysis has inherent limitations, this analysis produces net results for each joint and therefore cannot take biarticular or antagonistic muscles 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 plantigrade, digitigrade, and unguligrade animals, sagittal plane joint loading patterns appear to be 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.

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 bears. Instead, it appears that the forelimb of a grizzly bear 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 likely not energetically costly.

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Table 3.1 Segment Properties for Individual Bears

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

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

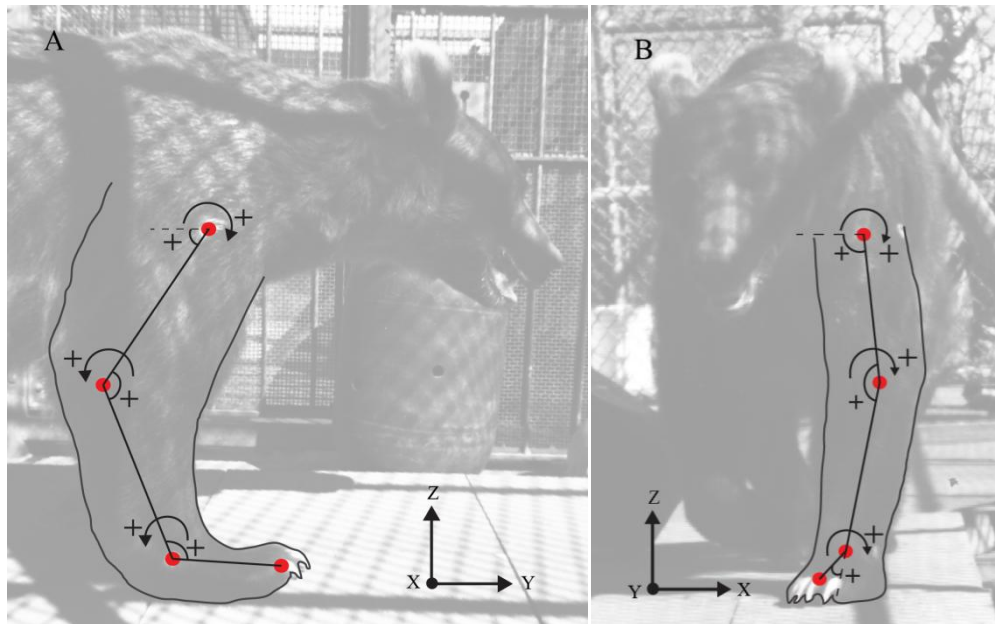


Figure 3.18 Schematic of Joint Angles and Moments.

A) Sagittal Plane. Shoulder 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 was 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. Shoulder joint angle was calculated relative to the horizontal. The wrist angle is calculated as the angle of the foot relative to the forearm. Abductor moments are positive for all joints.

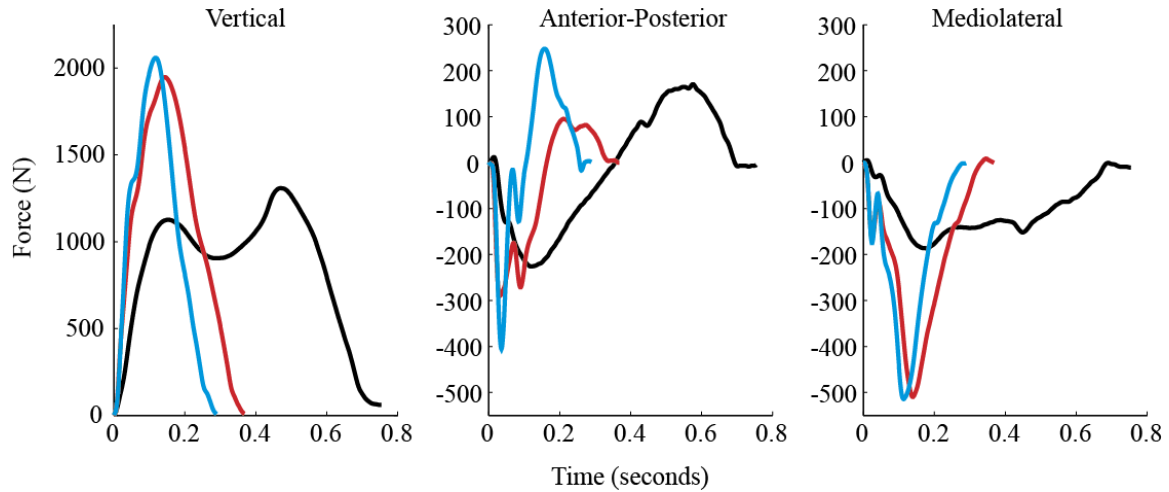


Figure 3.19 Representative Ground Reaction Forces.

Vertical, anterior-posterior, and mediolateral ground reaction force traces from representative trials at a walk (1.4 ms^{-1} ; black), running walk (2.5 ms^{-1} ; red), and canter (3.2 ms^{-1} ; light 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.

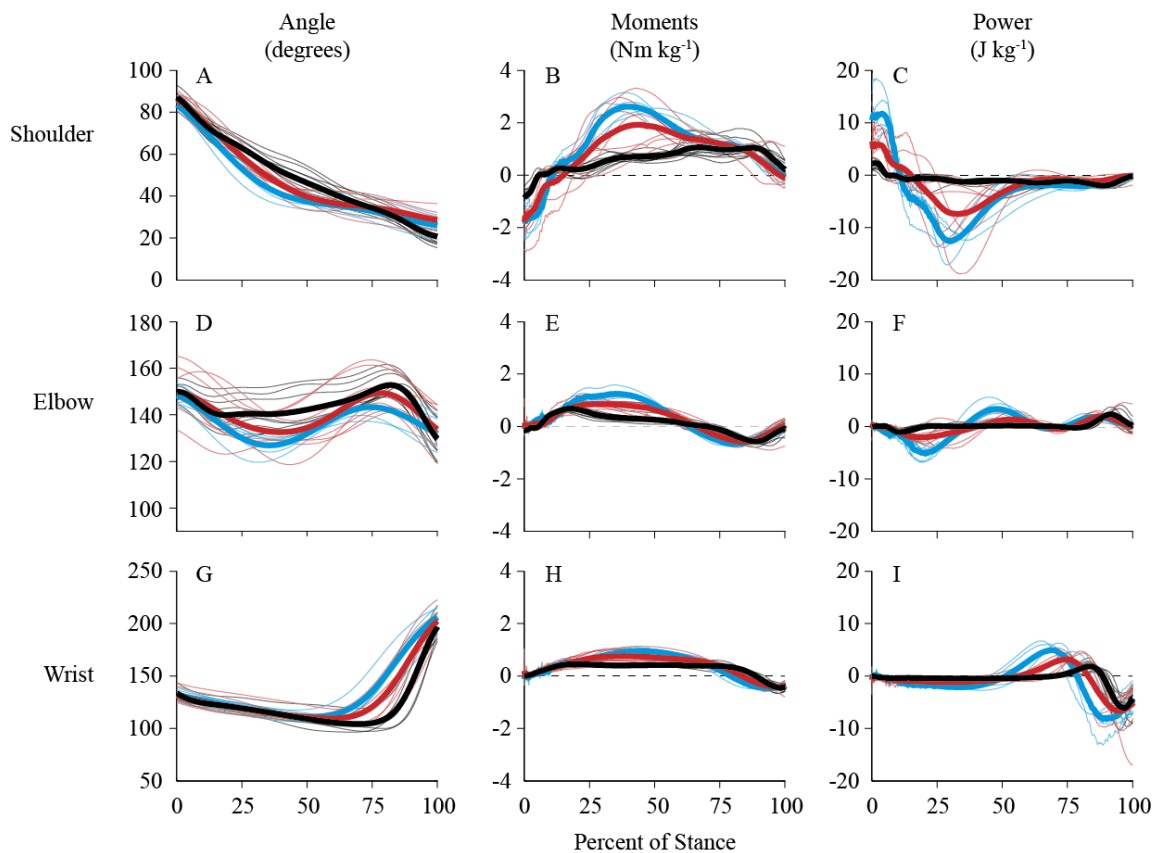


Figure 3.20 Angles, Moments, and Powers in the Sagittal Plane.

Joint angles, normalised joint moments, and normalised joint powers for the shoulder (A, B, C respectively), elbow (D, E, F), and wrist (G, H, I). Light blue represent canters ($\sim >3 \text{ ms}^{-1}$), red represents running walks ($\sim 2\text{-}3 \text{ ms}^{-1}$), and black represents walks ($\sim <2 \text{ ms}^{-1}$). 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 dotted black line for clarity.

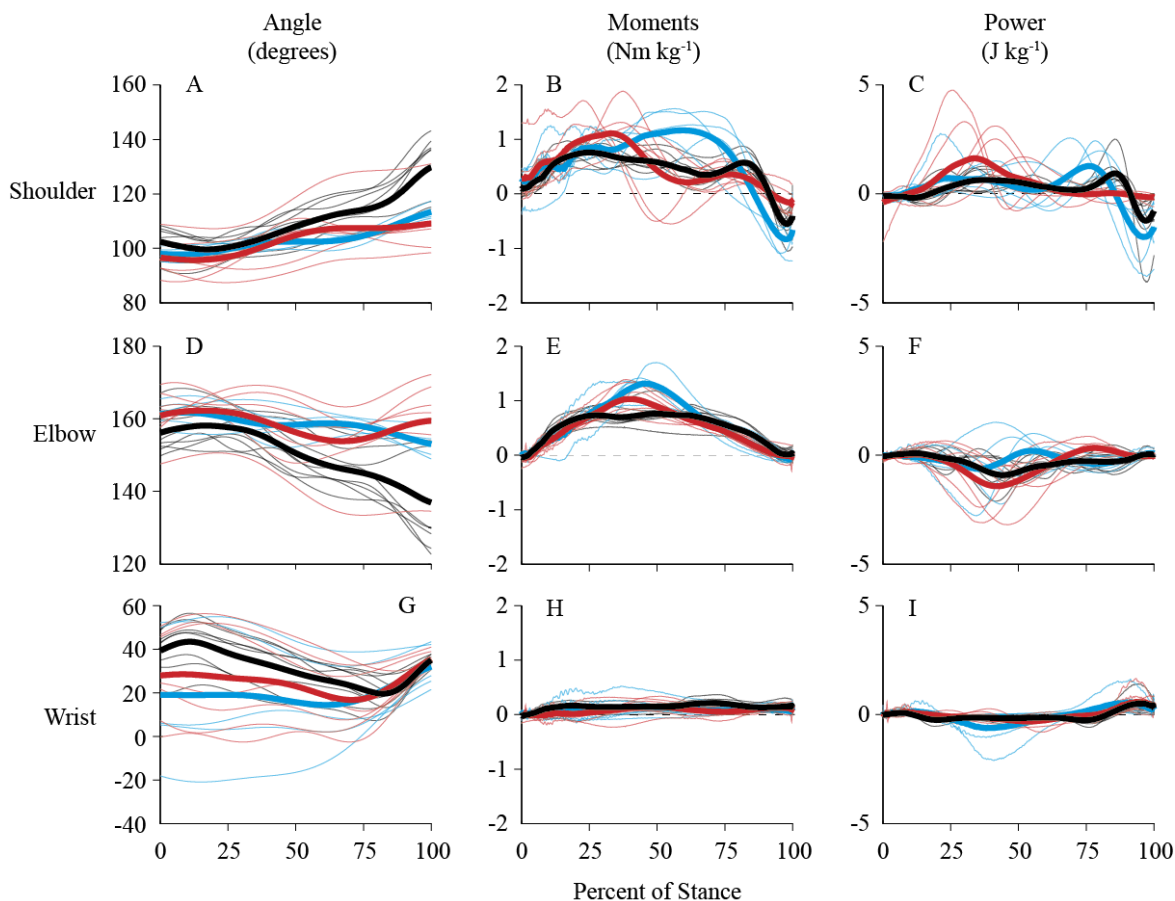


Figure 3.21 Angles, Moments, and Powers in the Frontal Plane.

