Chapter 2

Inferences from Footprints: Archaeological Best Practice

Matthew R. Bennett and Sally C. Reynolds

Abstract Animal footprints are preserved in the archaeological record with greater frequency than perhaps previously assumed. This assertion is supported by a rapid increase in the number of discoveries in recent years. The analysis of such trace fossils is now being undertaken with an increasing sophistication, and a methodological revolution is afoot linked to the routine deployment of 3D digital capture. Much of this development has in recent years been driven by palaeontologists, yet archaeologists are just as likely to encounter footprints in excavations. It is therefore timely to review some of the key methodological developments and to focus attention on the inferences that can and, crucially, cannot be justifiably made from fossil footprints with specific reference to human tracks.

Keywords African palaeoecology · Mammalian ichnology · East African fossil record · Laetoli · Hominin sites · Pliocene · Ichnology

Introduction

Every contact an animal makes with the ground has the potential to leave a trace, as set out in Locard's famous exchange principle. The average moderately active person, for example, takes around 7500 steps a day, and if maintained over a lifetime of 80 years, then they will have left the order of 216,262,500 steps with each step having a theoretical potential for preservation. Contrast this with the 206 bones in the human body, and it is not surprising that we frequently uncover fossil footprints. In fact, it is surprising that we don't find more. Something we would argue is due to the lack awareness and prospection, rather than any particular rarity in the geological or archaeological record. There is a well-documented recent examples where footprints of *Homo heidelbergensis* have been recovered (Altamura et al. 2018) but were not

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recognised by earlier excavators who destroyed tracks in their quest for more conventional archaeological materials. Increasing awareness of archaeologists of the potential to find footprints in excavations of all ages is an important endeavour, as is drawing attention to the convergence of methodological approaches, standards of recovery and best practice. Much of this best practice has been driven in recent years by the palaeontological community, and it is therefore timely, we believe, to review these developments for the benefit of all, especially for archaeologists.

There has been a rapid growth in recent years in the discovery of human fossil footprints around the world which questions the long-held and much-stated assumption that footprint preservation is a freak geological event (Bennett and Morse 2014). To give a flavour of the recent discoveries, in 2016 we saw the publication (Masao et al. 2016) of additional footprints at the famous 3.66-million-year-old footprint site at Laetoli in northern Tanzania first reported in 1979 by Leakey and Hay (1979). Not far from Laetoli, a Late Pleistocene site on the shores of Lake Natron was reported with hundreds of visible tracks (Balashova et al. 2016; Liutkus-Pierce et al. 2016; Zimmer et al. 2018). In 2018 the publication of children's footprints in association with butchered hippo carcasses was reported from Ethiopia (Altamura et al. 2018), and there are reports of human tracks in association with giant ground sloth in North America (Bustos et al. 2018). Footprints preserved in peat have been found on the Pacific Coast of Canada (McLaren et al. 2018), and a new footprint site in South Africa is reported by Helm et al. (2018). Footprints have been found in a diverse range of environments (Fig. 2.1a), and improved awareness by excavators, continued prospection and a revolution in digital techniques for their capture and analysis are perhaps responsible for the increasing discovery of new sites. There is much more to do however.

The aim of this contribution is explore modern tools for the capture and analysis of fossil footprints and to emphasise some of the challenges archaeologists face in making inferences from human footprints in particular. We have structured this review along three stages in what we see as the ichnological pipeline: (1) digital capture and documentation, (2) analysis and (3) inference. To aid cross-disciplinary convergence, the key terminology used in vertebrate ichnology is provided in Table 2.1.

