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RESEARCH ARTICLE

Goats decrease hindlimb stiffness when walking over compliant surfaces

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ABSTRACT

Leg stiffness, commonly estimated as the 'compression' of a defined leg element in response to a load, has long been used to characterize terrestrial locomotion. This study investigated how goats adjust the stiffness of their hindlimbs to accommodate surfaces of different stiffness. Goats provide a compelling animal model for studying leg stiffness modulation, because they skillfully ambulate over a range of substrates that vary in compliance. To investigate the adjustments that goats make when walking over such substrates, ground reaction forces and three-dimensional trajectories of hindlimb markers were recorded as goats walked on rigid, rubber and foam surfaces. Net joint moments, power and work at the hip, knee, ankle and metatarsophalangeal joints were estimated throughout stance via inverse dynamics. Hindlimb stiffness was estimated from plots of total leg force versus total leg length, and individual joint stiffness was estimated from plots of joint moment versus joint angle. Our results support the hypothesis that goats modulate hindlimb stiffness in response to surface stiffness; specifically, hindlimb stiffness decreased on the more compliant surfaces ($P<0.002$). Estimates of joint stiffness identified hip and ankle muscles as the primary drivers of these adjustments. When humans run on compliant surfaces, they generally increase leg stiffness to preserve their center-of-mass mechanics. We did not estimate center-of-mass mechanics in this study; nevertheless, our estimates of hindlimb stiffness suggest that goats exhibit a different behavior. This study offers new insight into mechanisms that allow quadrupeds to modulate their gait mechanics when walking on surfaces of variable compliance.

INTRODUCTION

Since the first conceptual models of spring-like gait were presented three decades ago (Blickhan, 1989; Blickhan and Full, 1993; McMahon, 1985; McMahon and Cheng, 1990), analyses of leg stiffness have provided valuable insight into the mechanics of legged locomotion. For the most part, such analyses have characterized the 'quasi-stiffness' (Latash and Zatsiorsky, 1993) as the average or peak 'compression' of a representative leg element in response to an applied load, often estimated from measured kinematics and ground reaction forces (GRFs). Therefore, as used in these studies, the term 'stiffness' refers to the leg's capacity to resist externally imposed displacements, and not the capacity of specific structures in the leg to store elastic energy. The earliest studies represented the body as a simple spring–mass system and established the utility of the leg stiffness metric in understanding hopping and running gaits. For instance, analyses of leg stiffness have been used to explain the preferred frequency of humans during hopping (e.g. Farley et al., 1991) and to predict observed increases in stride length with running speed (e.g. McMahon and Cheng, 1990; Alexander, 1992). Estimates of the quasi-stiffness of individual joints (Latash and Zatsiorsky, 1993), based on average or peak changes in joint angles and net joint moments, have also provided insights with translational relevance. For example, estimates of joint stiffness during human walking have informed the development of mechatronic control architectures designed to mirror human joint dynamics, such as those in robotic leg prostheses (Au et al., 2007; Herr and Grabowski, 2012). Comparative studies have assessed various leg stiffness metrics, across a range of bipedal and quadrupedal animals, to identify common biomechanical principles. For instance, studies have shown that leg stiffness is nearly independent of trotting speed (e.g. Farley et al., 1993) and that larger animals have stiffer 'leg springs' when trotting at equivalent speeds (e.g. Farley et al., 1993; Lee et al., 2014).

From experiments on human subjects, interpreted through spring–mass models, it is clear that leg stiffness can be modulated in response to substrate compliance. For example, McMahon and Greene (1979) demonstrated that the compliance of a track can be 'tuned' to increase running speed. Ferris and Farley (1997) showed that humans increase the stiffness of their legs when hopping on more compliant surfaces, noting that the hoppers in their study maintained the series combination of surface stiffness and leg stiffness in a manner that was nearly independent of surface stiffness. They postulated that such a strategy was beneficial because it allowed hoppers to preserve important mechanics, such as ground contact time and center of mass (COM) vertical displacement. Ferris et al. (1998) observed a similar inverse relationship between leg stiffness and surface compliance in humans during running, and Silder et al. (2015) showed that humans increase leg stiffness when running with a load. In a study involving drop jumps on a sprung surface, Arampatzis et al. (2001) proposed an energetic benefit of increasing leg stiffness on substrates with greater compliance: stiffer legs enabled the sprung surface to store and return more energy to the jumpers, leading to a concomitant decrease in the mechanical work produced by the jumpers to raise their COM. Inverse dynamics analyses of human hopping have further suggested that leg stiffness depends on the torsional stiffness of the ankle, with knee stiffness playing a minor role (Farley and Morgenroth, 1999; Hobara et al., 2009).

Although the modulation of leg stiffness has been well documented in humans, it is largely unknown whether, and to

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List of abbreviations

COM   center of mass
COP   center of pressure
DOF   degree of freedom
GRF   ground reaction force
MTP   metatarsophalangeal

what extent, leg stiffness is adjusted in response to changes in substrate stiffness in other species and gaits. In this study, we hypothesized that goats modulate the stiffness of their hindlimbs in response to the stiffness of the surface under foot (hoof) during level walking. Because the legs of goats shorten as they are loaded and rebound as they are unloaded during walking, trotting and galloping (Lee et al., 2007), the hindlimbs of walking goats are 'spring like' in their behavior (Geyer et al., 2006). Goats move with remarkable agility, and their natural habitats demand adaptability to a wide range of terrains. Thus, goats represent a relevant animal model for investigating how leg stiffness is modulated during walking in response to surfaces of different stiffness.

To evaluate our hypothesis, we collected three-dimensional (3D) kinematic and kinetic data as goats walked on three surfaces of different stiffness. Average total leg stiffness, defined as ΔGRF/Δtotal leg length, and individual joint stiffness, defined as Δnet joint moment/Δjoint angle, were estimated via regression over the stance period and compared across surfaces. Goats were not modeled as a single mass and a single 'virtual' leg spring from the COM to the center of pressure (COP) during walking, as is frequently done in studies of human leg stiffness, because this would have required resolving the goats' simultaneous, asymmetrical forelimb and hindlimb contacts during walking. Instead, we adopted an approach similar to that used by Lee et al. (2007, 2014) to characterize the quasi-stiffness of individual hindlimbs in quadrupeds; therefore, our estimates of leg stiffness throughout the paper represent the stiffness of a passive linear spring fitted to the measured task-specific kinetic and kinematic behaviors of the hindlimb, rather than the leg's true mechanical stiffness, which governs the instantaneous response to a perturbation (Latash and Zatsiorsky, 1993; Rouse et al., 2013). We

were particularly interested to see whether an inverse relationship between surface stiffness and leg stiffness would emerge for goat walking, similar to the relationship observed for human running based on a simple spring–mass model. Because preserving COM mechanics, or vertical excursions of the body, during locomotion could have benefits across species and gaits, we expected that the previously observed response of human runners to substrates of variable stiffness would be mirrored in the hindlimbs of goats. However, recognizing that quadrupedal walking is inherently different from bipedal running, we reasoned that alternative behaviors might be detected as a result of these differences.

