Interpreting locomotor biomechanics from the morphology of human footprints.

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Abstract

Fossil hominin footprints offer unique direct windows to the locomotor behaviors of our ancestors. These data could allow a clearer understanding of the evolution of human locomotion by circumventing issues associated with indirect interpretations of habitual locomotor patterns from fossil skeletal material. However, before we can use fossil hominin footprints to understand better the evolution of human locomotion, we must first develop an understanding of how locomotor biomechanics are preserved in, and can be inferred from, footprint morphologies.

In this experimental study, 41 habitually barefoot modern humans created footprints under controlled conditions in which variables related to locomotor biomechanics could be quantified. Measurements of regional topography (depth) were taken from 3D models of those footprints, and principal components analysis was used to identify orthogonal axes that described the largest proportions of topographic variance within the human experimental sample. Linear mixed effects models were used to quantify the influences of biomechanical variables on the first five principal axes of footprint topographic variation, thus providing new information on the biomechanical variables most evidently expressed in the morphology of human footprints. The footprint's overall depth was considered as a confounding variable, since biomechanics may be linked to the extent to which a substrate deforms. Three of five axes showed statistically significant relationships with variables related to both locomotor biomechanics and substrate displacement; one axis was influenced only by biomechanics and another only by the overall depth of the footprint. Principal axes of footprint morphological variation were significantly related to gait type (walking or running), kinematics of the hip and ankle joints and the distribution of pressure beneath the foot. These results provide the first quantitative framework for developing hypotheses regarding the biomechanical patterns reflected by fossil hominin

footprints by demonstrating the statistically significant effects of specific kinematic variables on patterns of variation in footprint topography.

Keywords: Locomotion; Ileret; Laetoli; Kenya

Introduction

Researchers have long recognized (e.g., Lamarck, 1809; Darwin, 1871) that habitual bipedalism is a unique behavioral characteristic that distinguishes modern humans from the other extant great apes and that would have played an influential role in many aspects of our evolution. Yet much remains unknown about this behavior's evolutionary history. Did bipedalism evolve in different ways within the hominin clade? Or did all early hominins walk bipedally in essentially the same manner as modern humans do today?

The locomotor styles of early hominins are often characterized as fitting into one side of a dichotomy, or somewhere along a continuum, between chimpanzee-like facultative bipedalism and human-like habitual bipedalism. However, this paradigm excludes the possibility that forms of habitual bipedal locomotion different from those of any extant species could have evolved throughout the history of the hominin clade. Robinson (1972) and Oxnard (1975) were among the first to hypothesize that the suites of postcranial features within particular fossil hominin taxa could imply locomotor styles that are in some ways similar to, but in other ways quite different from, those that are observed among modern taxa. The discovery of a 3.4 Ma hominin foot from Ethiopia with a startling combination of primitive and derived features previously thought to be incongruous with one another (e.g., a widely divergent hallux alongside other features functionally linked to terrestrial bipedalism) has provided hard evidence to support the

hypothesis that multiple forms of bipedalism must have evolved and persisted within the hominin clade, at least during the Pliocene (Haile-Selassie et al., 2012). This lends support to the idea that the evolution of bipedalism within the hominin clade was a process in which bipedalism formed larger portions of an overall locomotor repertoire in some hominin taxa relative to others (Rose, 1991). This discovery also suggests that we have much left to learn about the timing and nature of the evolution of a human-like form of bipedalism, and raises the question of how we can identify and characterize different modes of bipedalism that existed throughout the evolutionary history of the hominin clade.

Many recent hypotheses, and several ongoing debates, regarding the first emergence of a distinctly human-like form of bipedalism are centered around the interpretation of locomotor adaptations in two particular taxa, *Australopithecus afarensis* (dating to c.3-4 Ma) and *Homo erectus sensu lato* (dating to c.1.9 Ma-50 ka; Wood and Richmond, 2000). The postcranial anatomies of both taxa are relatively well-known compared to those of other fossil hominins and the current evidence even includes well-preserved partial skeletons of both (A.L. 288-1 and KNM-WT 15000 [Johanson et al., 1982, Walker and Leakey, 1993]). However, despite these relatively rich samples of fossil evidence, the interpretation of locomotor patterns practiced by *Au. afarensis* and *H. erectus s.l.* have been rife with debate.

The postcranial morphology of *Au. afarensis* has been viewed by some as incompatible with a form of bipedalism that directly mirrored that of modern humans (e.g., Jungers, 1982, Stern and Susman, 1983). Yet others have made the argument, based on the same assemblage of fossils, that locomotor adaptations in *Au. afarensis* bear a striking enough resemblance to those of modern humans that they must have used a similar mode of bipedal locomotion (e.g., Latimer and Lovejoy, 1989, 1990a,b; for a summary of the debate see Ward, 2002). Such debates have

continued with the interpretations of more recently discovered fossils, which have suggested to some, but not others, that *Au. afarensis* may have had human-like arches in their feet (Ward et al., 2011, but see Drapeau and Harmon, 2012) and had relatively longer legs than previously thought (Haile-Selassie et al., 2011; Pontzer, 2012).

