Wiseman, A and De Groote, I

A three-dimensional geometric morphometric study of the effects of erosion on the morphologies of modern and prehistoric footprints.

http://researchonline.ljmu.ac.uk/id/eprint/7468/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Wiseman, A and De Groote, I (2017) A three-dimensional geometric morphometric study of the effects of erosion on the morphologies of modern and prehistoric footprints. Journal of Archaeological Science: Reports, 17. pp. 93-102. ISSN 2352-409X

A three-dimensional geometric morphometric study of the effects of erosion on the morphologies of modern and prehistoric footprints.

Ashleigh L A Wiseman[1], Isabelle De Groote[1].

[1]Research Centre in Evolutionary Anthropology and Paleoecology, Liverpool John Moores University.

Contact email(s): A.L.Wiseman@2016.ljmu.ac.uk, I.E.DeGroote@ljmu.ac.uk.

Author for correspondence: Ashleigh LA Wiseman. Liverpool John Moores University,
Byrom Street, Liverpool, L3 3AF, United Kingdom.

Introduction: Fossilised footprints have been discovered all over the world and can provide information regarding the foot size and subsequent body size estimates of the track makers or an insight into the kinematics of the foot/lower limb. After exposure, these fossils rapidly erode. It is predicted that footprint morphology is compromised after creation, prior to fossilisation and that erosion after exposure will affect the morphology of a footprint after exposure. To date, no studies have assessed if degradation prior to fossilisation and/or after fossilisation, and subsequent exposure, affects the morphology of the print, thereby affecting any measurements taken. This study aims to quantify these pre- and post-erosional processes.

Materials and methods: A set of experimentally generated footprints were created to test the effects of degradation of footprint morphology prior to fossilisation. In addition, Holocene footprints were recorded at Formby Point, Sefton, UK. In just over a week tidal action had completely eroded the Holocene beds. Photogrammetry was applied to the experimental human footprints and a selection of Holocene human and animal footprints. Three-dimensional Geometric Morphometric methods were utilised to estimate differences in shape and size.

Results: Results from the experimental footprints indicate that weather action affects the size and shape of a footprint prior to fossilisation. When the weather was dry, footprint shape and size showed little difference for two weeks, but rainfall caused significant changes. The Holocene footprints show that after fossilisation and exposure to coastal erosion, footprint rigidity is highly compromised. The human footprint borders progressively recede, increasing length and width each day. Footprint depth, often used to inform upon speed and kinematics, varied considerably in one week. Some regions becoming shallower, others increasing in depth. Similar results were found for the animal footprints, but with less significant changes in shape and size determined.

Conclusion: Observed significant differences in measurements result in problems for predicting stature, mass, sex, and kinematic analyses. This warrants caution when making interpretations from fossilised footprints. Rapid recording of fossilised prints from first exposure and assessing pre-fossilisation processed are necessities when recording footprint surfaces.

Keywords: fossilised footprints, geometric morphometrics, erosion, photogrammetry, 3D modelling.

Conflicts of interest: None.

1.1 Introduction

Fossilised hominin footprint localities have been discovered across Africa, Eurasia, Australia and the Americas (Leakey and Hay 1979; Behrensmeyer and Laporte 1981; Roberts and Berger 1997; Mietto *et al.* 2003; Watson *et al.* 2005; Webb 2007; Bennett *et al.* 2009; Roberts 2009; Morse *et al.* 2013; Felstead *et al.* 2014; Aston *et al.* 2014; Masao *et al.* 2016). In lieu of skeletal material, fossil footprints can be used to infer body dimensions of the track makers (Bennett and Morse 2014). Numerous fossil and forensic-based studies have been conducted that have attempted to find a correlation between footprint measurements (e.g.; forefoot breadth, heel breadth, length, toe extremity length, etc.) and body dimensions, such as stature, body mass, hip height, sex and age (Krishan 2006; Kanchan *et al.* 2008; Avanzini *et al.* 2008; Bennett *et al.* 2009; Dingwall *et al.* 2013; Domjanic *et al.* 2015; Hatala *et al.* 2016a).

For example, stature is often predicted using the length of the foot by applying Martin's ratio of 0.15 (Martin 1914). Dependant on substrate material properties, these measurements extracted from a single trackway belonging to a single individual can vary substantially. Stature and mass predictions from just one trackway from Walvis Bay, Namibia have estimated that the individual ranged from 1.35metres to 1.73metres tall, with the individual being either malnourished or clinically obese (Bennett and Morse 2014). Evidently, slight variations in a trackway results in grossly variable biometric predictions.

In other locations, such as at Laetoli, Tanzania and Ileret, Kenya, the substrate material properties are much more uniform across a trackway, and biometric data that is extracted is much less variable (Bennett *et al*. 2009). Less variable measurements have resulted in numerous studies utilising these measurements to predict not only biometric data, but also kinematic data (Schmid 2004; Berge *et al.* 2006; Vaughan *et al.* 2008; Raichlen *et al.* 2008; Raichlen *et al.* 2010; Crompton *et al.* 2011; Bates *et al.* 2013; Dingwall *et al.* 2013; Bennett *et al.* 2016; Hatala *et al.* 2016b; Masao *et al.* 2016; Raichlen and Gordon 2017). These studies have allowed palaeoanthropologists to assess evolutionary trends in bipedal locomotion and body proportions.

It has been previously demonstrated that footprints are susceptible to taphonomic changes prior to diagenesis as the result of a number of variables; weather conditions, changes in surface hydrology or bioturbation (Marty *et al*. 2009; Bennett and Morse 2014). After the footprints have undergone diagenesis, and have either become exposed or excavated a number of variables can lead to the footprints becoming eroded, thus affecting footprint shape (Bennett *et al.* 2013). As with any archaeological material, once the fossils are uncovered and exposed to the elements they will begin to erode, with softer, lithified sediments being more susceptible to erosion (Bennett *et al.* 2013). It must be acknowledged that weather action, such as wind or rain, may affect the size and shape of a footprint in a similar manner that slight variations in substrate typology may affect a footprint (Marty *et al.* 2009; Bennett *et al.* 2013).

No studies to date have quantified the effects of degradation on morphology, and how this can affect measurements taken from a footprint. The current study aims to quantitatively assess the effects of taphonomy and erosion on footprint morphology through the assessment of experimental and Holocene footprints. New discoveries of human trackways at Formby Point, Merseyside has offered a unique opportunity to record a set of Holocene footprints as they rapidly eroded.

This study proposes that footprints are at risk of significant morphological change which will alter body size predictions at two stages. The first stage is immediately after footprint creation. The second stage is post-excavation. It is predicted that a delay in events leading to excavation and recording could result in changes in shape and size of a footprints, particularly in easily deformable softer sediments that are more susceptible to morphological changes (Bennett *et al*. 2006).

We use a selection of experimentally generated footprints to assess changes in footprint morphology prior to fossilisation. Holocene human and animal footprints discovered along the Sefton Coast were also assessed to determine if there is any changes in shape or size per day after exposure. It is predicted that the longer a footprint is exposed then there will be a significant change in shape and size of the print. Shape change is predicted to affect measurements of the foot used to inform upon body size estimates. An improvement on understanding the effects of erosion on morphology will improve the ability to accurately assess body size estimates from future footprint sites.

1.2 Geological and archaeological context

Formby Point is located along the Sefton Coast in Merseyside, England and is characterised by silty, fine-grained sands and peat sediments, and sand dunes (Roberts *et al*. 1996) preserved in unlithified, soft-sediments (Roberts 2009; Bennett and Morse 2014). Encroaching coastlines have led to the exposure of numerous ancient sediments since the 1970s, many of which contain over 145 Holocene human trackways and animal footprints along a 4km stretch of this coastline (Huddart *et al.* 1999; Roberts 2009). The Formby Point sediments are similar to other fossilised sediment beds at Terra Amata, a site containing a Neanderthal footprints (De Lumley 1966).

Carbon and optically stimulated luminescence (OSL) dating of the previously excavated sediments have yielded dates from 6650 ± 700 OSL BP ~ 3575 ± 45 ^{14}C BP (Roberts 2009). The latter date was obtained by dating roots that overlay the Holocene beds, indicating a *terminus ante quem* for the beds (Roberts *et al.* 1996; Huddart *et al*. 1999; Roberts 2009), confirming a Mesolithic age. These beds offer an interesting insight into human activity of the Late Mesolithic-Early Neolithic transition along the Sefton Coast.

In June 2016 three human trackways were exposed due to wave erosion at Formby Point immersed in over 700 animal footprints. Auroch, roe and red deer, crane bird, wolf/dog, and beaver footprints have been identified (Roberts *et al.* 1996; A. Burns 2017, pers. comm.). The interaction of many animal and human prints offer a glimpse into Mesolithic human activity, and even offer a unique opportunity to assess the gait dynamics of an extinct species of cattle, although this is not the focus of the current study.