MATERIALS AND METHODS
Animals and experimental setup

Four healthy African pygmy goats (*Capra hircus* L.) were selected from a breeding colony maintained by the Concord Field Station at Harvard University. All animal procedures were performed at the Massachusetts Institute of Technology and were approved by the institution's Committee for Animal Care. Two adult female and two adult male goats, with body masses ranging from 25.0 to 36.0 kg (mean 30.9±4.6 kg), were included in this study. To facilitate motion capture, the hair on each animal's hindquarters was clipped back to the skin, and 29 reflective spherical markers (14 mm; Vicon, Centennial, CO, USA) were affixed directly to the skin (Fig. 1A) using a silicone-based adhesive. Marker placement was designed to characterize the 3D kinematics of the hip and the sagittal plane motions of the knee, ankle and metatarsophalangeal (MTP) joints bilaterally (Fig. 1B). The hoof marker, which was of particular importance to COP estimates, was secured to the lateral surface of the hoof such that it was visible and continuously tracked via the high wall-mounted cameras on all three surfaces, including foam.

The 3D marker trajectories were recorded at 100 Hz, via an 8-camera motion-capture system (Bonita 10; Vicon), as goats ambulated freely on a 6.1 m indoor walkway with a modular surface (Fig. 2A). The walkway was instrumented with two force plates (OPT464508; AMTI, Watertown, MA, USA), which were centered in the motion-capture volume and arranged side by side, with one plate offset 30 cm in the direction of travel. Both force plates were
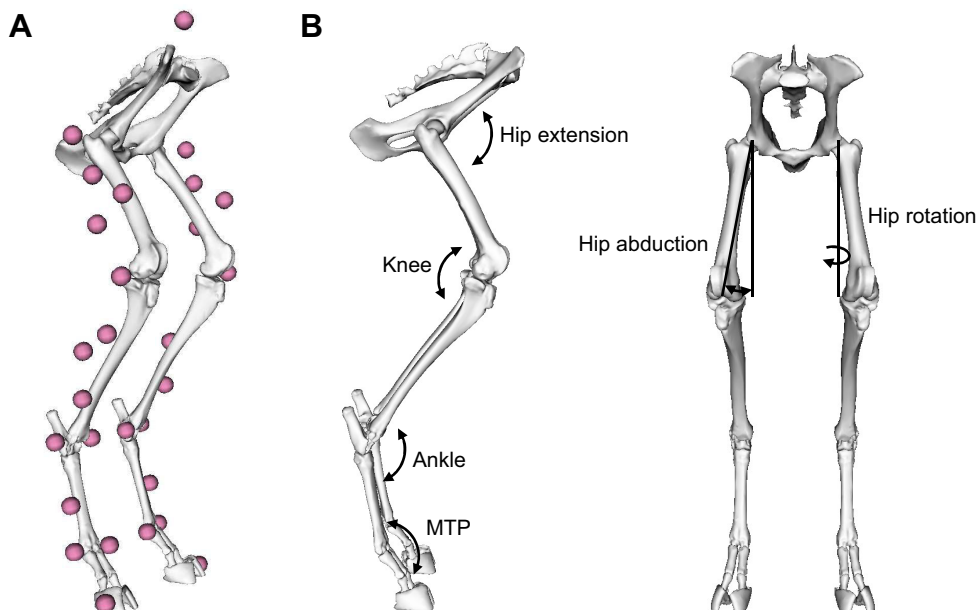

Fig. 1. Marker placement and joint angle definitions for the goat model. (A) Marker positions were chosen to enable 3D inverse kinematic reconstruction of each hindlimb joint. (B) Hip, knee, ankle and metatarsophalangeal (MTP) joint angles were determined from the relative orientations of adjacent segments.
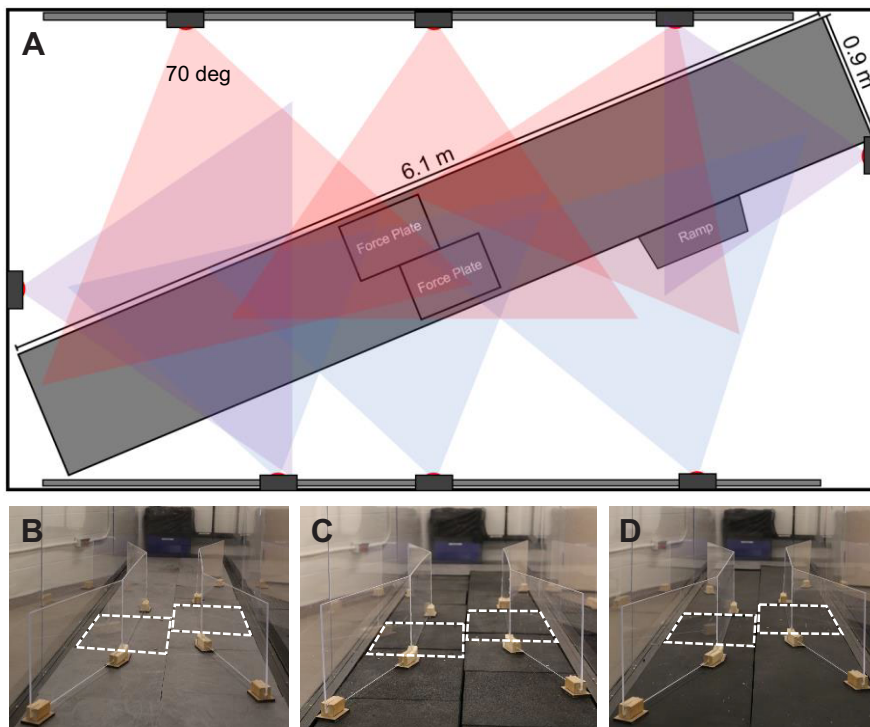
Fig. 2. Instrumented walkway with interchangeable surface materials. (A) The walkway was positioned such that an offset pair of force plates was centered in the capture volume of the 8-camera motion-capture system (Vicon). Rigid (B), rubber (C) and foam (D) surfaces were tested in this study. In the photos, force plates are outlined by dashed white lines.

recessed 15 cm below the surface of the walkway, allowing the surface material to be modified without moving the force plates. A 1 cm gap between each force plate and all surrounding surfaces ensured proper isolation of the measured forces. GRF signals from the walkway were amplified, sampled at 1 kHz, digitized and recorded using the OPTIMA system (OPT-SC; AMTI). The force signals were digitally synchronized with the motion-capture system using Nexus software (Vicon). Transparent Plexiglas on either side of the walkway restricted the goats' motion to the desired direction of travel.

Three distinct surfaces, made of rigid materials (i.e. metal and stacked particle board), rubber and foam, were explored in this study (Fig. 2B). The three surfaces were selected to capture a wide range of elastic moduli, representative of the variable stiffness terrains on which goats ambulate in the wild (Table 1). During each test session, goats walked back and forth across the walkway for

approximately 2 h on a single surface. Goats rested for at least 2 h between sessions, during which the surface material was exchanged by switching out 1.83 m-long panels on both ends of each force plate, as well as an isolated panel bolted to the top of each force plate. The order in which the surfaces were evaluated was pseudo-random for each goat.

