Project title: Fossil hominin footprints and the dynamics of footprint formation

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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 anatomy of fossil hominin species have analyzed data in many different ways only to arrive at conflicting conclusions regarding when and how bipedalism evolved. The proposed study offers a new approach to analyzing a different type of data, in the form of recently discovered fossil hominin footprints. First, biomechanical experiments on footprint formation will be conducted with habitually unshod modern human populations and with chimpanzees, to develop an understanding of how different details of human and chimpanzee foot anatomy and bipedal gait are preserved in footprints. These results will then be used to provide accurate interpretations of foot anatomy and walking gait from three different fossil hominin footprint sites at Laetoli, Tanzania (dated to about 3.7 million years ago), Ileret, Kenya (1.5 million years ago), and Engare Sero, Tanzania (120 thousand years ago). Evidence from these fossil footprints will be used to directly test the hypothesis that all features of a modern human-like foot anatomy and gait were present in *Australopithecus afarensis*, and foot anatomy and gait remained essentially unchanged in *Homo erectus* and later at the emergence of *Homo sapiens*. Additionally, experiments on footprint formation with modern runners will be combined with analyses of the oldest known fossil running footprints at Engare Sero, as the first direct test of hypotheses regarding the evolution of running in later *Homo*. Studying these direct snapshots of locomotion at three very different points in human evolutionary history will provide an opportunity to develop new hypotheses about the evolution of modern human-like bipedalism.

I. Research objectives

Researchers as early as Charles Darwin (1871) have described bipedalism – the ability to walk on two legs – as a unique evolutionary change that defined our human lineage. Yet despite general agreement that bipedalism is especially important to our species, there is no consensus among paleoanthropologists about its evolutionary history. Changes in anatomy between hominin species may have resulted in, or been adaptations to, different styles of locomotion and we know that these changes are related 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 a unique window into the evolutionary history of hominin locomotion. Fossil footprints preserve the only direct record of both the foot anatomy and gait of extinct hominins, and offer a new approach for developing functional interpretations of fossil evidence. Such an approach has already proven invaluable in reconstructing locomotor patterns of dinosaurs from fossilized footprints (Gatesy et al., 1999). However, until quite recently, hominin footprints were rare in the fossil record. One very well-known set of hominin prints dating to about 3.7 million years ago (Ma) was discovered in 1978 at Laetoli, Tanzania (Leakey and Hay, 1979) and later attributed to *Australopithecus afarensis* (White and Suwa, 1987). But aside from that site, fossil hominin footprint discoveries have either been from much younger Holocene sediments, or preserved in ways that inhibit detailed reconstructions of gait (e.g., Behrensmeyer and Laporte, 1981; Mietto et al., 2003; de Lumley, 1966; Mountain, 1966; Roberts and Berger, 1997).

Recent discoveries of probable *Homo erectus* fossil footprints at Ileret, Kenya (about 1.5 Ma; Bennett et al., 2009) provide new data that will allow for direct comparisons of the implied foot anatomy and gait of *H. erectus* and *Au. afarensis*, and the direct testing of hypotheses related to locomotion before and after the extensive anatomical changes that occurred in hominins around 2 Ma. Even more recently, one of the earliest modern human fossil footprint sites (~120 thousand years ago; 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 quantitative analyses of gait in the earliest *H. sapiens*, and provides a comparative sample to assess the 'humanness' of the Laetoli and Ileret footprints. Moreover, the site at Engare Sero preserves trails of footprints that reflect running gaits, allowing us to test hypotheses regarding the way that our immediate ancestors ran.

The growing sample of fossilized hominin footprints will allow us to address important questions about the evolution of bipedal gait within the hominin clade. However, before that process can begin, we need to generate a thorough understanding of the dynamic interaction between the foot and the soft sediment in which an impression is formed. We intend to develop such an understanding by using experimental biomechanical methods to demonstrate how aspects of foot anatomy and gait are reflected in the morphology of footprints. **This project will integrate experimental results with data from fossil footprints to directly test the hypothesis that all features of a modern human-like foot anatomy and gait were present in *Au. afarensis*, and foot anatomy and gait remained essentially unchanged in *H. erectus* and later at the emergence of *H. sapiens***. Additionally, experiments on footprint formation with modern runners will be combined with analyses of the oldest known fossil running footprints at Engare Sero, to directly test hypotheses regarding the evolution of running in later *Homo*. The 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 across a pressure pad, and to produce footprints by walking and running through soft sediments so that we can relate foot anatomy and the distribution of foot pressures to the morphology of footprints. For example, what relationships exist between peak pressures and footprint depth? How does walking speed affect pressure distributions and the form of footprints?
   b. *Chimpanzee experiments.* Experiments are planned with common chimpanzees to investigate how they distribute pressure and produce footprints while walking bipedally. How are any differences in pressure distribution, and any differences in foot anatomy (e.g., abducted hallux and lack of longitudinal arch), reflected in footprints formed by chimpanzees in soft sediment?
2) *The evolution of bipedal walking as inferred from fossil footprints.* Fossil *Au. afarensis*, *H. erectus* and modern human footprints will be examined in light of the results from experiments on footprint

