Project title: A novel experimentally-based investigation of Plio-Pleistocene fossil hominin footprints

Funding program: Wenner-Gren Foundation, Dissertation Fieldwork Grant

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Project abstract:

Bipedalism is a fundamental modern human behavior but many questions about the evolution of bipedalism in our extinct ancestors remain unanswered. Paleoanthropologists studying the skeletal anatomy of fossil hominins have analyzed data in many different ways only to arrive at conflicting conclusions regarding when and how bipedalism evolved. New approaches are necessary to resolve this ongoing debate.

This study applies novel methods to the analysis of a different type of data, in the form of recently discovered fossil hominin footprints. One well-known set of fossil footprints was uncovered over 30 years ago at Laetoli, Tanzania (dated to about 3.7 million years ago). Within the past three years, new discoveries have unearthed fossil hominin footprints from different time periods at Ileret, Kenya (~1.5 million years ago), and Engare Sero, Tanzania (~120 thousand years ago). With a growing sample of hominin fossil footprints from various times throughout the Plio-Pleistocene, these unique data can be used to test earlier hypotheses, and develop new ones, regarding the evolution of hominin anatomy and bipedal locomotion. However, much remains unknown about how anatomy and gait are recorded in footprints. The proposed study will use experimental biomechanics to determine, for the first time, how specific variables of foot anatomy and gait are preserved within footprint topography. The fossil footprints from Laetoli, Ileret, and Engare Sero will be analyzed in light of these experimental results to directly test the hypothesis that the same anatomical and functional adaptations for bipedal locomotion seen in modern humans were present in the hominins that produced these footprints at 3.7, 1.5, and 0.12 Ma.

Application discipline: Physical/Biological
Geographic research area: Africa
Sub-discipline: Hominid evolution

Key words: fossil footprints, experimental biomechanics, hominin locomotion

RESEARCH PROPOSAL

20. Are you resubmitting an application that was unsuccessful in a prior season? Yes

If the current application is a resubmission of a previous unsuccessful Dissertation Fieldwork grant application, you must include a resubmission statement. This statement should describe how your application differs from your previous submission and how you have addressed reviewers' comments. Include this resubmission statement whether or not the current project is similar to your previous one. A resubmission statement is often a benefit to an applicant in demonstrating how and why his/her thinking has changed.

In response to a number of excellent point raised by reviewers, the following changes have been made:

1) We emphasize the unique nature of this experimental study, and the novel approach it takes with respect to past studies of fossil hominin footprints. The project outlined here will be one of the very few to systematically break down the process of footprint formation into its component parts, in order to understand how specific variables related to foot anatomy, gait, and sediment properties, simultaneously and together influence footprint morphology. Past studies (e.g., Day & Wickens, 1980; Charteris et al., 1981, 1982; Tuttle et al., 1990; Musiba et al., 1997; Meldrum, 2004; Berge et al., 2006; Raichlen et al., 2008, 2010; Crompton et al., 2011) have often relied upon comparing the final products - footprints produced by human subjects, or sometimes nonhuman great apes - to footprints in the human fossil record in order to draw inferences about fossil hominin anatomy and gait. The studies to date leave open many questions about how anatomy, gait, and sediment properties influence print morphology, thereby limiting the conclusions that can be drawn from fossil footprints about hominin foot anatomy and gait. This project takes an alternative approach, to study how specific anatomical, functional, and sedimentary variables influence the morphology of footprints produced by humans and our closest living relatives, chimpanzees. We feel that such an approach is imperative in order to understand how specific anatomical and functional variables are recorded in footprint shape, given that we are ultimately trying to interpret footprints produced by fossil hominin taxa that almost certainly have no exact modern anatomical or functional analogue. D'Août and colleagues (2010) conducted the only prior study of the human footprint formation process, in which they examined the relationship between the distribution of plantar pressure and footprint depth. They found only weak relationships between pressure and depth, and concluded that a large amount of variation was probably left unexplained because they were unable to quantify and control variables related to foot anatomy and sedimentary properties. A similar result was found in a pilot study I conducted (see Question 4 and Hatala et al., 2012), where significant relationships were found between plantar pressure and footprint shape, but again the majority of the variation was left unexplained.