Joint angles, normalised joint moments, and normalised joint powers for the shoulder (A, B, C), elbow (D, E, F), and wrist (G, H, I). Light blue represent canters ($\sim 3 \text{ ms}^{-1}$), red represents running walks ($\sim 2\text{-}3 \text{ ms}^{-1}$), and black represents walks ($\sim <2 \text{ ms}^{-1}$). 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 dotted black line for clarity.

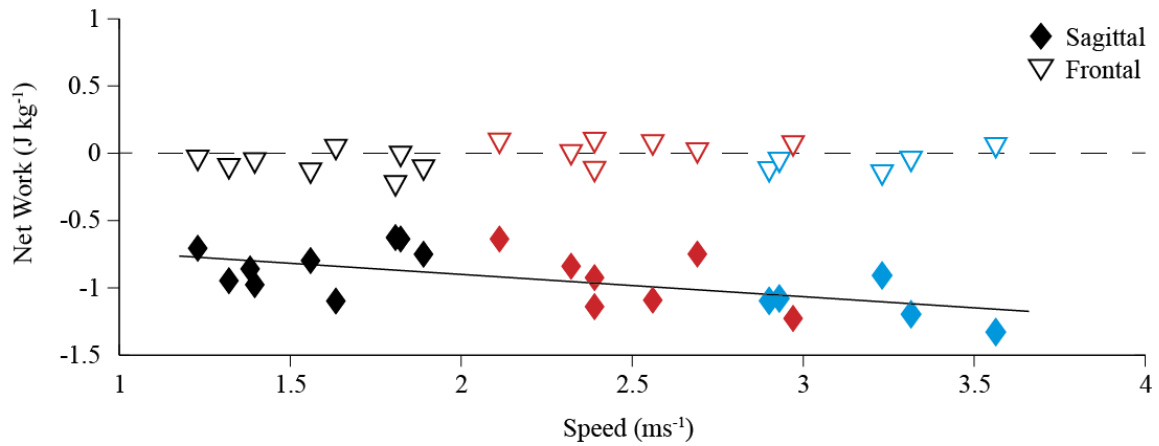


Figure 3.22 Limb Net Work across Speeds.

The net work for joints was summed to produce total limb net work in the sagittal (closed diamonds) and frontal (open 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 ($p < 0.01$). Gaits coloured as described in Figure 3.

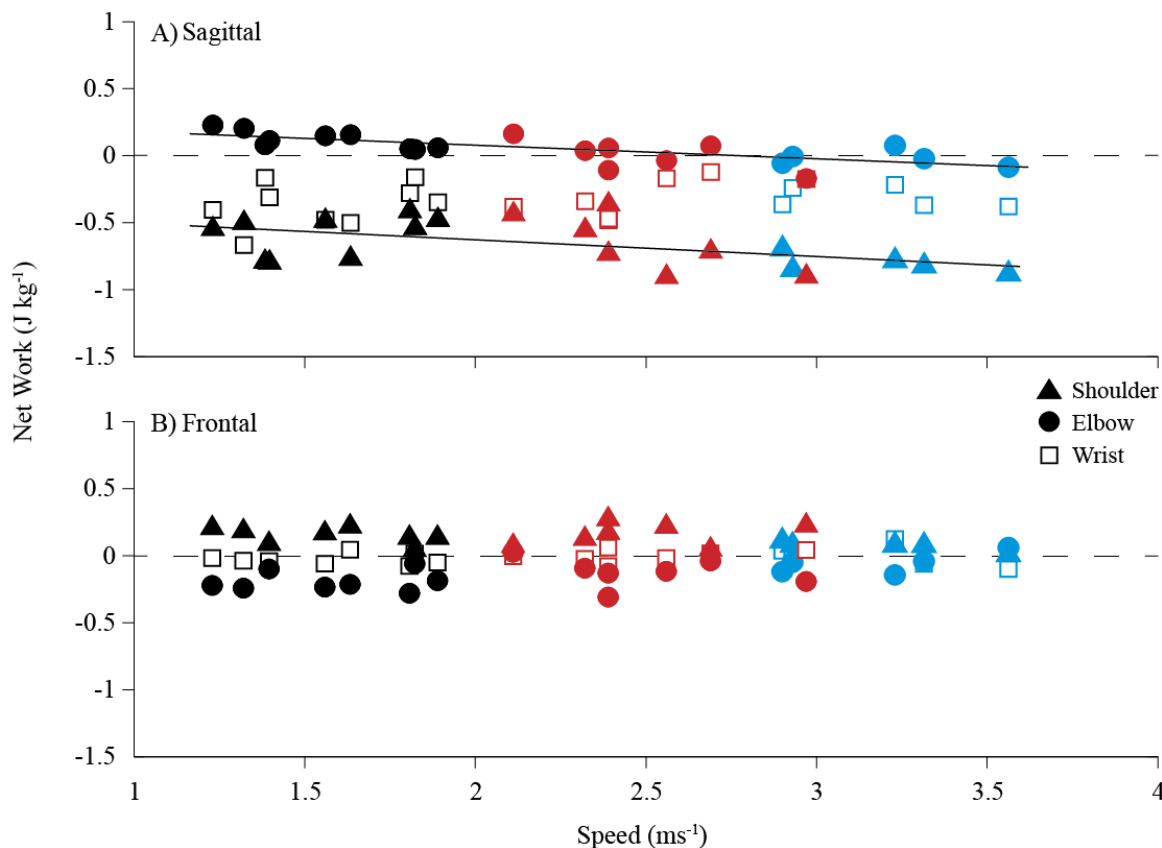


Figure 3.23 Joint Net Work across Speeds.

A) Sagittal Plane. The wrist absorbs energy at all speeds, although with low magnitude, and there is no significant relationship with speed (open squares). The net work produced by the elbow has a significant negative relationship with speed ($p < 0.001$; closed circles), beginning with positive net work at a walk, and becoming more negative during the running gaits. The shoulder absorbs energy at all speeds, and this increases with increasing speed ($p < 0.05$; closed triangles). B) Frontal Plane. The shoulder produces positive net work at all speeds (closed triangles). The elbow has a significant positive relationship with speed ($p < 0.05$; closed circles). The net work produced by the wrist was not significantly different from zero (open squares). Gaits coloured as described in Figure 3.

Chapter 4: Locomotor Behaviour of Plantigrade Carnivorans: Analysis of Forelimb Bone Morphology

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Abstract

Skeletal morphology studies have been used to help scientists understand the natural history and evolution of life on earth. Carnivora (Mammalia) has received particular attention due to the diversity in size, behaviour, and ecology of its species. Many of these studies have included representatives of digitigrade and plantigrade postures, which has led to outliers and results that may be confounded by shape due to posture as opposed to behaviour. In this study we used 3D geometric morphometrics on 44 extant species of plantigrade carnivoran, and analysed the forelimb long bones for differences in shape due to their locomotor behaviour. We also estimated the locomotor behaviour of two extinct bear species. The results showed that there were significant shape differences between the behavioural groups in the scapula, humerus, and ulna, but not the radius. Discriminant analysis had high error rates for all bones, likely due to the small sample size per behavioural group. Using the extant data as a model to estimate the behaviour of extinct bears suggests that *Arctodus* was arboreal; however the results for *Ursus spelaeus* were inconsistent. There was a significant phylogenetic effect in the shape data and bears were outliers for the scapula and ulna in the principal components analysis. Overall, the results of this study suggest that including both digitigrade and plantigrade species does not have an effect on the success of classification rates. However, phylogenetic effects need to be taken into account, especially when identifying locomotor behaviour of an extinct species from an outlying family, such as Ursidae.

Introduction

There have been a considerable number of bone morphology studies, across the whole of tetrapoda. These studies are often used to increase understanding of the life history and ecological niches of extinct species, using extant species for comparison (Ricklefs and Miles, 1994; Van Valkenburgh, 1994).

Carnivora has received particular attention (e.g. Ginsburg, 1961; Van Valkenburgh, 1987; Polly and MacLeod, 2008; Fabre et al., 2013). This order contains a wide range of morphology and behaviour, and contains species with body mass that ranges over four orders of magnitude (Samuels et al., 2013). The locomotor behaviours in this group are dispersed throughout the whole order, including caniforms and feliforms, demonstrating convergent or parallel evolution (Samuels et al., 2013). Canidae, felidae, and hyaenidae are families of digitigrade species (animals that stand only on their toes), and are mainly identified as being terrestrial or cursorial. The other ten terrestrial families (i.e. excluding Pinnipedia) in Carnivora are almost entirely plantigrade species (those that stand with their entire foot on the ground).

The plantigrade posture is ancestral for mammals (Ginsburg, 1961). The digitigrade posture likely evolved to increase running speed and endurance; however, the majority of Carnivora species maintain the plantigrade posture. The morphological differences between digitigrade and plantigrade species are substantial; these include limb and phalange proportions, as well as sizes of processes for muscle attachments on limb bones (Ginsburg, 1961). In part due to the lack of specialisations for cursoriality in plantigrade species, they are able to display a wider range of behaviours.

Previous morphological studies have included digitigrade and plantigrade species of carnivora. The inclusion of both postures may have led to lower classification rates in extant species that could otherwise be achieved. Some plantigrade species, in particular members of Ursidae, have been found to be outliers (Van Valkenburgh, 1987). However, if these data are viewed with digitigrade and plantigrade species separated, it is possible that the two postures have different trends in morphological variables. Recent studies seeking to identify locomotor behaviours of extinct species have also used representatives from both postures across Carnivora; however, the successful classification of extant species was 65.1% (Samuels et al., 2013), and the highest correct classifications were for digitigrade (cursorial) groups. Therefore the interpretation for extinct species, especially plantigrade species, may be less accurate than if postures are considered independently.

There are eight extant species of bear, but this group was previously much more diverse and there are many extinct species. The most commonly found fossils are from the short-faced bear (*Arctodus simus*) and the European cave bear (*Ursus spelaeus*). There has been a substantial amount of controversy regarding the locomotor behaviour of the short-faced bear. The short-faced bear is a particularly large Pleistocene bear that was sympatric with North American brown bears (Matheus, 1995). There have been suggestions that it was a hypercarnivorous bear, and a cursorial predator (Kurten, 1966). However, studies using stable isotope analysis to identify the diet of these bears have suggested that they were primarily carnivores, but more likely to be scavengers than active hunters (Matheus, 1995). A study of the craniodental morphology of *A. simus* suggested that although the isotopic analysis found the diet to consist mainly of meat, this species was more likely to be a resource dependent omnivore (Figueirido et al., 2010). In contrast, the limb morphology suggests that the short-faced bear may have adaptations for semi-fossoriality and used its robust limbs to dig (Samuels et al., 2013). The short-faced bear was likely to have been a plantigrade species, and therefore the use of solely the plantigrade posture in this study may help to identify the locomotor behaviour of this controversial species.

In this study we use 3D geometric morphometrics to analyse the shape change between locomotor behaviours. This method allows the entire shape of the bone to be incorporated in a way that linear or 2D analyses cannot. For example, some locomotor behaviours result in similar morphological adaptations for different functional reasons (Samuels et al., 2013). However, muscle attachment areas or articulation surfaces are likely to demonstrate different signals depending on the locomotor behaviour, and these are more easily incorporated into a landmarks based analysis. The additional dimension in 3D geometric morphometrics also allows the overall bone shape to be included, such as twisting that is present in long bones of some carnivorans (Ginsburg, 1961). We are focusing on the forelimb due to its essential role in all the locomotor behaviours included and it is therefore likely to have a strong functional signal.