formation. Are characteristics of a modern human-like foot (e.g., medial longitudinal arch) and gait (e.g., toe-off through the hallux) evident in *Au. afarensis* and/or *H. erectus* fossil footprints? What might comparisons among fossilized *Au. afarensis*, *H. erectus* and *H. sapiens* footprints tell us about similarities or differences in their foot anatomy and/or gait?

3) *The evolution of running in later* Homo. Runners who habitually forefoot-strike and others who heel-strike will be asked to run across a pressure pad and to produce footprints in sediment. These data will be compared with trackways of early modern human running gaits at 120 Ka, as the first direct test of hypotheses regarding the foot strike patterns used by human ancestors while running. Did anatomically modern humans at 120 Ka run with a forefoot-strike, as habitually unshod humans do today?

II. Significance of proposed research

Despite general agreement that bipedalism played an integral role in human evolution, paleoanthropologists have often disagreed over the evolutionary history of this behavior in our ancestors. Those debates based on fossil anatomy alone have reached an impasse, with researchers disagreeing over the functional interpretations of the same anatomical features (Ward, 2002). Fossil footprints provide unique windows to directly observe the foot anatomies and locomotor behaviors of extinct hominin species. Some intriguing fossil hominin footprint sites have been uncovered in recent years, and present a new source of data that can be used to directly test hypotheses about locomotion in the human fossil record. However, much preliminary research is necessary before we can understand how details of foot anatomy and gait are preserved in footprints. The proposed study will use an innovative experimental approach to analyze the dynamic processes of footprint formation with habitually unshod humans and chimpanzees, to understand how particular aspects of hominin anatomy and gait are preserved in footprints. These results will provide a foundation for detailed quantitative analyses of fossil hominin footprints, using techniques never before applied to the reconstruction of fossil human anatomy and behavior. Specifically, hypotheses will be tested regarding the foot anatomies bipedal locomotion of *Au. afarensis*, *H. erectus*, and the earliest members of *H. sapiens*. Furthermore, additional experiments with modern runners will provide the basis for the first direct tests of hypotheses regarding the evolution of running in later *Homo*. This project will use a novel approach to interpret new fossil footprint data, and will certainly provide new evidence to inform many long-standing debates over the evolutionary history of human gait.

III. History of attempts to answer related questions

The importance of the information preserved by fossil footprints has been recognized since the discovery of the Laetoli footprints in 1978 (Leakey and Hay, 1979). Some researchers have used experimental approaches to address questions about these fossil footprints but much remains unknown about the quantitative relationships between foot anatomy, gait, and sediment properties, and how this information can be used to better interpret fossil hominin footprints. The fact that clear connections between these factors have not yet been established has led different researchers to develop conflicting interpretations of the Laetoli footprints.

Day and Wickens (1980) conducted one of the earliest experimental analyses 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. However, the modern human subjects used in these experiments were habitually shod. Tuttle and his colleagues (1990) rightfully acknowledged that the use of footwear would postdate the Laetoli footprints (Trinkaus and Shang, 2008) and opined that this might have influenced their foot anatomy and function (see D'Août et al., 2009). Therefore, Tuttle and colleagues (1990) used a sample of footprints made by habitually unshod Machiguenga of Peru in their comparative study of the Laetoli prints. Regardless of methodological differences, both studies concluded that the foot anatomy and gait of the makers of the Laetoli footprints were similar to those of modern humans. Raichlen and colleagues (2010) later employed 3D laser scanning in an experimental analysis of the Laetoli prints, a marked technological improvement over earlier studies that allowed for more detailed and accurate measures of the complex topography of experimental and fossil prints. They concluded that the Laetoli footprints reflect a human-like extended-limb gait, rather than the bent-hip bent-knee (chimpanzee-like) gait that others have proposed (Raichlen et al., 2010).

However, other researchers have still maintained that the Laetoli prints reflect a foot anatomy and gait that differs from that of modern humans and more recent hominins, such as *H. erectus* (Stern and Susman, 1983; Bennett et al., 2009). They have cited features such as the more abducted angle of the hallux, long lateral toes, and shallowness of the region of the medial metatarsal heads as evidence that the Laetoli footprints reflect a more primitive, or ape-like, foot anatomy and/or gait. Interestingly, the only study to include experimentally-produced chimpanzee footprints in its interpretation noted qualitative similarities between chimpanzee footprints and those at Laetoli (Meldrum, 2004).