In the proposed project, we measure variables of hard tissue pedal anatomy including longitudinal arch height and hallux divergence angle, because these features have been critical in debates over the functional interpretation of fossil skeletal evidence and likely leave measurable impressions in footprints. In response to reviewer comments, we also employ an entirely new system, involving extremely thin and flexible sensors worn on the bottom of the foot (described above), to measure plantar pressure directly at the interface between the foot and soft sediment. Finally, we quantify sediment moisture levels and the sediment's resistance to deformation, in order to understand how these variables influence footprint morphology. We will use geometric morphometrics and multiple regression analyses to understand how these anatomical, functional, and sedimentary variables together govern the shapes of footprints. These results will enable the interpretation of fossil footprints in a new light, with the first quantitative basis for inferring how variables of foot anatomy and gait are expressed in fossil hominin footprints.

The analyses of fossil hominin footprints in this study are also unique. The framework of the experimental research will provide a novel approach for re-analyzing the famous and oft-studied Laetoli footprints. The other sets of fossil hominin footprints that will be analyzed, 1.5 Ma footprints from Ileret, Kenya and 120 ka prints from Engare Sero, Tanzania, represent new discoveries and this project will provide the first detailed, quantitative assessment of both of them. Using the proposed techniques to infer aspects of foot anatomy and gait from these three sets of fossil hominin footprints will provide a new comparative analysis of fossil hominin anatomy and gait at 3.7 Ma, 1.5 Ma, 120 ka, which will directly test the contentious hypothesis that the anatomical and functional adaptations of the modern human foot were present in all fossil hominin taxa that produced these footprints.

2) My collaborators and I concede that differences between the sediment that preserves the Ileret footprints and the ash at Laetoli may produce significant variation in footprint shape. As such, we now include a quantitative measurement of the sediment's resistance to deformation in our multivariate experimental approach. We will analyze how this variable influences footprint morphology, and also be able to test how it influences records of foot anatomy and gait. We believe that, with our data on the influence this variable has on footprint morphology, one will be able to theoretically predict how a more, or less, deformable substrate would behave in response to foot function.

3) We have revised our budget justification and now provide greater detail on how we intend to fund items for which we are not requesting funding in this proposal. The budget has been altered significantly because the applicant was awarded a research grant from The Leakey Foundation. Also, the use of the Novel Pedar pressure sensor system is new to this re-application because that system just recently became available.

4) We describe that no permits are needed to bring the fossil footprint-bearing sediment from Ileret back to the United States. The sediment has already been approved for export by the Kenya Plant Health Inspectorate Service (KEPHIS) after being found to contain no organic material. Per USDA regulations, inorganic sediment does not require an import permit. Therefore, the methodology proposed by the applicant will not be obstructed by potential difficulties in obtaining sediment import permits.

21. Project Description Question 1: *Describe your research question/hypothesis or research objective. That is, what will the focus of your investigation be?*

Researchers as early as Charles Darwin (1871) have described the evolution of bipedalism as a change that defined our human lineage. Yet there is still no consensus among paleoanthropologists about its evolutionary history. Did bipedalism evolve more than once? Can we reconstruct the ancestor/descendent sequence of changes leading to the type of locomotion practiced by modern humans? Changes in anatomy between hominin species may have resulted in, or been adaptations to, different styles of locomotion in our ancestors and we know that these changes eventually led to the type of bipedalism seen today in modern humans. However, the timing, nature, and ecological contexts of such changes remain largely unknown.