Generally, the overall body plan of *H. erectus s.l.*, including features such as its limb proportions (Ruff and Walker, 1993; Richmond et al., 2002) and the strength of its humerus relative to its femur (Ruff, 2009), bears a much closer resemblance than *Au. afarensis* does to the pattern observed in modern humans. Combined with the human-like morphology of the *H. erectus s.l.* inner ear and the ape-like morphology found in *Australopithecus* (Spoor et al., 1994), this evidence suggests to many researchers that *H. erectus s.l.* may have been the first hominin (or at least the first of those fossil taxa known today) to practice a human-like style of bipedalism. However, the morphology of a 0.9-1.4 Ma pelvis from Gona, Ethiopia, which has been assigned by its discoverers to *H. erectus* (Simpson et al., 2008), bears some resemblances to *Australopithecus* fossils (Ruff et al., 2010, but see Simpson et al., 2014) in ways that could imply that the taxonomic allocation of the specimen is incorrect, or that the bipedal locomotion of *H. erectus* was slightly different than that of modern humans.

It is evident that conflicting functional interpretations can be derived from the same assemblages of fossil skeletal evidence. This problem arises when analyzing an anatomical form from the fossil record that is not identical to the anatomy of any extant taxon (Richmond et al., 2012). This typically results in some level of subjectivity when reconstructing the behavioral repertoires of fossil hominins because their anatomies are in some ways similar to, but in other ways very different from, both modern humans and the other extant great apes.

The debates that have arisen from this approach emphasize the necessity of new objective techniques that can extract direct evidence of biomechanical function from the fossil record. In other words, one needs to identify ways in which biomechanical patterns leave unambiguous signatures that are preserved in the fossil record. While such evidence has been difficult to identify in skeletal material, footprints from the human fossil record offer unique direct windows to the mechanics of extinct hominin locomotion. Skeletal morphology is representative in some ways of habitual activity patterns, yet footprints preserve explicit evidence of locomotor behaviors on an immediate timescale. With footprints, one can be certain of where and how hominins were moving across their landscapes at moments in time millions of years ago. Importantly, the record of pre-*Homo sapiens* footprints in the human fossil record continues to grow, such that extensive assemblages are now known from both the Pliocene and the early Pleistocene. Hominin footprints dating to *c.*3.7 Ma were uncovered at Laetoli, Tanzania in the late 1970s (Leakey and Hay, 1979), and in more recent years multiple hominin footprint sites dating to *c.*1.5 Ma have been discovered and excavated at Ileret, Kenya (Bennett et al., 2009; Richmond et al., 2012, 2014; Dingwall et al., 2013). These sites offer rare opportunities to understand the nature of hominin bipedalism at two very different times in our evolutionary history and to address questions about when a human-like form of bipedalism first emerged. Furthermore, these data will allow us to build new hypotheses regarding the ways in which the ecological, energetic, and other effects of those locomotor patterns may have changed between the Pliocene and the Pleistocene.

However, before these data can better inform us of the detailed nature of early hominin bipedalism, we must understand how footprints actually record evidence of locomotor patterns. Beginning with the earliest analysis of the Laetoli footprints (Day and Wickens, 1980), many

researchers compared the shapes of fossil hominin footprints to those produced by modern humans and drew conclusions about foot function or locomotion based on differences in footprint morphology (e.g., Tuttle et al., 1991; Meldrum, 2004; Berge et al., 2006; Bennett et al., 2009; Crompton et al., 2012). These studies have required the assumption that footprint morphologies directly represent particular functional signals, yet this has never been validated experimentally. In order to avoid the same kinds of seemingly unsolvable debates we see in analyses of fossil hominin skeletal anatomy, we must move beyond comparative analyses that treat modern species as directly analogous models and instead understand how particular biomechanical variables influence footprint shape (Richmond et al., 2012). With this understanding of how the biomechanical variables affect variation in footprint morphology, we can then be confident in deriving functional interpretations from footprints that may have been produced by an extinct hominin whose postcranial anatomy did not match that of any living taxon.

Raichlen and colleagues (2010) demonstrated that certain biomechanical variables are tightly linked to footprint morphology, as they showed that one can distinguish between human footprints produced with an extended limb gait and those produced with bent hips and bent knees. But uncovering the relationships between biomechanical variables and footprint morphologies has proven to be complex, as other studies have found that some logically expected relationships were not observed between footprint shape and certain biomechanical variables. For example, D'Août and colleagues (2010) designed experiments to test directly the hypothesis that footprint depths preserve a record of foot function (in the form of the distribution of plantar pressure). They found that only a weak relationship existed between pressure and footprint depth, and suggested caution in directly interpreting foot function from footprints.