The chimpanzee foot is characterized by a transverse arch similar to modern humans (and other great apes), but they lack a longitudinal arch and have a more abducted hallux (Morton, 1922, 1924). An adducted hallux and a longitudinal arch are considered features of modern human foot anatomy that contribute to our unique, strict reliance upon bipedal locomotion (Harcourt-Smith and Aiello, 2004). These features also make our pattern of bipedal walking distinct from that of chimpanzees. Elftman and Manter (1935) found that the walking gait of modern humans involved a transfer of pressure to the medial forefoot during late stance phase, followed by a toe-off through the hallux. But chimpanzees seemed to lack this pattern, and this was explained by their lack of longitudinal arches and different hallucial morphologies. A similar pattern of pressure transmission was found in a more recent study of bonobo bipedal locomotion (Vereecke et al., 2003). A recent analysis of *Au. afarensis* foot morphology (Ward et al., 2011) has raised new questions about the evolutionary history of hominin foot anatomy by suggesting that *Au. afarensis* had a longitudinal arch, which would have allowed for a modern human-like medial transfer of pressure and toe-off through the hallux during bipedal locomotion. Evidence to inform this hypothesis is certainly present in the Laetoli footprints, although the relationships between characteristics of foot anatomy and gait and footprint morphology need to be established to move beyond conflicting interpretations of this direct evidence of fossil hominin locomotion.

In their interpretation, Day and Wickens (1980) understood that footprints are not simple mirror images of foot anatomy and that the dynamic propulsive forces beneath the foot must also significantly influence on footprint morphology. Although devices to measure pressures beneath the foot were developed long ago (Elftman, 1934), advances in computer technologies have made these systems exponentially more accurate and practical. D'Août and colleagues (2010) were the first to relate quantified foot pressure distributions to footprint morphology. They found a relationship between pressure and depth, but noted that "…the exact nature of the interaction between the dynamics of the foot and the substrate needs to be elucidated."

IV. Materials and Methods

Field experiments on footprint formation will be conducted with 30 consenting adult individuals (15 men, 15 women) from the Daasanach tribe living in and around the village of Ileret, Kenya. Most adults in the Daasanach tribe grew up either unshod or minimally shod. Also, the Daasanach are local to the site of ongoing fieldwork at Ileret, Kenya where the 1.5 Ma fossil footprints are located. We have collected pilot data from members of this population and they are consequently familiar with our research team and our protocol. IRB approval for these experiments has been granted (GW IRB#031030, expires 9/11/11, will be renewed).

A plantar pressure plate (RSscan International Footscan, 0.4m x 1.1 m^2, sampling frequency 250 Hz) will be placed on dry, firm ground in an open clearing with sufficient space prior to the pad for subjects to reach the desired experimental speeds. Approximately 2 m from the end of the pressure pad, a trackway measuring 125 cm long, 50 cm wide, and 15 cm deep will be dug out of the ground and filled with sediment directly excavated from the geological layer preserving the 1.5 Ma footprints at Ileret. Water will be added to the sediment in order to reconstitute a mud similar to that in which the fossil footprints were formed. It is not crucial (and nearly impossible) to know the exact saturation level of the mud in which the fossil footprints were made. However, given the high level of anatomical detail preserved in the Ileret prints, results from other experimental work would suggest that they were formed in a strong, firm mud (Allen, 1997). In these experiments, the sediment will be moistened until test footprints generate a depth and level of anatomical detail that mirrors that of the fossil prints. Prior to and following the addition of water, 300mL samples of sediment will be weighed using a balance, to obtain quantified sediment moisture levels for each trial.

First, biometric measurements will be taken from each subject. These will include height, weight, shoulder height, hip (greater trochanter) height, knee (tibial tuberosity) height, ankle (lateral malleolus) height, foot length, shoulder circumference, and waist circumference. Neon-colored adhesive markers will be placed at osteological landmarks at the hip, knee, ankle, and foot. These markers will allow for later digitization and analysis of kinematic data from video taken with a high-definition camcorder and imported into motion analysis software at George Washington University (**GWU**). Subjects will pass over the plantar pressure plate and through the sediment trackway, within the same trial, at five different speeds (slow walk, normal walk, fast walk, jog, fast run; speeds quantified from video). Each subject will complete at least 3 trials at each speed (total n>300). Subjects will be asked to repeat trials until they are able to land on the pressure pad and in the soft sediment trackway without adjusting their gait, while maintaining a constant speed of travel throughout the trial. After each trial, the footprint produced in the sediment trackway will be photographed in a particular manner (~15 photographs at specific angles, heights, etc.) that will allow for the later creation of 3-dimensional models using photogrammetric methods (see Appendix for description of technique). Following photography, footprints will be obliterated and the mud trackway leveled, using a trowel and a standard carpenter's level.