The Holocene sediment layer was excavated by staff and students of The University of Manchester. Unfortunately, the bed was destroyed in just under two weeks after exposure due to the destructive nature of the high tide. Twice a day the sediment layer was completely immersed by high tide, with the prints only reappearing with low tide. Visually, it was possible to see the daily erosion of the footprints as the direct result of wave action (Fig.1). The sediment bed was unlithified and despite efforts to prevent human and animal interference with the footprints, tidal action still led to the destruction of the footprint bed quite rapidly due to the bed being composed of soft, easily deformable silts. Such a rapid degradation of the footprints that was noticeable by the naked eye is hypothesised to have resulted in significant morphological change. Importantly, we expect that linear measurements of the foot will have changed on a daily basis. As previously discussed, these linear measurements are used to predict an individual's biometric information. Changes in these measurements are expected to produce highly variable predictions regarding body size estimations.

Holocene footprints have previously been exposed along the Sefton Coast (Roberts 2009), with fossilised footprints appearing at other coastal sites in the UK, such as at Happisburgh, Suffolk (Ashton *et al.* 2014). These beds containing unlithified footprints were also destroyed rapidly due to tidal action in a matter of weeks. If our study is successful in determining that morphological changes are paramount in coastal locations, particularly with footprints that are unlithified, then the biometric data that has been previously published from these sites, such as at Happisburgh (Ashton *et al.* 2014), is questionable. The sediments are variable between Formby Point and Happisburgh, but it is a fair assumption that two soft, unlithified sediment beds would have reacted similarly when exposed to the same variables: vigorous tidal action and poor weather conditions. Both of these beds deformed and were destroyed rapidly. It is expected that both sites also experienced changes in footprint morphology coinciding with the rapid destruction of the beds.

The rapid erosion of the footprints at Formby Point have offered a unique opportunity to quantitatively assess the effects of daily degradation on footprint morphology. If the current study is successful in determining that footprints undergo daily morphological changes, then our results will have considerable implications for future studies that assess footprint discoveries from coastal locations.

2.1 Materials

2.1.1 Experimental set-up

A selection of experimental footprints were created in homogenous fine-grained sand composed of rounded to sub-angular particles measuring ~0.06-0.7mm in diameter with ~20% saturation at a 40mm depth (Fig.2). Previous experiments have determined that this is the optimal saturation for footprint definition, whereby sand composition has no significant effect on morphology after saturation (D'Août *et al.* 2010; Crompton *et al.* 2011). The footprints were created inside a container with a drainage system in place. The base of the tray allowed any rainwater that saturated through the overlaying sediment to drain through to the ground to prevent the tray from flooding. Netting was placed over the footprints to prevent animal interference, but still allowed wind and rain to penetrate through.

The experimental prints were placed outdoors in an open area in Liverpool, Merseyside during winter. During the first 14 days the weather was dry with low wind speeds and near-freezing temperatures. There was rain and medium-to-high wind speeds during the remaining six days of the experiment. Rain resulted in small dents across the sediment to form. Footprint features progressively eroded in the final days of the experiment.

These experimental footprints were not created in a material that reflect any sediments belonging to fossilised beds containing footprints. We have deliberately chosen a homogenous material of uniform particle distribution and water content. The rationale for using this material is to demonstrate that footprints are susceptible to morphological change prior to becoming covered with overlaying material, a process that often leads to fossilisation (Morse *et al.* 2013). By using this homogenous material, we have avoided the problem of attempting to replicate sediments from Formby Point, Ileret or Laetoli, etc. Any unlithified material (e.g., volcanic ash, fluvial or lacustrine deposits composed of silt, sand or clay of varying material properties) is expected to behave in a similar manner as the container of sand: it is expected that there will be morphological change as the direct result of weathering or coastal action. If a material can be deformed to produce a footprint with anatomical features, then the material is certainly capable of deforming as the result of weather action in the period before the material becomes covered by overlaying sediment. This must remain an important consideration when analysing fossilised footprints: any information extracted from the footprints can only be classed as relative information about the track-maker.

2.1.2 Holocene footprint data collection

Three human trackways were discovered at Formby Point containing a total of seventeen complete human footprints of definite ichnology. Due to daily time constraints of the incoming high tide, only one human footprint was recorded daily and used for this study. It was the longest surviving print. Others were initially selected in addition, but were rapidly destroyed after just a few days warranting their removal from the dataset. One auroch and two roe deer footprints were also selected (Fig.3). The auroch prints offer a unique opportunity to assess the gait dynamics of an extinct species of cattle.

Due to a combination of excavation limitations and bad weather the human footprint was only recorded on four days out of a possible 7 days, and the animal prints were recorded on a total of five days. On the seventh day the section of bed containing the human print had completely degraded. The animal prints were destroyed the following day.

A DSLR D3300 Nikon camera with a macro 60mm lens of fixed zoom was used to photograph each footprint each day. Due to sporadic weather conditions (a mix of cloud cover and bright sunlight) camera settings were consistently altered to accommodate weather. The first model of the animal prints were made using a GoPro Hero4 due to time constraints of the incoming high tide.

2.2 Methodology

Photogrammetry was applied to create 3D models of each footprint daily on the licensed software Pix4D. Weather conditions during the experiments were consistent with heavy cloud cover. Conditions at Formby Point were mostly very bright, with the ground quite wet, which has reduced the resolution for two models. All photographs were taken during dry periods of the day. Model editing was completed using Avizo 9.0.

Footprint length was calculated by measuring the distance between the most distal point of the hallux and the most inferior point of the pternion. Length was then used to predict stature using Martin’s ratio of 0.15, which has repeatedly been found to positively predict stature in modern habitually unshod populations (Martin 1914; Hrdlicka 1935; Dingwall *et al*. 2013), and has been previously applied at fossilised sediment localities such as such as Laetoli (Tuttle 1987) and Happisburgh (Ashton *et al.* 2014).

2.2.1 Geometric morphometrics

Geometric morphometrics (GM) is a suite of statistical methods employed to measure and compare patterns of similarity and differences in many objects through the process of datum acquisition, processing, analysis and visualisation of geometric information (Bookstein 1991; Slice 2005). These methods allow for morphological changes to be quantified from the statistical application of landmarks (Oxnard and O'Higgins 2009). These techniques will be applied in the current study to determine if shape/size change occurs between daily models, and if this is the direct result of coastal erosion. All analyses were computed in *R*, and two *R* packages: morpho (Schlager 2017) and geomorph (Adams and Otárola-Castillo 2013).

A total of 44 models were landmarked, representing the experimental prints and Holocene human print. A further 15 models were landmarked, representing the animal prints. A total of 20 type II landmarks were used for the human dataset and a total of 10 landmarks were used for the animal dataset (five for the first roe deer print, three for second, and three for the auroch print). All landmarks were found to be homologous between each daily model. Landmarks were digitised on 3D .ply surfaces in Avizo 9.0 (Fig.4).

Prior to any geometric morphometric applications, the depth of four landmarks were calculated for all experimental and Holocene human prints: the medial and lateral forefoot region at the deepest points, and the medial and lateral heel at the deepest points. The depth of these landmarks are expected to change, corresponding to increased degradation of the footprint. The landmarks that synthesised the most concave points on the medial and lateral heel and forefoot were used to calculate the linear distance across these region. Depths were thus measured using simple trigonometry for all human prints.

A General Procrustes Analysis (GPA) was performed, which translates and rotates each homologous landmark to the origin, whilst scaling to unit-centroid size (Zelditch *et al.* 2012). These configurations are all aligned to a single reference specimen, representing the mean shape. The resulting Procrustes coordinates compose the shape of each specimen within Kendall's shape space (Kendall 1984).

Shape variation was then assessed using a Principle Components Analysis (PCA), which is a non-parametric statistical technique used to examine the relationship between a set of variables by calculating the maximum distance between each individual landmark (Zelditch *et al* 2012). Each principle component (PC) was examined to determine shape variability. Shape change was visualised by non-affine partial warp grids called thin plate splines (TPS). These grids allow for the visual representation of relative shape deformation and display landmark transformation which maps a set of GPA-aligned configuration of landmarks between a set of structures, with the grid lines representing the relative amount of bending energy between each landmark (Rohlf and Splice 1990). TPS grids were not created for the animal prints due to a reduced landmark dataset.

An ANOVA was computed to assess the relative amount of shape variation per day. Categorical variables were created for each landmark configuration to assist in assessing the cause of shape change. By adopting the use of categorical variables in the dataset, information about the footprints – such as the sudden appearance of holes in the surface as the direct result of rain – can be included in the analyses. Their inclusion in the dataset assigns each configuration of landmarks to a group, allowing for groups to be statistically compared. For example, group one contains two variables: the presence or absence of raindrops. This group can then be statistically compared with the second group whereby the configurations have been assigned a variable stating if the footprint has experienced a reduction in height of the landmarks relative to landmark height on day one. Subsequently, it will be possible to determine if rain action has resulted in the reduction of landmark height, and if these variables have cumulatively resulted in changes to the shape and size of a footprint.

Two categorical variables were developed for the experimental prints. The first describes the presence of rain drops in the bed that left small dents in the sediment towards the end of the experiment. The second describes the reduction in height of several landmarks in the forefoot region, corresponding to degradation. Two categorical variables were created for the animal prints: the presence/absence of toe ridges in the roe deer and the severe erosion of the posterior border of the auroch footprint.