Footprints are usually ephemeral but a few sets of footprints made by extinct hominins have fossilized, providing unique windows into the evolutionary history of hominin locomotion. Fossil footprints preserve the only direct record of both the foot anatomy and gait of extinct hominin species, and offer a new approach to address debates over the functional interpretation of fossil evidence. Footprint analysis has proven invaluable in reconstructing the locomotion of dinosaurs from fossilized footprints (e.g., Gatesy et al., 1999). But until recently, hominin footprints were rare in the Plio-Pleistocene fossil record. One oft-studied set was discovered in 1978 at Laetoli, Tanzania (Leakey & Hay, 1979). These prints definitively show that hominins, often assumed to have been *Australopithecus afarensis*, walked bipedally about 3.7 Ma (million years ago; White, 1980). However, studies continue to arrive at conflicting conclusions regarding the 'humanness' of the foot anatomy and locomotion implied by these footprints (e.g, Stern & Susman, 1983; Deloison 1991; Bennett et al., 2009 contra Day & Wickens, 1980; White & Suwa, 1987; Raichlen et al., 2011). A new approach, such as the experimental one proposed here, is required to move this discussion forward. Further, additional sites preserving Plio-Pleistocene fossil hominin footprints have been discovered in the past three years. The recently discovered fossil hominin footprints at Ileret, Kenya (about 1.5 Ma; Bennett et al., 2009) can provide new data that will enable the direct comparison of the implied foot anatomy and gait of hominins at 3.7 and 1.5 Ma. These data will facilitate the direct testing of hypotheses related to locomotor behavior before and after the extensive changes in hominin anatomy that occurred around 2 Ma (Wood & Collard, 1999). The Ileret footprints offer the only opportunity presently available to study East African hominin foot anatomy at 1.5 Ma, as relevant skeletal material is virtually unknown. Even more recently, one of the earliest modern human fossil footprint sites (~120 Ka) was uncovered at Engare Sero, Tanzania (Hatala et al., 2011; Richmond et al., 2011). This sample of fossil footprints presents the first opportunity for a quantitative analysis of gait in the earliest members of *H. sapiens* and, if properly analyzed, will provide a comparative context to assess the 'humanness' of the Laetoli and Ileret footprints. Moreover, the site at Engare Sero preserves footprints of individuals who were almost certainly running, allowing us to test hypotheses regarding the way that our immediate ancestors ran (e.g., Lieberman et al., 2010).

However, before these unique and invaluable data can be used to directly inform hypotheses about the evolution of hominin anatomy and locomotion, we need to thoroughly understand the dynamic interaction between the foot and the soft sediment in which footprints are formed. We intend to develop such an understanding by using experimental biomechanical methods to demonstrate how specific variables of foot anatomy and gait are reflected in the morphology of footprints. Results from these experiments will be integrated with analyses of fossil footprints in order to interpret the foot anatomies and gaits that produced three different sets of fossil human footprints. This project will use evidence from fossil footprints to directly test the hypothesis that all features of modern human foot anatomy and gait were present in the maker of the Laetoli footprints, and foot anatomy and gait remained essentially unchanged in the hominins that created the Ileret and Engare Sero footprints. Approaches that will be taken include:

1) Understanding the dynamics of footprint formation.

a. Human experiments. Habitually unshod subjects will be asked to walk and run through soft sediments to produce footprints. They will also do so while wearing a custom-designed pressure-sensing 'sock' to directly measure the dynamic distribution of pressure beneath their feet as they walk and run on soft sediment. Aspects of foot anatomy will be measured and sediment saturation levels and mechanical properties will also be quantified. These controlled experiments will enable us to gain the first understanding of how specific anatomical and functional variables are recorded in footprint morphology. For example, are variations in foot anatomy (e.g., divergence angle of hallux, height of longitudinal arch) discernible from footprints? Do consistent relationships exist between the distribution of plantar pressure and footprint topography? Do relationships between anatomy, gait, and footprint morphology change with variation in sediment properties?

b. Comparative primate experiments. Similar laboratory experiments are already underway with chimpanzees at Stony Brook University, in order to understand how their foot anatomy and function are recorded in the footprints they produce when walking bipedally. This comparative research is critical, given hypotheses that early hominin anatomy and bipedal locomotion may have resembled modern chimpanzees'. How are differences between human and chimpanzee foot anatomy (e.g., position of hallux and presence of longitudinal arch) and foot function (distribution of plantar pressure) reflected in their footprints formed by walking through soft sediment? Do these relationships change with variation in sediment properties?