The chimpanzees that will be used in this study are held at Stony Brook University (**SBU**) in Stony Brook, NY. Approval has been granted by the institution to conduct these experiments (see attached documentation). Experiments on the distribution of foot pressure and footprint formation will follow the same protocol as the experiments on human subjects. A wooden trackway will be constructed and filled with sediment in the lab at SBU. Sediment will be of the same type as in the field experiments (that preserving the fossil footprints at Ileret), as several 10-gallon containers will be filled with sediment and shipped back to the United States. Length, width, and depth will be identical to the trackway used in the human experiments. A wooden platform will be built to the height of the sediment trackway, and the pressure pad will rest upon it. Gradually-inclined ramps will lead up to and down from the platform, with space for the chimpanzees to reach their preferred speeds before passing over the pressure pad. The chimpanzees will be habituated to walking over this setup prior to experimentation. The same biometric measurements taken in the human experiments will be taken from the chimpanzees. Markers will be placed at the same osteological landmarks and trials will be recorded with a high-definition video camera for later digitization using motion analysis software at GWU. Each chimpanzee will conduct 10 trials at their preferred speed and up to 10 at faster speeds, depending on the trainer's ability to motivate speed. Speeds will be quantified after digitization. Trials will only be included if the chimpanzee continues walking at a constant speed across the full length of the platform. The footprints that the chimpanzees create will be photographed for the later production of 3-dimensional photogrammetric models at GWU.

Pressure distribution maps and 3D footprint models will be analyzed according to 12 anatomical areas of interest, corresponding to the heel, lateral midfoot, metatarsal heads 1-5, and each of the five toes (see Appendix for detailed workflow). Measures of peak pressure and pressure-impulse (pressure*time) at each of these landmarks will be exported. Positional (x-y-z coordinate) data will be collected at each landmark on the 3D footprint model. The plane of the ground can be easily established, since the 3D models will always include at least 10 cm of flat, undisturbed ground around the perimeter of the footprint. The flat ground will be fixed to a plane, so that linear measurements can capture depth at each landmark. Data analysis will test the hypothesis that a correlation exists between pressure and footprint depth in each region of the foot. Multiple regression analyses will examine within- and among-group relationships between footprint depths at landmarks and several predictor variables, including pressure, speed, joint angles, and biometric measurements.

The fossil footprint sample will consist of footprints from Laetoli, Ileret, and Engare Sero (see Appendix for sample details). Fossil footprints will be documented by photogrammetry. This will take place in the National Museums of Kenya (**NMK**) for the Laetoli prints (see attached documentation), whereas the Ileret and Engare Sero footprints will be photographed in the field (KH and BR are actively involved in fieldwork at these sites). Landmarks will be placed on 3D footprint models at the 12 anatomical landmarks listed previously. Multivariate statistical methods will examine within- and among-site variation in footprint morphologies, and also compare morphologies of fossil and experimental footprints. Geometric morphometric analyses will elucidate shape differences among the morphologies of footprints produced by *Au. afarensis*, *H. erectus*, and *H. sapiens*, and also among fossil and experimental prints. Differences will be examined in light of experimental results, to relate footprint morphologies to particular characteristics of anatomy and/or gait. For example, shallow footprint depths underneath the hallux and first metatarsal head may indicate the lack of a modern human-like medial transfer of pressure during late stance phase.

A sample of 20 subjects (10 male, 10 female, 5 forefoot-strike and 5 heel-strike runners of each sex) will be recruited from GWU and the broader Washington, DC area. The experimental setup will be identical to that for the chimpanzee experiments at SBU, but will take place in the Motion Capture and Analysis lab at GWU. Subjects will be asked to run across the pressure pad and through sediments for at least three trials at each of two speeds (jog and fast run; quantified from video). Subjects will repeat trials and adjust their starting position until they strike the pressure pad and land in the sediment trackway at a constant speed, without altering their gait. Footprints will be documented using photogrammetric techniques for the later construction of 3D models. Analysis will first determine the relationships between maximum pressures and maximum footprint depths. Geometric morphometric analyses will compare experimental footprints to fossil running prints from Engare Sero. Landmarks will be mapped onto 3-dimensional models of the fossil prints to determine if the topography of those prints is most similar to those produced by forefoot- or heel-strike runners. This analysis will allow us to hypothesize whether these early modern humans, at 120 Ka, ran with a forefoot- or a heel-strike.

V. Previous experience

All equipment for studies of gait (pressure pad, video camera) and photogrammetry (camera, lenses, software) are currently available at GWU and I have experience with all methods for data collection and analysis (see preliminary results). I have received training and gained experience in field excavation techniques, including those specific to fossil footprints, during participation as a member of the Engare Sero Research Project and as an instructor on the Koobi Fora Field School. Results from preliminary analyses of fossil footprints have been presented at professional conferences.