Two categorical variables have been established for the Holocene human dataset: the grade of footprint degradation and depth. Two grades have been established for degradation: the presence and absence of the forefoot region. Footprint depth was measured at five separate points across the foot (Table.1). Two grades were established for depth based upon the significant reduction in hallux depth relative to an increasing heel depth. This is split between the first two days and the final two days for the Holocene print.

Finally, the relationship between footprint degradation and size was assessed by regressing log-centroid size (CS) to the first PC. Levels of significance were computed by permutation tests to a 95% confidence level, using 1000 permutations which tests the sampling distributions. Finally, morphological disparity tests were computed which performs a pairwise comparison between groups.

3.1 Results

3.1.1 Morphological change prior to fossilisation

Foot length was calculated for each model (S1), with stature being predicted using Martin's ratio (Martin 1914). Different statures were produced for the models representing the final two days of the experiment, with foot length increasing as much as 6.016%.

PCA of the experimental prints over a period of 20 days revealed that shape variance can be explained by the first two PCs that account for more than 84% of total variance (Fig.5a). The first two axes (PC1 and PC2) can be cumulatively surmised as accounting for the observations previously accounted for in the creation of the categorical variables: the reduction in height of the toe ridges (identified in PC2) and the appearance of numerous holes as the direct result of rain/weather (identified in PC1). The maximum (PC1+) and minimum (PC1-) shape difference indicates that changes in foot length are associated with poor weather conditions, with an increased distance between anterior and posterior landmarks as ridges become shallower and less convex. As expected, weather action has cumulatively resulted in changes in shape/size of the footprint (according to PC1) and changes in footprint depth (according to PC2). This is characterised by the strong separation of negative PC scores for the final two days of the experiment and positive PC scores for the first 18 days of the experiment. The least displacement for both the experimental and Holocene prints occurs in the heel region, with shape remaining almost static with increasing erosion.

To analyse if degradation affects size, shape variability (assessed by using PC1) was regressed against log-CS for all footprints. Results indicate that size is significantly affected by degradation in the final two days of the experiment and that the null hypothesis can be rejected, and that there is a statistically significant difference in shape and size between the models, as shown by a one-way ANOVA. This is corroborated by the change in length and the change in foot width for the right foot as the direct result of rain. Shape change has a significantly strong association with log-CS (R^2=0.57524; P=0.002), that has a weak positive correlation with weather action (R^2=0.22281; P=0.002).

A morphological disparity test found that shape change is only significantly affected by weather in the final six days of the experiment with the severe degradation of the toe ridges (P=0.004) and the increased presence of raindrops (P=0.002). No statistically significant shape/size change occurred in the first fourteen days of the experiment when weather remained dry. The null hypothesis can be rejected as there is a significant association between weather and shape change, as supported by a Pairwise test.

3.1.2 Morphological change after exposure/excavation

Upon visual inspection it was clear that all of the Holocene footprints selected displayed the collapse of key features of the footprints. The human footprint suffered severe degradation in the forefoot, the roe deer prints lost toe ridges, and the auroch print, which was located on the edge of the sediment bed, progressively lost the posterior region of the footprint each day alongside the erosion of the bed edge. If the bed had been discovered during the final two days of exposure then it is questionable whether the footprints would have been identified as human or animal, as the hollows that remained resembled bed damage, rather than footprints.

Foot length was calculated (S1). As expected, four different foot length measurements were generated, although the variance between day one and day two is only 3.8mm and is not deemed significant. Measurements from the final two days are quite different. The tip of the hallux is still easily distinguishable in the day three model, although the ridge is much less prominent. In day four a more inferior point has been identified as the tip of the hallux, although this is roughly one centimetre shorter than the first two days, and two centimetres shorter than the third day. Evidently, a large margin of error exists in determining footprint extremities after prolonged exposure.

Stature was then predicted using Martin's ratio. Different statures were produced in accordance with varying foot length, with the percentage increase in foot length increasing as much as 6.21% with erosion.

PCA of the Holocene human print revealed that shape variance can be explained by the first two axes that account for more than 81% of total variance (Table 4). The first axis can be surmised as describing the significant degradation of the forefoot region and the collapse of ridges between the 2nd to 5th metatarsals that are prominent in the first two days only – these observations were previously identified during the creation of the categorical variables, and have thus informed on the major shape change of the Holocene footprint. The forefoot region becomes flat (supported by a loss of depth, as discussed in section 2.1.2), with no clear identifiable structures, with two exceptions: the hallux and the ridge surrounding the extremity of the 5th toe. This is characterised by the strong separation of individual PC scores, represented by negative PC scores for the first two days and positive PC scores for the final two days that the footprint was recorded. This division can be emphasised by the dotted line along the PC1 axis (Fig.5b).

Variation along the second PC described changes in depth of the footprint as a whole. The hallux is seen to be decreasing in depth relative to the heel which increases depth. The depth of the lateral foot (2nd to 5th metatarsals) is found to decrease. The region under the 1st metatarsal slightly decreases in depth during the first two days then increases in depth relative to the loss to the lateral border of the foot. The midfoot region (area lateral to the medial arch) remains almost static in depth, displaying the least amount of depth and shape variance across the footprint.

The shape differences depicted reveal that footprint shape can be warped into two different shapes, per the forefoot region. The maximum (PC1+) and minimum (PC1-) shape difference along PC1 indicates that the forefoot region becomes much more constricted as erosion increases, with a reduced height and a reduced amount of bending energy (PC1-) between each landmark. A likely cause in this displacement may be the degradation of numerous distinguishable features in this region, and a reduction in the height of numerous landmarks. Similarly, the most obvious shape change along PC2 in the experimental prints occurs in the forefoot region, explaining a reduction in the height of the toe ridge landmarks as the ridges are slowly eroded.

The most obvious shape change along PC2 in the print would appear to be around the head of the metatarsals. This area seems to be wider between PC2+ and PC2-, with the landmarks characterising the medial border of the foot being stretched relative to the lateral border of the foot. The lateral border of the foot becomes much less distinguishable during the last two days making this the likely cause in this displacement. The loss of the medial ridge may further explain this shape variance. This is further corroborated by the depth test which found this area lost considerable depth relative to the medial border of the foot.

A morphological disparity test found that shape change is significantly correlated with changes in size ($P=0.0038$), with depth also significantly affected ($P=0.00452$). CS is very weakly correlated to changes in depth ($R^2=0.00723$). A poor R^2 value may be explained by a reduced dataset ($n=4$). Regardless, the null hypothesis regarding depth cannot be rejected as a positive association could not be established. Similarly, a Pairwise test was computed to establish the amount of shape change relative to footprint depth. The null hypothesis cannot be rejected as the interaction between depth and shape/size was not found to be significant ($P>0.05$).

3.1.3 Morphological change in the Holocene animal prints

Shape change of the animal prints can be explained by the first three PCs that account for more than 97% of total variance (Fig.5c). The first axis can be surmised as describing the degradation of the of the auroch footprint, which was discovered at the edge of Bed III. By the second day half of the print had completely disappeared, with the lateral and medial edges of the footprint progressively eroding until its complete disappearance on the fifth day. By the third day it is no longer identifiable as a print. The loss of identifiable features of this print has resulted in the strong separation of individual PC scores along the first axis, represented by negative PC scores for the first two days and positive PC scores for the last three days.

Shape change along the second axis can be surmised as describing relative changes in depth. With the loss of the toes the base of the print became less convex. This loss is more evident on the fifth day, represented by negative PC scores for the first two days and a positive PC score for the final day. Variation along the third and fourth axes cumulatively describe changes in the loss of toe ridges in the roe deer footprints. The ridge between the medial and lateral toes had completed vanished by the fourth day. The borders of one of the roe deer prints are no longer undercut, but are shallow and slanted. This results in a considerable lack of distinction of internal morphology.

4.1 Discussion

4.1.1 Taphonomic changes to footprint morphology prior to diagenesis

GM methods were applied to quantitatively assess the effects of erosion on footprint morphology and to assess if degradation affects body proportion estimates. One Holocene human footprint, two experimental human prints and three Holocene animal prints were chosen to be recorded daily (n=59). This study was testing the hypothesis that footprint morphology will change in shape and size prior to fossilisation and after fossilisation and subsequent exposure. It was predicted that prolonged exposure will significantly affect measurements taken of the foot, thereby decreasing the accuracy of biological inferences.

It has been previously demonstrated that footprints undergo significant taphonomic processes prior to burial and diagenesis (Marty *et al.* 2009), that may alter the shape of a footprint thus affecting any inferences extracted, such as body proportion predictions (Bennett and Morse 2014). However, to date no study has quantified morphological change due to taphonomic processes and how these changes may affect body proportion predictions.

The results from the current study have demonstrated that significant morphological change may occur in softer sediments prior to diagenesis, according to weather conditions. Shape and size will change significantly after rainy periods or high wind speeds. These shape/size changes have affected measurements taken of the foot (length has been used in this study as an example) thereby producing inaccurate predictions of stature. Although not the focus of this study, it can be assumed that other biological predictions will vary greatly if a footprint is exposed to adverse weather conditions prior to fossilisation. While the current study has only focused on weather action as a taphonomic variable, it is a fair assumption to say that other taphonomic processes such as bioturbation, will also affect footprint morphology.

