Early Hominin Movement Patterns at Laetoli, Northern Tanzania

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ABSTRACT

The site of Laetoli in northern Tanzania is famous for its preservation of 3.66-million-year-old footprint trails, among which are several belonging to upright walking hominins (Day and Wickens 1980; Leakey and Hay 1979; Masao et al. 2016; McNutt et al. 2021). These footprints provide the earliest definitive evidence of bipedal locomotion in the hominin lineage and have undergone intense research. While much has been written about the taxonomy and gait characteristics of the hominins that produced them, researchers have not yet investigated the directions in which the printmakers were traveling. Here we show that all five hominin trails are oriented in a non-random, northerly direction. Using the original M.D. Leakey survey maps of the Laetoli site, we calculated the direction of travel for 49 footprint trails including 461 individual footprints spanning 11 different taxonomic groups. The majority of the footprint trails were oriented in random directions, but all the hominins were moving north, potentially toward the water source of paleolake Olduvai. This northward movement of the hominins suggests either group travel or movement toward a common destination. These data provide significant insight into early hominin behavior and add an important layer to our understanding of the Laetoli hominins.

INTRODUCTION

The paleoanthropological site of Laetoli, Tanzania, preserves the footprints of a range of Pliocene mammalian taxa embedded in 3.66-million-year-old layers of volcanic ash (Deino 2010) (Figure 1). Included among these are several hominin trackways, each of which clearly demonstrates an upright walking gait (Day and Wickens 1980; Leakey and Hay 1979; Masao et al. 2016; McNutt et al. 2021). The most famous hominin trails were found at Site G by Paul Abell and Ndibo Mbuika, members of a team led by Mary Leakey, in 1978. The trackways record at least three separate individuals (G1, G2, and G3) (Leakey 1981).

The preservation of these fossil footprints has allowed for biomechanical gait analyses of the Site G hominins, however, interpretations of the resulting analyses have reached what appear to be contrasting conclusions. Some researchers have focused on the ways in which footprint morphology is more human-like than nonhuman ape-like (i.e., a non-divergent hallux, shorter lateral toes, and evidence of a heel-strike) and concluded that they evidence an

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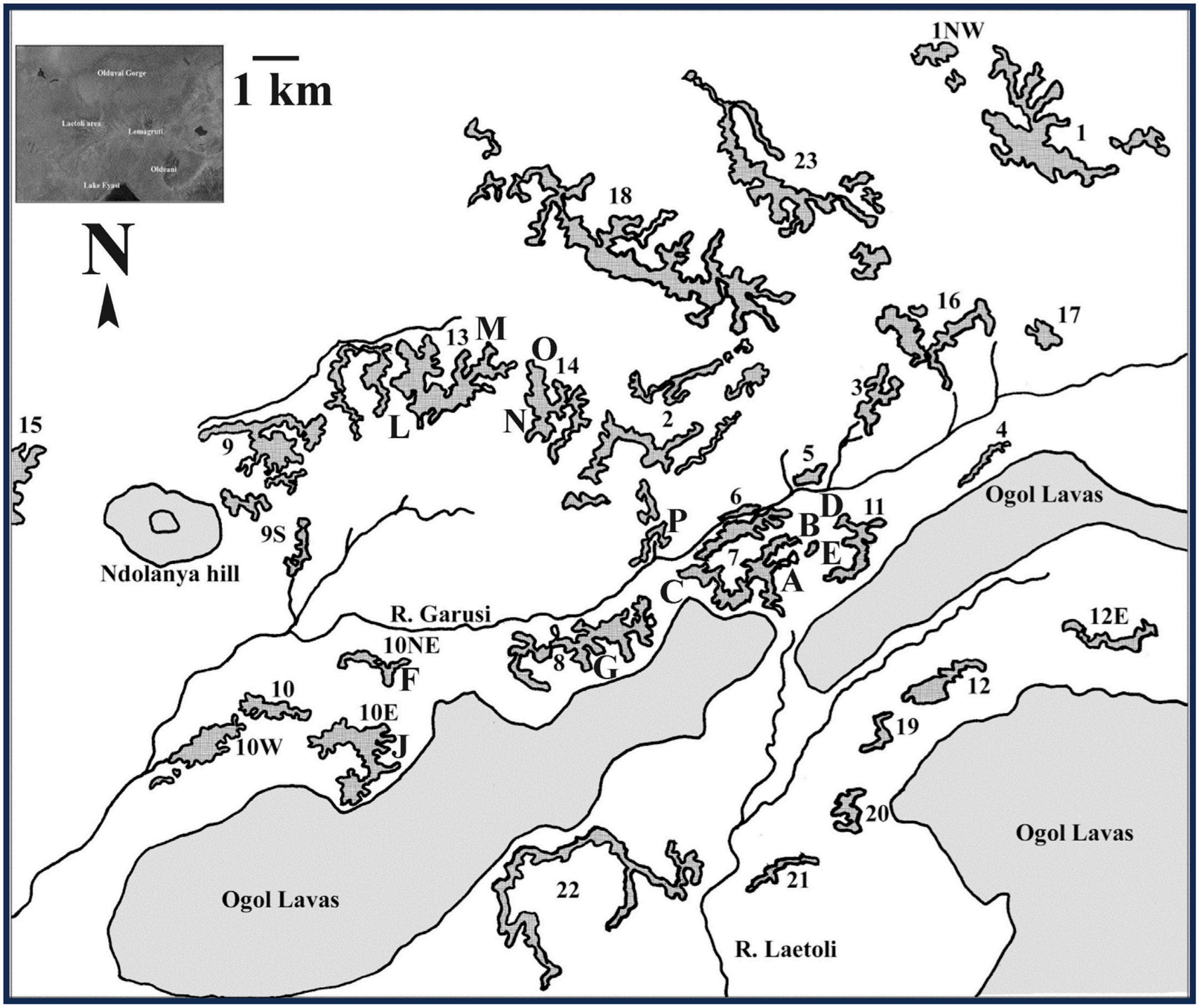