VI. Preliminary results

A pilot study was conducted with 13 consenting adults (5 male, 8 female) from the habitually unshod Daasanach tribe at Ileret, Kenya. This study followed the protocol outlined previously for experiments aimed at understanding the dynamics of footprint formation. Data were collected on the pressure distribution across the foot, and the morphology of footprints produced when subjects walked at both normal and fast speeds. Analyses for this pilot study focused on the metatarsal heads alone. This part of the foot, along with the toes, is involved in the active transmission of propulsive forces between the foot and the ground. This is also the location of the medial transfer of pressure late in stance phase that characterizes human gait.

When walking at normal, preferred speeds, subjects distributed pressure evenly, as standardized maximum pressures (the proportion of total maximum pressures attributed to a given metatarsal) were not significantly different among any of the metatarsal heads (Figure 1). The same was true of standardized pressure-impulse, which refers to pressure experienced by the metatarsal heads over time (Figure 2). These results were comparable to those of D'Aoȗt and colleagues in their study of unshod foot function (D'Aoȗt et al., 2009).

When the same subjects produced footprints at the same normal walking speed, the area under the first metatarsal head was actually significantly deeper than that underneath the 4th and 5th metatarsal heads (Figure 3). The area under the 5th metatarsal head was also significantly shallower than the area under the second and third metatarsals. The fact that significant differences were seen in footprint depth but not pressure across the metatarsals implies that something other than pressure influenced print depth at these locations. More data are necessary, but I hypothesize that such a pattern might always occur when a medial longitudinal arch is present.

A different pattern of pressure was found when subjects increased to faster walking speeds. Maximum pressure underneath the first metatarsal head was significantly greater than that under the 4th or 5th metatarsals. Maximum pressure underneath the 5th metatarsal head was also significantly less than that under the 2nd and 3rd metatarsal heads (Figure 4). Pressure-impulse under the 1st metatarsal was also significantly greater than that under the 5th (Figure 5). As subjects increased walking speed, they applied greater amounts of pressure medially, rather than continuing to distribute it evenly across the foot. Rosenbaum and colleagues (1994) found similar results in their study of the effects of speed on plantar pressure distribution.

When walking at fast speeds, footprint depths under the 4th and 5th metatarsal heads were still shallower than that under the 1st metatarsal (Figure 6). The area under the 5th metatarsal head was also significantly shallower than the 2nd, 3rd, and 4th metatarsal heads. While the general pattern of footprint depths remained similar, with the area under the first metatarsal head being the deepest, the area under the 5th metatarsal head tended to be even shallower at fast walking speeds than it was at a normal walking pace. This is likely connected to the medial transfer of pressure associated with increasing walking speed.

The correlations between maximum pressure and footprint depth, as well as that between pressure-impulse and depth, were statistically significant at both normal and fast walking speeds (Table 1).These results demonstrate that footprint depth is related to foot pressure. However, the small values of correlation coefficients show that other factors do certainly play a role in determining footprint depth. It is important to know that the relationship between pressure distribution and footprint morphology changes with speed, emphasizing the importance of estimating speed for fossil footprint trackways before interpreting foot anatomy or gait.

To relate these pilot results to some fossil hominin footprints, I gathered a small subset of data from both Laetoli and Engare Sero footprints. The Laetoli sample consisted of data captured by photogrammetry from a second-generation cast of three consecutive prints from the G1 trackway at the NMK. The Engare Sero data was collected from a photogrammetric model of one footprint created in the field. Predicted velocities for the Engare Sero and Laetoli trackways are similar (about 1.1m/s and 0.99 m/s, respectively; Hatala et al., 2011; Raichlen et al., 2008). In the Laetoli footprints, the area under the first metatarsal head is quite shallow compared to the central metatarsals, a pattern not typically seen in the footprint experiments (Figure 7). This could suggest that the foot anatomy of the maker of the Laetoli prints differed from that of modern humans, or perhaps that their gait involved relatively little medial transfer of pressure. The morphology of the Engare Sero footprint was more similar to the experimentally-produced footprints (Figure 8). While the deepest point was underneath the third metatarsal, the first metatarsal depth was still greater than that of the fifth, as was the case in our footprint experiments. With further work, I hope to be able to say a lot more specifically about what these similarities and differences mean in relation to foot anatomy and gait.

VII. Broader impacts

The experimental results of this project have the potential to benefit fields outside of paleoanthropology. Studies of foot anatomy and function in habitually unshod populations are of interest to fields such as podiatry and footwear science, as they provide a better understanding of how feet develop and function without the influence of modern footwear. Results from experiments with forefoot- and heel-strike runners are of interest to fields of exercise science and orthopedics in light of recent enthusiasm for barefoot running.