Bates et al. (2013) addressed the same question with different statistical techniques, and Hatala et al. (2013) conducted similar experiments but with habitually barefoot people making prints in the same cohesive sediments that preserve the 1.5 Ma Ileret hominin footprints. Yet both of these studies still found very similar results to those of D'Août et al. (2010), with weak relationships between the magnitude of normal forces beneath the foot and the depth of footprints in analogous regions. Together, these studies demonstrate that footprints represent a complicated dynamic interaction between anatomical, functional, and sedimentary variables. The interpretation of functional patterns from footprint morphology requires approaches that extend beyond simply translating deep impressions as direct indications of high normal forces.

In this paper, controlled biomechanical experiments were conducted and analyzed in a manner that explicitly examines how variables related to locomotor biomechanics are recorded in, and can be inferred from, patterns of variation in footprint morphology. This included a consideration of multiple kinetic and kinematic variables that could potentially influence the patterns by which the foot applied forces to move across the substrate. To build this understanding, the following three questions were asked: First, in what ways do the morphologies of footprints tend to vary when produced by different people using different gaits (walking and running)? Second, how and to what extent do specific kinetic and kinematic variables affect those patterns of footprint morphological variation? And last, how and to what extent are those relationships influenced by the compliance of the substrate in which the footprints are produced?

Based on the results of previous studies, we hypothesized that certain relatively large-scale joint motion patterns (e.g., flexion of the hip and knee) would be significantly related to principal axes of footprint shape variation (as found by Raichlen et al., 2010) and therefore most

easily interpretable from footprint morphologies. Meanwhile, finer details of locomotion (e.g., regional peak pressures) might be less likely to influence principal axes of footprint topographic variation (following D’Août et al., 2010; Bates et al., 2013; Hatala et al., 2013) and are therefore more difficult to infer from footprint shapes.

Materials and Methods

Experimental subjects

Experiments were conducted with habitually unshod and minimally shod subjects from the Daasanach tribe near the town of Ileret, Kenya. The habitually unshod human foot is known to differ both anatomically (Hoffmann, 1905; Wells, 1931; Sim-Fook and Hodgson, 1958; Barnett, 1962; Ashizawa et al., 1997) and functionally (D’Août et al., 2009) from the habitually shod foot. It is critical to conduct these biomechanical experiments with habitually unshod subjects in order for the results to be applicable to the analysis of fossil footprint assemblages such as those at Ileret, Kenya or Laetoli, Tanzania, which were made by barefoot hominins and pre-date the earliest proposed evidence for the habitual use of footwear (*c.*40 ka, Trinkaus and Shang, 2008).

Twenty-nine adults (15 male, 14 female, ages 18 and above) and twelve children (10 male, 2 female, ages 4-15) participated in these experiments. All subjects were recruited, and provided their informed consent to participate, through a protocol approved by the Institutional Review Boards of The George Washington University and James Madison University. All subjects were pooled in this analysis because we sought to uncover generalizable biomechanical relationships that could be detected regardless of the age or sex of an individual producing a footprint. Age and sex may be difficult, if not impossible to know from fossil hominin footprints.

The nature of our analysis accounted for the random effect of subject identity allowing, in a way, for each subject to have a ‘baseline footprint’ and for us to measure biomechanically-induced deviations from that baseline shape. Furthermore, studies of plantar pressure have revealed no significant between-sex differences in foot function among either children or adults (Hennig et al., 1994; Bosch et al., 2010; Putti et al., 2010, but see Unger and Rosenbaum, 2004) despite some differences in foot anatomy (Wunderlich and Cavanagh, 2001; Bosch et al., 2010). While peak pressures and forces increase with age, the distribution of relative forces across the foot (which we use in this analysis) appears to vary only slightly past the age of 4.5 years (Bosch et al., 2010). Therefore, anatomical differences between subjects due to sex or age should not influence our results.

Experimental setup

The experimental setup (Fig. 1) was the same as one published previously (Dingwall et al., 2013; Hatala et al., 2013). A trackway was cleared in a large, flat and open space adjacent to the site of ongoing fossil footprint excavations at site FwJj14E at Ileret, Kenya. A one-meter-long pressure pad (RSScan International, Olen, Belgium) was placed about eight meters from the start of this trackway. One meter from the end of the pressure pad, a pit was dug that measured 150 cm long, 50 cm wide, and 15 cm deep. This pit was then filled with sediment taken directly from a layer (Lower Footprint Layer) that preserves fossil hominin footprints at Ileret, Kenya (Fig. 2). That sediment was variably hydrated before trials such that the overall depths of the experimentally-produced footprints encompassed the range of depths of the fossil hominin footprints preserved at both Ileret and Laetoli. The sediment patch was mixed with a trowel and lightly smoothed after each trial, to minimize compaction over time and provide a clear surface

for the footprint in the subsequent trial. The experimental trackway extended about eight meters beyond the end of the sediment pit. A video camera was placed perpendicular to the trackway, such that it could record all actions that occurred both on the pressure pad and along the patch of hydrated sediment. These experiments were conducted over the course of two field seasons, in 2011 and 2012. Because of differences in equipment availability, all 2011 trials were recorded at 210 Hz and all 2012 trials were recorded at 60 Hz.