Digital Capture, Documentation and Stratigraphic Context

A quiet revolution during the last decade has transformed human ichnology from an essentially descriptive discipline into one that is now both data- and hypothesis-driven. This transformation started with the introduction of optical laser scanners to capture 3D tracks and has been completed with the routine availability of Structure from Motion-based photogrammetry (Bennett and Budka 2018). While 3D documentation is not necessarily new, having been applied in the late 1970s to the Laetoli tracks (Day and Wickens 1980; Leakey and Harris 1987), it has now become routine for all modern practitioners, although there remain situations where it has not been

Fig. 2.1 (a) Sketch showing the typical types of location in which fossil footprints have so far been found after Bennett and Morse (2014); (b) the power of independent lines of investigation leading convergence and/or corroboration

successfully applied or has failed due to environmental conditions (e.g. Ashton et al. 2014). Collecting 3D data allows the user to test assumptions and inferences that previously were made simply by assertion, as exemplified by the work of Roberts et al. (1996). There are those that argue that assertions made by expert trackers (Pastoors et al. 2015, 2016) provide a valid alternative, and while the skill of the

Table 2.1 Commonly used terms with respect to footprint or footwear impression. After Marty et al. (2009)

Term	Definition
Track	A single footprint or partial impression made by the foot of shod or unshod animal or human
Trackway	A series of tracks made by a single individual
Trail	A series of signs or objects left behind by the passage of someone or something. In this context it might be multiple tracks left by one or more individuals, forming a path, for example
Trackmaker	The animal that made the track
Tracked surface	The surface on which the trackmaker walked/moved
Over-printing	Caused by an individual or animal over-printing an original track
Displacement rim	A marginal rim to a track formed by the upward displacement of sediment, sometimes referred to as a push-up structure or a bourrelet
Track ejecta	Material ejected by the removal of the trackmaker's foot from a track. This often forms a debris trail in front of a track
Plantar surface	The base of the trackmaker's foot or shoe
Ichnosurface	A surface with multiple tracks which may have either formed in an isochronous (synchronous) or diachronous (time-averaged) fashion

trackers is not in dispute, the inability of a reader to question and/or test those assertions themselves limits the scientific credibility of such approaches.

The authors have developed, along with colleagues, freeware (www.digtrace.co.uk) that enables the capture of tracks in 3D using the open source software OpenMVG (Bennett and Budka 2018). Not only can you create 3D models, but the freeware provides a series of analytical workbenches with tools specific to the analysis of footprints. Commercial alternatives exist in the form of such things as PhotoScan by Agisoft (<http://www.agisoft.com>), and while they create excellent 3D models, they do not provide analytical tools specific to footprint analyses, and the user has to rely on expensive 3D modelling software or freeware tools such as MeshLab (www.meshlab.net) or CloudCompare (www.danielgm.net/cc). Structure from Motion relies on multiple oblique digital photographs from which individual pixel clusters are placed in 3D space. Almost any digital camera can be used provided its sensor size is known or can be calculated (Bennett and Budka 2018).

The archaeologist who arrives at a field site or encounters a series of footprints for the first time needs a plan. Figure 2.2 lists some of the key elements of any plan and reviews the things that need to be considered. Assuming that one has the necessary permits and permissions, the first step is to consider whether the tracks can be preserved or whether it is a case of conservation by rescue. Preserving soft-sediment footprints is challenging, if not impossible (Bennett et al. 2013), and 3D digital capture is often the only way to create a permanent record of the tracks (Bennett and Morse 2014). This is especially true of those tracks preserved in coastal exposures (Bennett et al. 2010; Falkingham et al. 2018; Wiseman and De Groote 2018) or where the act of excavation disturbs a fragile surface, thereby allowing erosion.

Arrival at Field Site

1

Pause

- Do you have the necessary permits and permissions?
- What are the objectives of the study?
- Where are the main areas of interest?
- Are the tracks exposed or do they need to be excavated?
- What is known, what is the current working hypothesis or hypotheses?
- Why and how were the tracks preserved? Keep an open mind.
- Who, what made the tracks? Keep an open mind.
- Actions should be proportionate to the objectives.