Experimental data and inverse dynamics

Motion-capture and GRF data were post-processed in Nexus software (Vicon). For this study, a 'trial' consisted of one complete stance phase of a gait cycle in which a goat walked steadily within 10% of its median velocity, and contacted at least one of the two force plates cleanly with its right or left hindlimb. Trials were excluded if the measured GRFs were not isolated to the hindlimb of interest, if the goat was noticeably accelerating or decelerating, or if the average velocity of the sacrum marker was more than 10% above or below the goat's median velocity, in the direction of travel, for that particular surface. With this methodology, a total of 58 single-leg trials were deemed appropriate for inverse dynamics analysis, including 20 rigid ground trials, 20 rubber trials and 18 foam trials. The non-dimensionalized walking speeds of the goats (Arnold et al., 2013) were conserved across surfaces (Table 1). Markers from the included trials were labeled manually, and any gaps in marker trajectories were filled with built-in spline or neighbor-tracking algorithms. GRF and marker data were digitally low-pass filtered using a zero-phase fourth-order Butterworth filter with a 15 Hz cutoff frequency (MATLAB; MathWorks, Natick, MA, USA). The data were then transformed to be consistent with the ground coordinate frame used in OpenSim (Seth et al., 2018).

A 3D musculoskeletal model of the goat hindquarters was used for inverse kinematic and dynamic analysis. The model was constructed, in SIMM (Delp and Loan, 2000), based on cadaveric dissections of the pelvis and hindlimbs of one formalin-fixed adult male specimen (mass 46 kg). Briefly, we characterized the passive

Table 1. Non-dimensionalized walking speed and surface stiffness properties

	Non-dimensionalized speed	Approximate elastic modulus (MPa)	Analogous natural material
Rigid	0.53±0.08	4000	Sandstone (Dvorkin and Nur, 1996)
Rubber	0.55±0.07	2.0	Soft silts with low plasticity (Kezdi, 1974)
Foam	0.52±0.06	0.1	Very soft clays with high plasticity (Kezdi, 1974)

Non-dimensionalized walking speed was calculated as the square root of the Froude number (that is, by dividing the goat's measured speed by the square root of the product of the acceleration due to gravity and the animal's hip height at mid-stance) and did not differ significantly across the three surfaces. Values are presented as means±s.d.
Surface materials were chosen to represent a broad range of elastic moduli, similar to those found in the goat's natural environment. The elastic modulus of each surface was determined from the datasheet for the substrate material.

kinematics of the right hip, knee, ankle and MTP joints using a magnetic tracking system (Fastrack; Polhemus, Colchester, VT, USA). After disarticulating the specimen, the pelvis and the right femur, tibia, patella, tarsus, phalanges and hoof were cleaned and digitized using a 3D laser scanner (NextEngine 2020i and ScanStudio 1.7 Pro; NextEngine, Inc., Santa Monica, CA, USA). The left limb was used to experimentally determine the segments' mass and inertial properties (Arnold et al., 2013). Polygonal meshes characterizing 3D bone morphology were re-articulated and animated in SIMM, based on the experimental measurements of joint motions, and assuming right–left symmetry. The resulting musculoskeletal model had 9 segments and 18 degrees of freedom (DOF). The pelvis was defined as the base segment, with 6 DOF relative to the ground. Each hip was modeled as a ball-and-socket joint with three DOF. Each knee had one flexion–extension DOF, with the translations, varus–valgus, and internal–external rotations of the tibiofemoral joint defined as functions of knee flexion angle. Each ankle and each MTP joint had one DOF, with axes of rotation determined from the articulated bone geometry. Each hoof was modeled as a rigid segment; thus, relative motions of the proximal and distal phalanges were ignored (Arnold et al., 2013).

After importing the musculoskeletal model and the kinematic and kinetic data into OpenSim (v3.3), we used OpenSim's Scale and Inverse Kinematics Tools to determine the joint angles of each goat during walking. First, we scaled the model to the anatomical dimensions of each goat. Bone dimensions and all length-dependent quantities were scaled in OpenSim by a constant scale factor, identified from radiographs of the tibia and tarsus bones from each goat. All mass-dependent quantities, including the mass of each segment, were scaled based on measured body mass. The segment moments of inertia were scaled based on the relative body mass and segment lengths of each goat. Next, for each trial, a static frame was identified in which the goat's stance-limb position most closely matched the model's rest position; this frame was used to adjust the positions of the markers on the model to match the measured marker locations. Joint angles during walking were determined by tracking the marker trajectories. In particular, we used the Inverse Kinematics Tool in OpenSim v3.3 (Seth et al., 2018) to solve a weighted least squares problem, the solution of which aimed to minimize marker errors given the model's kinematic constraints at the joints (Lu and O'Connor, 1999). Across goats, RMS errors between the models' markers and the experimental markers were generally less than 1.5 cm.

We used OpenSim's Inverse Dynamics Tool, together with the measured GRFs (Fig. S1) and the joint angles obtained from inverse kinematics, to estimate the net joint moments of each goat during walking. We estimated the location of the COP as a fixed point in the hoof frame for all trials; we adopted this approach because our calculations of the COP, based on force plate data, were not robust for the more compliant surfaces as a result of the non-linear impedance of the interfacial material. For each goat, we based the COP estimates on the rigid surface trials – during which our COP calculations from force plate data were reliable – as the average location of the calculated COP in the hoof frame throughout stance. We then solved for each goat's net joint moments during walking using the measured GRFs and the hoof-fixed COP. To assess the accuracy of this approach, we compared inverse dynamics results using the hoof-fixed COP with those obtained using the calculated COP for the rigid surface trials. The resulting net joint moments were nearly identical, with the exception of a few frames near the beginning and end of hoof contact where low GRFs lead to inaccurate COP calculations (Fig. S2).

Analysis of net joint moments, power, work and stiffness

Kinetic and kinematic descriptors of hindlimb biomechanics, including the joint angles and the net joint moments, power and work, were calculated for each trial and compared across surfaces. From these descriptors, we estimated hindlimb stiffness and identified joint-level factors that potentially contributed to stiffness modulation. All analyses of these data, including the statistical tests, were performed in MATLAB (MathWorks). The stance phase of each gait cycle was identified as the period over which there was a sustained positive vertical component of the GRF vector. Joint angular velocity was calculated over the stance phase as the time derivative of joint angle. Net power at each joint was calculated by multiplying the net joint moment by the joint angular velocity. Net work at each joint was calculated by integrating net joint power with respect to time over the stance phase. Positive work represents mechanical energy generated by muscles, and negative work represents mechanical energy absorbed by muscles and tendons. To enable comparisons across trials and animals, joint moments, power and work were normalized to body mass, and all time-varying trajectories were plotted with respect to percentage of the stance phase. After normalization, we calculated the average joint angle, moment and power trajectories for each surface as the arithmetic mean of all individual trials from that surface (n=20 for rigid, n=20 for rubber and n=18 for foam). We then compared these averaged trajectories across surfaces.

A few key metrics allowed us to make further comparisons across surfaces at the level of the individual joints. Angular excursion was calculated for each joint and trial as the maximum joint angle minus the minimum joint angle for that trial. Peak extension moments were defined as the maximum moment recorded for each trial. Average values were calculated for each surface as the arithmetic mean of the values from all individual trials for that surface; these averages were then plotted with their 95% confidence intervals and compared across surfaces using a one-way ANOVA. Differences across surfaces were considered significant for P<0.05.