INSERT FIGURE 1 HERE

INSERT FIGURE 2 HERE

Experimental protocol

The experimental protocol closely resembled one that has been published previously (Dingwall et al., 2013; Hatala et al., 2013). After each subject provided their informed consent to participate, biometric measurements were taken including stature, body mass, functional leg length, and foot length. Fluorescent adhesive markers were placed at the greater trochanter, tibial plateau, lateral malleolus, and fifth metatarsal head of the leg and foot that faced the camera's view. Each subject performed at least six walking trials (three at their normal, preferred speed and three at a faster speed; average walking speed = 1.78 m/s), and six running trials (three at their preferred endurance running speed and three at faster speeds; average running speed = 4.24 m/s), in which they passed over the entire trackway including both the pressure pad and the hydrated sediment. Trials were discarded and repeated if subjects visibly targeted the pressure pad or sediment patch. In most cases, subjects showed no evidence of targeting the pad or sediment. For example, subjects typically did not contact both the pressure pad and the hydrated

sediment in the same trial. Additional trials were performed until 3 pressure readings and 3 footprints were generated by each subject at each of the qualitative speeds being examined. Multiple photographs were taken of each footprint such that 3-dimensional models of each one could be rendered using photogrammetry software (PhotoModeler Scanner 2013, EOS Systems, Inc., Vancouver, BC).

There were two trials that seemed successful at the time of experimentation, yet had to be discarded later when poor geometric solutions prevented the rendering of scaled 3-dimensional footprint models by the photogrammetry software. This resulted in a total experimental sample of 490 trials (12 per subject for 41 subjects, minus 2) that were analyzed in this study.

Data processing

Kinetic and kinematic variables were quantified in each trial. Within RSScan International Footscan 7 software (Olen, Belgium), peak plantar pressure readings were extracted for 10 regions of the foot: medial and lateral heel, midfoot, metatarsal heads 1-5, the hallux, and the lateral toes. Videos of each trial were digitized in ImageJ software (Rasband, 1997-2012) in order to measure speed, stride length, and stride frequency. MaxTraQ software (Innovisions Systems, Inc., Columbiaville, MI) was used to digitize and quantify the angles of the hip, knee, and ankle joints at foot strike, midstance, and toe-off. Using Geomagic Studio (3D Systems, Inc., Rock Hill, SC), the depth of each footprint was measured at 14 functionally-relevant locations: the medial and lateral heel, medial and lateral midfoot, metatarsal heads 1-5, the hallux, and toes 2-5 (Fig. 3). For each model, 25 points were selected along the undisturbed substrate that surrounded the perimeter of each footprint. A least-squares algorithm was used to create a best-fit plane from those 25 points, which represented the ground plane. All depths were measured as

orthogonal distances from this plane. Despite the fact that these are not discrete anatomical landmarks, repeatability tests performed on a subset of 14 footprints revealed that these functionally-relevant locations could be measured in a replicable manner (paired t-test, $p = 0.7555$; mean difference between replicates = 0.005 cm).

INSERT FIGURE 3 HERE

D'Août and colleagues (2010) argued that larger individuals have larger feet with greater surface area over which to distribute their weight and the surface area of the foot effectively 'cancels out' the influence of body mass on footprint depth such that the average depth of a footprint is influenced to a larger degree by the compressive strength of the substrate. But foot area may not fully 'cancel out' the effect of body mass on print depth, since body mass ought to scale to the third power and foot surface area to the second. Furthermore, in this study we examined gaits that involve different amounts of force transmission to the ground (i.e., walking and running) and are therefore likely to result in footprints of different depth for the same individual moving across the same substrate. Due to these issues, attempts were made to measure substrate strength directly using a penetrometer. However, obtaining a repeatable measurement across the sediment patch was precluded by heterogeneity of the substrate. As a result, a similar approach to D'Août et al. (2010) was applied, simply to obtain a quantified measure of the amount of sediment displaced in a particular trial due to substrate mechanical, but also biomechanical, factors. The mean of the 14 depth measurements across each footprint was calculated and this measure of substrate deformability was then included in linear models as a variable that could influence footprint topography.

Analysis – Influences of biomechanical variables on footprint variation

Because a footprint is a complex shape that results from dynamic interactions within the foot but also between the foot and the deforming substrate, there is no reason to expect that the different functional areas from which footprint depth was measured should vary independently. As a result, principal components analysis (using the singular value decomposition) was used as a variable-reduction technique, which provided multiple orthogonal axes along which human footprint shapes were inclined to vary.