Our study aims to determine whether using a model created using only plantigrade species produces higher correct percent of classification of locomotor behaviour in extant species. We

use 3D geometric morphometrics of surface scans of the forelimb long bones of plantigrade carnivorans. We hypothesise that our model will be more accurate at placing plantigrade extant species in their correct locomotor behavioural groups, than a model that includes species representing other postures, and will therefore produce more reliable estimations for the locomotor behaviours of extinct species with the same posture. We will test the second part of this hypothesis using extinct bears *Arctodus* and *Ursus spelaeus*.

Materials and Methods

Specimens

We scanned one specimen (a representative from a species, usually consisting of a complete skeleton) of 44 extant species and two extinct genera (Table 4.1). The extant specimens include representatives from all ten families of Carnivora that contain plantigrade species. We are defining species as plantigrade according to their foot posture at rest as in Carrano (1997). Because the analyses were being carried out on behavioural groups as opposed to individual species, we did not consider it necessary to create a species average from several specimens. The shape change between different species, especially those with different behaviours, will be greater than the variation identified between individuals of the same species. Bones included in the analyses are the left scapula, humerus, ulna and radius of each specimen. If bones were missing or broken from one specimen, then these bones were scanned from another specimen where available. For some of the smaller species, the ulna and radius were not disarticulated in the specimen. In these cases only the scapula and humerus have been included in the analyses. All scans were taken from adults specimens, as identified by fusion of the epiphyseal plates.

Extinct specimens included were from Ursidae (Figure 4.1). All bones for *Ursus spelaeus* were from the same specimen. *Arctodus* bones were from different specimens and were not all identified to species.

Data were collected from several institutions: Idaho Museum of Natural History, Idaho State University ID (IMNH), Museum of Comparative Zoology, Harvard University, MA (MCZ), California Academy of Sciences (CAS), Museum of Vertebrate Zoology, University of

California Berkeley (MVZ), University of California Museum of Palaeontology (UCMP), National Museum of Natural History, Smithsonian Institution (USNM). Location of each specimen is listed in Table 4.1.

Locomotor Behaviours

Our study included six locomotor behaviours: terrestrial, scansorial, semi-aquatic, semi-fossorial, arboreal, and digitigrade (Table 4.2). One specimen from each of Canidae, Felidae, and Hyaenidae were included as digitigrade species. These were given their own behavioural group to determine whether plantigrade and digitigrade species would be grouped independently. Species were assigned to their groups based on previous studies (Table 4.1). All locomotor behaviour categories contained species from at least three families, and five species (Table 4.3).

Scanning and Digitising

All bones were scanned using the NextEngine Desktop Scanner (Model 2020i; ShapeTools LLC and NextEngine, Inc.). At least two scans were taken of each bone and were aligned using ScanStudio HD software (Version 2.0.2). The complete scan was then fused to fill any holes, simplified to reduce file size, and exported as an STL file. Photographs were taken of the bones in several views; these were used to measure the bone (Schneider et al., 2012) and therefore scale the 3D scan. Humerii, ulnae, and radii were scaled using total bone lengths, scapulae were scaled using the distance from the distal point of the glenoid to the top of the scapula spine. All bones were scaled with at least two photographs; four were used wherever possible.

The scans were imported into Landmark Editor (Wiley, 2006) for digitising. Digitised points included single landmarks and curves (sliding semi-landmarks). Each bone had at least twelve landmarks and two curves (Figures 4.2, 4.3). Due to the variation in shape of the scapulae, we used four curves to encompass the entire edge of the bone. Landmark coordinates were exported, using dimensions from the photographs, as PTS files and converted to TXT files manually. The TXT files were formatted, combined, and exported as a single CSV file for

each of the scapula, humerus, ulna, and radius using Matlab (Mathworks, Inc., Natick, MA, USA).

Geometric Morphometric Analyses

Morphometric analyses were conducted in R (R Core Team, 2015). Geometric morphometric analyses were carried out using the *geomorph* package (Adams and Otárola-Castillo, 2013). The CSV files created in Matlab were imported into R, and the sliding semi-landmarks were identified manually. Independent scripts were written for the analysis of the scapula, humerus, radius, and ulna. Bones were aligned using a generalised Procrustes analysis. The Procrustes coordinates were used to create a variance-covariance matrix, which was used to calculate principal components. The principal component scores were used for further analyses of differences in behavioural groups (see *Statistics* section below). Principal component analyses were analysed using only the extant species. The analysis was rerun including the fossil species to provide the principal component scores for the fossil bones to be included in the discriminant analysis.

Phylogenetic Analysis

Shape differences were assessed for phylogenetic signal using a Carnivora phylogeny adapted from (Nyakatura and Bininda-Emonds, 2012; Figure 4.1). This tree was edited using Mesquite (Maddison and Maddison, 2015) to remove species that were not included in this study, in particular all of the digitigrade families, as well as include an extra six species that had not been included in the original study. The tree was scaled in two ways, first where all branch lengths were equal to 1 (unit tree), and second where all terminal nodes were equal height (Grafen tree). As not every bone was available for every specimen, the phylogeny was adjusted for each type of bone. The morphometric data was tested for a phylogenetic signal (*geomorph*; Adams and Otárola-Castillo, 2013), and a phylogenetic generalised least squares (pGLS) test was used to determine whether the morphological signal was still present once phylogeny was taken into account.

Statistics

Statistical tests were also conducted in R. Overall differences between behaviour groups were assessed using a MANOVA (*vegan*; Oksanen et al., 2016). Pairwise tests were conducted to compare differences between specific groups (*geomorph*; Adams and Otárola-Castillo, 2013). A discriminant analysis was run to determine the accuracy of the model for placing extant species in their respective groups, and also estimating the locomotor behaviour of extinct species (Iida, *MASS*; Venables and Ripley, 2002). Due to the inclusion of semi-landmarks, the LDA was run using the principal component scores (Zelditch et al., 2012). Scores that cumulatively accounted for 95% of the shape variation were included, this varied per bone from 11 to 16 scores. Classification error rates were calculated using 80% of the dataset per bone as a training set, and then placing the remaining specimens in their respective groups.

Results

Group Differences

Locomotor behavioural groups were significantly different for the scapula ($p=0.028$), humerus ($p=0.002$), and ulna ($p=0.002$). Overall the behavioural groups were not statistically different for the radius ($p=0.078$).

In the pairwise comparisons the semi-fossorial species were different from the most other behavioural groups. Semi-fossorial species were significantly different from terrestrial species for the scapula, humerus, and radius ($p<0.05$). Semi-fossorial and scansorial species were also significantly different for the humerus ($p=0.01$) and radius ($p<0.05$). The humerus also showed a significant difference between semi-fossorial and arboreal groups ($p=0.015$).

Arboreal species have shape differences from several groups, which were significantly different for different bones. The scapula showed that arboreal and terrestrial species were significantly different ($p<0.01$). For the ulna, arboreal and semi-aquatic species were significantly different ($p<0.05$).

Scansorial species were significantly different from semi-aquatic species in the ulna ($p<0.01$), and terrestrial species for the scapula ($p<0.01$). Across all pairwise comparisons and bones,

every group was significantly different from at least one other group for at least one bone. The ulna was the only bone to show significant differences between semi-aquatic species and any other behavioural group. Similarly, terrestrial species were significantly different from other groups only for the scapula.

Phylogenetic Analysis

All bones had a significant phylogenetic signal in the shape data, regardless of the model used for scaling branch lengths (Table 4.4). Results of the pGLS showed that when phylogeny was taken into account using a Grafen modelled tree the shape changes were no longer statistically significant (Table 4.4). This result is likely due to my small sample size in each behavioural group. However, the areas of shape change identified in the analysis are still likely to be biologically relevant and therefore worth discussing for distinguishing between different groups.

Shape changes

Scapula

The first two principal component axes accounted for 63.9% of the shape variation (PC1 = 51.6%, PC2 = 12.3%; Figure 4.4). The eight specimens at the negative end of the first principal component axis are all bear species. These are therefore not representative of shape change due to locomotor mode. Positive scores on PC1 are represented by a triangular shape, with a fairly short acromion, and a symmetrical anterior-posterior curvature. Semi-aquatic, semi-fossorial and terrestrial species have generally positive PC1 scores; however these may be more extreme due to the bears representing the negative PC1 scores.

The second principal component axis differentiated between rounded and rectangular scapula shapes, with long or short acromia. Arboreal and scansorial species tend to have positive PC2 scores, which represent a more rounded overall shape with a longer acromion, whereas semi-fossorial species have negative PC2 scores with a more rectangular shape and a short acromion.

Humerus

The first two principal component axes accounted for 56.1% of the shape variation (PC1 = 43.5%, PC2 = 12.7%; Figure 4.5). The first principal component analysis is a measure of robustness. Positive PC1 scores are robust humeri with an overall curvature to the bone, while negative PC1 scores are much more gracile bones with less curvature. Scansorial and terrestrial species tend to have negative PC1 scores. Positive scores on the first principal component axis are mainly found in the semi-fossorial and semi-aquatic species. However, there is one semi-fossorial species with a negative PC1 score; this species is the meerkat (*Suricata suricatta*), which is the only feliform semi-fossorial specimen in the analysis.

The second principal component analysis is also a measure of robustness. On this axis, positive scores are more gracile shapes, while negative scores are more robust. This axis appears to differentiate between semi-fossorial species (positive scores) and semi-aquatic species (negative scores). Arboreal, scansorial, and terrestrial species are all approximately neutral on this axis.

Ulna

The first two principal component axes accounted for 55.4% of the shape variation (PC1 = 35.7%, PC2 = 19.6%; Figure 4.6). The first principal component axis for the ulna is a measure of robustness. Positive scores relate to a robust shape, with a laterally directed and long olecranon that possesses a large medially directed process. This shape is shown mostly in semi-aquatic species. Negative PC1 scores are very gracile bones with short, straight olecranons. Terrestrial species tend to have negative PC1 scores.

Positive PC2 scores are dominated by Ursidae, with six bear species having the most positive values (Figure 4.6). As with the scapula, these values are not representative of shape change due to locomotor behaviour. Semi-fossorial species tend to have negative scores on the second principal component axis, and this shape is represented by an intermediate robustness, a long and slightly laterally directed olecranon, with a minimal medial process.

Radius

The first two principal component axes accounted for 70.4% of the shape variation (PC1 = 53.3%, PC2 = 17.1%; Figure 4.7). Positive scores on the first principal component axis represent a gracile shape, with a slight curvature, and narrow epiphyses. These scores are mostly represented in semi-fossorial species. Negative PC1 scores are more robust bone shapes, with a more curved diaphysis, and broader epiphyses, particularly at the distal end. Semi-aquatic species are the most representative of this shape; however, arboreal species are also slightly negative on PC1.

The second principal component axis is a measure of robustness in the radius. Positive scores are gracile shapes but with a broader distal epiphysis than positive scores on PC1. This shape is demonstrated by scansorial and terrestrial species. There are only two specimens at the extreme negative end of PC2, which is a very robust and curved bone, with broad epiphyses. These specimens are the semi-fossorial striped skunk (*Mephitis mephitis*; 13 on Figure 4.7) and the semi-aquatic giant otter (*Pteronura brasiliensis*; 27 on Figure 4.7).

Linear Discriminant Analysis

Misclassification rates were high for all four bones, which is most likely a factor of low sample sizes in each behavioural group. The scapula (60.0% error rate), humerus (61.5%), and ulna (53.3%) had slightly lower rates than the radius (72.8%). This is likely a result of the radius not having significant differences between the behavioural groups in the principal components analysis.