Figure 1. Layout of the Laetoli fossil sites. Numbers represent paleontological localities while letters represent the animal trackway sites. More detailed maps of three of the animal trackway sites used in this study (Site C West, Site D, and Site F) can be seen in Figure 2 (image adapted from Musiba et al. [2007]).

extended limb bipedal gait broadly similar to that of modern humans (Crompton et al. 2012; Day and Wickens 1980; McClymont et al. 2021; Raichlen et al. 2010; Tuttle 1987; Tuttle et al. 1991; White 1980; White and Suwa 1987). Others have used both experimental and morphological data to highlight inconsistencies between the G prints and those of modern humans. Even if they might agree with the broad characterization of Site G hominin bipedalism as more similar to that of modern humans than to that of nonhuman apes, they have also identified evidence that these hominins moved with a gait that was kinematically distinct in many aspects (Bennett et al. 2009; Hatala et al. 2016a; Hatala et al. 2023; Meldrum et al. 2011; Stern and Susman 1983).

Enduring debate surrounds other aspects of the Laetoli hominins, including their taxonomic identity. The fossil record at Laetoli would suggest that these hominins belong to *Australopithecus afarensis*. Laetoli is home to the type specimen of *A. afarensis* (LH 4), which is the only fully described hominin species from this site with the same geological age as the footprints (but see Musiba et al. 2010). But while it is generally accepted that the Laetoli Site G tracks were made by *A. afarensis*, some have argued against this designation, suggesting that the footprints are those of a still undiscovered—and more human-like—hominin taxon (Harcourt-Smith and Aiello 2004; Tuttle et al. 1991).

Two additional hominin trackways were discovered in 2016 at Laetoli Site S (S1 and S2) in the same 3.66 Ma layer of volcanic ash (Masao et al. 2016). Given their morphological similarities to the Site G prints, these trails are also attributed to *A. afarensis.* The large size of the S1 footprints compared with some of those from Site G led the authors to conclude that *A. afarensis* had a significant degree of body size dimorphism (Masao et al. 2016).