The loadings on each principal component were examined to determine the general shape change described by each (e.g., the first principal component was generally characterized by diametric variation in the depth of the forefoot relative to the heel). Biomechanical hypotheses were then developed to explain the ways in which the kinetic and kinematic variables that were quantified in these experiments could induce the types of variation in footprint shape that were described by each principal component axis. Linear mixed effects models were used to assess the competing, but not exclusive, hypotheses for each scenario. In these mixed models, subject identity was designated as a random effect, in a way controlling for anatomical variation and other peculiarities of individual subjects. Mixed effects models did not always result in a statistically significant increase in model fit (evaluated via log-likelihood) compared to standard multiple regression models. However, the inclusion of subject identity as a random effect tended to both eliminate structure from model residuals and decrease the value of the Akaike Information Criterion (AIC) for a given model. Because it is biologically sensible to include the random subject effects in these models, the variable was retained in all cases (following Zuur et al., 2009).

In the initial phase of this analysis, an inclusive mixed effects model was developed for each principal component of footprint topographic variation, which included as fixed effects all functional variables that were hypothesized to explain variation along that particular principal component axis. A maximum likelihood approach was used to eliminate variables sequentially if their independent effects were non-significant ($p>0.05$); in this process ANOVA was used to compare log-likelihood values of inclusive versus reduced models. Non-significant fixed effects were removed if their absence did not significantly affect the fit of the mixed model and if their removal reduced the value of AIC. The residuals of the final models were examined to ensure that they met the assumptions of normality and homoscedasticity.

The functional variables considered in this analysis of effects on axes of footprint topographic variation included gait type (walking or running), joint angles at foot strike, mid-stance and toe-off, joint excursions between those three phases, and various measurements of the distribution of peak pressures beneath the foot. It is important to note that in this analysis we were primarily interested in uncovering broad relationships between movement patterns and footprint morphologies. This led us to consider gait type as a categorical variable, rather than speed as a continuous variable. A complete analysis of speed effects within gaits could be a productive target of future work.

Results

Principal components analysis of the 14 regional footprint depth measurements revealed that only the first five principal component axes individually explained more than 5% of total variance in footprint topography (Fig. 4). Those first five axes together explained slightly more than 85% of total variance. Because of their relatively large contributions to describing variance

in footprint topography, these were the axes whose relationships with biomechanical variables were analyzed.

INSERT FIGURE 4 HERE

The rotation matrix that described the relationships of the original depth measurements to those first five principal component axes was then examined to understand the type of shape variation that each component described (Fig. 5; Table 1). Multiple biomechanical hypotheses were developed to explain variation along each of these principal component axes. Linear mixed effects models were based upon those biomechanical hypotheses.

INSERT FIGURE 5 HERE

INSERT TABLE 1 HERE

The first principal component axis can be summarized as describing depth in the region of the heel versus depth in the forefoot (Fig. 5; Table 1). Through mixed effects modeling, PC1 was found to be significantly influenced by both the total amount of deformation of the substrate and the type of gait used (Fig. 6; Table 2). Variation along the second principal component axis described depth at the first and second toe relative to the heel and lateral metatarsal heads (Fig. 5; Table 1). This component was significantly influenced only by the angular excursion about the hip during the second half of stance (Fig. 7; Table 2). The third principal component described depth at the heel and toes relative to the midfoot and metatarsal heads (Fig. 5; Table 1). This component was affected by only the total deformation of the substrate (Fig. 7; Table 2). The axis

of PC4 was generally related to depth at the first metatarsal head and the hallux, relative to the lateral metatarsal heads and toes (Fig. 5; Table 1). Mixed effects modeling revealed significant effects of substrate deformability, and also the relative amount of pressure along the transverse toe-off axis of the foot (mean of peak pressures on the first and second metatarsal heads minus mean of peak pressures on second through fifth metatarsal heads) on variation along PC4 (Fig. 7; Table 2). Finally, the fifth principal component axis described depth at the lateral midfoot and second toe relative to depth at the fifth toe (Fig. 5; Table 1). This component was significantly influenced by gait type, the angle of the ankle at toe-off, and the deformability of the substrate (Fig. 7; Table 2). In each of these linear models gait type was not collinear with mean footprint depth, which was used as the proxy for substrate deformability. This result supports the hypothesis that, at least in this study, variation in the average depth across entire footprints more closely reflected the mechanical properties of the substrate than the total amount of force applied beneath the foot.

INSERT TABLE 2 HERE

INSERT FIGURE 6 HERE

INSERT FIGURE 7 HERE

Discussion

The results of this study demonstrate that biomechanical variables related to lower limb kinematics leave discernible signatures in the morphology of human footprints, which is encouraging for the potential of fossil hominin footprints to afford a better understanding of the evolution of human bipedalism. Large-scale joint motion patterns tended to show stronger

relationships with principal axes of footprint topographic variation than did finer-scale biomechanical variables such as regional peak plantar pressure measurements. These results provide further evidence that the inference of functional patterns from footprint morphologies is much more complex than simply relating deep impressions to high normal forces.