Fossil Species

Fossil species were placed into behavioural groups based on their PC scores using the discriminant analysis described above. *Ursus spelaeus* was placed into the semi-fossorial group for the scapula, the arboreal group based on the humerus, and in the scansorial group for the radius.

The scapula of *U. spelaeus* has a rounded shape similar to positive scores on the second principal component axis for this bone, which is mostly seen in scansorial and arboreal

species. However, the bears are separated from the rest of the species in this principal component analysis, and therefore the scapula of *U. spelaeus* is likely bear shaped and therefore difficult to accurately place in a behavioural group.

The *U. spelaeus* humerus is intermediately robust, with minimal curvature of the bone overall. This bone also has a well defined humeral head and a broad distal epiphysis. The overall shape of this bone when compared to the shapes from the principal component analysis suggest that it is fairly neutral on both axes, which is why it was placed in the arboreal behavioural group.

The radius of *U. spelaeus* is generally straight, with a broad distal epiphysis. This is similar to the shape represented by positive principal component scores on the second axis, and therefore this shape is similar to that seen in scansorial species.

Arctodus was placed into the arboreal behavioural group based on both humerus and ulna shape. The *Arctodus* humerus is not particularly robust, with minimal curvature, a broad distal epiphysis, and a shallow humeral head. These characteristics suggest that this bone would be neutral on the second principal component axis and more negative on PC1. This could place this species in either the arboreal group (as suggested by the discriminant analysis) or the scansorial group.

The ulna of *Arctodus* has a short, posteriorly directed olecranon, and has a straight diaphysis. This shape of bone is similar to arboreal or terrestrial species, based on the results of the principal components analysis. The arboreal species demonstrate the average shape in the principal components analysis for the ulna. However, positive scores on the second principal component axis are only represented by bears. It is therefore likely that this is affecting the estimated behaviour of the extinct species.

Discussion

The aim of this study was to determine whether using plantigrade species to produce a model of the relationship between long bone morphology and locomotor behaviour produces lower

error rates than a model which includes different foot postures. The results of our study suggest that this is not the case.

Group Differences

The principal component analysis in this study tended to differentiate between robust and gracile bone shapes most effectively. Across all bones terrestrial, scansorial, and arboreal species were most often statistically different from semi-aquatic and semi-fossorial species. This would be expected, and a similar result to that found in other studies. Both semi-aquatic and semi-fossorial species have to face resistance of the medium in which they move (Fabre et al., 2015), which is likely to result in similar levels of robustness in the forelimb bones. Interestingly, the ulna showed significant differences between semi-aquatic species and other groups, whereas the semi-fossorial species were most often significantly different from other groups in the humerus. The differences between each type of bone and the behavioural groups that they differentiated between, demonstrate the importance of including as many bones as possible in morphological studies.

Only the scapula showed significant differences between the three locomotor behaviours with more gracile bone shapes. The scapula has been previously shown as an excellent indicator of locomotor behaviour (Davis, 1949). However, it is infrequently preserved in fossils, particularly in a suitable form to be included in morphological studies (Van Valkenburgh, 1987), and therefore often excluded from studies. The results of this study highlight the importance of including the scapula where ever possible. This is particularly true for estimating the locomotor behaviour of fossil species, if the scapula were not included then it would be more difficult to predict membership of behavioural groups, aside from semi-aquatic and semi-fossorial.

Discriminant Analyses

Although the groups were overall significantly different in three of the four bones, and there were significant results in the pairwise analysis for all bones, the discriminant analysis did not produce high classification rates. This is likely due, at least in part, to the small sample sizes per behavioural group included in this study.

Previous studies have shown different behavioural groups produce different classification error rates. The more generalised behavioural groups, terrestrial and scansorial, have lower successful classification rates (Samuels et al., 2013). This may relate to the low classification rates in this study due to the generalised morphology already associated with the plantigrade posture.

In a previous study, semi-aquatic species also had high classification error rates (Samuels et al., 2013). Although the principal components analysis in this study found semi-aquatic species to be significantly different from other groups (in the ulna) there are variations in the locomotor patterns within semi-aquatic species that could result in differences in morphology. For example, otters are generally hind limb paddlers (Salesa et al., 2013), while polar bears and mink use their forelimbs to paddle (Samuels et al., 2013). A future study will analyse the hind limb bones, which will help to clarify the morphological patterns present in this behavioural group.

The behavioural group of some species is not completely resolved, and therefore they can be placed in different groups (Table 4.1), depending on the reference data used for classification. These species are likely to vary in their locomotor behaviour, and therefore their morphology may not be as well defined as other species. The arboreal and scansorial groups were not significantly different for any of the bones, and most of the species that have previously been assigned to more than one category came from one of these two groups (Table 4.1). It is possible that the species in these groups overlap in both their behaviour and their morphology, which results overlap in both the principal component and linear discriminant analyses, and therefore a lack of statistical significance. Alternatively, the groups we have chosen to use may not represent the dominant behaviour of each species. This would result in species being classified incorrectly, affecting both of the analyses conducted. Re-running the analyses with these species in their alternative groups may produce different results; however further research into the observed behaviour of these species would be beneficial to any future studies.

Species are classified into behavioural groups based on observational data. For some species, such as polar bears, this can result in a classification that may not relate to their evolved morphology. Polar bears are classified as semi-aquatic in most studies, including this one; however they have relatively recently evolved from the terrestrial brown bears to live on sea ice. Generally polar bears will swim for long distances or long periods of times only when necessary for safety or food. Therefore the morphology for this species could potentially be more similar to terrestrial species, both due to phylogeny and preferred behaviours. These factors are likely to have an effect on the overall classification rates in this, and other, studies.

Phylogenetic Analysis

The results of this study show that there is a significant effect of phylogeny in all bones, using both models of branch lengths. As discussed above, Ursidae could be a large factor in this result due to their unusual morphology, which results in them being separated from all other species in the principal components analysis for both the scapula and ulna. Additionally, seven out of the eight semi-fossorial species are from relatively closely related families, Mustelidae and Mephitidae. The meerkat (*Suricata suricatta*) is a member of Herpestidae, which is a feliform family, and is therefore more distantly related to the other families. This is likely to be the cause of the meerkat being an outlier for the semi-fossorial species in the humerus, and will also contribute to the phylogenetic effects.

The different results produced using the different models of branch lengths highlights the need to include a scaled tree. The two models of branch lengths used here, using a Brownian motion model of evolution, are commonly used for taxa without a phylogeny that has been scaled using character states or evolutionary distance. The humerus and the ulna maintained statistical significance between behavioural groups using the unit tree, where all branch lengths are equal to 1 (Table 4.4), and we are therefore satisfied that the morphological signal is stronger than the phylogenetic signal for these two bones. However, more accurate results could be obtained using a tree that has scaled branch lengths.

Bears

Bears have previously been shown as outliers in studies of ecology and limb bone morphology in mammals (Van Valkenburgh, 1985; Van Valkenburgh, 1987; Bertram and Biewener, 1990). In two of the four bones included in this study bears were outliers in the principal components analysis; they were separated from all other species along one of the first two axes. Our results showed a strong phylogenetic signal, and it is possible that this is substantially a result of the Ursidae family. “Bear-like” morphologies are not found in other clades of Carnivora (Losos and Miles, 1994) and they are therefore a distinct group, which may confound morphological signals due to locomotor behaviour. Recent research has also shown that grizzly bears have unusual locomotor patterns, which may relate to their distinct morphology (Shine et al., 2015).

Fossil Species

The predicted locomotor behaviour for fossil species was different depending on the bone used in the analysis. The high error rates in classification for the discriminant analysis are likely to have affected our prediction for extinct species. *Ursus spelaeus* was classified as semi-fossorial (scapula), arboreal (humerus), and scansorial (radius). Due to the variety of classifications of this species, it is possible that it is a generalist and therefore does not have particularly distinct morphology for one behavioural group. As discussed above, bears represent a unique morphology aside from their locomotor behaviour, which may also affect the classifications for this species.

Our results assigned *Arctodus* to the arboreal group. This seems to be an unlikely behaviour for this species, due to the estimated body mass (up to 1000kg; Figueirido et al., 2010). However, this result suggests that *Arctodus* may have more gracile forelimb bones than has previously been suggested. A recent study using linear morphometrics estimated *A. simus* to be unlike any other bears and this species was placed in the semi-fossorial behavioural group (Samuels et al., 2013). Polar bears were also misclassified as semi-fossorial in the same study, and therefore this classification may be due to the robustness of bear bones as a result of their size. The use of 3D geometric morphometrics will limit the effect of allometry (although it is still present) due to the inclusion of landmarks across the whole bone. As our results suggest

an unlikely behavioural group for this genus, in particular one that is opposite in morphospace from previously suggested behavioural groups, we are unable to provide any additional insight that may benefit the current controversy surrounding the behaviour of this genus.

The use of extant species to estimate the locomotor behaviour of fossil species, relies on the assumption that there is a representative with a homologous morphology. This assumption does not always hold true, for example, there are no extant species with skull morphology similar to that of the saber-tooth cats. As extant bears are outliers when compared to other plantigrade carnivorans, it is possible the extinct bears, in particular *Arctodus*, have morphological adaptations that are also unlike extant bears and are therefore difficult to classify based on living species.

Conclusions

The results of this study did not support our hypothesis that using only plantigrade carnivorans would produce a more accurate model for estimating locomotor behaviour. However, the significant differences between the behavioural groups, and the shape changes identified, will be useful for future studies to estimate the locomotor behaviour of extinct plantigrade species. We estimated the locomotor behaviour of extinct bears to be different that previous studies, which may benefit from further investigation. The results of this study could be improved by including a larger number of species per behavioural group and incorporating a phylogeny with scaled branch lengths.

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Table 4.2 List of Species and their Corresponding Locomotor Behaviour

Species included in the study and their locomotor behaviour classification. Some species have been classified into different groups in previous studies. Plain text refers to the behaviour used in this study; alternative behaviour groups are included in italics for discussion. Museum abbreviations are explained in the text. Numbers in the first column refer to labels on figures.