A recent analysis of the footprint trail at Site A has added new complexity to the evidence of hominin bipedal locomotion preserved at Laetoli. This footprint trail was originally discovered in 1976, just prior to the discovery of the famous Site G trails. The first publication of the Laetoli footprints by Leakey and Hay (1979) described the Site A prints as those of a hominin with a shambling gait. Later, Tuttle (1985, 1987, 1990; Tuttle et al. 1991) raised the possibility that these unusually shaped prints were made by an ursid. This hypothesis, along with the subsequent attention focused solely on the Site G trails, left the Site A footprints relatively undiscussed in the paleoanthropological discourse.

However, in 2019, our team returned to Site A and relocated these footprints to test hypotheses about their taxonomic identity. The successful re-discovery allowed for updated analyses and led to the rejection of the ursid hypothesis (McNutt et al. 2021). McNutt and colleagues instead concluded that these footprints were made by a hominin. However, the dimensions of the Site A footprints and the biomechanical implications of their morphology do not align with those found at Sites G and S. This finding suggests that the Laetoli landscape was home to at least two hominin species around 3.66 Ma, consistent with interpretations of bipedal diversity during the Pliocene based on the hominin pedal fossil record (e.g., Haile-Selassie et al. 2012).

While the hominin footprint trails at Laetoli have been the subject of intense scientific investigation, many researchers have focused on locomotor biomechanics, with less attention paid to the behavioral implications of the hominin—and other animal—trails regarding collective movement. Here, we look specifically at the directionality of the hominin footprint trails within the context of all other fossil footprint trails at Laetoli. While directionality has been reported for the individual hominins at Laetoli, no study has yet looked at the Laetoli hominins collectively, nor at their direction of travel as it compares to the fossilized prints of other taxa at the site. A significant amount of research has targeted questions about how the Laetoli hominins moved, but this paper asks, where were they going and were they potentially traveling to or from the same place? Comparisons of directionality between taxa further add an additional piece to our understanding of hominin behavior and paleoecology at Laetoli. Here, we test the null hypothesis that movement of the animals, including hominins, at Laetoli was random. We evaluate this against the alternate hypothesis that hominins and/or other animals moved in directionally coordinated ways. Acceptance or rejection of either hypothesis has important implications for understanding hominin and other animal behavior, and for understanding how they were interacting with this landscape at the time when they produced these footprints.

METHODS

Digital images of the maps from the original M.D. Leakey surveys of the Laetoli sites (found in Leakey and Harris 1987; Figure 2) were created and aligned with a north-south vertical axis. The images of each were processed using ImageJ to determine the coordinates of the midpoint of each marked footprint. These coordinates were then plotted into a graph using Microsoft Excel. Lines of best fit were applied to the stride midpoints within each footprint trail to determine the slope (m) of the direction of travel. In cases where individual trails would dramatically change directions (N=5; Table S1), the final direction of travel was used for alignment of the line of best fit. It is worth noting that none of the hominin trails exhibit a change of direction. The slopes were then converted to specific degrees from north using the equation $(90 + \tan^{-1}(m))$ and compared with visual interpretations of the maps. Footprints in which the shape of the print could not be used to determine the general direction of travel along the footprint trail (e.g., some hyaenid tracks) were excluded. The slopes from each of the lines of best fit were then plotted on a 360-degree circular graph and color-coded per taxonomic group (Figure 3). A total of 49 footprint trails encompassing 461 individual footprints of 11 different taxonomic groups were included.

Patterns of randomness were then evaluated within R Studio using R (version 4.2.1). A test of significance (r.test) was done using the circular package, CircStats. For each taxonomic group, a value of randomness (Rbar) and statistical significance (p-value) were calculated as well as a standard deviation (Jammalamadaka et al. 2001). This statistical circularity method was successfully applied to fossilized footprints in a previous study by Roach and colleagues (2016).

RESULTS

Circular maps of trackway orientations (see Figure 3a, b) indicate a common direction just slightly east and west of north for all the hominins. This observation is supported by the statistical test of randomness that resulted in an Rbar value of 0.969 and a p-value of 0.002 suggesting that the hominins were moving in a statistically significant, non-random direction. (Rbar values closer to 1 indicate greater uniformity, Rbar values closer to 0 indicate greater randomness). Similar calculations of randomness for the entire set of footprint data result in an Rbar value of 0.196 with a p-value of 0.14 indicating that the collective group of animals that made footprints at Laetoli was not moving in any one direction.