To make comparisons across surfaces at the level of the whole hindlimb, a total leg vector was defined from the hoof COP to the hip joint center in 3D space (Fig. 3A). Total leg length was calculated throughout the stance phase as the instantaneous magnitude of this total leg vector. To facilitate making comparisons across animals of different sizes, we scaled the total leg length of each goat by a constant, unitless factor relating that goat's height to the height of the largest goat; in other words, all length values are reported in absolute length units, as if measured from the 36 kg animal. Total leg force was calculated as the magnitude of the projection of the GRF vector onto the total leg vector. Total leg velocity was calculated as the time rate of change of the total leg length; to obtain net total leg power, total leg force was multiplied by this total leg velocity at each time point. Net total leg work was calculated by integrating net total leg power with respect to time over the stance phase. Total leg forces and power were normalized to body mass, and all time-varying trajectories were plotted with respect to percentage of the stance phase. After normalization, we calculated the average total leg length, force and power trajectories for each surface as the arithmetic mean of all individual trials from that surface.

To test our primary hypothesis that goats modulate the stiffness of their hindlimbs in response to the stiffness of the walkway surface, we estimated hindlimb stiffness and compared these estimates across surfaces. For each trial, total leg stiffness was estimated as the slope of the least-squares regression line through the plot of total leg length versus total leg force, over the entirety of the stance phase.
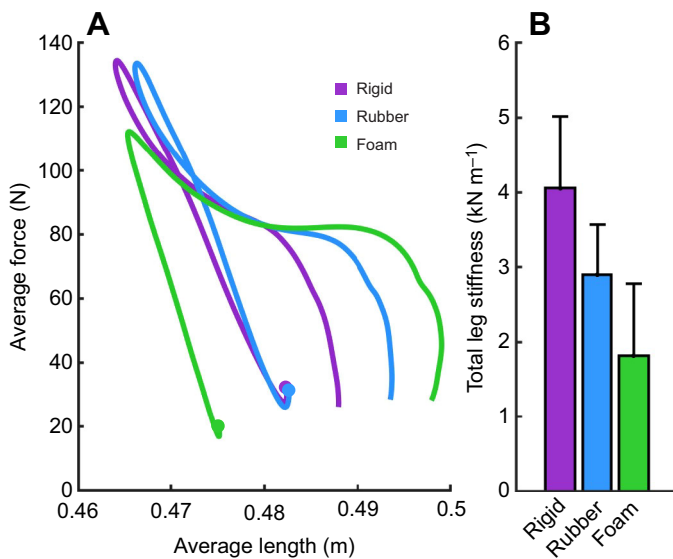
Fig. 3. Total leg stiffness during walking on rigid, rubber and foam surfaces. Leg stiffness was estimated, on a per-trial basis, as the slope of the least-squares regression line through the plot of total leg length versus total force during stance; the figure shows the averaged force–length trajectories (A) and slopes (B) for each surface. Dots in A indicate hoof strike. Error bars in B represent 95% confidence intervals (n=20 trials for rigid, n=20 trials for rubber, n=18 trials for foam).

We performed a similar analysis at the level of each individual joint, estimating joint stiffness as the slope of a least-squares regression line through the plot of joint angle versus joint torque. Appropriateness of fit was assessed via the coefficient of determination, R^2. Several studies have shown that stiffness values calculated from such data are sensitive to the particular method used to quantify the slope (e.g. Günther and Blickhan, 2002). We chose a linear regression approach

because it was generally less variable across goats and surfaces than other methods we tried (e.g. Farley and Morgenroth, 1999; Günther and Blickhan, 2002), and it led to conclusions that were consistent with those of other methods (Fig. S3). In this study, we were particularly interested in whether hindlimb stiffness would change as goats walked over different surfaces; thus, our comparisons of relative stiffness across surfaces are more relevant to the present hypothesis than the absolute stiffness values that were calculated.

Average stiffness for each surface was calculated as the arithmetic mean of stiffness values from all individual trials for that surface; these averages were then plotted with their 95% confidence intervals and compared across surfaces using a one-way ANOVA. Differences across surfaces were considered significant for $P<0.05$.

RESULTS

Total leg stiffness and individual joint stiffness on rigid, rubber and foam surfaces

Consistent with our hypothesis, the goats in this study altered the stiffness of their 'leg spring' in response to changes in the stiffness of the walkway surface (Fig. 3). In particular, goats walked with stiffer hindlimbs on the rigid walkway than on the more compliant rubber or foam surfaces tested ($P<0.002$). The leg shortened in early stance on all surfaces but extended farther and contacted the ground longer, on average, on the foam than on the rubber or rigid surfaces (Figs 3 and 4A,B). For example, the average stance duration was 0.41 s on the foam surface, 0.35 s on the rubber surface and only 0.34 s on the rigid surface. The total leg force was significantly reduced ($P<0.0001$) on the foam surface (Fig. 4C), and less energy was stored in the leg spring during early stance, as estimated from the total leg power (Fig. 4D).

Analysis of individual joint stiffness (Fig. 5) revealed that muscles crossing the hip and ankle likely contributed to the changes in total leg stiffness across the different surfaces. Notably, stiffness at the hip and at the ankle varied significantly when goats walked
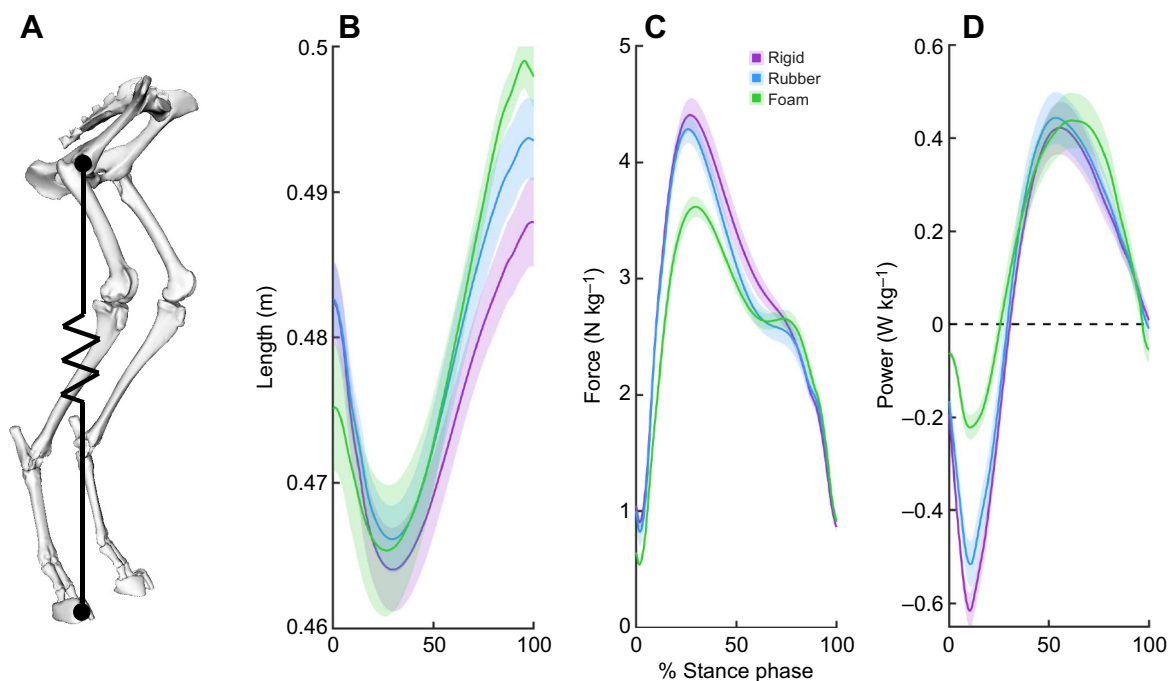