The results of the current study have considerable implications for the human evolution fossil record: how accurate are previously published body proportion estimates of fossil footprints? As previously stated, by analysing the morphology of a footprint numerous inferences can be made. For example, foot parameters (such as using foot length to predict stature and foot index to predict body mass) have been used in conjunction with contemporaneous skeletal data from north-western Europe dating to 950-850Kya to assign *Homo antecessor* as the maker of the footprints from Happisburgh (Ashton *et al.* 2014). Taphonomic processes, such as changes in surface hydrology or even bioturbation, after footprint creation may have affected the shape and size of these prints, thus altering taxon assignment and body proportion predictions. Similarly, taphonomic processes of the footprints from either Laetoli or Ileret may have resulted in the hominin body proportion estimates being under- or over-estimated.

It is suggested that sediment beds should be inspected for evidence of weather damage, particularly in softer lithified sediments, in future fossilised bed discoveries as the surface area may have been exposed for several days prior to fossilisation, with a potential loss of information. In particular, an archaeologist should inspect the sediment bed for rain drops.

4.1.2 Morphological changes to a human footprint after exposure/excavation

After a footprint has become covered by overlaying sediment and has begun the process of diagenesis, and subsequently exposed the print is susceptible to significant changes in shape and size, thereby affecting body size estimates. An example of how degradation can affect footprint inferences can be found in the high variance of predicted stature values presented in the current study. The first 3D model was created just under a week after the footprint was first exposed. The rapid degradation of the print after this point has significantly affected stature predictions. Shape change during the first two days is miniscule, and any analyses and subsequent results would not have produced drastically different results. As such, foot size and subsequent body size estimates can be reliably predicted in the first few days of exposure, assuming that minimal change occurred as a result of taphonomic processes prior to diagenesis. Prolonged exposure after excavation has significant implications for extracting reliable data. This problem is not unique to Formby Point, it was paramount during the excavations at Happisburgh. The Happisburgh footprints were also found on the coastline and were destroyed rapidly due to tidal action (Ashton *et al*. 2014). Any delay in recording the footprints may have resulted in stature and mass values that are not true representations of the Happisburgh hominins.

This has considerable implications for other footprint sites The Ileret and Koobi Fora, Kenya footprints are the oldest footprints attributable to the genus *Homo* (Bennett *et al*. 2009), and are thus of great scientific importance. The sediment bed containing the footprints are composed of fine-grained silt and sands that are unlithified and highly erodible (Bennett *et al*. 2013). These sediments are quite comparable to the fine-grained sand and peaty sediments from Formby Point. Similarly, the Kenyan footprints are at threat of flooding and storm action (Bennett *et al.* 2013) – two variables that are somewhat comparable to the Formby Point sediment beds. With the exception of changes in water salinity (Formby Point is characterised by salt-water immersion and the threat of flooding at Kenya relates to non-saline lake inundation), the variables highlighted in the current study are applicable to the highly-erodible Kenyan footprints. Fortunately, the Kenyan tracks have been covered post-excavation in an attempt to geo-conserve the footprints. However, if the footprints are exposed for excavation or geo-tourism during periods of stormy weather or flooding, then it is expected that the footprints will undergo significant morphological change that may affect our interpretation of the track-makers.

The Laetoli footprints which were formed in natrocarbonatite ash (Leakey and Hay 1979) are only partially lithified, resulting in these footprints being much more robust and firm than the unlithified footprints from Ileret (Bennett *et al.* 2013). It is expected that the Laetoli sediments will be less-susceptible to morphological change as the direct result of wind or rain action, due to much firmer substrates. However, the threat of degradation as the direct result of exposure is not redundant. Despite being much more robust and composed of a different substrate than that of Formby Point, it is expected that constant or prolonged exposure will likely result in the partially lithified Laetoli prints undergoing morphological changes. It is expected that any material that is not fully lithified and preserved will undergo significant changes in shape and size due to a number of external factors. Care should be taken for the immediate preservation of footprints of high interest, such as footprints from Laetoli. Without preservation, a footprint will continue to be subjected to considerable morphological change, and eventually the footprint may be unrecognisable. This occurred with the human footprint at Formby Point. Due to the severe degradation in the forefoot region in the Holocene human print, it is questionable as to whether the print would have been declared human, if discovery was delayed. If it had been declared human, remarkable differences in footprint measurements would have been made. These measurements are used to determine body size estimates (age, sex, mass and stature). Any inferences or estimations that could be calculated from these measurements taken in the final few days would have changed drastically from those made from the first model.

Happisburgh is a prime example of severe degradation hampering ichnotaxonomy. Numerous hollows were excluded in the analyses of the Happisburgh footprints due to questionable ichnology; only 14 footprints out of a total of 152 could be definitively declared hominin (Ashton *et al*. 2014). These hollows could be remnants of hominin footprints whereby only the heel and border of the prints – the deepest regions that are preserved the longest – have survived, as has been observed at Formby Point (Fig.7). Alternatively, the hollows could be eroded animal footprints. Tidal erosion and a delay in recording these footprints that potentially belong to an extinct *Homo* species may have resulted in a considerable loss of data.

The results from the current study are a prime example of how rapidly a footprint can degrade. Within two weeks the Holocene sediment bed had completely vanished. During this time, one of the human trackways had completely eroded, with only one very deep trackway remaining *in situ*. The footprint that formed the basis of this study lay towards the west of Bed II and was the first print to be immersed by high tide. By the end of the first week Bed II had completely eroded, revealing another sediment bed below. Bed III (towards the north) was the final bed to disappear. Severe erosion in Bed III by this point made 3D modelling impossible due to the numerous pockets of water that remained during low tide. The rapid degradation of these footprints have demonstrated the pivotal need for digital recording for the preservation and future scientific investigation of these fragile fossils.

4.1.3 Morphological changes in animal footprints after exposure/excavation

In the current study it was demonstrated that the Holocene animal footprints also experienced a significant change in shape and size as the direct consequence of weather action. The roe deer prints, which were deeply pressed, demonstrated no significant shape change or change in size (except for the toe ridge region). This implies that lightly pressed prints are more susceptible to degradation. Prolonged exposure will affect print definition and depth.

The complete loss of the posterior region of the auroch print from Formby Point further raises questions regarding ichnology. By the second day the print would have been identified as damage to the bed, rather than an extinct species of cattle. Although not the focus of the current study, the auroch trackways provide a unique opportunity to study the gait dynamics of an extinct animal that could have been lost if the Formby Point prints were not rapidly recorded. Similarly, the delayed excavation at Happisburgh resulted in numerous damaged prints – poor anatomical definition has resulted in many of the Happisburgh footprints not being assigned to any taxa (Ashton *et al.* 2014) – being unidentifiable and rightly excluded from analyses. However, the loss of this data may have resulted in a lost opportunity to identify an extinct species of animal present in Britain during MIS 21/25.

Fortunately, better preservation resulted in the identification of numerous animal hollows within the Laetoli tracks, representing a range of extinct Pliocene species within the carnivora, equidae, suidae, and bovidae mammalian orders (Leakey and Hay 1979). However, taphonomic and/or post-excavation erosion of these prints may have resulted in a warping of anatomical features. A loss of this data may have resulted in the incorrect ichnotaxonomy of the prints, or unreliable biological data of the species.

While rapid recording is recommended in order to extract the most reliable data, it must be acknowledged that taphonomic changes may have occurred prior to diagenesis, resulting in a loss of reliable data. Prints that display poor anatomical features are concluded to be unreliable. Prints that are deeply pressed, with clear anatomical details will undergo insignificant morphological changes in the period immediately after exposure. It is expected that clearly defined footprints will be the most reliable to inform on the track makers.