	Species	Family	Behaviour	References*	Museum(s)
1	<i>Ursus maritimus</i>	Ursidae	Semi-aquatic	3,5,7,8	CAS
2	<i>Mustela vison</i>	Mustelidae	Semi-aquatic	6,7,8	IMNH
3	<i>Enhydra lutris</i>	Mustelidae	Semi-aquatic	6,7,8	CAS
4	<i>Cynogale bennettii</i>	Viverridae	Semi-aquatic	5,7,8	USNM
5	<i>Atilax paludinosus</i>	Herpestidae	Semi-aquatic	4,5,7	MCZ
6	<i>Lontra canadensis</i>	Mustelidae	Semi-aquatic	8,9	IMNH
7	<i>Pteronura brasiliensis</i>	Mustelidae	Semi-aquatic	8	USNM
8	<i>Aonyx cinerea</i>	Mustelidae	Semi-aquatic	8	MVZ
9	<i>Tremarctos ornatus</i>	Ursidae	Arboreal/ <i>Scansorial</i>	3,7,8	CAS, USNM
10	<i>Helarctos malayanus</i>	Ursidae	Arboreal/ <i>Scansorial</i>	1,3,7, 8	CAS
11	<i>Potos flavus</i>	Procyonidae	Arboreal	1,7,9	MVZ
12	<i>Nasua narica</i>	Procyonidae	Arboreal/ <i>Scansorial</i>	7,9	MCZ
13	<i>Arctictis binturong</i>	Viverridae	Arboreal	1,7,8,9	CAS
14	<i>Prionodon linsang</i>	Prionodontidae	Arboreal	1,7	USNM
15	<i>Nandinia binotata</i>	Nandiniidae	Arboreal	7	USNM
16	<i>Paradoxurus hemaphroditus</i>	Viverridae	Arboreal	8,9	MVZ
17	<i>Ursus thibetanus</i>	Ursidae	Scansorial	1,7,8	CAS
18	<i>Ursus americanus</i>	Ursidae	Scansorial	1,7,8	IMNH
19	<i>Ailurus fulgens</i>	Ailuridae	Scansorial/ <i>Arboreal</i>	1,7, 9,8	CAS
20	<i>Eira barbara</i>	Mustelidae	Scansorial/ <i>Arboreal</i>	1,7,12,8	CAS
21	<i>Gulo gulo</i>	Mustelidae	Scansorial/ <i>Terrestrial</i>	1,7,12,8	IMNH
22	<i>Bassariscus astutus</i>	Procyonidae	Scansorial	1,7,9	IMNH
23	<i>Martes americana</i>	Mustelidae	Scansorial	8	IMNH
24	<i>Mustela erminea</i>	Mustelidae	Terrestrial	8	CAS
25	<i>Melursus ursinus</i>	Ursidae	Terrestrial	7,8	CAS
26	<i>Ursus arctos</i>	Ursidae	Terrestrial	1,7,8	IMNH
27	<i>Ailuropoda melanoleuca</i>	Ursidae	Terrestrial	3,7,8	USNM
28	<i>Martes pennanti</i>	Mustelidae	Terrestrial/ <i>Scansorial</i>	7,8,9	IMNH
29	<i>Herpestes javanicus</i>	Herpestidae	Terrestrial		IMNH
30	<i>Viverra zangalunga</i>	Viverridae	Terrestrial	8	USNM
31	<i>Galidictis fasciata</i>	Eupleridae	Terrestrial	8	USNM

	Species	Family	Behaviour	References*	Museum(s)
32	<i>Fossa fossana</i>	Eupleridae	Terrestrial	8,9	USNM
33	<i>Galerella pulverulenta</i>	Herpestidae	Terrestrial	8	CAS
34	<i>Galictis vittata</i>	Mustelidae	Terrestrial	8	MVZ
35	<i>Mustela putorius</i>	Mustelidae	Terrestrial	8	CAS
36	<i>Mustela frenata</i>	Mustelidae	Terrestrial	8	CAS
37	<i>Ictonyx striatus</i>	Mustelidae	Semi-fossorial	1,7,8	MVZ
38	<i>Taxidea taxus</i>	Mustelidae	Semi-fossorial	1,7,9	IMNH
39	<i>Meles meles</i>	Mustelidae	Semi-fossorial	1,7,8,9	MCZ, MVZ
40	<i>Arctonyx collaris</i>	Mustelidae	Semi-fossorial	1,7,8	USNM
41	<i>Mephitis mephitis</i>	Mephitidae	Semi-fossorial	1,7,8	IMNH
42	<i>Suricata suricatta</i>	Herpestidae	Semi-fossorial	8	USNM
43	<i>Mephitis macroura</i>	Mephitidae	Semi-fossorial	8	MVZ
44	<i>Conepatus mesoleucus</i>	Mephitidae	Semi-fossorial	8	MVZ
	<i>Arctodus</i> [†]	Ursidae			UCMP
	<i>Ursus spelaeus</i> [†]	Ursidae			UCMP

*References: 1 – Van Valkenburgh (1987); 2 – Ginsburg (1961); 3 – Brown (Brown, 2009); 4 – Somers and Purves (1996); 5 – Bininda-Emonds et al. (2001); 6 – Williams (1998); 7 – Nowak (1999); 8 – Samuels et al. (2013); 9 – Gould (2014)

Table 4.3 Descriptions of Locomotor Behaviours

Locomotor Behaviour	Description
Semi-aquatic	Species that rely heavily on water for survival, including foraging and escape behaviour.
Arboreal	Species that spend substantial amounts of time in trees, including foraging, escape behaviour, and breeding.
Scansorial	Species that are able to climb, and may do so readily for escape, but do not spend significant portions of time in trees.
Terrestrial	Species that are either unable to climb or chose not to. These animals may still swim occasionally but spend the majority of their time on land.
Semi-fossorial	Species that dig burrows greater than themselves, but do not live exclusively underground.

Table 4.4 Distribution of Families and Species per Locomotor Behaviour

The number of bones varies per group depending on availability. There are at least three families and five species per group.

	Semi-aquatic		Arboreal		Scansorial		Terrestrial		Semi-fossorial	
	Fam	sp	Fam	sp	Fam	sp	Fam	sp	Fam	sp
Scapula	4	7	5	7	4	8	5	11	3	8
Humerus	4	7	5	7	4	8	5	12	3	8
Ulna	4	7	3	5	4	7	5	7	3	6
Radius	3	6	3	5	4	7	3	5	3	7

Table 4.5 Phylogenetic Results

All bone had significant phylogenetic signal in the shape data, with both models of branch lengths. Grafen tree = all terminal nodes are equal height. Unit tree = all branch lengths are equal to 1. None of the bones had significant differences between groups when the phylogeny was included using a Grafen model of branch lengths; however the humerus and ulna did maintain a level of significance between groups when using the unit tree.

	Grafen Tree	Unit Tree	pGLS (Grafen Tree)	pGLS (Unit Tree)
Scapula	0.001***	0.001***	0.109	0.178
Humerus	0.003**	0.048*	0.187	0.047*
Ulna	0.001***	0.006**	0.199	0.042*
Radius	0.03*	0.002**	0.192	0.11

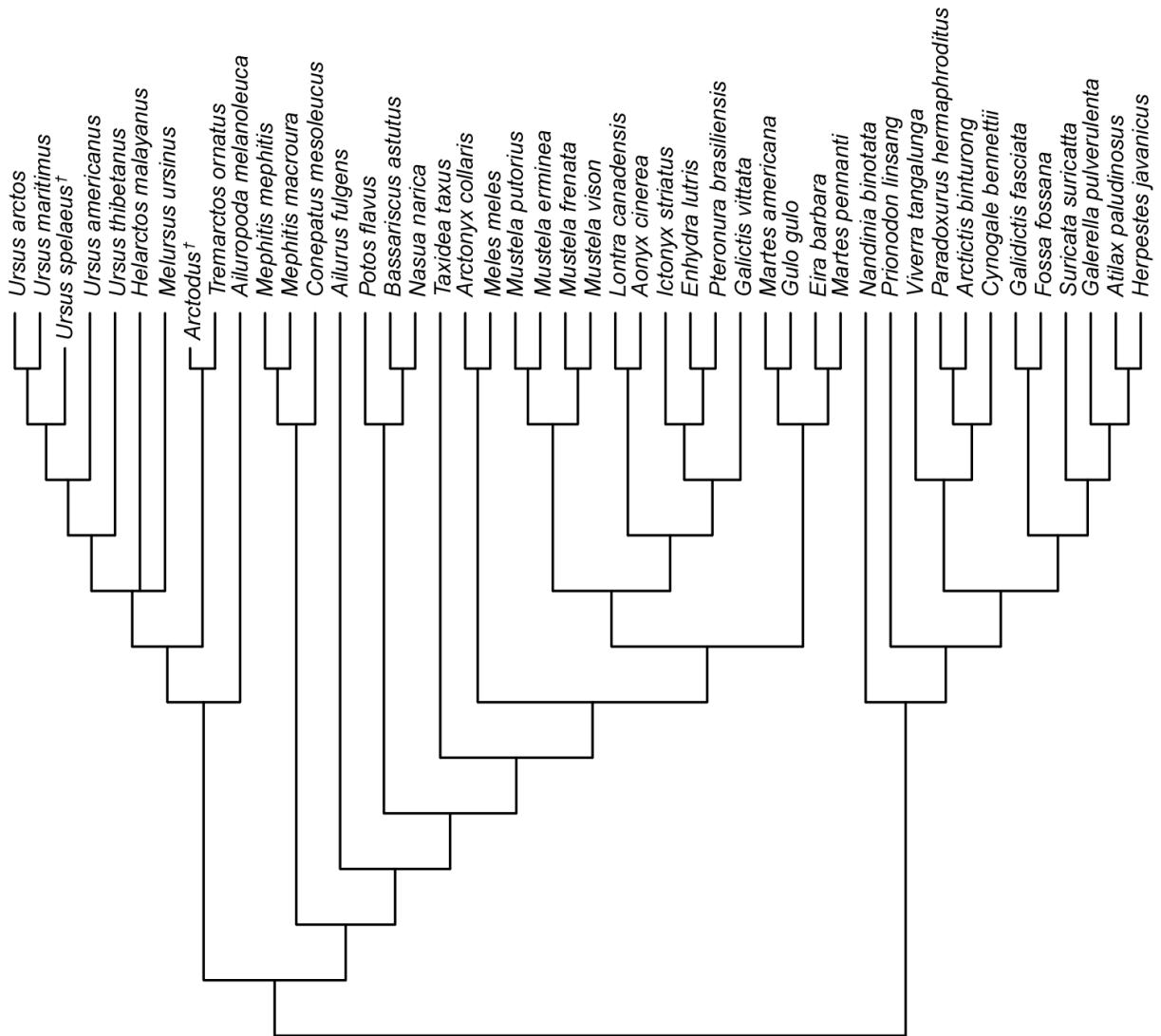


Figure 4.24 Phylogeny of Species Included in this Study

Not drawn with scaled branch lengths. Extinct species are placed on shorter branches and labelled (†).

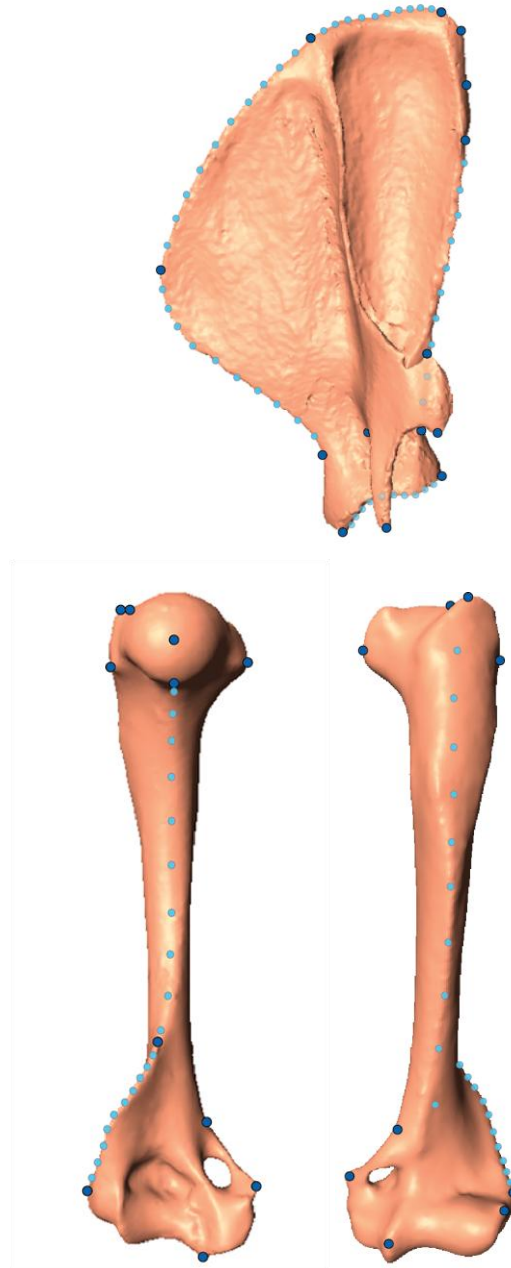


Figure 4.25 Proximal Bone Digitising

Left: scapula, right: humerus. Fixed landmarks (dark blue) and semi-sliding landmarks (light blue) were used on all bones. Landmarks were selected to encompass the entire shape of the bone, with particular focus on articulation surfaces and areas of muscle attachment. Some landmarks are visible in both views of the humerus; there are a total of 13 fixed landmarks, and 3 curves totalling 24 semi-sliding landmarks. Example specimens are from *Mustela vison*.