Fig. 4. Leg spring analysis during steady-state level walking over rigid, rubber and foam surfaces. (A) Leg spring representation. Total leg length (B), force (C) and power (D). Plots represent mean trajectories (shaded regions represent s.e.m.) across all trials from all goats (n=20 trials for rigid, n=20 trials for rubber, n=18 trials for foam).
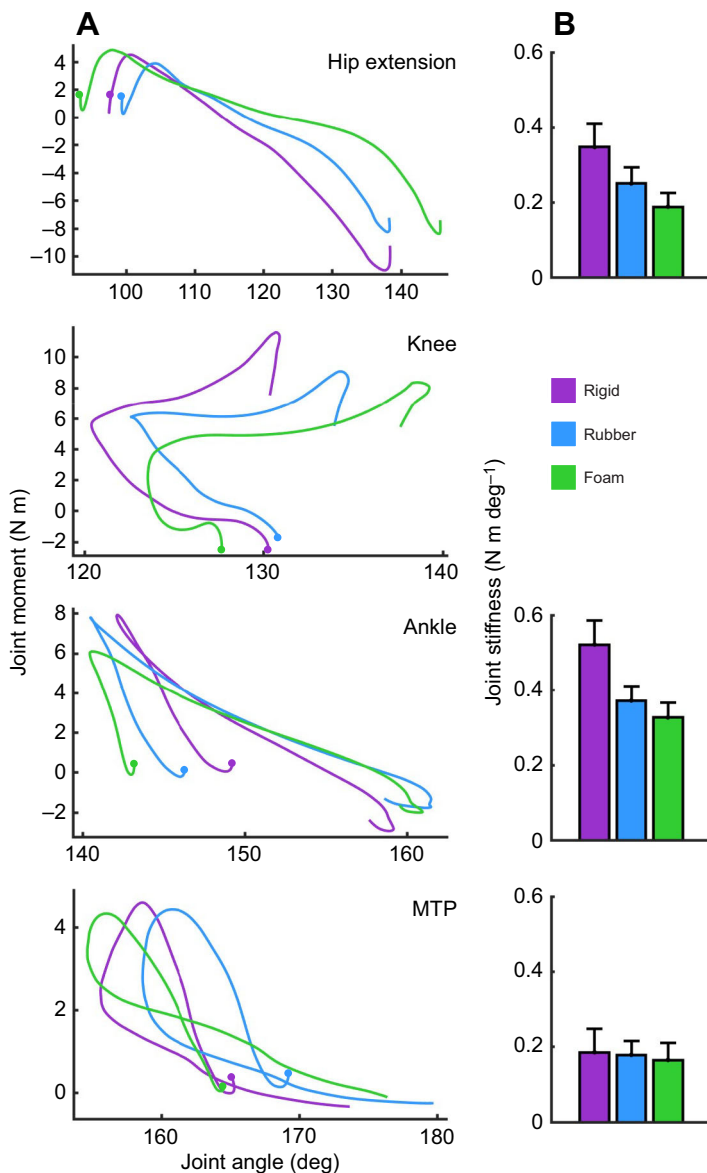
Fig. 5. Individual joint stiffness during walking on rigid, rubber and foam surfaces. Joint stiffness was estimated, on a per-trial basis, as the slope of the least-squares regression line through the plot of joint angle versus net joint moment during stance; the figure shows the averaged torque–angle trajectories (A) and slopes (B) for each surface. Because the linear spring model did not yield useful information for the knee, the stiffness bar graph was excluded. Dots in A indicate hoof strike. Error bars in B represent 95% confidence intervals (n=20 trials for rigid, n=20 trials for rubber, n=18 trials for foam).

across the rigid, rubber and foam surfaces ($P<0.0001$), with the more compliant surfaces eliciting lower joint stiffness on average (Fig. 5). At both the hip and the ankle, plots of net joint torque versus joint angle were spring like during the stance phase, with coefficients of determination ranging from 0.65 to 0.81 (Table 2). Coefficients of determination for the knee and MTP plots, by contrast, were relatively low, indicating that a linear spring poorly approximated the torque–angle behavior of these joints (Fig. 5 and Table 2). At the knee, in particular, joint stiffness analysis did not

Table 2. Average coefficients of determination for fit with a linear spring

	Rigid	Rubber	Foam
Total leg spring	0.78±0.11	0.65±0.20	0.33±0.22
Hip	0.81±0.18	0.65±0.26	0.72±0.14
Knee	0.28±0.22	0.21±0.21	0.41±0.28
Ankle	0.77±0.23	0.74±0.13	0.72±0.11
MTP	0.37±0.22	0.41±0.21	0.50±0.28

Coefficients are interpreted as a measure of the appropriateness of fit for the linear spring model; values are reported as means±s.d. Coefficients were calculated for each trial and were then averaged across all trials and goats for each surface (n=20 trials for rigid, n=20 trials for rubber, n=18 trials for foam).

yield useful results, consistent with previously published kinematic and kinetic data from trotting goats (Lee et al., 2007).