Three-dimensional scan data from both individual fossil footprints and complete footprint layers will be stored in museum databases. This will address the important issue of preservation since fossil footprints are vulnerable to degradation once they are exposed. The same data will also allow museums to easily create highly accurate models of the footprints and footprint sites that can be used for educational purposes.

This project will provide research experience and training for several undergraduate students. One female undergraduate student is already being trained in both field and laboratory methods in Kenya and at GWU. Excavations and field experiments will be conducted in collaboration with the Rutgers University and NMK Koobi Fora Field School, where undergraduate students from the United States, Kenya, and South Africa will be trained in methods of excavation, experimental biology, and biomechanics. Consistent efforts will be made to recruit undergraduate research assistants from groups historically underrepresented in physical anthropology.

VIII. Research schedule

Academic year 2011-2012 – conduct experiments with chimpanzees at Stony Brook University
Summer 2012 – conduct experiments with Daasanach, continue excavations at Ileret and Engare Sero
Fall 2012 – analyze experimental data
Spring 2013 – conduct laboratory experiments with modern forefoot- and heel-strike runners
Summer 2013 – continue Ileret/Engare Sero excavations, collect Laetoli footprint data, analyze fossil print data
Academic year 2013-2014 – completion of data analysis, write and defend dissertation

Figures and Tables

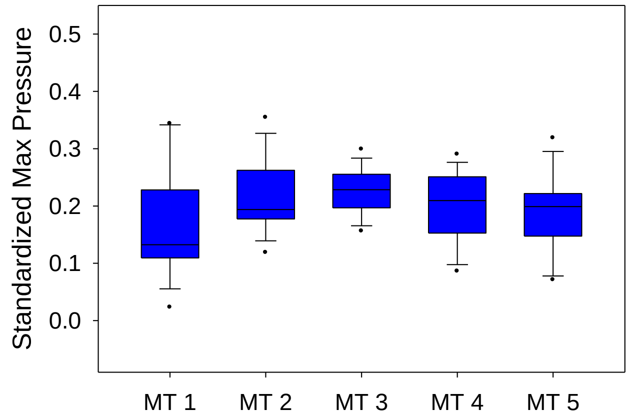

Figure 1. Standardized maximum pressures at metatarsal heads, normal walking speed.

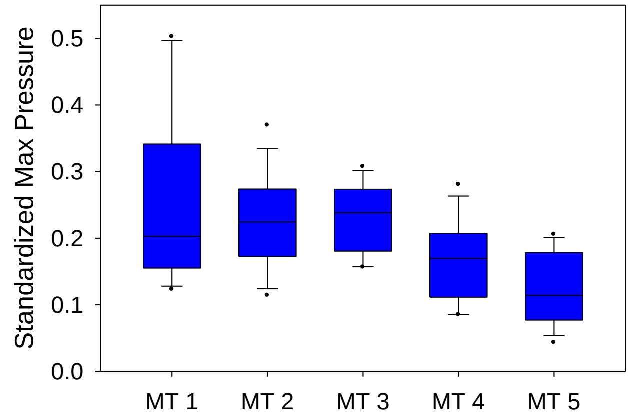

Figure 4. Standardized maximum pressures at metatarsal heads, fast walking speed.

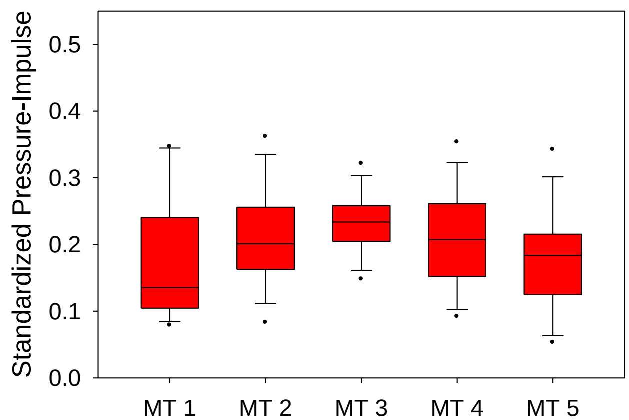

Figure 2. Standardized pressure-impulse (pressure-time integral) at metatarsal heads, normal walking speed.