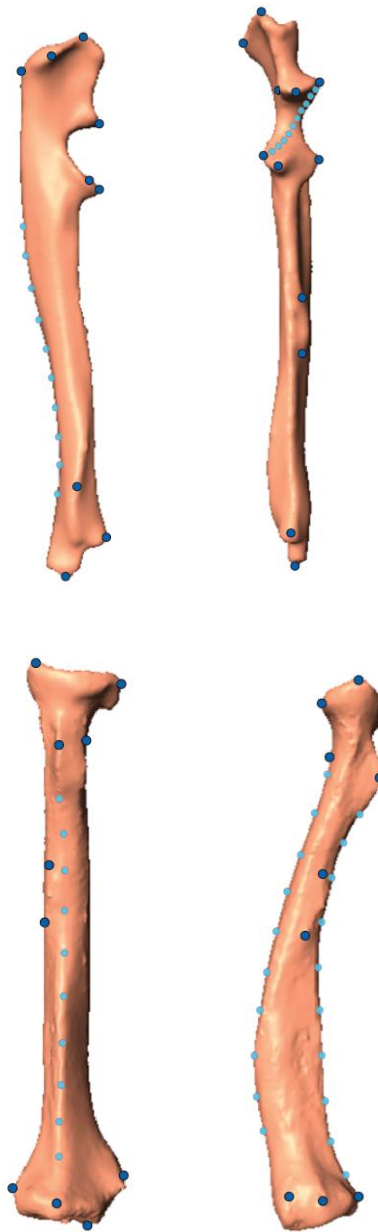


Figure 4.26 Distal Bone Digitising

Fixed landmarks (dark blue) and semi-sliding landmarks (light blue) were used on all bones. Landmarks were selected to encompass the entire shape of the bone, with particular focus on articulation surfaces and areas of muscle attachment. Some landmarks are visible in both views; there are a total of 14 fixed landmarks for the ulna, 13 fixed landmarks for the radius, and each bone has 2 curves totalling 16 semi-sliding landmarks. Example specimens are from *Mustela vison*.

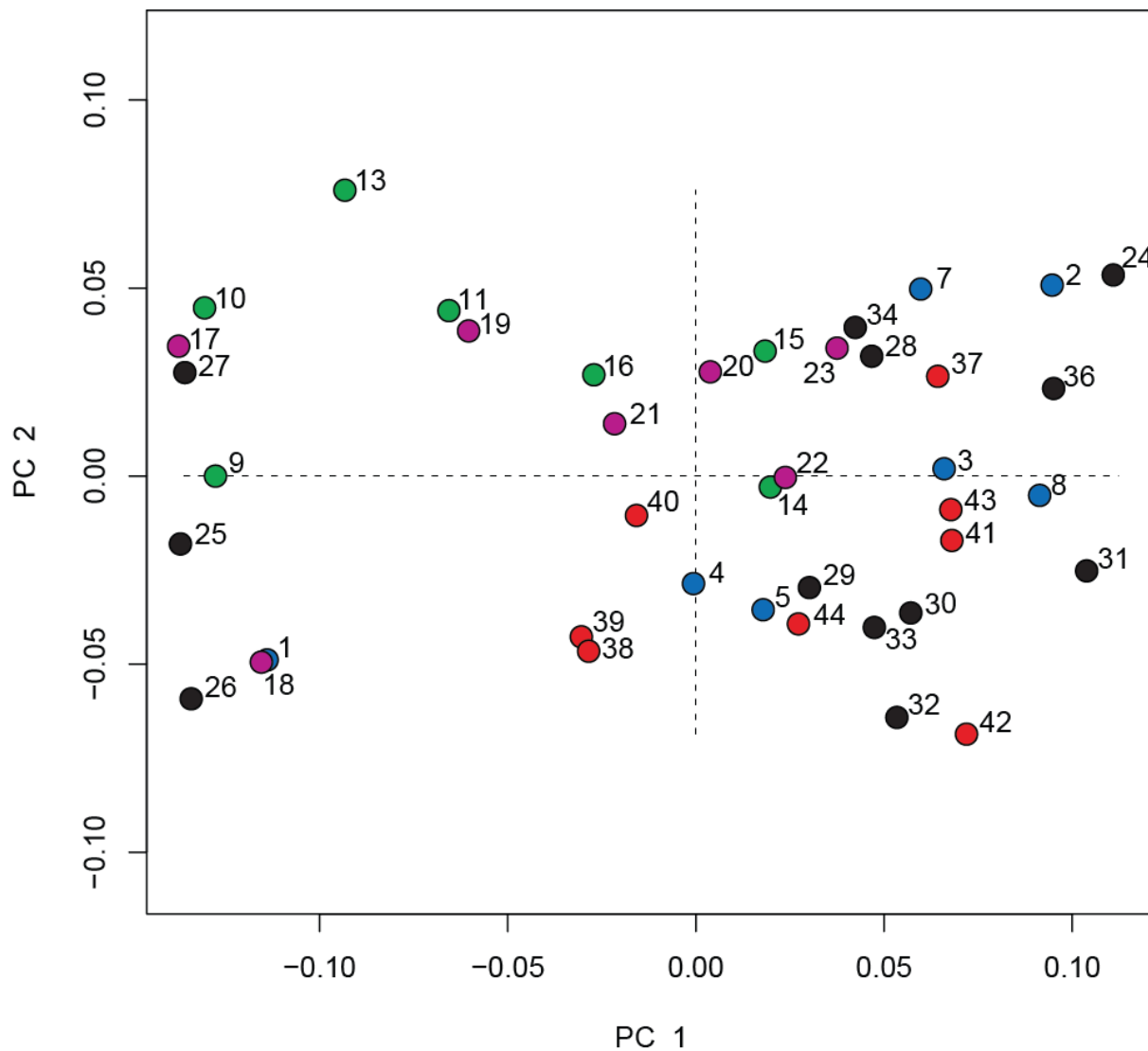
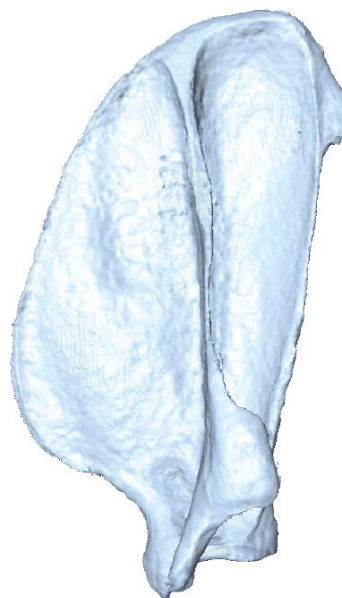


Figure 4.27 Principal Components Analysis of the Scapula

The first two principal component axes account for 63.9% of shape variation: PC1 = 51.6%, PC2 = 12.3%. Groups were significantly different ($p=0.028$). The eight species with the most negative PC1 scores are bears. Each colour represented a behavioural group: aquatic = blue, arboreal = green, scansorial = magenta, semi-fossorial = red, and terrestrial = black. Specimen identification is given in Table 4.1.



Negative PC1: *Tremarctos ornatus* (9)



Positive PC1: *Aonyx cinerea* (8)



Negative PC2: *Taxidae taxus* (38)



Positive PC2: *Eira barbara* (20)

Figure 4.28 Representative Scapula Specimens for Principal Components 1 and 2

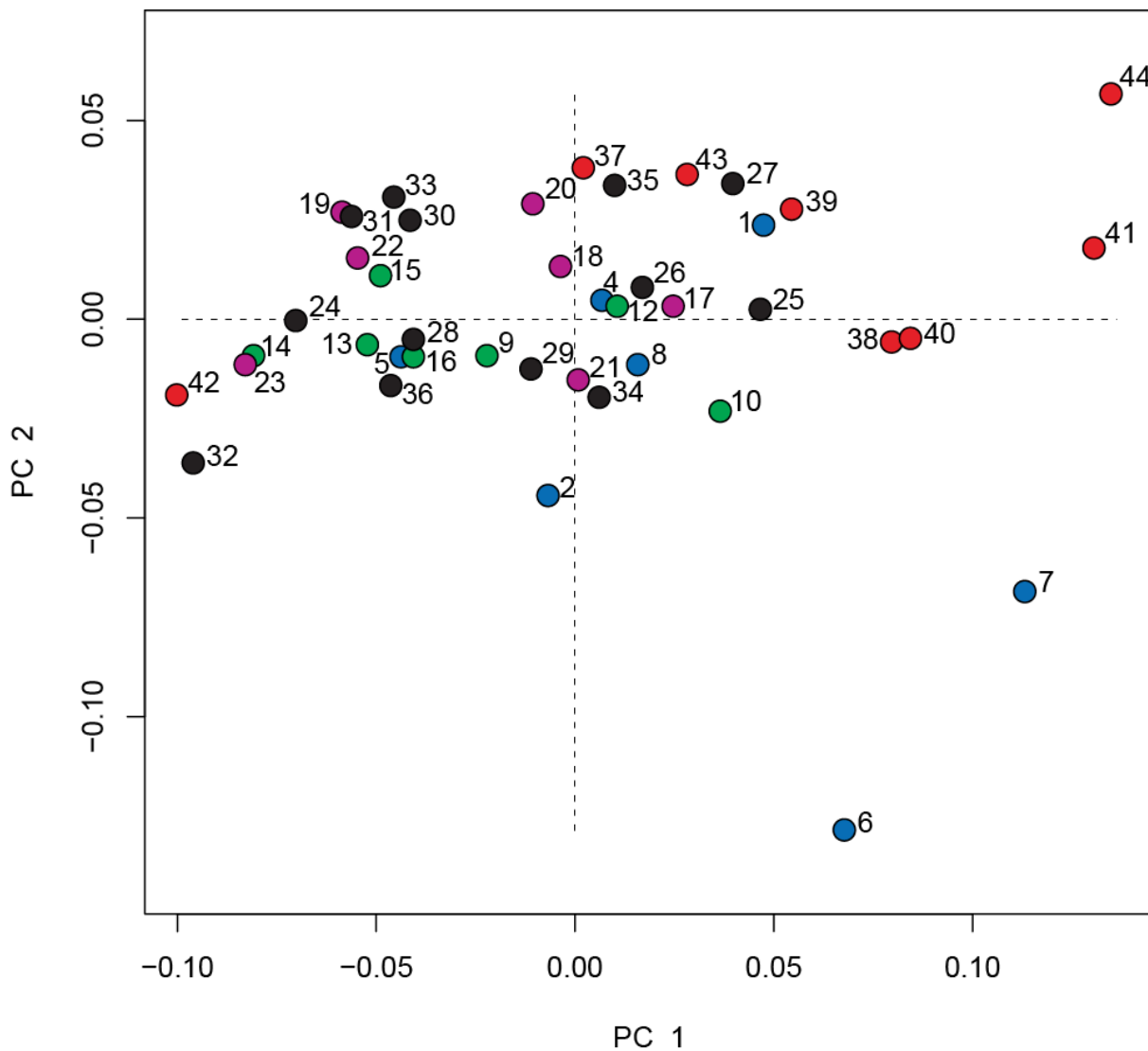


Figure 4.29 Principal Components Analysis of the Humerus

The first two principal component axes account for 56.1% of shape variation: PC1 = 43.5%, PC2 = 12.7%. Groups were significantly different ($p=0.002$). Colours as described in Figure 4.4. Specimen identification is given in Table 4.1. Specimen 42 (semi-fossorial, negative PC1) is the only feliform semi-fossorial species and this outlier is likely due to phylogenetic effects.