Perhaps most importantly, this experimental study found that distinct patterns of variation in footprint morphology can be linked to certain movement patterns across the lower limb. The second principal component axis of footprint shape variation was related to motion at the hip joint, the fourth was driven by foot motion, and the fifth was influenced by motion at the ankle (Fig. 7; Table 2). These relationships provide novel insight into how an entire sequence of lower limb motions can be reflected in different ways by the morphology of a footprint.

The statistically significant relationships observed here between biomechanical variables and principal components of footprint topographic variance are unlikely to be mere statistical coincidences given that the linear models were based on *a priori* hypotheses of biomechanical variables that could induce particular patterns of footprint shape variation. For example, the pattern of variation described by PC2, which essentially captures depth at the forefoot relative to the heel, was hypothesized to be affected by hip excursion because it influences how far forward the body's center of mass travels before the foot leaves the ground. With a high magnitude of hip excursion during the second half of stance phase, the foot leaves the ground as the center of mass is far ahead of the ground contact point and one would expect that in such a scenario a relatively higher load would be generated through the forefoot compared to the heel. There could very well be different anatomical, biomechanical, or substrate mechanical variables that influence particular patterns of footprint shape variation that were not quantified and included in our models. Yet certain biomechanical variables do seem to have strong relationships with particular

patterns of footprint shape variation, and these relationships would be expected to be consistent even outside of this human sample.

This study also provides a new quantitative understanding of the ways in which certain patterns of human footprint topographic variation, and relationships between human locomotor biomechanics and footprint shape, are influenced by substrate mechanics. The results demonstrate that most patterns of footprint shape variation that are related to biomechanical variables are also sensitive to the amount of substrate displaced in a particular trial (this was the case for the first, fourth, and fifth principal component axes; Table 2). Furthermore, substrate deformability appeared to be solely responsible for variation along the third principal component axis of human footprint topographic variance which reflected the relative amount of deformation along an anteroposterior axis (heel/toe versus midfoot/metatarsal heads).

Bates and colleagues (2013), and also Morse and colleagues (2013), found that footprints in more deformable sediments tended to have deeper forefoot than heel impressions. That result corresponds well with the model describing variation along the first principal component axis of footprint topographic variance in this study. However, this study also found the pattern of shape variation (i.e., PC1) to be significantly influenced by gait type (Table 1). This study did not identify a clear ‘change point’ in footprint depth at which the primary influence on PC1 shifted from a biomechanical to a substrate mechanical effect, although Bates and colleagues (2013) proposed that such a transition may occur once footprints exceed 20 mm in depth.

It is interesting to note that while the effects of substrate compliance on patterns of variation in footprint morphology were statistically significant, their effects were typically in the same direction as the effects of biomechanical variables but of a smaller magnitude. First, this means that one can more confidently compare functional signals preserved in different footprints

so long as they are of comparable overall depths. If, for example, one came across two trails of footprints with similar stride lengths and similar overall depth, but one had a much deeper forefoot relative to heel impression than the other, then it is likely that differences in gait type produced those morphological differences. The reason for this is that the magnitude of the effect of gait type on PC1 is much greater (about three times greater) than the magnitude of the effect of sediment deformability. One would have to be much more cautious though in developing functional interpretations in cases where footprints differ significantly in their depths.

Second, the fact that substrate and biomechanical effects act in similar directions could also reflect relationships between bipedal biomechanics and substrate compliance. For example, one could tend to use an ‘exaggerated’ medial transfer of pressure as substrates become more compliant. The exact relationships between human biomechanics and substrate compliance, and their effects on footprint morphology, are relatively under-studied. However, simulation studies of the formation of theropod tracks have shed important light on this issue, and have revealed that differences in substrate properties can cause footprint morphologies to be misleadingly suggestive of locomotor differences (Falkingham et al., 2011).

Applying results to fossil hominin tracks

Some of the variables that significantly influence patterns of variation in footprint morphology directly contribute to certain definitions of ‘human-like’ bipedalism. For example, much debate has surrounded the reconstruction of early hominin limb joint postures during bipedal locomotion, and conflicting ideas exist regarding whether or not early hominins were capable of walking with a human-like posture. Based on skeletal anatomy, some researchers have argued that members of the genus *Australopithecus* likely employed somewhat compliant