2

Assess and Preserve

- How large is the ichnosurface, is there more than one surface/site?
- What is the stratigraphic context and dating potential?
- What were the environmental conditions at the time the tracks were made?
- What are the current weather conditions?
- What can be excavated and uncovered easily? Do you have permission?
- What are the temporal relationships between ichnites?
- What ichnites are not relevant to your objective and need to be eliminated?
- Focus on areas of surface change and transitions between geological materials.

3

Evidence Recovery Plan

- Risk assessment, health and safety considerations.
- Prioritise vulnerable ichnites and consider sequential documentation/collection.
- Constantly change the line of sight and use different lighting options.
- Ensure excavation approaches do not damage the tracks as they are uncovered.
- Don't stop searching once the visible evidence is removed.
- Try to leave items in situ if possible and only recover/cast if they will be lost.

4

Record Throughout

- Known information prior to attending.
- Site assessment and recovery plan.
 - Surfaces/horizons searched.
 - Types of surfaces encountered.
- Location of all ichnites recovered/documented.
 - Ichnites eliminated.
- Decision log for the above.

1-4

5

Review

- New evidence may come to light, so always be prepared to evolve your plan.
- Review and learn from experience and mistakes if made.

Fig. 2.2 The basic structure of an ichnological field survey plan, modified from Bennett and Budka (2018)

Interestingly, recent work using geophysics (magnetometry and ground-penetrating radar) shows promise with respect to how tracks may be prospected for without surface disturbance or excavation (Urban et al. 2018).

The basic information that is required is (1) spatial information showing the relative position of one track to another (i.e. some form of map); (2) detailed 3D models of all or a selection of individual tracks; (3) detailed vertical photographs, written observations and measurements; (4) facies descriptions of the containing sediments both vertically and spatially; and (5) detailed sampling for datable materials both below and above the tracked layer. Spatial mapping can be achieved in a variety of different ways, although traditional field survey techniques, coupled with low-level aerial photographs, are now the norm. Traditionally plastic sheets have been placed over tracked surfaces, and footprint outlines have been traced onto them. These have to then be reduced to make them manageable, the advantage of vertical images is that, if the surface is not horizontal, contours can be added using photogrammetry or portable LiDAR devices. Working at White Sands National Park (WNSA), Bustos et al. (2018) used Agisoft's PhotoScan to produce photomosaics of large areas, supplemented with detailed 3D models of individual tracks made with DigTrace.

Tracks need to be documented individually, or in combination. Deciding what the sampling strategy should be is critical here. For example, how many tracks should be excavated out of the total population? What proportion should be conserved, if any, for future investigators? This clearly depends on the total available track count, but at sites like those described by Morse et al. (2013) and Bustos et al. (2018) where there is a surplus of tracks and excavation limits long-term preservation, then these are real questions for which there are few definitive answers. As working principle excavating/disturbing the minimum number of tracks is usually the general practice, unless the site is at risk. Sampling strategies are not necessarily relevant where there are a small number of endangered tracks. Anything and everything that is excavated needs to be captured in 3D. Where a whole surface has been scanned, or a 3D mosaic created, there is a temptation to simply crop this down to create individual track models. Large-scale models do not always have the resolution, however, for detailed topological study and rarely deal with undercut edges well. It is therefore advisable to also make close-up models where lines of sight can be improved. It is also worth noting that photogrammetry, or laser scanning for that matter, is not always a perfect solution especially where the tracks are deeply incised in soft ground. The use of an endoscope can help with this, but it may be necessary to adopt alternative strategies. For example, Altamura et al. (2017) excavated deep hippo tracks and then infilled these with plaster before excavating the surrounding surface to reveal the cast. The casts can be laser scanned subsequently, if required. Once the individual tracks have been documented, it is then necessary to describe and sample the tracked units and surrounding lithofacies, using standard procedures.