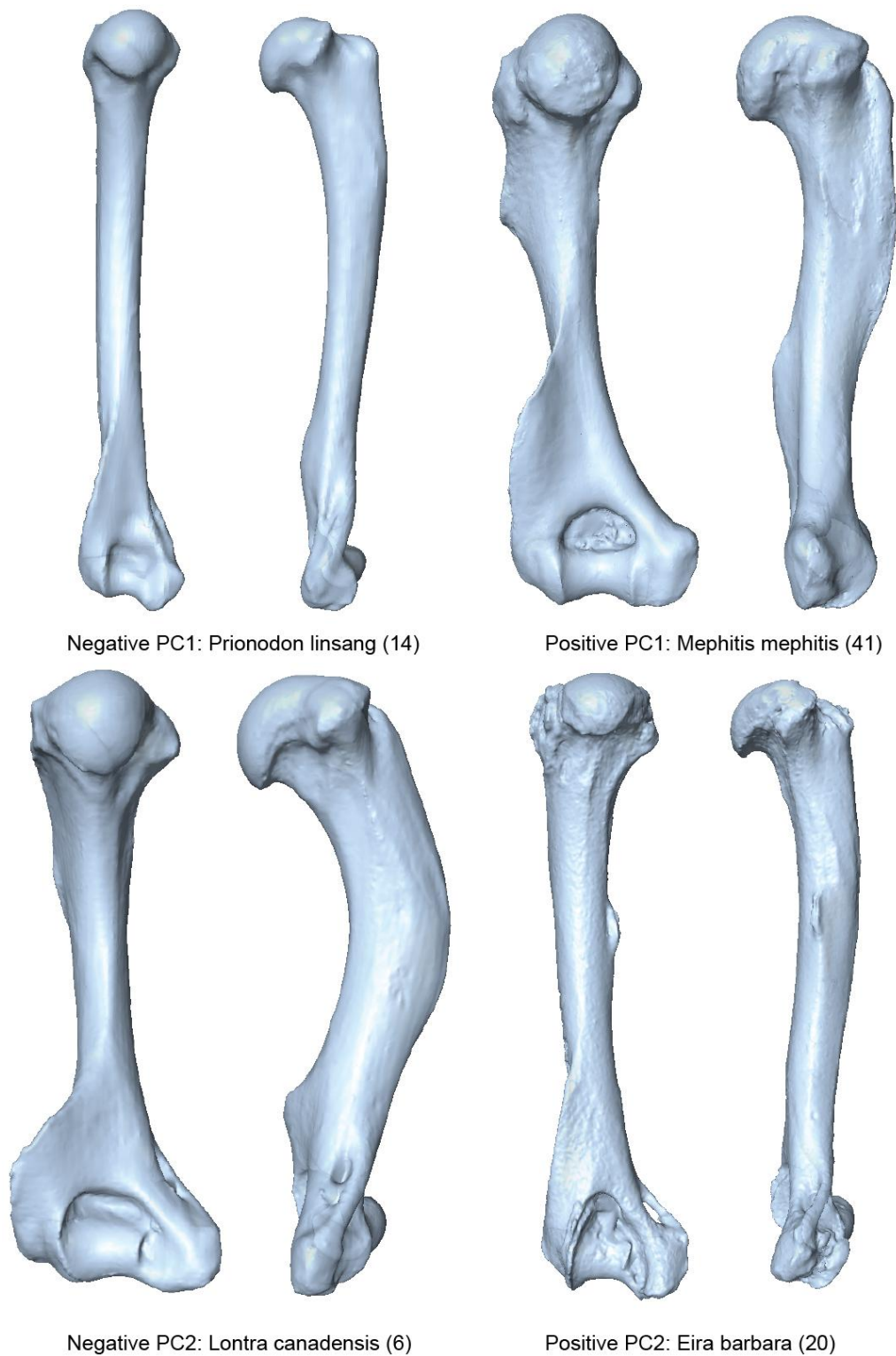


Figure 4.30 Representative Humerus Specimens for Principal Components 1 and 2

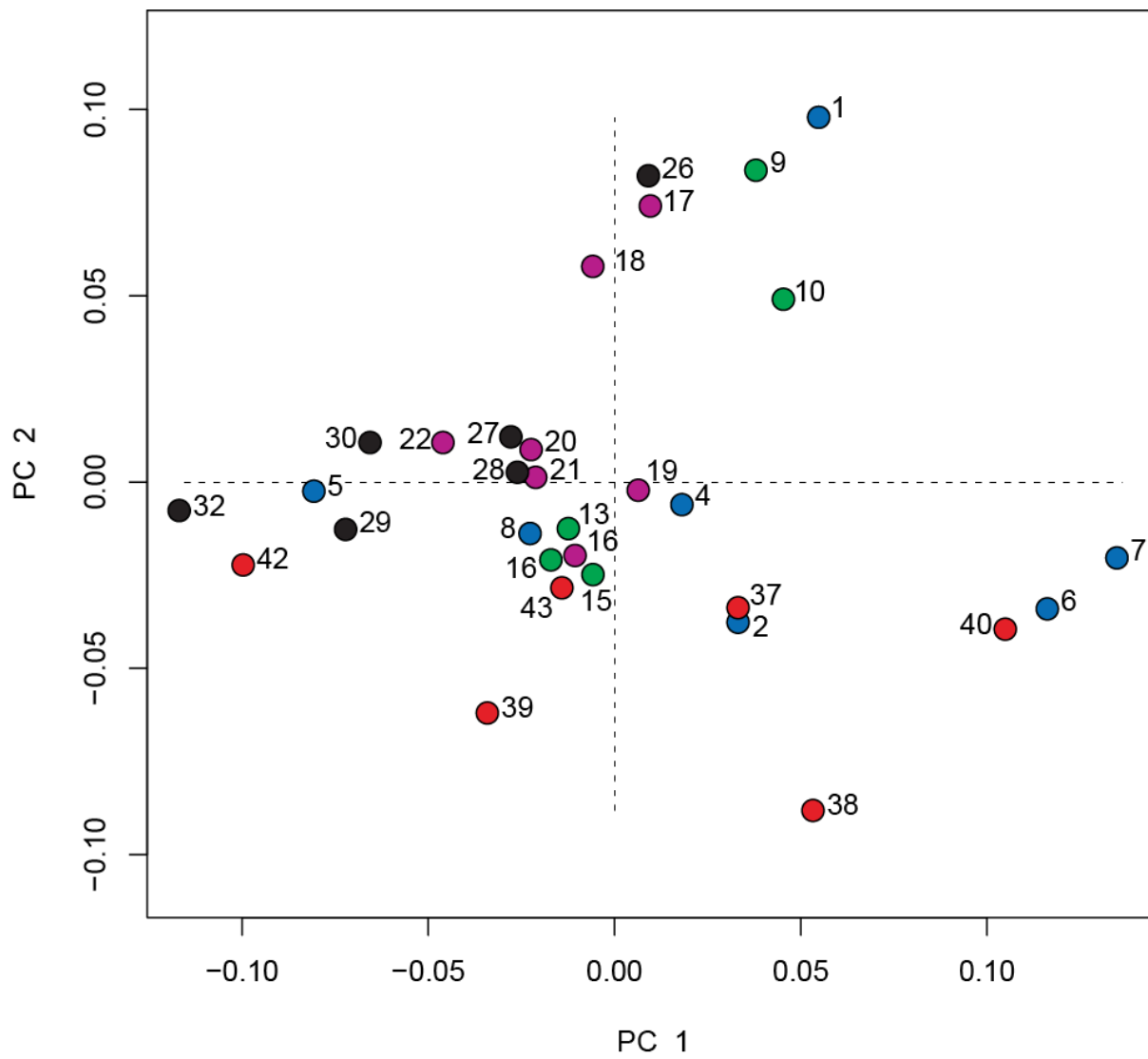


Figure 4.31 Principal Components Analysis of the Ulna

The first two principal component axes account for 55.4% of shape variation: PC1 = 35.7%, PC2 = 19.6%. Groups were significantly different ($p=0.002$). Colours as described in Figure 4.4. Specimen identification is given in Table 4.1. The six species with the most positive PC2 scores are bears.