Joint angles and net joint moments, power and work on rigid, rubber and foam surfaces
Joint angle trajectories and net joint moments calculated for goats walking on the rigid runway (Fig. 6) were qualitatively similar to data reported previously for goats walking on level surfaces (Arnold et al., 2013; Pandy et al., 1988). However, when the goats walked on rubber and foam surfaces, distinct differences emerged in the behaviors of the hip and ankle joints. Goats extended their hips throughout the stance phase on all surfaces (Fig. 6A), yet the total angular excursion of the hip was significantly different across the three surfaces ($P<0.0002$) and was largest on the foam. At the ankle, goats generated a net plantarflexion moment for most of the stance phase (Fig. 6B), absorbing energy in early stance, as the leg flexed, and generating energy in mid-stance, as the ankle extended and the plantarflexion moment peaked. However, the peak plantarflexion moment was significantly different across the three surfaces ($P<0.0001$) and was smallest on the foam. These data suggest that the hip muscles' contributions to the observed changes in total leg
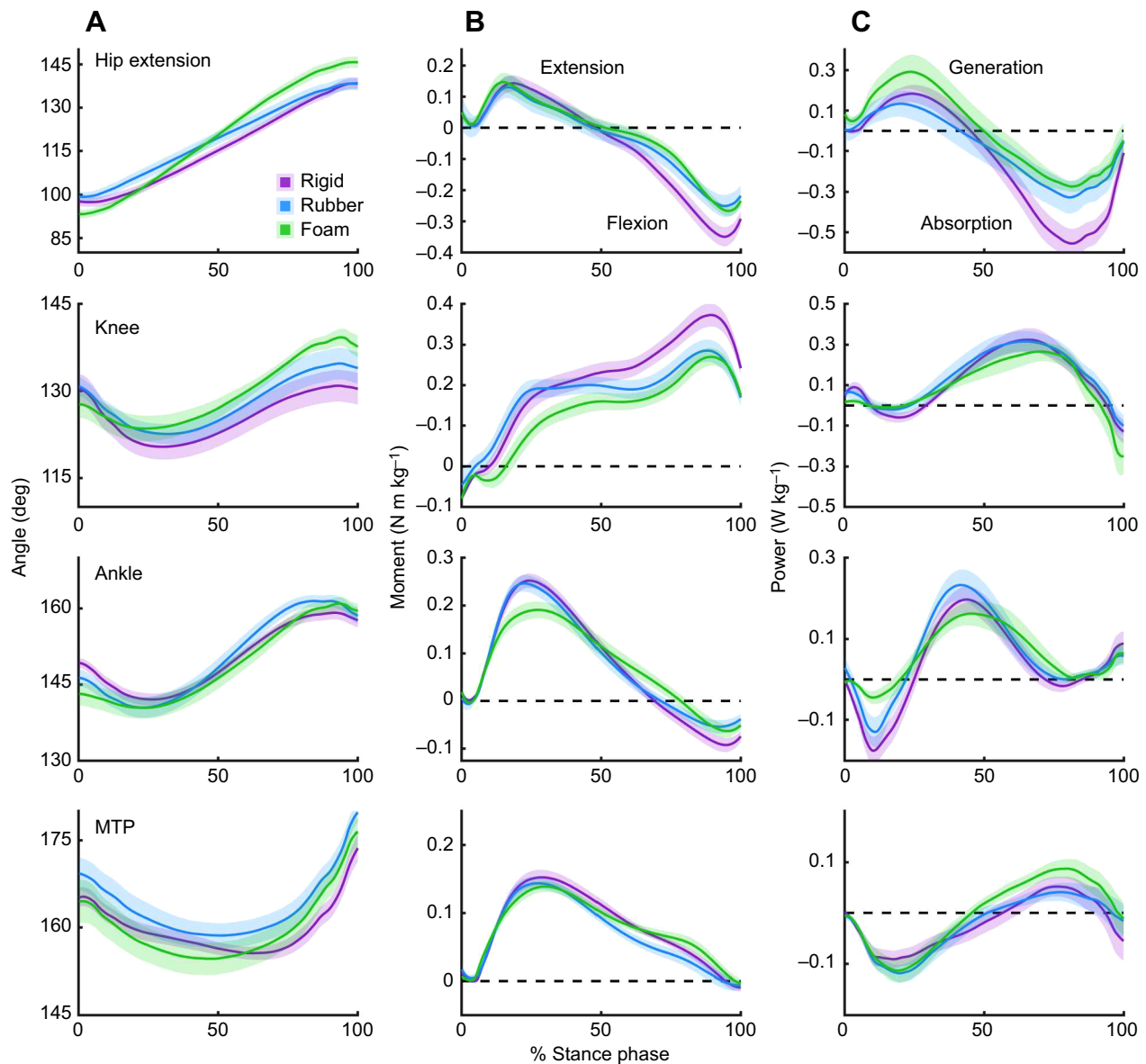
Fig. 6. Joint-level biomechanics during steady-state walking over rigid, rubber and foam surfaces. Hindlimb joint angle (A), net joint moment (B) and net joint power (C). Plots represent mean trajectories (shaded regions represent s.e.m.) across all trials from all goats (n=20 trials for rigid, n=20 trials for rubber, n=18 trials for foam).

stiffness were primarily kinematic (larger joint excursions on compliant surfaces), while the ankle muscles' contributions were primarily kinetic (smaller plantarflexion moments on compliant surfaces). On foam, these changes resulted in greater power generation at the hip and less power absorption at the ankle during early stance (Fig. 6C).

Although the torque–angle plots for the knee were not well characterized by a linear spring (Fig. 5), changes in the net knee moments on the different surfaces likely helped to modulate total leg stiffness. For instance, the knee extension moment increased sooner on the rigid and rubber surfaces than on the foam (Fig. 6B). Peak knee extension moment, which occurred on all surfaces at approximately 90% of stance, was also significantly greater on the rigid surface than on either the rubber or the foam (P<0.05).

The amount of energy stored and released by the hindlimb 'leg spring' during walking varied with surface stiffness. Notably, the net work differed significantly across the rigid, rubber and foam

surfaces (P<0.005), with the greatest net work, and the greatest positive work, occurring on the foam (Fig. 7A,B). These trends were generally mirrored at the hip, ankle and MTP joints (Fig. 7C,D). On the rigid walkway, goats absorbed substantially more energy at the hip than when walking on the foam.

DISCUSSION

This study tested the hypothesis that goats modulate the stiffness of their hindlimbs in response to stiffness properties of the surface under foot. This hypothesis was evaluated by modeling the goat's hindlimb as a spring and estimating leg stiffness from 3D kinematic and GRF data, during level-ground walking, over three different synthetic substrates. In addition, we analyzed the net moments and angular excursions of the joints, providing insight into factors that led to the changes in total leg stiffness. We were particularly interested to see whether an inverse relationship between surface stiffness and leg stiffness would emerge for goat walking.
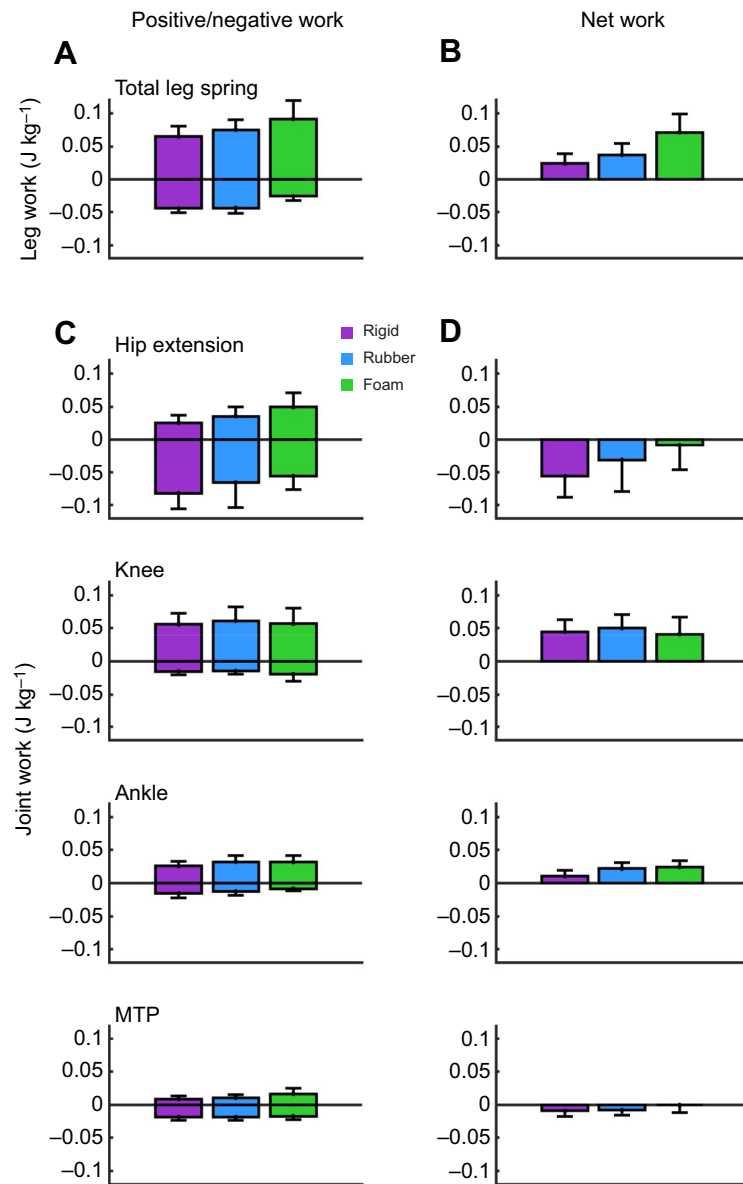
Positive/negative work

A

Total leg spring

Net work

B

Fig. 7. Changes in hindlimb work with surface stiffness during steady-state walking. Negative and positive work (left) and net work (right) over the stance phase were estimated for each trial for the total leg (A,B) and for each individual joint (C,D). These values were then averaged across all trials and goats for each surface (n=20 trials for rigid, n=20 trials for rubber, n=18 trials for foam). Error bars represent 95% confidence intervals.