2) The evolution of bipedal gait as inferred from fossil footprints. Fossil hominin footprints from three different locations and times (Laetoli, 3.7 Ma; Ileret, 1.5 Ma; Engare Sero, 0.12 Ma) will be examined in the light of results from experiments on footprint formation. Are the distinguishing characteristics of a modern human-like foot anatomy (e.g., adducted hallux, medial longitudinal arch) and gait (e.g., toe-off through hallux) evident in all three samples of fossil hominin footprints? What do comparisons among these fossilized hominin footprints tell us about similarities or differences in their foot anatomy and/or gait?

22. Project Description Question 2: *How does your research build on existing scholarship in anthropology and closely related disciplines? Give specific examples of this scholarship and its findings.*

While fossil hominin footprints provide unique opportunities for studying locomotion, they also present the complex problem of interpreting the dynamic interaction between a foot and soft sediment that results in a footprint. Some researchers have used experimental approaches to address questions about fossil footprints but much remains unknown about the quantitative relationships between the anatomical, functional, and sedimentary variables that control footprint morphology, and how this information can be used to accurately interpret fossil hominin footprints.

Day and Wickens (1980) conducted the earliest experimental analysis of the Laetoli footprints, in which they asked modern humans to produce footprints in fine-grained sand and then compared contour maps of these prints to the fossil footprints from Laetoli. These authors explained that a footprint is not simply a mirror image of foot anatomy and must also reflect the process by which the foot generates propulsive forces. However, Day and Wickens (1980) did not directly measure those forces and relate them to footprint shape. Many others have pursued similar approaches, asking humans (or occasionally nonhuman great apes) to produce footprints and then comparing aspects of their prints to those from Laetoli. In some cases the Laetoli prints have been found to be human-like (e.g., Day & Wickens, 1980; Charteris et al., 1981, 1982; Tuttle et al., 1990; Raichlen et al., 2008, 2010; Crompton et al., 2011), but others have noted important differences (e.g., Meldrum, 2004, Berge et al., 2006). Much of this debate comes from disagreement over how to interpret anatomy and gait from footprints.

A study by D'Août and colleagues (2010) was the first to break down the process of footprint formation, and it compared quantified measures of foot pressure to footprint morphology. These authors found that a relationship existed between foot pressure and footprint depth, although they noted (p.524) that "…the exact nature of the interaction between the dynamics of the foot and the substrate needs to be elucidated." D'Août and colleagues (2010) conceded that their study would ideally utilize a "pressure sock" that could measure pressure at the foot-soft substrate interface, although no such equipment was available. Since we are primarily interested in relating footprint morphology to the distribution of propulsive forces at the foot-substrate interface, I have worked with Novel, a leading manufacturer of pressure-sensing equipment, to develop an innovative custom-made system that integrates a flexible sensor on the bottom of the foot within a neoprene sock, thereby minimally obstructing the natural movements of the foot. Our use of this system will produce the first quantitative data on the dynamic distribution of plantar pressure at the foot-substrate interface as subjects walk through soft sediment. The proposed study will also include direct measurements of foot anatomy (hallux divergence angle and longitudinal arch height) and sediment properties (moisture content and resistance to deformation). Together, these three variables - foot anatomy, foot function, and sediment properties - are the primary determinants of footprint morphology. Consequently, this study will be the first to quantify and investigate all variables governing footprint formation so that we can understand the simultaneous effects of, and relationships between, these variables. We will then be able to apply this unique, new information to the interpretation of fossil footprints and develop specific hypotheses about how variables of foot anatomy and gait were expressed in fossil hominin species that have no exact modern analogue.