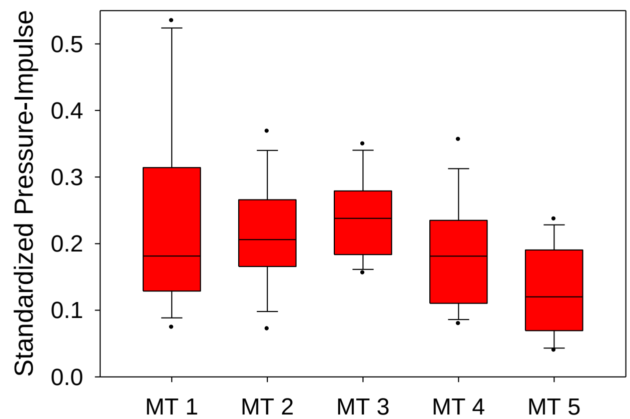

Figure 5. Standardized pressure-impulse (pressure-time integral) at metatarsal heads, fast walking speed.

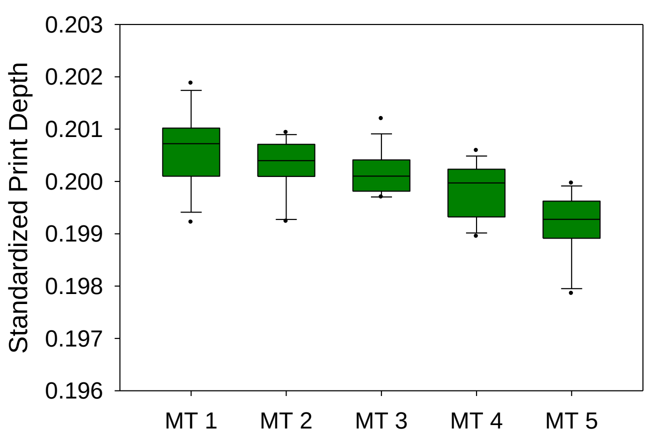

Figure 3. Standardized footprint depths at metatarsal heads, normal walking speed.

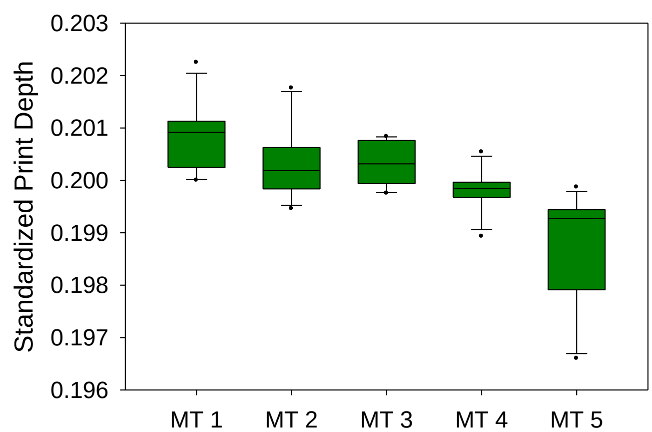

Figure 6. Standardized footprint depths at metatarsal heads, fast walking speed.

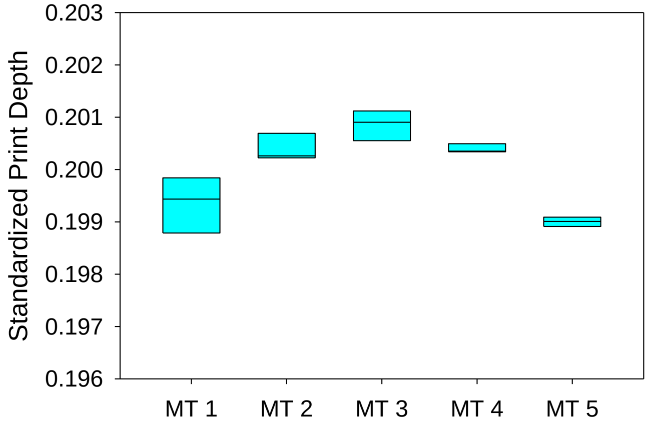

Figure 7. Standardized footprint depths at metatarsal heads, Laetoli G1 trackway.

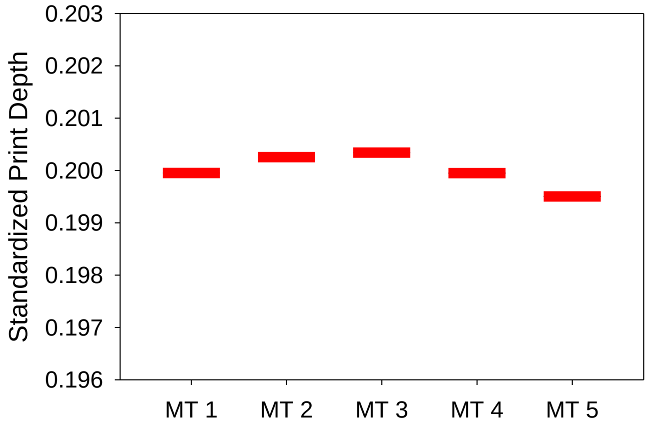

Figure 8. Standardized footprint depths at metatarsal heads, Engare Sero footprint R1.