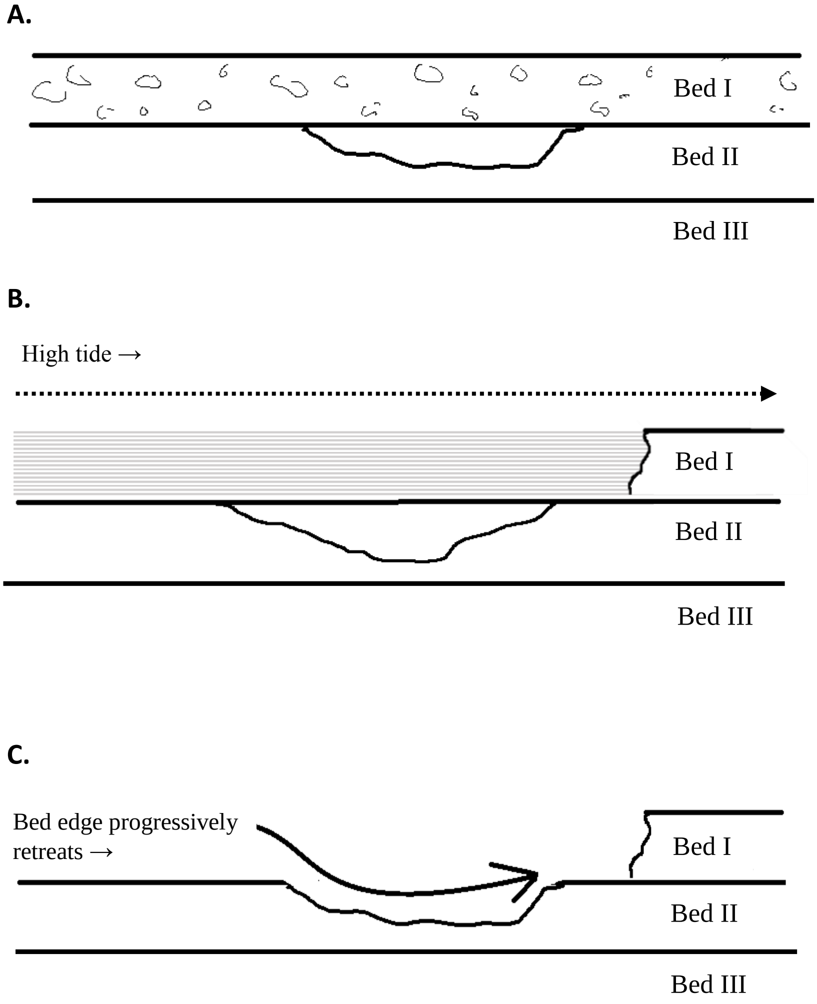
5.1 Concluding remarks

By applying GM techniques it was possible to identify the effects of erosion on footprint interpretation, particularly in softer sediments. The use of statistical techniques created a fundamental tool for the evaluation of footprint erosion. Results have shown that weather action can result in significant morphological change to a footprint prior to and after fossilisation. If a surface is free from weather damage then it may be assumed that there has been no loss of reliable data prior to fossilisation. After fossilisation and exposure a footprint will undergo considerable morphological change directly associated with weather and coastal activity. Morphology was not found to be significantly affected in the first few days after initial exposure, necessitating the need for rapid recording to provide the most accurate results, particularly in highly erodible substrates. It is recommended that inferences made on footprints that have a questionable time frame of exposure should be treated with caution. By creating high resolution 3D models rapidly these fragile fossils have been digitally preserved for further analyses.

N.B. Color should be used in the following figures in print:

Figure 2
Figure 3
Figure 4
Figure 5
Figure 6
Figure 7

Figure 1. Diagram explaining the destructive nature of the high tide. Twice a day the beds were flooded by high tide which resulted in damage to the bed edges and the loss of ~60cm of the west-facing bed daily. Large sand particles and water eroded the footprint edges resulting in changes in shape and size.



Bed stratigraphy after initial exposure

Tide completely immerses prints and destroys the overlaying sediment

Large sand particles remove infilled sediment revealing footprint. Twice daily the beds are flooded with high tide that rapidly erode the bed edges and compromise footprint morphology, resulting in changes in shape and size.

Figure 2. Set-up of the experimentally generated footprints on the first day of the experiment. Netting was placed over the prints each day to prevent animal interference. Photographs were taken with a camera mounted to a tripod.

Figure 3. (A) High tide completely immersed the bed each day. Ai shows the incoming high tide that later reached on average 8metres high. Overlaying beds were rapidly removed by the tide, revealing lower beds below (Aii). After repeated tidal immersion, the fossilised beds were destroyed. Aiii shows the bed after just one week. Around 5metres of the west-facing bed was lost in just one week. (B) Photograph of the selected animal prints on the second day. Bi and Bii belong to roe deer. Biii belongs to auroch. Note the fragmented posterior region of the auroch print. (C) Photographs of the human print during the four days of recording, with Ci belonging to day one and Civ belonging to day four.

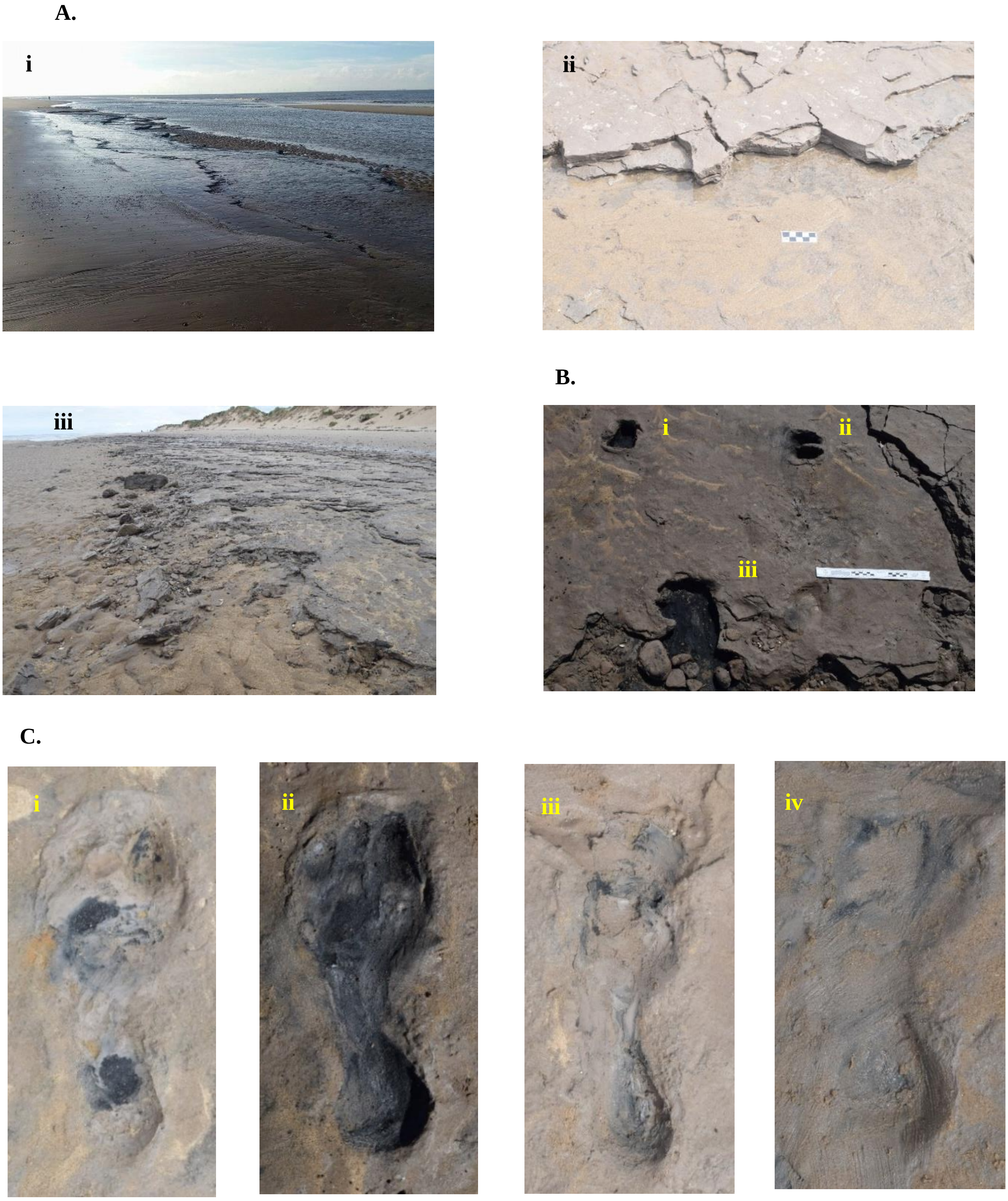


Figure 4. Landmark datasets for the human prints and animal prints. A lack of homologous landmarks in the animal dataset has resulted in a reduced landmark dataset.