The potential of the information preserved within fossil hominin footprints was immediately recognized upon the discovery of the Laetoli footprints in 1978 (Leakey & Hay, 1979). While hard tissue evidence indicated that members of the genus *Australopithecus* were bipedal, the Laetoli prints pushed back the oldest evidence of bipedalism from 3.0 Ma to around 3.7 Ma (White, 1980). Several researchers supported the idea that these footprints reflect a modern human-like form of bipedalism (see refs. above). However, others have argued that the Laetoli prints reflect a foot anatomy and gait that differs from, and is more primitive than, that of modern humans and more recent hominins (refs. above; Deloison, 1991; Bennett et al., 2009). This project will take a novel approach to the interpretation of the Laetoli footprints by re-analyzing them in the context of experimental results obtained from humans and chimpanzees. Specifically, we will derive the relationships between anatomical and functional variables and experimentally-produced human and chimpanzee footprints, then use 3D analytical methods to quantify the differences and similarities among the experimental, Laetoli, and other fossil hominin prints. The inclusion of chimpanzees in this study is crucial given that they are modern humans' closest living relatives (Page & Goodman, 2001) and one prominent hypothesis in paleoanthropology suggests that early hominin postcranial anatomy is consistent with a bent-hip bent-knee compliant bipedal gait, similar to that observed in chimpanzees (Stern & Susman, 1983; Schmitt, 2003). This study differs dramatically from recent analyses (e.g., Raichlen et al., 2010; Crompton et al., 2011) in that we will use experimental results to generate the first quantified estimates of variables related to the foot anatomy (e.g., longitudinal arch height) and foot function (e.g., distribution of plantar pressure) reflected in the Laetoli footprints.

We will also provide the first detailed analysis of recently discovered 1.5 Ma fossil footprints from Ileret, Kenya. Preliminary analyses have suggested that these footprints reflect aspects of a modern human anatomy and gait (Bennett et al., 2009). The proposed study will expand upon the previous work by establishing an experimentally-derived quantitative foundation for interpreting specific variables of foot anatomy and function from fossil hominin footprints. Applying our results to the Ileret fossil prints will unlock the information held within the most complete evidence of hominin foot anatomy at 1.5 Ma.

Finally, we will analyze the 350 footprints uncovered to date at the ~120 ka site of Engare Sero, Tanzania. This sample comprises more than 30 trackways of multiple prints. This exceeds, by two orders of magnitude, the footprint totals at the South African sites of Nahoon Point (~124 ka, only 2 prints preserved; Roberts, 2008) and Langebaan Lagoon (~117 ka, 3 prints; Roberts, 2008), making Engare Sero the appropriate location for detailed analyses of early *H. sapiens* locomotion. The analysis of these footprints will provide a comparative context to interpret the anatomy and gait of earlier hominins and permit the first quantitative analysis of foot anatomy and gait in early *H. sapiens*.

23. Project Description Question 3: *What evidence will you need to collect to answer your research question? How will you go about collecting and analyzing this evidence?*

1) Understanding the dynamics of footprint formation.

a) Human experiments (data collection Summer 2013). Field experiments on footprint formation will be conducted with 20 consenting Daasanach adults (10 men, 10 women) living near Ileret, Kenya. Anthropologists working in Ileret since the 1960s have attested that the Daasanach grow up unshod or, just within the last five years, have been minimally shod (JWK Harris & AK Behrensmeyer, pers. comm.). Thus, their foot development is not influenced by modern footwear.

A 15-m long trackway will be cleared in a flat space adjacent to the site of fossil footprint excavations. In the middle of it, we will dig a pit measuring 150 cm long, 60 cm wide, and 25 cm deep and fill it with sediment directly excavated from a geological layer preserving the 1.5 Ma footprints at Ileret. Water will be progressively added to this sediment during the experiments, beginning with the level at which a footprint is barely visible and proceeding to the point at which footprints are so soft that preservation in the fossil record would be impossible. Prior to each trial, moisture levels will be quantified using a digital moisture meter. A portable penetrometer, a standard piece of equipment in soil mechanics, will be used to measure the pressure required to depress the sediment to a specified depth, in KPa.