C

Hip extension

Knee

Ankle

MTP

D

- Rigid
- Rubber
- Foam

Our results provide evidence that hindlimb stiffness is indeed modulated as goats adjust their gaits to different terrains. However, interestingly, we observed that goats decrease hindlimb stiffness on more compliant surfaces (Fig. 3). This is in contrast to the changes in leg stiffness that have been observed in humans during running and hopping, as interpreted via spring–mass models at the COM, in which stiffness increased on more compliant terrains (e.g. Ferris et al., 1998).

Based on joint-level analyses, our study highlights the role of muscles acting about the goat hip and ankle in modulating hindlimb stiffness. These two joints were the most 'spring like' of the goat's hindlimb during the stance phase, as evidenced by their relatively high coefficients of determination (Table 2). In addition, the changes in torsional stiffness of the hip and ankle joints on the rigid, rubber and foam surfaces (Fig. 5) followed the trends observed for the total leg model. Statistical analyses of the inverse dynamics data also indicated that the observed decrease in hip joint stiffness on softer surfaces was driven primarily by joint kinematics: hip angular extension, under similar loads, was greater on the softer surfaces than on the rigid walkway (Fig. 6). Changes in ankle stiffness, in

contrast, were primarily kinetic in nature: stance-phase ankle motions were induced by a net plantarflexion moment that was lower on the softer surfaces than on the rigid walkway. These stiffness adaptations led to a significant increase in total leg positive work and a decrease in total leg negative work on the softer terrains (Fig. 7).

Substantial consideration was given to selecting an appropriate metric for assessing leg stiffness. We did not model the goats as a single mass and a single 'virtual' leg spring from the COM to the COP, as frequently done in studies of human leg stiffness, because this would have required resolving the goats' simultaneous, asymmetrical forelimb and hindlimb contacts during walking. In the only prior study looking specifically at leg stiffness in goats, Lee et al. (2007) introduced a metric, termed 'actuator–spring leg stiffness', to analyze hindlimb compliance. In their formulation, the stance leg was modeled as a passive linear spring in series with an actuator; stiffness of the spring was then optimized to minimize the work performed by the actuator. Using that metric, Lee et al. (2007) showed, for example, that the hindlimb is less spring like when goats trot downhill, as the leg muscles absorb more energy.

The formulation of Lee et al. (2007) differs in a fairly significant way from the regression approach chosen here. In their most basic interpretations, both the actuator–spring leg formulation and the regression approach are optimization methods intended to characterize leg stiffness by minimizing some cost function. Where the two strategies differ is in the construction of that cost function. The actuator–spring leg formulation minimizes the integrated difference between predicted and measured power trajectories for a measured load profile. In other words, the cost function is specified to reduce the error in predicted versus measured velocity trajectories, weighted by the magnitude of the measured force (or net joint moment) at each time point. In this way, the algorithm is structured so that the behavior of the resultant spring best matches the behavior of the biological leg (or joint) at points when the loads are greatest. The regression approach, in contrast, minimizes only the integrated error of the force (or net joint moment) predicted by the linear spring for a given deformation trajectory. We ultimately selected the regression approach because we did not feel justified in enforcing a load-dependent weighting on the optimization function, given that the purpose of the study was to best approximate the stiffness of an assumed spring-like leg/joint. Certainly, stiffness values will depend on the particular method used to model the 'virtual' leg and quantify its behavior. In this study, our hypothesis was that hindlimb stiffness would change as goats walked over different surfaces; for this reason, our comparisons of relative stiffness across surfaces were of greater interest than the absolute stiffness values that we calculated.

It is important to acknowledge that the data collected for this study did not allow us to analyze the goats' COM dynamics or to estimate the stiffness of the forelimbs. Of course, the changes in total leg length, as calculated here, are not necessarily representative of the goat's COM motion, and forelimb–hindlimb function is known to be asymmetrical (e.g. Griffin et al., 2004; Lee et al., 2007; Maes et al., 2008). It is therefore possible that the observed changes in hindlimb stiffness could be better understood in the context of forelimb behavior or full-body dynamics; this remains a future study objective. Although the facility used in the present study was not large enough to allow for trotting or galloping, with the proper environment it would be interesting to test whether these stiffness changes hold across speeds and gaits. In addition, the data presented here do not allow us to draw conclusions as to the neuromuscular mechanisms underlying the observed changes in individual joint or total leg stiffness. In a future study, it could be informative to couple these analyses with data describing individual muscle state and activation profiles.

In conclusion, this study provides evidence that goats decrease the stiffness of their hindlimbs when walking on softer surfaces. Without concrete evidence as to the evolutionary origin of the goat's gait patterns on natural terrains, we offer a speculative explanation for why goats appear to adopt different strategies to humans when running over compliant surfaces. The human tendency to increase leg stiffness in response to unknown terrains helps to preserve COM kinematics; because humans are bipedal, preserving these kinematics is essential to gait stability. Goats, as quadrupeds, may not have the same need to preserve COM kinematics, especially during walking when multiple limbs are in contact with the ground and their gaits are more stable. In the absence of this constraint, goats may benefit from softening the stance limb on foam or other compliant surfaces that have a relatively high capacity to store and release energy, because doing so might allow these animals to absorb energy from the unsure ground without disrupting or perturbing overall body dynamics.