Rbar and p-values were calculated separately for 9 of the 11 taxonomic groups, excluding those that only include one individual (i.e., Suidae and Felid) (Table 1). From these, two groups were shown to be moving in a significant, non-random direction in addition to the hominins (see Figure 3c, d). These are the Hyaenidae (Rbar=0.985, p-value=0.008) moving east and the Equidae (Rbar=0.965, p-value=0.046) moving north. Results of tests applied to all other groups were not statistically significant. Those groups for which the Rbar value is closer to zero, indicating more directional spread, also had a higher standard deviation (see Table 1).

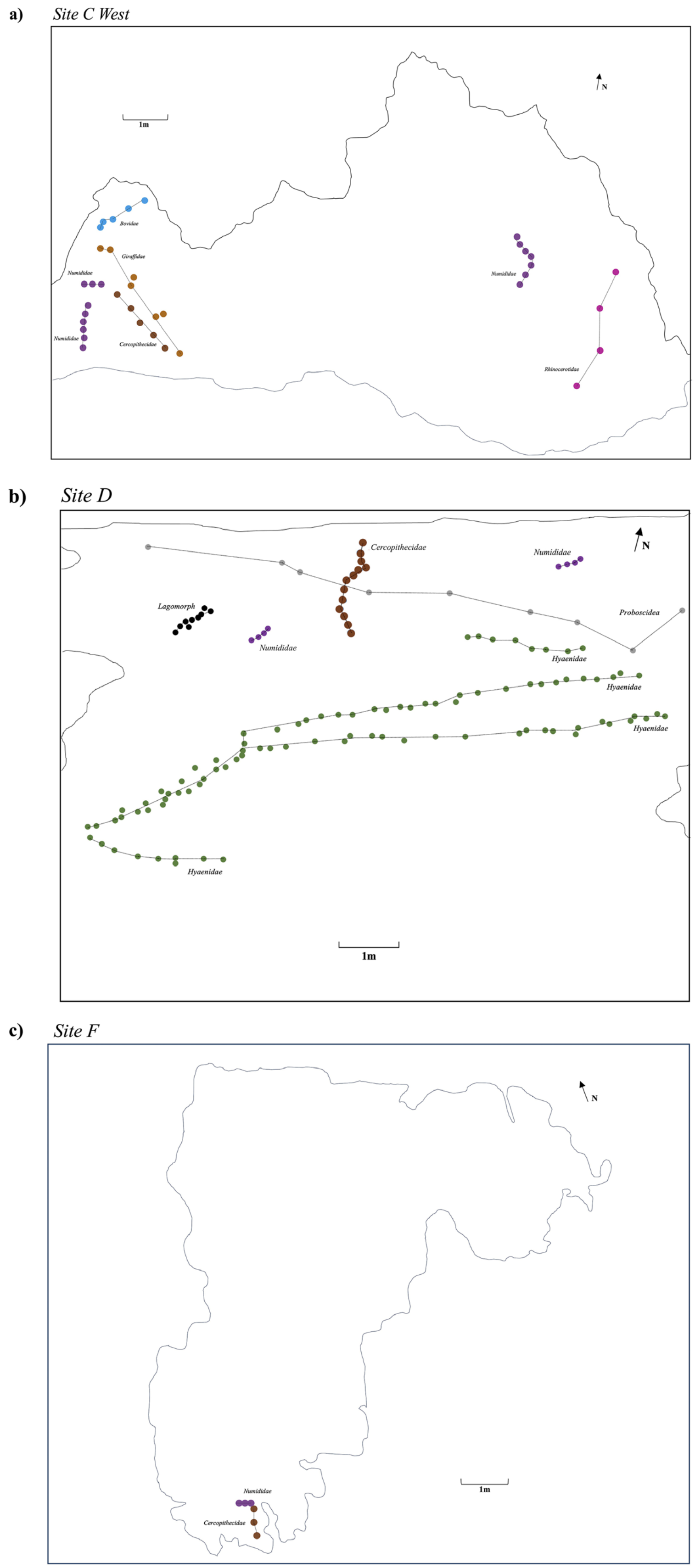

Figure 2. Individual footprint maps. Maps of three of the trackway sites used in this study. Individual trails are depicted with colored circles. Only those footprint trails that were included in the current study are indicated on the map. **a)** *Site C West, which includes 7 footprint trails;* **b)** *Site D, which includes 9 footprint trails;* **c)** *Site F, which includes 2 footprint trails. See Leakey and Harris (1987) for the original maps that were used for this study.*