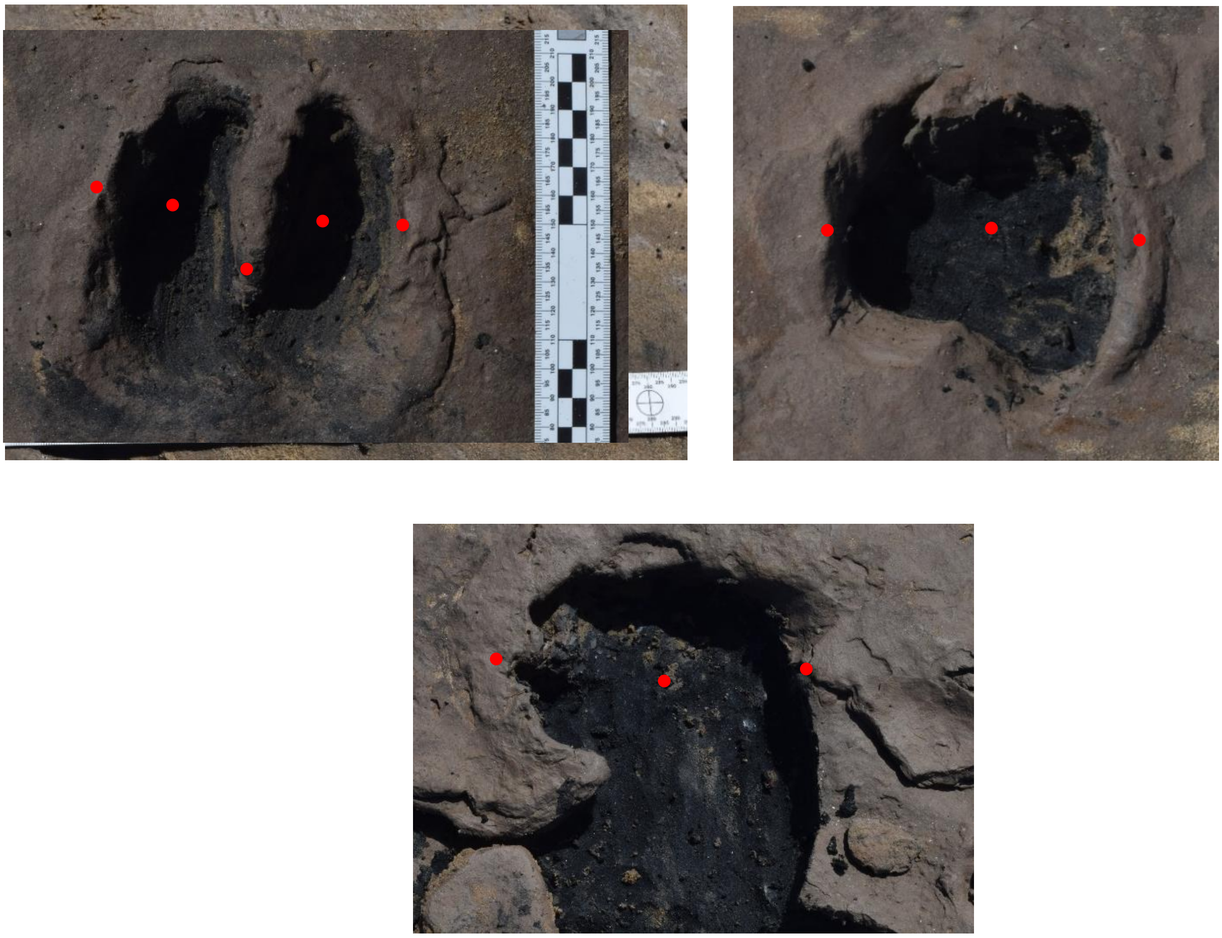


Table 1. The depth of the Holocene human footprint at five separate locations taken from each model. Measurements are in mm. See Supporting Information 1 for experimental print measurements.

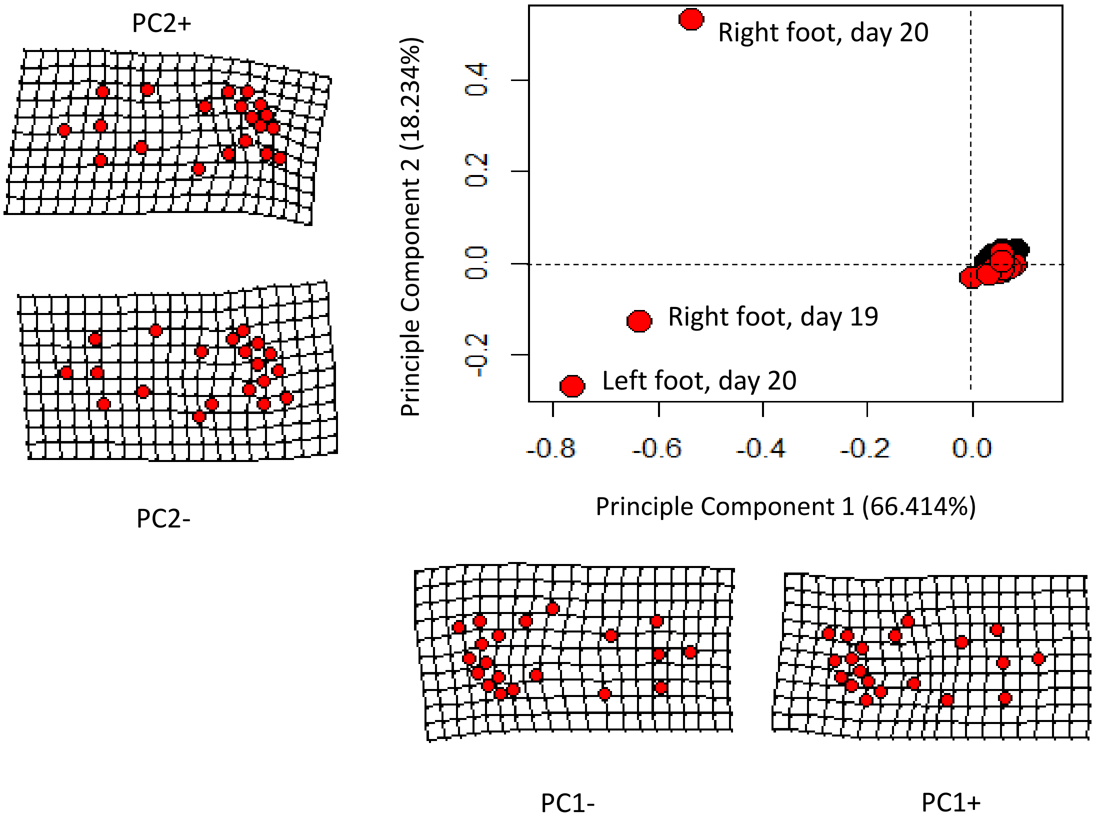
	Model one	**Model two**	**Model three**	**Model four**
Depth of hallux	15.34486	14.28583	2.656838	1.894133
Depth of 2nd to 5th metatarsals	19.20728	12.09233	11.39923	11.32415
Depth of 1st metatarsal	11.54887	8.409708	10.03207	13.9389
Depth of midfoot	6.422628	6.482933	8.004055	5.766013
Depth of heel	12.11445	16.10337	17.66635	18.48052

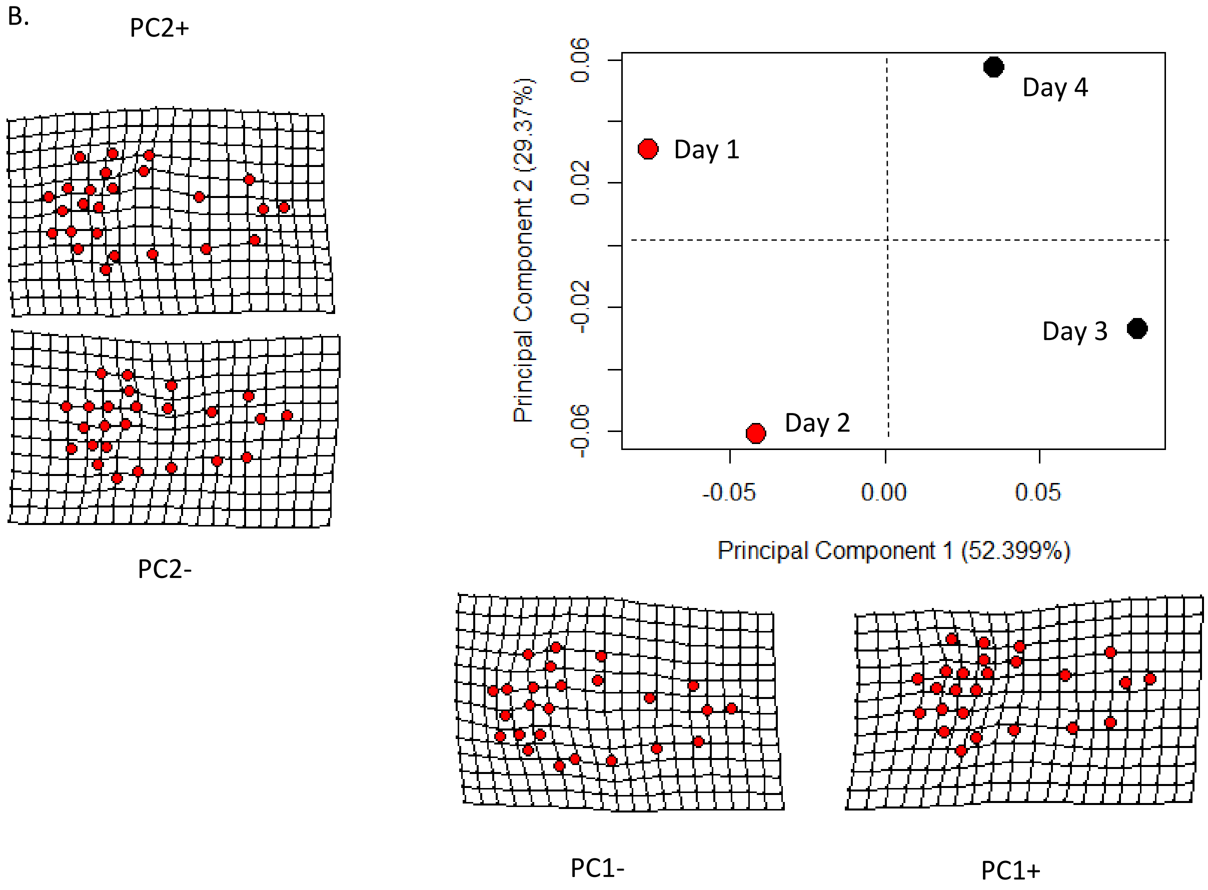
Table 2. Relative warps analysis of all footprints showing the first four principle components for the Holocene human print, the first five for the animal prints and the first 11 for the experimental prints, accounting for over 98% of variance.