467 bipedal gaits, and walked upright with greater degrees of hip and knee flexion than modern
468 humans do today (e.g., Stern and Susman, 1983; Schmitt, 2003). Others contend that the hip and
469 lower limb anatomy of *Australopithecus* would not have precluded them from fully upright,
470 human-like bipedalism (e.g., Lovejoy et al., 1973). These conflicting results and interpretations
471 continue due to the lack of clear skeletal signatures of the habitual motion patterns employed by
472 these early hominins during their bipedal locomotion. Previous research has demonstrated that
473 the footprints of humans walking with normal and compliant (bent-hip-bent-knee) gaits can be
474 distinguished, and that the *c.*3.7 Ma presumed *Australopithecus* footprints from Laetoli more
475 closely resemble those produced with extended limbs (Raichlen et al., 2010). This study has built
476 upon those results by showing that hip, and ankle joint motions are reflected in specific patterns
477 of footprint shape variation (specifically in the second and fifth principal component axes of
478 human footprint shape variation) within a large sample of humans who were all walking with
479 their normal extended limb gaits. This implies that even more subtle differences in lower limb
480 kinematics could be detected from the footprints of fossil hominins. Given the known influence
481 of even minor changes to limb compliance on locomotor energetics (e.g., Pontzer et al., 2009)
482 this could lead to the development of new hypotheses regarding the metabolic costs of bipedal
483 locomotor patterns employed by fossil hominins at various footprint sites.

484 Additionally, the results of this study show that a specific feature that is diagnostic of
485 human foot function, the transfer of plantar pressure to the medial metatarsal heads for
486 propulsion, can be detected within one specific pattern of footprint shape variation (along the
487 fourth principal component axis). This pattern of foot function is unique to humans compared to
488 other primates who occasionally walk bipedally, including chimpanzees (Elftman and Manter,
489 1935), bonobos (Vereecke et al., 2003), gibbons (Vereecke et al., 2005), and possibly orangutans

and gorillas (Crompton et al., 2012). The medial transfer of pressure allows humans to use their hallux for propulsion. Other primates do not exhibit such a pattern when walking on the ground because their halluces are adapted primarily for grasping during arboreal locomotion. Earlier researchers have suggested that the relatively shallow depth in the region of the first metatarsal head among the Laetoli hominin footprints may reflect a pattern of foot function that differs from what is seen in modern humans (e.g., Stern and Susman, 1983; Schmid, 2004; Bennett et al., 2009; but see White and Suwa, 1987). This study provides a better understanding of how the human toe-off mechanism is reflected in human footprint topography, and offers a framework for testing whether or not fossil hominin footprint morphologies fit within the human range of variation.

It is important to consider though how the results presented here can specifically be applied to analyses of fossil hominin footprints. As with any modeling approach, significant relationships merely inform us of how well the experimental data fit a particular linear model that we specify. These are not absolute, causal relationships. However, the significant relationships that we have uncovered can be used to suggest how different footprint shapes may reflect particular functional patterns. For example, if one were to uncover a trackway of fossil hominin footprints where traveling speed can be estimated from stride length, they could be compared to human tracks produced at similar speeds, on similar substrates, and of similar overall depths. In such a comparison, if the fossil hominin track were shown to have markedly deeper hallux and second toe impressions than the average human footprint, one could hypothesize that the hominin who created that track likely used a greater amount of hip retraction than the average human (based on the relationship between PC2 – which reflects relative medial toe to heel depth – and hip retraction). Of course if this interpretation coincides with other lines

of supporting evidence, such as morphological data, of the taxa presumed to have produced the footprint then one can make a stronger case for the functional interpretation of the tracks.

Limitations of this study for the analysis of fossil hominin tracks

This study does not provide any predictive models through which one could generate a prediction of the exact joint movements (e.g., x degrees of knee flexion) used by the hominin who produced a particular track. Future work in this direction, which could build on the results found here, would be very fruitful and may provide new avenues for interpreting biomechanics from fossil hominin footprints. Furthermore, one should be wary of confounding effects of speed and substrate on footprint morphology that were not explicitly accounted for in this experimental design. Interpretations of fossil hominin footprints based on these results should be, at the least, limited to comparisons that involve footprints created at similar speeds and of similar overall depths.

Conclusions

The results of the study presented here offer a novel quantitative framework from which to understand how biomechanical variables related to locomotor patterns are expressed in human footprint morphological variation. But they also offer a new understanding of some of the ways in which a substrate's mechanical properties influence the expression of biomechanical variables in footprints, and reveal patterns of footprint shape variation that do not appear to be biomechanically relevant. These results offer a framework that can be used, with appropriate caution, for developing biomechanical hypotheses from comparisons of fossil hominin footprint morphologies.

By building upon this understanding of how ‘human-like’ patterns of bipedalism manifest themselves in footprint morphological variation, fossil hominin footprints can be used in new ways to better understand detailed similarities or differences in the locomotion of different extinct hominin taxa. This experimental study provides the first means for quantitative, rather than qualitative, interpretations of locomotor patterns represented by different footprint assemblages. The linear mixed effects models presented here are characterized by relatively high residuals (Table 2) and therefore future work should pursue the development of robust predictive models from which one could generate more specific and more accurate predictions of the biomechanical pattern being expressed by a given footprint assemblage (e.g., the exact angles, +/- prediction error, of joints across the lower limb throughout a stride). However, the quantitative framework established here will allow comparisons to be made between different sets of fossil hominin footprints. It will also support the development of new hypotheses about how footprint morphologies reflect specific aspects of the locomotor patterns that produced them.