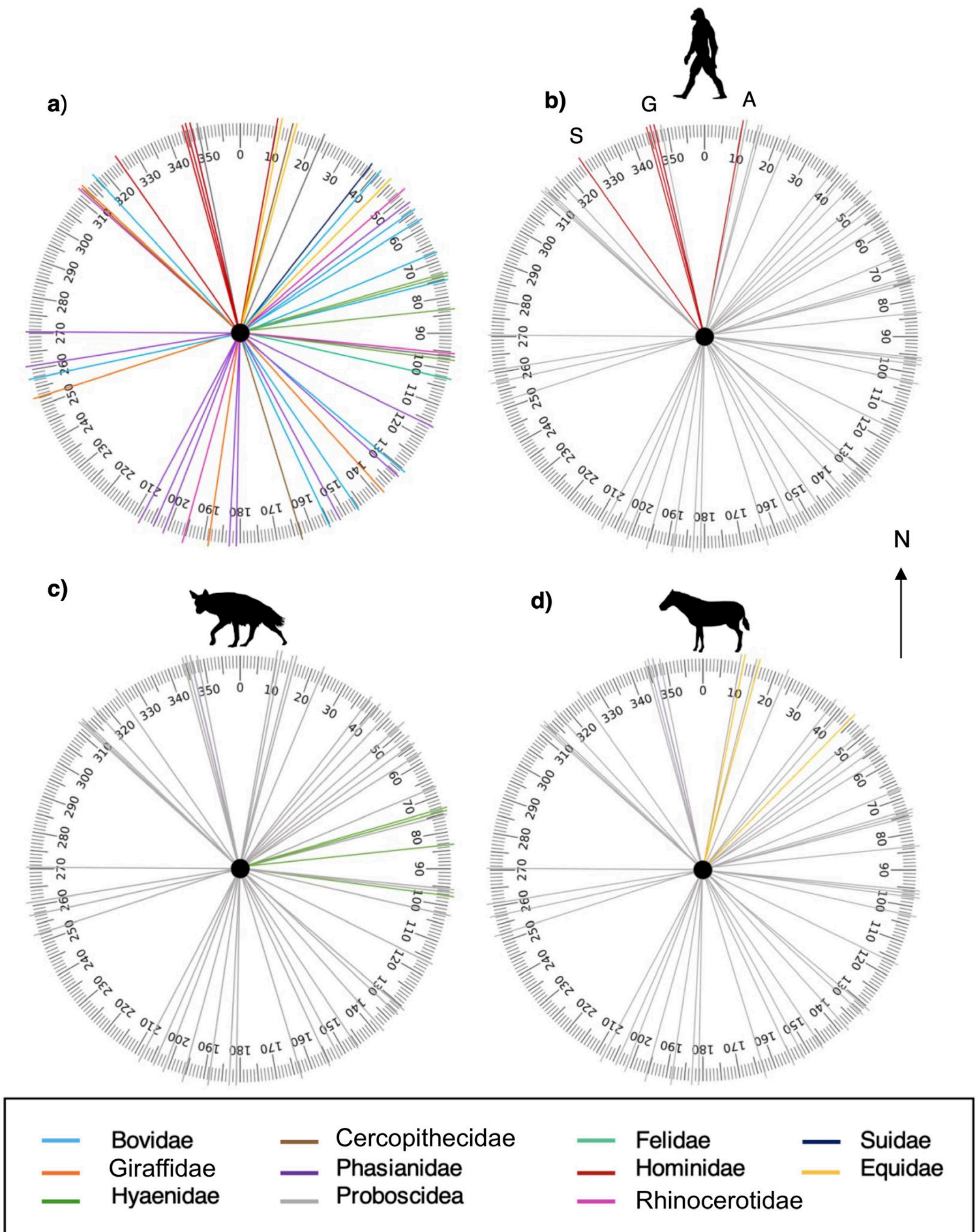

Figure 3. Circularity maps showing the directional movement of 11 Laetoli taxonomic groups. **a)** *all taxa;* **b)** *hominins are indicated in red and show a northward direction of movement. S, G, and A represent the respective site where those hominin prints are found;* **c)** *hyaenids are indicated in green and show an eastward direction of movement;* **d)** *equids are indicated in yellow and show a northward direction of movement. Hominins, hyeanids, and equids are the only taxonomic groups moving in non-random directions. Silhouettes from PhyloPic.*