	PC	Singular value	% explained variance	Cumulative variance
Fossilised human print				
	1	0.07182	0.52399	0.52399
	2	0.05377	0.29370	0.81769
	3	0.04237	0.18231	1
	4	6.266E-17	0	1
Animal prints				
	1	0.08068	0.66746	0.66746
	2	0.04558	0.21304	0.88250
	3	0.02975	0.09079	0.97128
	4	0.01673	0.02872	1
	5	5.848E-17	0	1
Experimental prints				
	1	0.1932	0.6636	0.6636
	2	0.1013	0.1822	0.8458
	3	0.06836	0.08304	0.92883
	4	0.03668	0.02391	0.95274
	5	0.02638	0.01237	0.96510
	6	0.02009	0.00171	0.97227
	7	0.01599	0.00454	0.097681
	8	0.01400	0.00348	0.98030
	9	0.01231	0.00269	0.98299
	10	0.01096	0.00241	0.98513
	11	0.0106	0.0020	0.9871

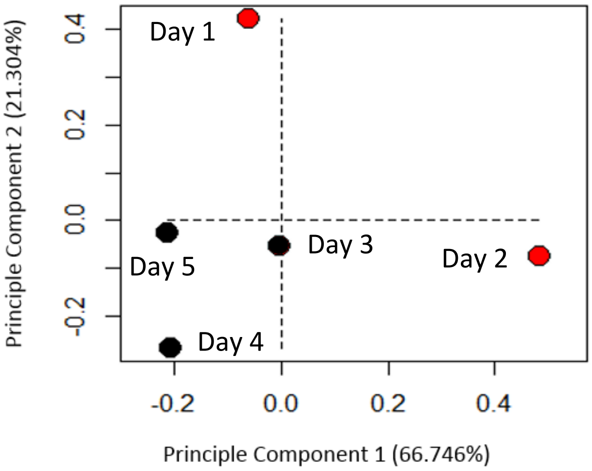
Figure 5. A. This PCA graph illustrates the shape change in the experimental footprints (n=44). Projection of each of the experimental prints on PC1 and PC2. Red dots represent the presence of rain damage which increased in the final two days of the experiment. Black dots represent the experiments before weather damage. B. This PCA graph illustrates the shape change in Holocene human footprint (n=4). Red dots represent the presence of the forefoot. Warp grids display the maximum and minimum relative shape changes along each PC axis. Black dots represent the severe degradation of the forefoot. C. This PCA graph illustrates the shape change in Holocene animal footprints (n=5). Red dots represent the first two days of recording. Black dots represent the last days of recording when the auroch print became severely degraded.

A.




B.
PC2+
PC2-
Principal Component 2 (29.37%)
0.06
0.02
-0.02
-0.06
Day 4
Day 1
Day 3
Day 2
-0.05
0.00
0.05
Principal Component 1 (52.399%)
PC1-
PC1+

C.



Day 1
Day 2
Day 3
Day 4
Day 5
Principle Component 2 (21.304%)
Principle Component 1 (66.746%)
0.4
0.2
0.0
-0.2
-0.2
0.0
0.2
0.4

Figure 6. Linear regression establishing the positive relationship between centroid size and shape of the the experimental prints, as explained by PC1. Red dots represent the presence of rain damage, which increased in the final two days of the experiment. Black dots represent the experiments before weather damage, which are clustered in the graph.

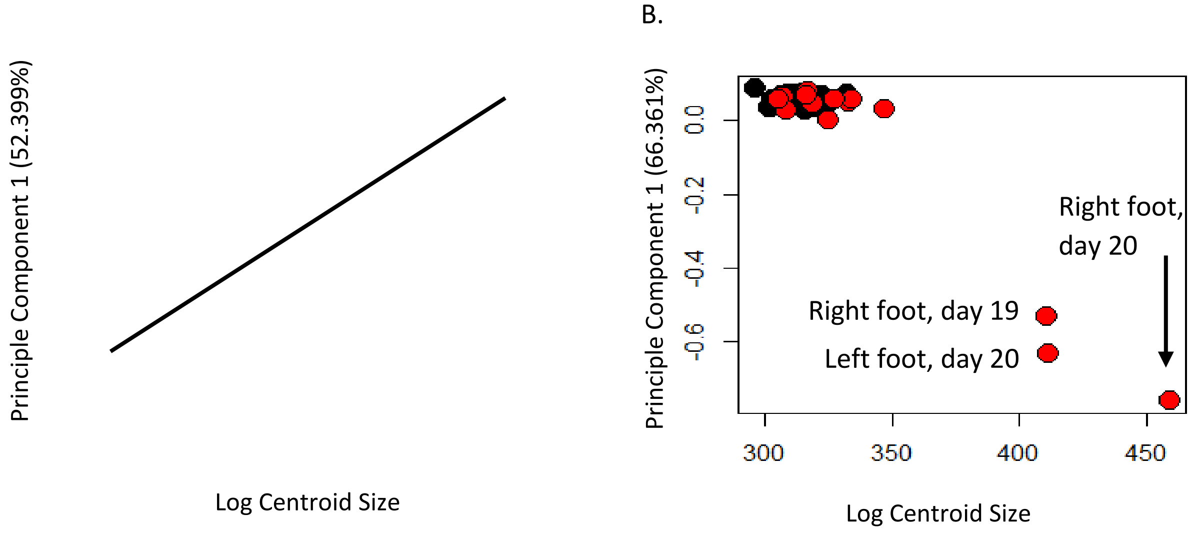


Figure 7. Comparison of hollows from Happisburgh (top) and Formby Point (bottom). Many of the hollows that were disregarded by Ashton *et al.* (2014) that have questionable ichnology from Happisburgh could have been identified as hominin if a delay in recording had not occurred. The photograph from Formby was taken on the penultimate day of excavation. The red highlighted footprints were previously identified as human, but on this day appeared as oval hollows with no distinctive features. Photo credit: Photograph of Happisburgh sediment bed by Simon Parfitt, May 2013.

Acknowledgements.

The authors would like to thank the National Trust Formby and Natural England for access and permission to carry out research. We would also like to thank Simon Parfitt for use of an image taken at Happisburgh, Norfolk in May 2013.

References

Adams, D. C., Otárola-Castillo, E. 2012. 'geomorph: an R package for the collection and analysis of geometric morphometric shape data', *Methods in Ecology and Evolution*. 4: 393-399.

Ashton, N., Lewis, S. G., De Groote, I., Duffy, S. R., Bates, M., Bates, R., Hoare, P., Lewis, M., Parfitt, S. A., Peglar, S., Williams, S., Williams, C., Stringer, C., 2014. 'Hominin footprints from Early Pleistocene deposits at Happisburgh, UK', *PLoS ONE* 9(2):e88329.

Avanzini, M., Mietto, P., Panarello, A., De Angelis, M., Rolandi, G., 2008. 'The Devil's Trails: Middle Pleistocene human footprints preserved in volcanoclastic deposit of southern Italy', *An International Journal for Plant and Animal Traces* 15(3-4): 179-189.

Bates, K. T., Savage, R., Pataky, T. C., Morse, S. A., Webster, E., Falkingham, P. L., Ren, L., Qian, Z., Collins, D., Bennett, M. R., McClymont, J., Crompton, R. H. 2013. 'Does footprint depth correlate with foot motion and pressure?', *Journal of the Royal Society Interface* 10: 20130009.

Behrensmeyer, A. K., Laporte, L. F. 1981. 'Footprints of a Pleistocene hominid in northern Kenya', *Nature Letters* 289: 167-169.

Bennett, M. R., Harris, J. W. K., Richmond, B. G., Braun, D., Mbau, E., Kiura, D. O., Kibunjia, M., Omuombo, C., Behrensmeyer, A. K., Huddart, Gonzalez, S., 2009. 'Early Hominin foot morphology on 1.5-million-year-old footprints from Ileret, Kenya', *Science Report* 323(5918): 1197-1201.

Bennett, M. R., Morse, S. A., Bates, K., Crompton, R. H., 2006. 'Preserving the impossible: Conservation of soft-sediment hominin footprint sites and strategies for three-dimensional digital data capture', *PLoS ONE* 8(4): e60755.

Bennett, M. R., Falkingham, P., Morse, S. A., Bates, K., Crompton, R. H. 2013. 'Preserving the impossible: conservation of soft=sediment hominin footprint sites and strategies for three-dimensional digital data capture', *PLoS ONE*

Bennett, M. R., Morse, S. A. 2014. *Human Footprints: Fossilised Locomotion?* Springer International Publishing: London.

Bennett, M. R., Reynolds, S. C., Morse, S. A., Budka, M. 2016. 'Laetoli's lost tracks: 3D generated mean shape and missing footprints', *Nature Scientific Reports* 6: 21916.

Berge, M. R., Penin, X., Pelle, E., 2006. 'New interpretation of Laetoli footprints using experimental approach and Procrustes analysis: Preliminary results', *Comptes Rendus Palevol* 5(3-4): 561-569.

Bookstein, F. L., 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press: New York.

Crompton, R. H., Pataky, T. C., Savage, R., D'Août, K., Bennett, M. R., Day, M. H., Bates, K., Morse, S., Sellers, W. I., 2011. 'Human-like external function of the foot, and fully upright gait, confirmed in the 3.66 million year old Laetoli hominin footprints by topographic statistics, experimental footprint-formation and computer simulation', *Journal of the Royal Society Interface*: doi:10.1098/rsif.2011.0258.