Measurements of height, weight, greater trochanter height, tibial tuberosity height, lateral malleolus height, and foot length will be taken from each subject. Digital calipers will be used to measure longitudinal arch height, as well as hallux length and horizontal displacement (to derive divergence angle) on the subjects' weight-bearing feet while standing. Neon markers will be placed at the hip, knee, ankle, and foot, allowing for later digitization and analysis of kinematic data (velocity and joint angles) from high-speed video using ImageJ software at George Washington University (GWU). Subjects will be outfitted with Novel Pedar insoles, enclosed within NRS Hydroskin neoprene socks. This apparatus is pliable and minimally obtrusive to movements of the foot (only 2.5 mm thick), providing a snug fit that moves with the toes and all other joints. The insole will be connected by a thin wire to an interface box on the subject's hip, which sends real-time (100 Hz) pressure data to a laptop via Bluetooth. Subjects will pass over the trackway at five different speeds (slow, normal, and fast walks, jog, sprint; quantified from video). Each subject will complete at least 3 trials wearing the Pedar sensor, and 3 barefoot, at each speed. After each barefoot trial, the footprint will be photographed about 15 times at a variety of angles and heights, allowing for the later creation of 3-dimensional models using photogrammetric software at GWU. Following photography, footprints will be obliterated and the sediment leveled.

b) Chimpanzee experiments (data collection Spring-Fall 2012). The chimpanzee experiments will take place at Stony Brook University and data collection methods will be similar to those described above. However, given the limitations presented by working with chimpanzees, a meter-long plantar pressure pad (RSScan International) will replace the pressure-sensing insoles. The pad will rest upon a trackway, approximately 0.5 meters before a container filled with the sediment. Comparable RSScan data have already been collected from 38 Daasanach adults and will provide a method for directly comparing the relationships between pressure and footprint morphology in humans and chimps (see Question 4; Hatala et al., 2012). The sediment used in field experiments has already been shipped back to the US for these experiments. Biometric measurements will be identical to the human protocol and 40 bipedal pressure/footprint trials will take place with 2 chimpanzees, covering a range of walking speeds.
c) Analysis of experimental data (2013-2014). Data will be collected from the following 11 anatomical regions on the pressure distribution map (using pressure software) and on the 3D footprint model (using Geomagic Qualify): the medial and lateral heel, medial and lateral midfoot, metatarsal heads 1-5, hallux, and second toe. Measures of peak pressure and pressure-impulse (pressure*time) at each of these landmarks will be exported. Positional (x-y-z) data for each landmark on the 3D footprint model will be collected within Geomagic Qualify. We will test hypotheses that correlations exist between anatomical variables (e.g., arch height) and/or functional variables (e.g., peak pressures, joint angles) and relative footprint depths in each region of the foot. Geometric morphometric analyses will be used to examine within- and between-subject relationships between footprint shape and multiple 'predictor variables', including measures of speed, joint angles, medial longitudinal arch height, hallux divergence, plantar pressure, sediment saturation level, and resistance of the sediment to deformation. Footprints will be transformed using a Procrustes fit, then principal components analyses will be conducted. Multiple regression analyses will be used to determine the influence of the 'predictor variables' on the principal components that describe variation in footprint shape. This innovative approach will provide the first information about the quantitative relationships between specific anatomical, functional, and sedimentary variables and footprint shape.
2) The evolution of bipedal gait as evidenced by fossil hominin footprints (data collection 2012-2013, analysis 2013-2014). All fossil footprints will be documented using photogrammetry. First-generation casts of the Laetoli prints will be scanned at the National Museums of Kenya, and the Ileret and Engare Sero footprints will be photographed in the field. As described previously, about 15 photographs at a variety of angles and heights will be taken of each footprint. Both trackways and isolated prints will be documented, although the focus will be on footprint trails. Trails are necessary to calculate stride and step lengths, which will be important for discerning walking speed prior to any comparative analyses. Landmarks will be placed at the 11 anatomical landmarks listed previously. Multivariate statistical methods will be used to examine within- and among-site variations in footprint morphologies. Geometric morphometric analyses will elucidate shape differences between the morphologies of the 3.7, 1.5, and 0.12 Ma fossil hominin footprints. Differences will be examined in light of experimental results on footprint formation, to relate morphological differences between footprints to particular characteristics of foot anatomy, gait, and possibly sedimentary differences. These results will enable a unique test of the hypothesis that all features of human foot anatomy and gait were present in the hominins that made the Laetoli, Ileret, and Engare Sero fossil footprints.