DISCUSSION

Footprint surfaces offer remarkable snapshots of hominin behavior, and they can provide unique opportunities to develop and test hypotheses about coordinated group activity (Hatala et al. 2022). For example, analyses of Late Pleistocene human and nonhuman animal trackways at White Sands, New Mexico, have revealed potential evidence of humans hunting ground sloths (Bustos et al. 2018) and of an adult carrying a child for an out-and-back journey of more than 1.5km (Bennett et al. 2020). Others have analyzed hominin trackways in Africa (Altamura et al. 2018; Hatala et al. 2016b; Hatala et al. 2020) and Pleistocene Europe (Ashton et al. 2014; Duveau et al. 2019; Mayoral et al. 2021) to develop hypotheses regarding group composition and coordinated group travel. These questions may be difficult or impossible to address with other forms of fossil or

TABLE 1. COMPARATIVE STATISTICS.*

Family	N	Rbar	p-value	SD
Hyaenidae	4	0.985	0.008	0.17
Hominidae	5	0.969	0.002	0.25
Equidae	3	0.965	0.046	0.27
Proboscidea	2	0.801	0.321	0.67
Giraffidae	4	0.445	0.482	1.27
Phasianidae	12	0.443	0.092	1.28
Bovidae	11	0.399	0.174	1.35
Cercopithecidae	3	0.239	0.863	1.69
Rhinocerotidae	4	0.196	0.871	1.80
All footprint trails	**47**	**0.196**	**0.140**	**1.80**

*Statistical results for tests of directional randomness and average direction for the nine taxonomic groups. This table excludes Felidae and Suidae as each of these has only one trail and thus no average direction or randomness could be calculated. Therefore, while direction of travel was measured for 49 total trails, average direction and randomness were only calculated for 47 footprint trails.

archaeological data.

This paper presents the first study focused on the directionality of all mammalian fossil footprints at Laetoli in order to develop testable hypotheses about Laetoli hominin behavior. Using the original excavation maps, the directions of 49 individual footprint trails representing 11 different taxonomic groups were calculated. Visualization and statistical analyses of these directional data reveal several key observations. The first is the concentrated directionality of the hominins, all of which (N=5) are traveling north. This is shown clearly on the circularity maps (see Figure 3b) and is supported by the statistical significance of tests of non-randomness (see Table 1). Additionally, although the S2 hominin footprint trail is only represented by a single print, Masao et al. (2016) note that it is oriented in the same direction as footprints from the S1 individual and the three hominins at site G.

In addition to the hominins, both the hyaenids and equids exhibit directional movement, with the hyaenid tracks oriented to the east and the equids to the north. All remaining taxa were moving in random directions, though a limitation of the study is that many of the taxonomic groups are represented by five or fewer trails, which could impact the robusticity of the statistical results. Nevertheless, the movements and behaviors of the hyaenids and equids may help inform our understanding of the Laetoli hominins. Leakey and Harris (1987) noted that the fossilized hyaenid tracks were all oriented due east and interpreted this as group movement but did not comment on the common directions of the equid tracks. Roach et al. (2016) found strong directionality among bovid tracks preserved on 1.5 Ma footprint surfaces near Ileret, Kenya. They interpreted those trackways as possible evidence for movement to and from a water source, given that similar behaviors were observed among modern bovids near Lake Turkana. Similar reasoning may be applied to the hominins suggesting that they, too, were intentionally moving as a group, or perhaps traveling at different times but towards a common destination.