D’Août, K., Meert, L., Van Gheluwe, B., De Clercq, D., Aerts, P., 2010. ‘Experimentally generated footprints in sand: Analysis and consequences for the interpretation of fossil and forensic footprints’, *American Journal of Physical Anthropology* 141(4): 515-525.

De Lumley, H. 1966. ‘Les fouilles de Terra Amata à Nice’, *Premiers résultats Bulletin du Musée d’Anthropologie Préhistorique de Monaco* 13:29–51.

Dingwall, H.,L., Hatala, K.,G., Wunderlich, R.,E., Richmond, B.,G., 2013. ‘Hominin stature, body mass, and walking speed estimates based on 1.5 million-year-old fossil footprints at Ileret, Kenya’, *Journal of Human Evolution* 64: 556–568.

Domjanic, J., Seidler, H., Mitteroecker, P. 2015. ‘A combined morphometric analysis of foot form and its association with sex, stature, and body mass’, *American Journal of Physical Anthropology* 157: 582-591.

Felstead, N. J., Gonzalez, S., Huddart, D. 2014. ‘Holocene-aged human footprints from the Cuatrociénegas Basin, NE Mexico’, *Journal of Archaeological Science* 42:250–259.

Hatala, K. G., Dingwall, H. L., Wunderlich, R. E., Richmond, B. G. 2016a. ‘The relationship between plantar pressure and footprint shape’, *Journal of Human Evolution* 65: 21-28.

Hatala, K. G., Wunderlich, R. E., Dingwall, H. L., Richmond, B. G. 2016b. ‘Interpreting locomotor biomechanics from the morphology of human footprints’, *Journal of Human Evolution* 90: 38-48.

Hrdlička, A., 1935. ‘The Pueblos. With comparative data on the bulk of the tribes of the Southwest and northern Mexico’, *American Journal of Physical Anthropology* 20: 235–460.

Huddart. D., Roberts, G., Gonzalez, S., 1999. ‘Holocene human and animal footprints and their relationships with coastal environmental change, Formby Point, NW England’, *Quaternary International* 55(1): 29-41.

Kanchan, T., Menezes, R. G., Moudgil, R., Kaur, R., Kotian, M. S., Garg, R. K. 2008. ‘Stature estimation from foot dimensions’, *Forensic Science International* 179: 241.e1-241.e5.

Kendall, D. G., 1984. ‘Shape-manifolds, Procrustean metrics and complex projective spaces’, *Bull. London Math. Soc.*, 16: 81–121.

Krishan, K. 2006. ‘Individualising characteristics of footprints in Gujjars of North India – Forensic aspects’, *Forensic Science International* 169: 137-144.

Leakey, M. D., and Hay, R. L., 1979. ‘Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania’, *Nature* 278: 317-323.

Martin R (1914) *Lehrbuch der Anthropologie 2*. Jena: Fischer.

Marty, D., Strasser, A., Meyer, C. A. 2009. ‘Formation and taphonomy of human footprints in microbial mats of present-day tidal-fl at environments: implications for the study of fossil footprints’, *Ichnos* 16:127–142.

Masao, F. T., Ichumbaki, E. B., Cherin, M., B, A., Boschian, G., Iurino, D, A., Menconero, S., Moggi-Cecchi, G., 2016. ‘New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins’, *eLife* 5: e19568.

Mietto, P., Avanzini, M., Rolandi, G. 2003. ‘Palaeontology: Human footprints in Pleistocene volcanic ash’, *Nature* 422: 133.

Morse, S. A., Bennett, M. R., Liutkus-Pierce, C., Thackeray, F., McClymont, J., Savage, R., Crompton, R. H., 2013. ‘Holocene footprints in Namibia: the influence of substrate on footprint variability’, *American Journal of Physical Anthropology* 151(2): 265-279.

Oxnard, C.E. and O’Higgins, P. (2009). ‘Biology clearly needs Morphometrics? Does Morphometrics need Biology?’, Biological Theory 4(1): 84-97.

Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E. H., Foster, A. D., Randall, W. M., Haas, J., 2008. ‘Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics’, *PLoS ONE*: 5(3): e9769.

Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E. H., Foster, A. D., Haas, W. R. J. 2010. ‘Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics’, *PLoS ONE* 5(3): e9769.

Raichlen, D. A., Gordon, A. D. 2017. ‘Interpretation of footprints from Site S confirms human-like bipedal biomechanics in Laetoli hominins’, *Journal of Human Evolution* 107: 134-138.

Roberts, G., 2009. ‘Ephemeral, subfossil mammalian, avian and hominid footprints within Flandrian sediment exposures at Formby Point, Sefton Coast, North West England’, *An International Journal for Plant and Animal Traces* 16(1-2): 33-48.

Roberts, D., Berger, L. R. 1997. ‘Last interglacial (c.11k kyr) human footprints from South Africa’, *South African Journal of Science* 93: 349-350.

Roberts, G., Gonzalez, S., Huddart, D.,1996. ‘Intertidal Holocene footprints andtheir archaeological significance’, *Antiquity* 70(269): 647-651.

Rohlf, F. J., Slice, D. E., 1990. ‘Extensions of the Procrustes method for the optimal superimposition of landmarks’, *Syst. Zool.*, 39: 40–59.

Schlager, S. 2017. “Morpho and Rvcg – Shape Analysis in R.” In Zheng G, Li S and Szekely G (eds.), *Statistical Shape and Deformation Analysis*, pp. 217–256. Academic Press.

Schmid, P., 2004. ‘Functional interpretation of Laetoli footprints’ in Meldrum, D. J. and Hilton (ed), *From Biped and Strider: The Emergence of Modern Human Walking, Running and Resource Transport*, 49-62. Springer US, New York.

Slice, D., E. (ed.) 2005. *Modern Morphometrics in Physical Anthropology*. Kluwer Academic/Plenum.

Tuttle, R., 1987. ‘Kinesiological inferences and evolutionary implications from Laetoli bipedal trails G-1, G-2/3’, in Leakey, M., D. and Harris, J., (ed), *Laetoli A Pliocene site in northern Tanzania*, 503–523. Oxford UK: Clarendon Press.

Vaughan, C. L., Blaszczyk, M. B., 2008. ‘Dynamic similarity predicts gait parameters for *Homo floresiensis* and the *Laetoli hominins*’, *American Journal of Human Biology* 20(3): 312-316.

Watson, P. J., Kennedy, M. C., Willey, P., Robbins, L., Wilson, R. C. 2005. Prehistoric footprints in Jaguar Cave, Tennessee. *Journal of Field Archaeology,* 30: 25–43.

Webb, S. 2007. ‘Further research of the Willandra Lakes fossil footprints site, southeastern Australia’, *Journal of Human Evolution* 52: 711-715.

Zelditch, M. L., Swiderski, D. L., Sheets, H. D., Fink, D. L., 2004. *Geometric Morphometrics for Biologists: A Primer*. Elsevier Academic Press: London

Supporting Information

Supporting Information table 1 (S1). Measurements in centimetres taken of the foot length and the predicted stature using Martin's 0.15 ratio (Martin 1914). Percentage change difference in foot length values from the first day were calculated. Robbin's ratio of 0.14 was used for the experimental prints (EP), owing to the print maker being habitually shod. Model numbers correspond to the day that the model was made.

	Model no.	Foot length	% change in foot length	Predicted stature
Formby print	1	24.64	/	164.26
	2	24.64	0.01%	164.28
	3	25.75	4.42%	171.68
	4	23.11	6.47%	154.05
EP left foot	1	21.59	/	154.24
	2	21.46	0.62%	153.29
	3	21.37	1.06%	152.61
	4	20.64	4.40%	147.45
	5	20.56	4.78%	146.86
	6	20.99	2.80%	149.92
	7	20.54	4.87%	146.74
	8	20.30	6.02%	144.96
	9	20.79	3.74%	148.47
	10	20.98	2.86%	149.84
	11	21.21	1.76%	151.52
	12	21.32	1.26%	152.29
	13	21.62	-0.13%	154.44
	14	21.65	-0.25%	154.63
	15	21.59	0.01%	154.22
	16	22.96	-6.32%	163.99
	17	22.20	-2.79%	158.55
	18	22.07	-2.20%	157.63
	19	22.19	-2.76%	158.49
EP right foot	1	22.12	/	157.98
	2	21.84	1.26%	155.99
	3	21.35	3.46%	152.51
	4	21.32	3.58%	145.17
	5	20.84	5.77%	148.86
	6	20.97	5.20%	149.76
	7	21.06	4.77%	150.44
	8	21.70	1.89%	155.00
	9	22.60	-2.20%	161.45
	10	20.89	5.54%	149.22
	11	21.16	4.34%	151.13
	12	21.28	3.80%	151.97
	13	21.41	3.19%	152.94
	14	21.91	0.93%	156.51
	15	22.38	-1.19%	159.86
	16	22.94	-3.74%	163.89
	17	23.42	-5.89%	167.28
	18	22.15	-0.16%	158.23
	19	22.36	-1.08%	159.69