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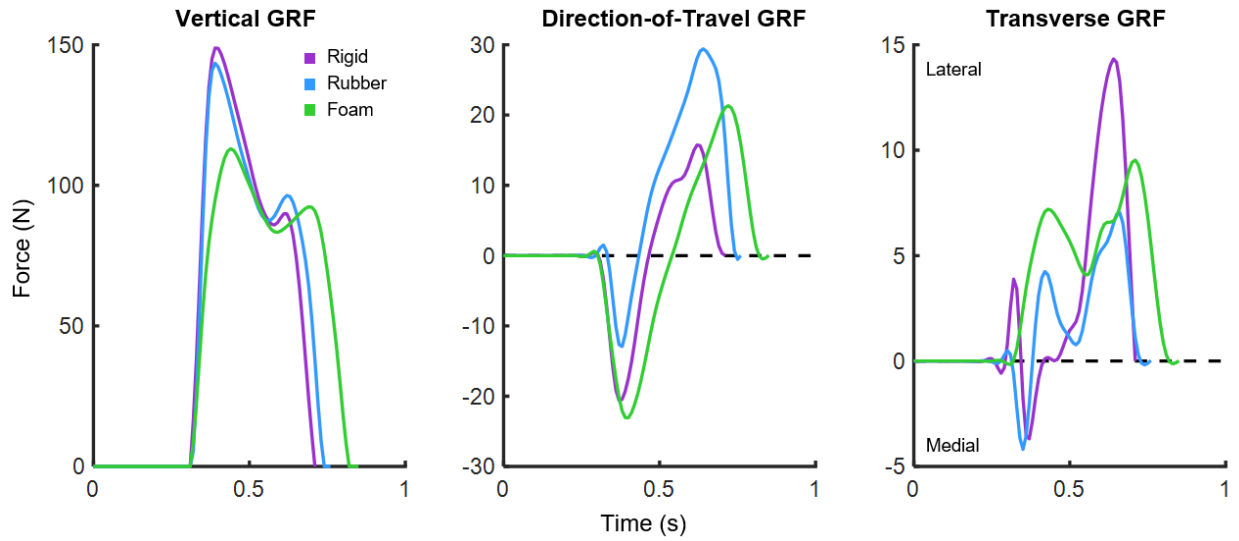
Fig S1. Representative absolute GRF measurements from Goat 63. Plots show three-component GRFs from a single representative trial (Goat 63) on each surface, as measured by walkway force plates. Trials are plotted in absolute time. Y-axis scales have been adjusted for each plot to show the relevant range of forces.
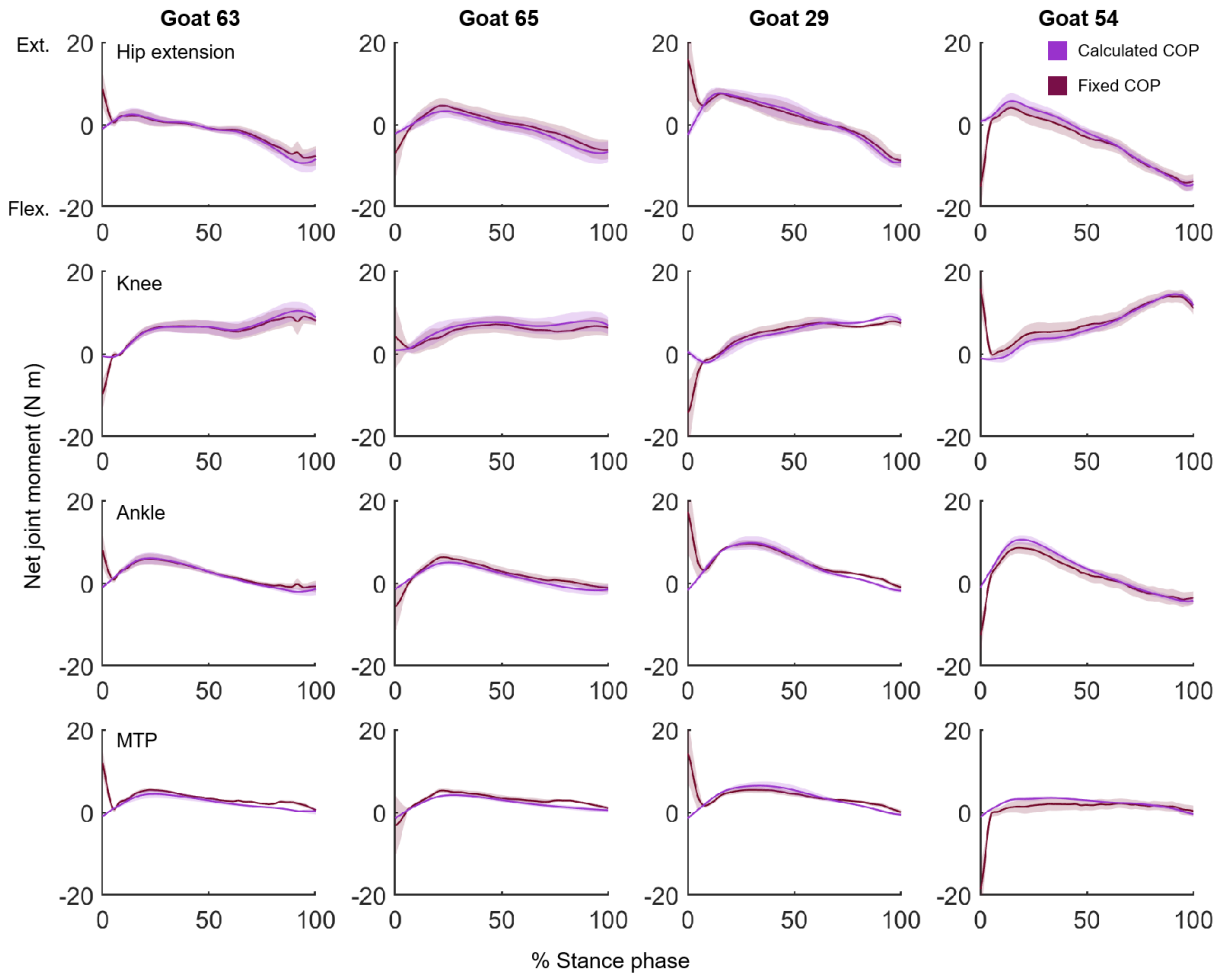
Fig S2. Net joint moments on the rigid surface, estimated using the GRF-calculated and hoof-fixed COPs. Plots represent average net joint moment across all trials from each goat. Shaded regions represent s.e.m. across all trials from each goat.
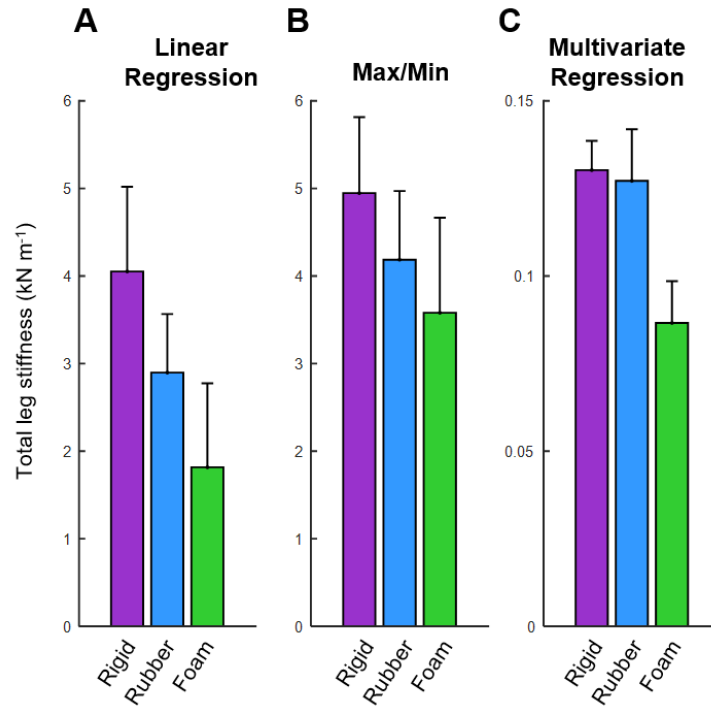
Fig S3. Total leg stiffness of the goat hindlimb during walking on rigid, rubber, and foam surfaces, as estimated three ways. In addition to the linear regression method described in the manuscript (A), we estimated stiffness at the point of maximum force (B), as was done by Farley and Morgenroth (1999) and others. We also estimated stiffness using the nonlinear approach (C) described by Gunther and Blickham (2002).