Evidence for hominin group movement from footprints has been established at other sites. Several ~1.5 Ma footprint sites are known from areas near Ileret, Kenya (Hatala et al. 2017), and among these there is one track surface (site FwJj14E Upper Footprint Layer) that preserves several trails with hypothesized attributions to *Homo erectus* (Bennett et al. 2009; Hatala et al. 2016b). Comparisons between the fossil track surfaces and modern tracks produced along the shores of Lake Turkana suggested that these footprints were likely created within hours to days of each other (Hatala et al. 2016b; Roach et al. 2016). The authors found that most of the hominin trails were sub-parallel and did not overlap, despite being oriented in the same direction and located within meters of each other. Given the small time-window available for footprint deposition, they hypothesized that these trackways could reflect coordinated group movement or at least movement towards some common destination (Roach et al. 2016; Hatala et al. 2017). On the FwJj14E Upper Footprint Layer, the parallel arrangement of the hominin trackways contrasts with the random orientations of the trackways of other animals, suggesting that the directionality of hominin movement was not forced by features of the landscape. This adds further support to the hypothesis of coordinated group movement in the hominins (Hatala et al. 2016b; Roach et al. 2016).

More than 400 preserved human footprints were found at the site of Engare Sero in Tanzania located about 100km northeast of Laetoli (Hatala et al. 2020). These prints date between 5.7 to 19.1 ka and represent the largest assemblage of hominin footprints currently known from the African fossil record. The trackways cluster in two groups based on their orientations—one in a northeastern direction and the other in a southwestern direction. Analyses showed significant directionality for both groups, and similar estimated traveling speeds despite body size variation, again strongly suggesting coordinated group movement (Hatala et al. 2020). There were roughly ten times as many hominin tracks as nonhuman animal tracks preserved on that surface—a total of only 43 nonhuman animal prints were uncovered (Hatala et al. 2020). Of these, 19 bovid tracks made up four trackways that were found in close proximity to the hominin tracks. Each bovid trackway was oriented in a southwestern direction, as was one of the two groups of hominin trackways (Hatala, unpublished data). It is possible that this indicates that a landscape feature constrained movement, and/or that the hominins and bovids were moving towards a common destination. But given the scarcity of nonhuman animal tracks relative to the abundance of human tracks, it is difficult to compare and evaluate their movement patterns in the same ways that have been possible elsewhere.

Previous interpretations of group movement derived from hominin footprints provide a foundation for hypothesized group movement at Laetoli. Similar to the evidence found at Ileret (and in contrast to that from Engare Sero), abundant hominin and non-hominin trackways are present, and their orientations can be analyzed. The directionality of the Laetoli hominin trackways contrasts with the randomness of the trackways made by most non-human taxa. This suggests that movement was not limited by features on the landscape and supports the possibility of intentionally coordinated movement by the hominins. However, the interpretation of group movement should be evaluated within the context of the location and taxonomy of the hominin footprints at this locality. Site G is only about 150 meters south of Site S and both sites preserve footprints interpreted by most as belonging to *Australopithecus afarensis*. The proximity and shared taxonomical attribution of these footprints, combined with the common orientations of their trackways, raises the possibility that the Site G and S hominins were moving together. This has been hypothesized by Masao et al. (2016) but not in the context of comparisons with the trackways of nonhuman taxa. The recently reinterpreted Site A footprints are located 2km east of Sites G and S and have been proposed to represent a different hominin taxon, yet that trackway is oriented in the same direction as the others. It is possible, therefore, that the hominin trails may not be directed northward because of coordinated group behavior, but due instead to the hominins seeking a common destination. However, variation in the exact northward direction of the hominin prints and a lack of knowledge concerning the exact timing of footprint formation precludes a confident interpretation.

One possibility is that both the hominins and equids were traveling north in search of water. Paleoenvironmental data from Laetoli suggest that this landscape was a mosaic environment with ephemeral water sources that would have been choked by volcanic ash from the eruptions and thus unreliable at the time the footprints were made (Su and Harrison 2008). Levin et al. (2008) analyzed oxygen isotopes in the enamel of African mammals and were able to distinguish between taxa that required a consistent water source (evaporative-insensitive) and those that were less dependent on water (evaporative-sensitive). Both hominins and equids fall into the category of evaporative-insensitive, indicating a strong dependency on an available water source and providing a potential explanation for the shared northward travel of these two groups.