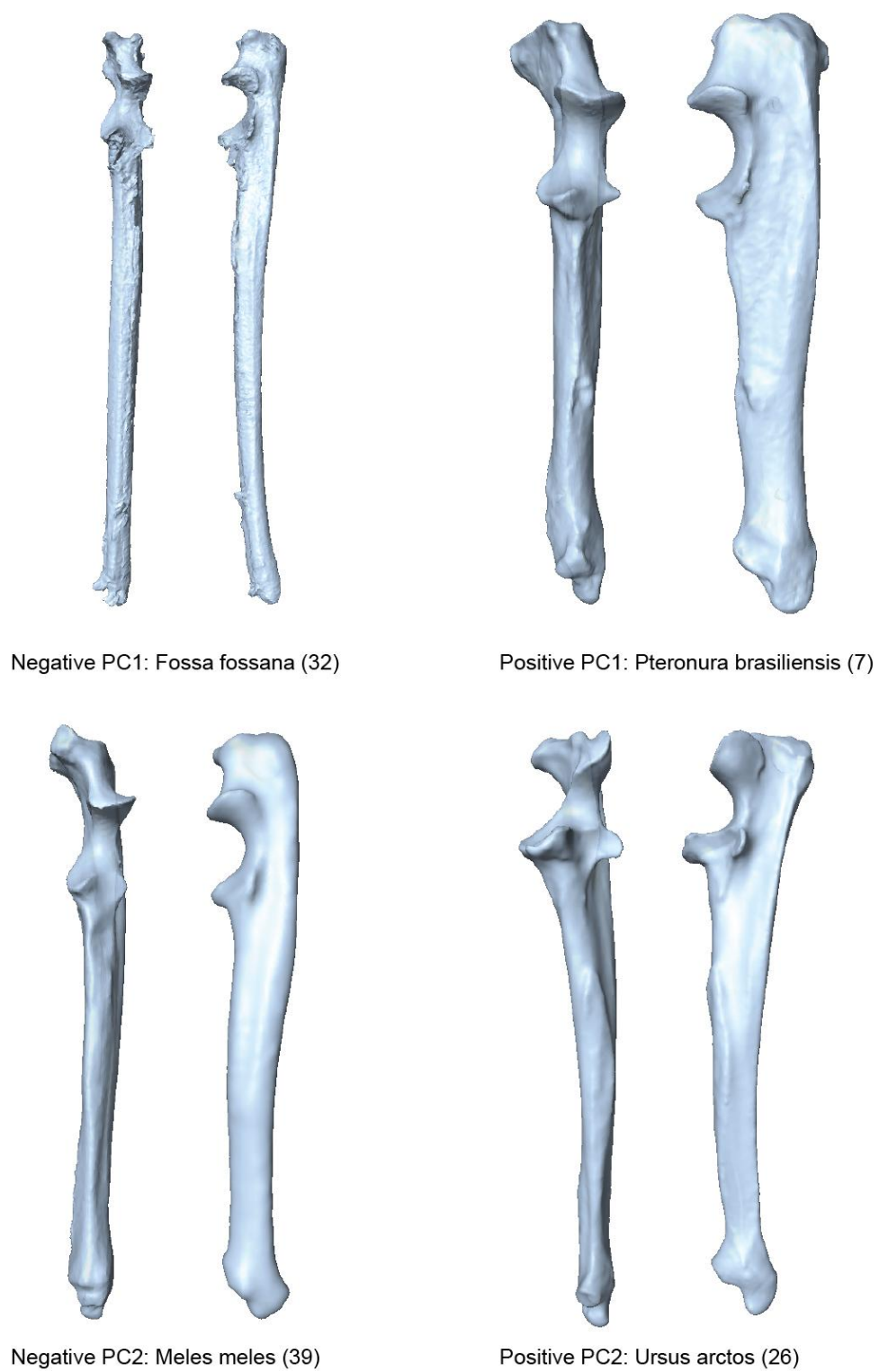


Figure 4.32 Representative Ulna Specimens for Principal Components 1 and 2

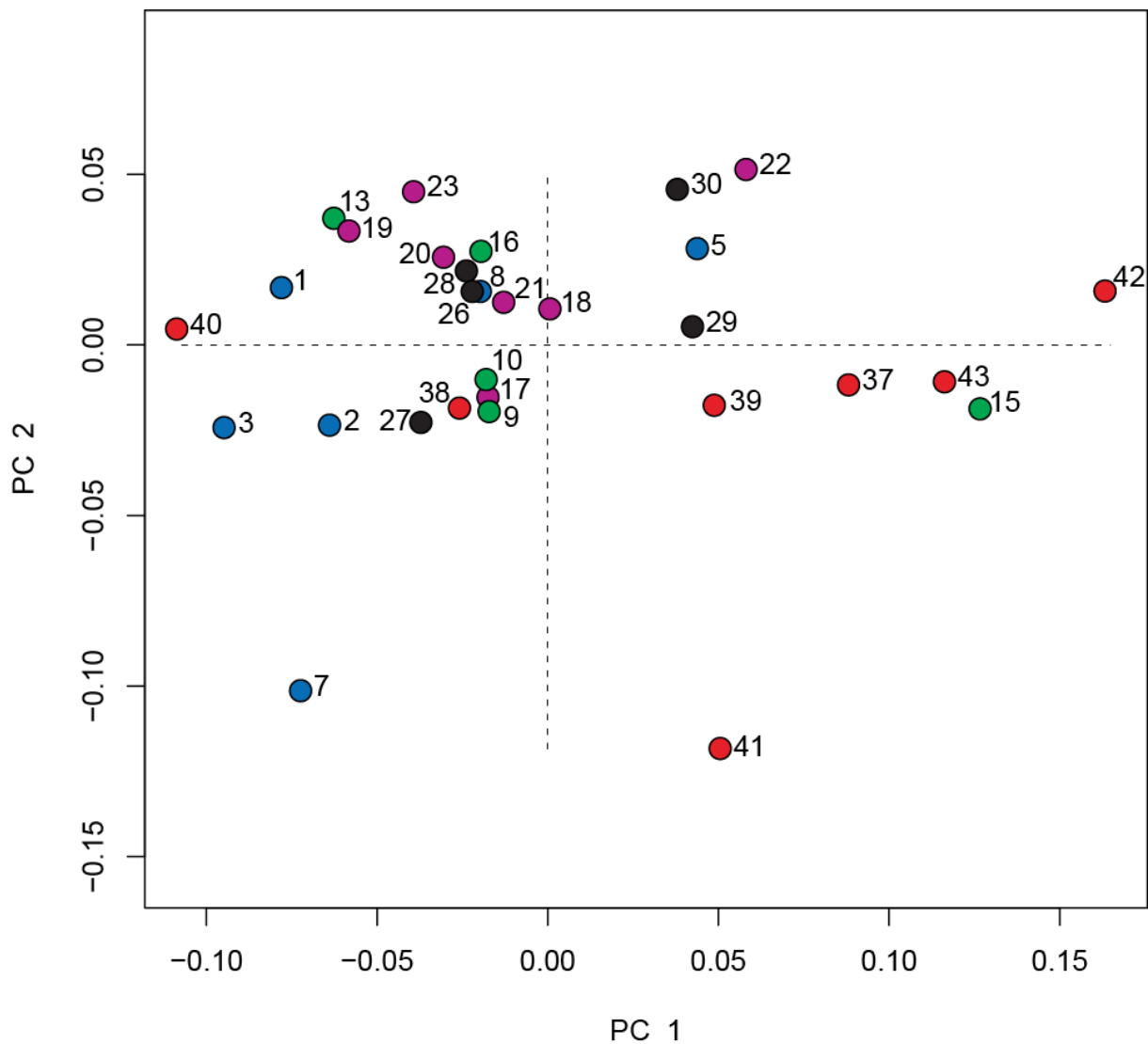


Figure 4.33 Principal Components Analysis of the Radius

The first two principal component axes account for 70.4% of shape variation: PC1 = 53.3%, PC2 = 17.1%. Groups were not significantly different ($p=0.075$). Colours as described in Figure 4.4. Specimen identification is given in Table 4.1.

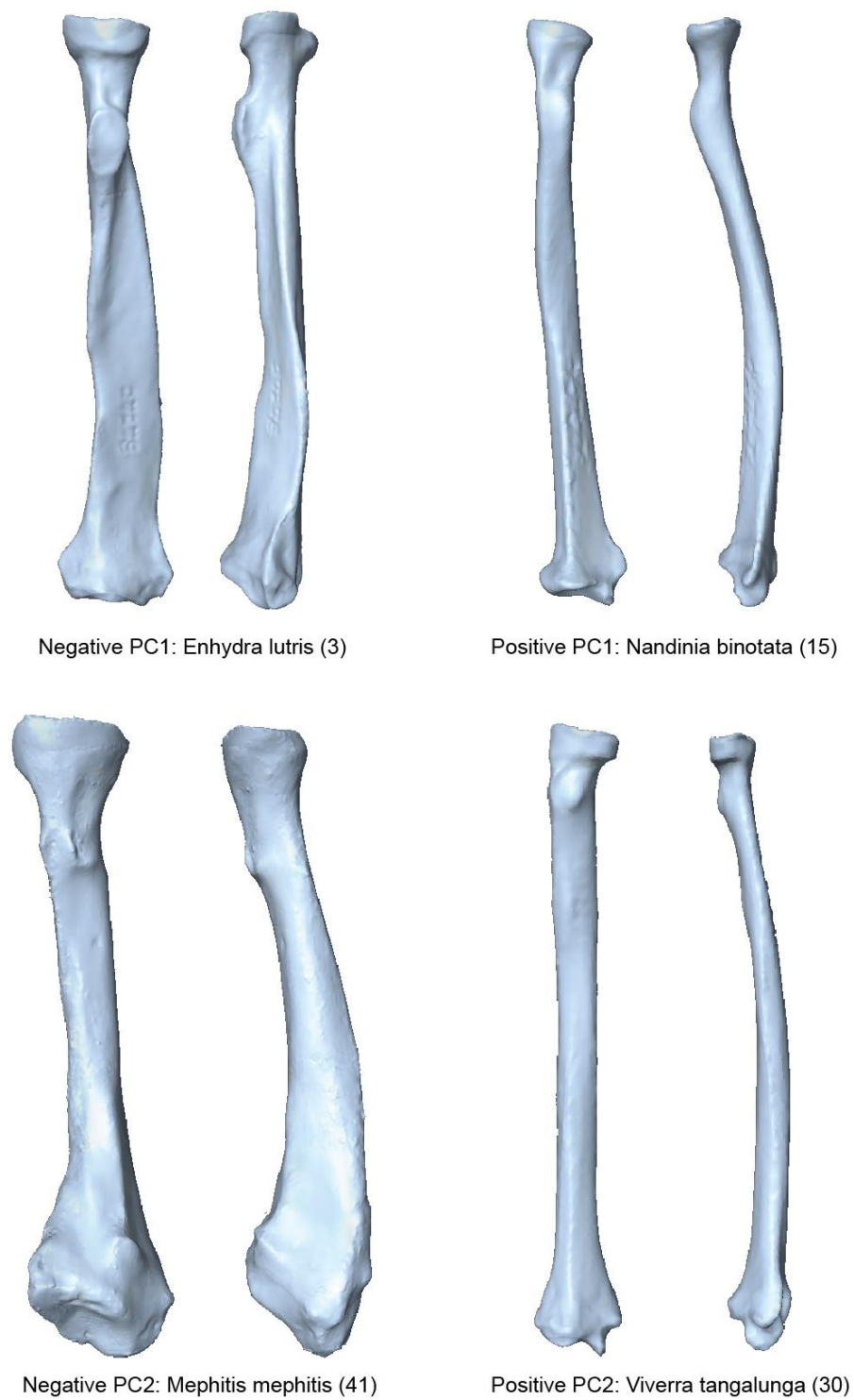


Figure 4.34 Representative Radius Specimens for Principal Components 1 and 2

Conclusions

My dissertation focuses on locomotion of a representative plantigrade carnivoran species, grizzly bears (*Ursus arctos horribilis*), and begins to interpret this locomotion with the morphology of this and related species, and therefore aims to increase understanding of the evolution of locomotion in plantigrade carnivorans as a whole.

Plantigrade species have previously been less studied than their digitigrade counterparts because they do not possess the evolutionary adaptations for cursoriality. This research demonstrates that plantigrade species, although considered generalists, have locomotor and morphological characteristics that make them fascinating study subjects.

We found that grizzly bears produce a lateral force that is greater in magnitude than would be expected for an upright mammal (Chapter 1). Bears as a group were also found to be outliers in two of the four forelimb bones analysed (Chapter 4). A detailed dissection of grizzly bear forelimb showed that bears have an unusual elbow joint, and that the medial deviation of the foot during stance is potentially passive. A detailed musculoskeletal model of the grizzly bear forelimb will be created using these previously collected data. This should enable a deeper understanding of how the musculature and bone morphology coordinate to produce the movements seen in the live grizzly bears.

As yet, we cannot determine whether the results found here are representative of bears, or whether grizzly bears are unique. We have collected data from American black bears (*Ursus americanus*) and will be analysing this in order to compare the locomotion of grizzly bears and black bears. Black bears are sympatric with grizzly bears; however, they are not sister taxa, and they are not classified in the same behavioural category (see Chapter 4). These factors could produce interesting results in the comparison of the gaits used and the forces produced by the different bear species. If the two bear species appear to use similar gaits and produce similar forces, it is possible that all bear species locomote in a similar way. However, if the two bear species are different, this leads to more research questions regarding other bear species and plantigrade species as a whole.

In the future I intend to collect kinematic and kinetic data from other plantigrade Carnivora species. The comparison of these smaller species to the larger Ursidae family will provide a more complete understanding of plantigrade locomotion. This biomechanics research, coupled with the morphological research already undertaken, will greatly enhance our understanding of the evolution of locomotion in plantigrade species, and allow us to gain better insight into the behaviour of extinct species.

Appendix I: Grizzly Bear Protocol Approval

11/10/2014

University Research Office Regulatory Compliance System

University of Idaho Institutional Animal Care and Use Committee

Date: Monday, November 10, 2014
To: Craig McGowan
From: University of Idaho
Institutional Animal Care and Use Committee
Re: Protocol 2014-89
Kinematics and Joint Dynamics During Bear Locomotion

Your animal care and use protocol for the project shown above was reviewed and approved by the Institutional Animal Care and Use Committee on Monday, November 10, 2014.

This protocol was originally submitted for review on: Thursday, October 02, 2014
The original approval date for this protocol is: Monday, November 10, 2014
This approval will remain in affect until: Tuesday, November 10, 2015
The protocol may be continued by annual updates until: Friday, November 10, 2017

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.



Barrie Robison, IACUC Chair