24. Project Description Question 4: *What is your training; how are you prepared to do this research? List examples of your language competence, technical skills, previous research, and any other relevant experience. Describe any work you have already done on this project, and/or how it relates to your prior research. If you are collaborating with other academic personnel describe their role/s in the project and the nature of the collaboration.*

Most equipment for studies of gait (pressure pad, video camera) and photogrammetry (camera, lenses, software) are currently available at GWU and I previously worked with nearly all methods for data collection and analysis during the pilot project, described below. I will be trained to use the new Novel pressure system by an external advisor (Wunderlich) who has extensive experience using a similar system. I am collaborating with three external advisors (Demes, Larson, Wunderlich) and a supervisor (Richmond) who have years of experience in biomechanical experiments with nonhuman primates. All have worked with me to design the chimpanzee experimental protocol and two (Demes and Larson) will be on site during experimentation. I have gained extensive training and experience in field excavation techniques, including those specific to fossil footprints, during my ongoing tenure as a member of the Engare Sero Research Project and as a researcher and instructor with the Koobi Fora Field School. My supervisor (Richmond) also has years of paleontological field experience, and serves as the lead hominin paleontologist of the Koobi Fora research team.

During the 2010 and 2011 field seasons, I led a pilot study with 38 consenting adults (19 male, 19 female) from the habitually unshod Daasanach tribe at Ileret, Kenya (Hatala et al., 2012). This study followed the protocol outlined above, but with pressure data collected from the RSScan pressure pad rather than the custom-designed 'pressure sock', which had not yet been conceived and developed. This pilot study assessed the relationship between the distribution of plantar pressure and footprint depths across 10 regions of the foot (medial and lateral heel, lateral midfoot, all 5 metatarsal heads, hallux, second toe). Data were collected from subjects walking at normal and fast speeds.

The cumulative assessment of the correlation between pressure and depth revealed that the two were significantly correlated. Maximum pressure explained a greater amount of variance in footprint depth (Spearman's $\rho = 0.4860$) than did pressure-impulse ($\rho = 0.2906$), although both measures of plantar pressure were significantly correlated with measures of print depth ($p<0.0001$). When data from each walking speed were analyzed separately, we found that the relationship between plantar pressure and footprint depth changed with walking speed. A stronger relationship between maximum pressure and depth existed at fast walking speeds ($\rho=0.5725$) than at normal speeds ($\rho=0.3853$) but both relationships were significant ($p<0.0001$). The same was true of the correlations between pressure-impulse and depth at fast ($\rho=0.3890$, $p<0.0001$) and normal ($\rho=0.1841$, $p = 0.0003$) walking speeds.

It was possible that between-subject differences in foot anatomy led to smaller-than-expected correlation coefficients between plantar pressure and footprint depth. Further analyses tested the correlation between pressure and depth for each subject independently. Significant correlations between maximum pressure and depth were found in 26 of the 38 subjects. Correlations between impulse and print depth existed in only 13 subjects. We also explored the general patterns by which peak plantar pressure and footprint depths were distributed and found similarities between them. Both peak pressure and footprint depth were greatest at the heel and hallux, intermediate at the metatarsal heads, and least at the lateral midfoot. The second toe left deep impressions despite low peak pressures, probably an effect of its small surface area relative to the other regions examined.

This pilot study established that the distribution of plantar pressure is correlated with the topography of footprints created in the sediment that preserves the 1.5 Ma fossil footprints at Ileret. This result differed from those of D'Août and colleagues (2010) who found that the distribution of plantar pressure at the foot-pressure pad interface was not correlated with the morphology of footprints made in sand. Differences in sediment mechanics likely account for why the sediment from Ileret preserved footprints that were topographically linked to the distribution of pressure measured on a pressure pad, but the sand used by D'Août and colleagues (2010) did not. These pilot results support the hypothesis that relationships between foot anatomy, foot function, and footprint morphology change with sediment properties.