Walking Speed	Correlation	Correlation coefficient	95% Confidence interval	p-value
Normal	Maximum pressure & depth	0.2955	0.0556-0.5031	0.0169
	Pressure-impulse & depth	0.3406	0.1055-0.5397	0.0055
Fast	Maximum pressure & depth	0.6196	0.4240-0.7600	<0.0001
	Pressure-impulse & depth	0.5589	0.3447-0.7178	<0.0001

Table 1. Correlations between standardized maximum pressures, and standardized pressure-impulse, and standardized footprint depth for experimentally-produced footprints at normal and fast walking speeds.

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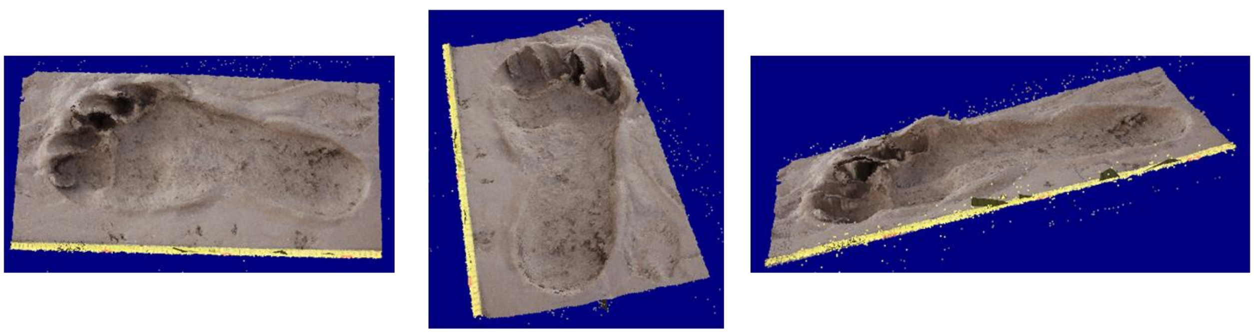
I. Photogrammetry

Photogrammetry is a technique by which multiple digital photographs of the same object, taken from different heights, angles, and orientations, can be merged together to create a 3-dimensional model of that object. Such an approach is most feasible to the current project because it is both portable, for use in the field, and capable of creating accurate, high-resolution 3-dimensional models. Appendix Figures 1 and 2 show 3D models of two different footprints, the former scanned with a 3D laser scanner and the latter created using photogrammetry. The photogrammetric model preserves a much more detailed record of the 3D topography of the footprint and also preserves color information, useful not only for interpreting 3D shapes but for preservation purposes as well. All camera equipment for this method is at GWU, and the processing of images is done in the computer lab there, using the program PhotoModeler Scanner 2011.

Appendix Figure 1. Footprint model created by 3D laser scanning.



Appendix Figure 2. Footprint model created by photogrammetry.

II. Detailed workflow for analysis of foot pressure data and 3D footprint models

Pressure distribution maps will be saved within Footscan software (Footscan 7.011). Measures of peak pressure and pressure-impulse (pressure*time) at each of the 12 anatomical landmarks listed in the proposal will be exported from the Footscan software to a Microsoft Excel spreadsheet.

Digital photographs of footprints will be imported to the program PhotoModeler Scanner 2011, and 3D footprint models will be created. These models will be exported as .stl files and then imported to the freely-available program MeshLab (http://meshlab.sourceforge.net/). Landmarks will be placed at the 12 different anatomical landmarks on the 3D footprint model (within MeshLab). Positional (x-y-z coordinate) data for each landmark point on the 3D footprint model will be collected within MeshLab software. As mentioned in the proposal, the plane of the ground can be easily established, since the 3D models will always include at least 10 cm of flat, undisturbed ground around the perimeter of the footprint. The flat ground will be fixed to the x-y plane in MeshLab, so that a landmark's position on the z-axis will correspond to its 'depth'. These measurements can also be exported to a Microsoft Excel spreadsheet.

All pressure data and coordinate data from 3D models will be imported to the program JMP for univariate and multivariate statistical analysis. Geometric morphometric analysis of 3-dimensional models will use the EVAN Toolbox software package (http://www.evan-society.org/node/23).

III. Details of fossil footprint samples

Sample	Location	Number of trackways	Total number of footprints
Laetoli	National Museums of Kenya (first-generation casts and molds)	3 (only G1 will be analyzed)	
Ileret	Ileret, Kenya	4*	21*
Engare Sero	Engare Sero, Tanzania	24*	353*

*At both Ileret and Engare Sero, footprint trackways lead directly into sediments that are currently unexcavated, making it almost certain that additional footprints will be uncovered in subsequent field seasons. These footprints will be added to the study sample as they are uncovered.