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702

703 **Figure legends**

704 Figure 1: Lateral photograph of volunteer performing footprint formation experiments. Subjects

705 passed over a trackway approximately 20 meters in length, and in the center of this trackway

706 were both a plantar pressure pad and a pit filled with hydrated sediment from a layer which

707 preserved 1.5-million-year-old fossil hominin footprints at Ileret, Kenya. Trials were discarded

708 and repeated if subjects visibly altered their gait to ‘target’ any part of the apparatus along this

709 trackway.

710

711 Figure 2: Stratigraphic section of FwJj14E site at Ileret, Kenya, with labeled locations of fossil

712 hominin footprint layers (figure from Dingwall et al., 2013; adapted from Behrensmeier, 2011).

713 The sediment used in these experiments came from the layer which contains “FLT 1”; all

714 footprint surfaces in this section are typologically very similar.

715

Figure 3: Image of 3-dimensional footprint model with markers identifying the regions from which footprint depths were measured. These regions mirrored those from which plantar pressure measurements were taken, but with an additional depth measurement taken from the medial midfoot (an area that typically did not experience any pressure when subjects walked across the firm pressure pad). All depth measurements were normalized in the same way as those of plantar pressure.

Figure 4: Scree plot showing the proportion of variance (y-axis) explained by the first ten principal component axes describing variation in the 14 regional measurements of footprint depth.

Figure 5: Bar plots showing the rotations which were applied to the 14 original footprint depth measurements in order to produce each of the first five principal components of footprint topographic variation. Positive loadings on a given axis are plotted in dark grey, while negative loadings are plotted in light grey.

Figure 6: Demonstrative boxplot of PC1 values (y-axis) and gait type (x-axis). This plot represents one experimental subject, allowing for easier visualization of the significant effect of gait type on PC1. The mixed effects models include random intercepts for individual subjects but the value of the slope (the magnitude of the effect) is calculated across all subjects. A summary of the model describing variation in PC1 across all subjects can be found in Table 2.

738 Figure 7: Demonstrative plots, from individual subjects, of PC2-5 values (y-axis) and different
739 variables that have significant effects on those principal components (x-axis). As in Figure 6,
740 these plots each show data from only one subject, to improve visualization of the significant
741 fixed effects. Summaries of the models describing variation in PC2-5 across all subjects can be
742 found in Table 2. These mixed effects models include random intercepts for individual subjects
743 but values of the slope (magnitudes of the effects) are calculated across all subjects.

744

fig 1

fig 2

fig 3

fig 4

fig 5

Region

fig 6

fig 7

Table 1. Summary table describing the original regional depth measurements that have the largest positive and negative loadings on the first five principal components of footprint depth variation (displayed in Figure 5). Those regions listed here had loadings that exceeded either the mean positive or the mean negative loadings for the given principal component axis.

Component	Primary positive loadings	Primary negative loadings
PC1	Metatarsals 1-4	Lateral and medial heel
	Toes 3-4	
PC2	Lateral and medial heel	Hallux
	Lateral midfoot	Toe 2
	Metatarsals 3-4	
PC3	Lateral and medial midfoot	Toes 2-4
	Metatarsals 4-5	
PC4	Metatarsals 1-2	Metatarsal 5
	Hallux	Toes 4-5
PC5	Lateral midfoot	Metatarsal 1
	Toe 2	Toe 5

Table 2. Summary of linear mixed effects models describing variation along the first five principal component axes of footprint topographic variance. The original inclusive linear models considered all of the variables in the corresponding row, while the reduced models retained only the statistically significant fixed effects (see Materials and Methods). The effects of gait type are directionally calculated as the effects of a walk relative to a run; for instance walking had a negative effect on PC1 scores.

Component	Median standardized residual	Fixed effect 1 (slope, <i>p</i> -value)	Fixed effect 2 (slope, <i>p</i> -value)	Fixed effect 3 (slope, <i>p</i> -value)	Effects lacking statistical significance
PC1	0.090		Substrate deformability (0.12, <0.001)		Hip excursion during first half of stance; hip excursion during second half of stance; maximum forefoot pressure relative to heel
PC2	0.109	Hip excursion during second half of stance (-0.28, 0.02)			Gait type; peak pressure beneath toes 2-5; peak pressure beneath hallux; substrate deformability
PC3	-0.003	Substrate deformability (-0.06, 0.01)			Gait type; angle of hip at foot strike; angle of ankle at foot strike; angle of hip at toe-off; angle of ankle at toe-off

PC4	0.107	Relative pressure across transverse toe-off axis (0.17, 0.05)	Substrate deformability (0.06, <0.001)		Gait type; angle of ankle at toe-off
PC5	-0.050	Gait type (-0.14, <0.001)	Angle of ankle at toe-off (-0.19, 0.05)	Substrate deformability (-0.04, 0.02)	Relative pressure across transverse toe-off axis; peak pressure beneath hallux; angle of ankle at toe-off