Most importantly, these pilot results illustrate the utility of a multivariate approach in the investigation of the footprint formation process. The coefficients of correlation between pressure and footprint depth demonstrate that plantar pressure significantly influences footprint depth, but explains less than half of its variation. This provides further justification for the methods of the proposed study, in which we will control and quantify anatomical, functional, and sedimentary variables, and analyze their simultaneous effects on footprint shape. Furthermore, the relationship between plantar pressure and footprint morphology may be different when new methods are applied to measure pressure at the interface of the foot and soft sediment. Our results highlight the fact that it is necessary to gain a more complete understanding of how specific anatomical, functional, and sedimentary variables influence footprint morphology before we can develop accurate functional interpretations of fossil hominin footprints. These invaluable data will enable the construction of better informed hypotheses regarding the evolution of human foot anatomy and locomotion.

I have been committed to presenting results of this research at professional meetings (e.g., Hatala et al., 2011; Hatala et al., 2012) and have also made consistent efforts to make my research available to the broader public. For example, I frequently participate in education and outreach programs organized through collaboration with the Smithsonian Institution's Human Origins Program (see Curriculum Vitae). Also, building on recent coverage of this research (e.g., Science in 2011, History Channel in 2012), my supervisor and I plan to continuing working with broader media to communicate this research to the public. This project will directly contribute to training Kenyan, South African and US undergraduate students, including those from underrepresented groups, in scientific research and paleoanthropology. All field experiments are conducted in collaboration with the Koobi Fora Field School, through which ten undergraduates from Kenya, South Africa, and the US were already trained as research assistants during the pilot phase of this project.

25. Project Description Question 5: *What contribution does your project make to anthropological theory and to the discipline? Please note that the Foundation's mission is to support original and innovative research in anthropology. A successful application will emphasize the contribution its proposed research will make, not only to the specific area of research being addressed, but also to the broader field of anthropology.*

Bipedalism is a defining characteristic of modern humans and it has had profound effects on the evolution of our species. For example, it freed the hands from locomotor obligations, which eventually allowed fossil hominins to develop new technologies, such as stone tools, and exploit new resources. It permitted long-distance travel, opening up new territories and potential migration routes. In many ways, bipedalism set the course for the evolution of our species. Yet despite its significance, the origins and evolution of bipedalism remain poorly understood.

This situation persists in large part because of debates over the interpretation of the fossil record. Fossil bones have revealed that early hominins possessed unique combinations of some primitive anatomical traits, which would have been advantageous for tree-climbing, alongside other derived traits, which are undoubtedly adaptations for terrestrial bipedalism. Despite close examination and detailed analyses of the fossil skeletal evidence, paleoanthropologists remain at an impasse regarding the interpretation of anatomies with no exact modern analogues.

Fossil footprints offer a new approach that circumvents the problems that arise from indirect functional interpretations of fossil bones by providing direct snapshots of both foot anatomy and gait. However, before these invaluable data can be extracted from fossil footprints, quantitative methods must be developed for interpreting specific aspects of foot anatomy and locomotion from footprint morphology. While it is obvious that the makers of the Laetoli, Ileret, and Engare Sero fossil footprints walked on two legs, there are currently no methods for determining whether or not they possessed the full suite of anatomical and functional attributes that characterize modern human bipedalism. The proposed project will develop such a method.

This project is transformative in that a novel experimental approach will be used to garner the first quantitative understanding of the footprint formation process. These experiments will assess the relationships between footprint morphology and specific variables of foot anatomy, gait, and sediment properties. Doing so will provide a new approach for developing accurate interpretations of specific features of foot anatomy and gait from fossil hominin footprints.

These results will then be used as a framework for analyzing three sets of Plio-Pleistocene fossil hominin footprint data, including two that are new discoveries. In doing so, this study will provide a unique and innovative test of the hypothesis that the full suite of modern human bipedal adaptations were present in the foot anatomies and gaits of fossil hominins at 3.7 million, 1.5 million, and 120 thousand years ago. This project will shed new light on long-standing debates and allow new hypotheses to be developed regarding the timing and nature of the evolution of human bipedalism.

PROJECT BIBLIOGRAPHY

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