It must be noted, however, that the hominins and equids are not traveling in the exact same northerly direction and are not the only water-dependent groups in the current dataset. Other evaporative-insensitive groups include Cercopithecidae, Proboscidea, and Rhinocerotidae. Statistical analyses of footprint directionality of these taxonomic groups show that they were moving in random directions and not only toward the north. Thus, there were clearly additional variables besides water dependence impacting animal movement on the landscape.

To be sure, there are other possibilities that could explain this concerted movement in the Laetoli hominins. Perhaps they were searching for additional food resources or tracking game. Alternatively, the Laetoli hominins may simply have been trying to find an area away from the ashy landscape. Whatever the reason, the important result of these data is the shared directionality of the trackways toward the north raises the distinct possibility of either group travel or common destinations for the hominins whose footprints have been uncovered at Laetoli. As more sites are discovered and excavated, those new trackway data will allow us and others to continue to test and refine these hypotheses regarding how and why the Laetoli hominins trekked north across an ashen plain.

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AUTHOR CONTRIBUTIONS

CKM contributed to study design, analyses, and wrote the manuscript. RAM contributed to study design and data collection. KGH contributed to analyses and assisted with the manuscript. CM assisted with the manuscript. JMD contributed to study generation and design and assisted with the manuscript.

COMPETING INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data are included in manuscript and supplemental material.

AI STATEMENT

No generative AI was used in this study or manuscript.

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Supplement 1: Early Hominin Movement Patterns at Laetoli, Northern Tanzania

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SUPPLEMENT 1
This file includes: Supplementary Table S1.

TABLE S1. COMPLETE SET OF DATA INDICATING THE INDIVIDUAL FOOTPRINT TRAILS.*

Taxon	Site	Degrees from North	Number of Prints	Change in Direction
Hominidae	A	9.4	4	
Hominidae	G (trails G2 and G3)	-14.4	12	
Hominidae	G	-14.3	13	
Hominidae	S	-35	7	
Numididae	A	152.5	6	
Numididae	D	-155.3	4	
Numididae	D	132.8	4	
Numididae	East C	52.2	3	
Numididae	East C	-151.6	13	
Numididae	East C	-13.3	3	
Numididae	East C	-179.5	4	
Numididae	F	116.4	3	
Numididae	Northern G	-98.3	7	
Numididae	West C	-176.8	6	
Numididae	West C	-89.2	3	
Numididae	West C	-158.9	7	Yes
Proboscidea	D	96.9	10	Yes
Proboscidea	East C	23.3	2	
Cercopithecidae	D	163.4	21	
Cercopithecidae	F	14.3	3	
Cercopithecidae	West C	-47.2	5	
Hyaenidae	D	83.8	9	
Hyaenidae	D	73.9	37	Yes
Hyaenidae	D	74.5	38	Yes
Hyaenidae	D	97.8	9	
Leporidae	D	-146.3	9	
Bovidae	East C	155.2	3	
Bovidae	East C	146.3	6	
Bovidae	East C	-42.7	4	
Bovidae	Upper A	-102.5	9	
Bovidae	Upper A	130.3	8	
Bovidae	West C	54.6	5	
Giraffidae	East C	-107.7	8	
Giraffidae	Northern G	-46.6	5	
Giraffidae	Upper A	-171.1	13	
Giraffidae	West C	138	7	
Rhinocerotidae	East C	-47.3	4	
Rhinocerotidae	Lower A	48.7	7	
Rhinocerotidae	Lower A	96.1	29	Yes
Rhinocerotidae	West C	-164.2	4	
Felidae	Lower A	101.9	13	
Bovidae (Simatherium)	Lower A	-11.6	15	

Bovidae (Simatherium)	Lower A	57.6	22	
Bovidae (Simatherium)	Upper A	67.4	18	
Bovidae (Simatherium)	Upper A	75.4	20	
Bovidae (Simatherium)	Upper A	40.8	10	
Chalicotheriidae	West C	-110.6	2	
Suidae	Upper A	37.8	4	

*Taxon, site location, orientation of the trail, number of prints per trail, and change in direction are listed for each individual. Because the hominin trackways for G2 and G3 are superimposed on one another, they have the same degrees from north and are reported accordingly in the table.