Analytical Tools in Ichnology

Traditionally good science requires a separation between description and interpretation. The description will always stand if done well, but the interpretation may change with time and new ideas or discoveries. In the context of a track, this is the separation between describing a track's topological properties and making inferences about the trackmaker from them. There are lots of examples where a trackmaker is inferred without such description (e.g. Musiba et al. 2008). In describing and/or measuring a track of whatever origin, we have three main independent properties to consider. Firstly, we have size defined by a single, or more usually, a combination of linear measurements. Typically these include measures of length, area and volume. Secondly, we have shape or form which describes how the track is defined by intersecting lines, edges or textural boundaries. For example, do the edges define a triangle or square? Finally we have topology which is the geometrical properties, and their spatial relationships to one another, such as the spatial disposition of different component shapes and depth variations. The morphology (or anatomy) of a track is the sum of the above properties, and all three dimensions need to be considered when describing a track (Fig. 2.3a).

Separating aspects of shape and size is an important part of any anatomical description and is usually achieved by the superposition and transformation of geometric forms such that size is removed. This is a standard part of most geometric morphometric analysis and is commonly attained via some form of Generalised Procrustes Analysis (GPA; Zelditch et al. 2012; Gómez-Robles et al. 2008; Friess 2010). Berge et al. (2006) pioneered the application of GPA to human tracks, an approach adopted and refined by Bennett et al. (2009) in their analysis of the Ileret footprints and used by others since (e.g. Wiseman and De Groote 2018). All the above require the placement of some form of homology-based landmark, that is, a landmark that relates to a biologically or anatomically homologous structure and crucially one that can be recognised consistently by observers. Even a single linear measurement of length requires landmarks to be placed at the start and finish of the measurement line. Defining landmarks consistently across different studies and operators is a source of error especially where linear properties such as length are not clearly defined (Bennett and Morse 2014).

Concern over landmark placement led Crompton and his team at the University of Liverpool to develop a whole-foot comparison method in which tracks are co-registered allowing measures of central tendency to be determined for entire track populations. Taking their lead from the mathematics behind the analysis of magnetic resonance imaging (MRI), they developed pedobarographic statistical parametric mapping (pSPM). It was designed to co-register multiple pressure records obtained from individuals walking on a treadmill, once co-registered pixels in similar anatomical positions are compared (Crompton et al. 2012). By substituting depth for pressure, one can apply it to tracks, although it requires the removal of all marginal structures for automated registration since it can only match recurrent plantar surfaces. Manual registration gets around this problem, but in doing so the

Fig. 2.3 (a) Components of track morphology; (b) analytical questions that can be addressed by quantitative analysis when 3D digital data is collected

objectivity obtained by auto-registration is lost. It is important to note that marginal deformation structures are as equally valid as the plantar surfaces in interpreting tracks.

Bennett et al. (2016a) use an alternative approach in which tracks are co-registered by matching common structures, via placed landmarks. These matched points are then used to guide the registration, and this approach has the advantage of being driven by a simple user interface. Whichever approach is used to register a population of tracks, once co-registered, one can create measure of central tendency, pixel by pixel, in the form of a mean/median track and measured of statistical variability around this (Crompton et al. 2012). This allows both dimensions of track variability to be explored, namely, (1) intra-trackway variance, that is, the variation between different tracks made by the same trackmaker in a trackway due to variation in substrate and inter-step biomechanics, and (2) inter-trackway variance, that is, the difference between two different trackways that may, or may not, have been made by the same individual. Both are critical to determining whether a set of tracks were made by the same trackmaker or not. If the intra-trackway variance is greater than the inter-trackway variance, then you have a problem in making a definitive qualitative or quantitative distinction between them. Belvedere et al. (2018) introduce two new terms, the stat-track and the mediotype (Fig. 2.3b). The former refers to any statistically produced measure of central tendency for a population of tracks, while the latter refers specifically to a mean or median track created from those holotype specimens. They also provide a range of examples of how whole-track methods can be used to help formalise the description of formal ichnotaxa (Marty et al. 2009, 2016).

Types of Inference from Human Footprints

The discovery and/or excavation of a fossil trackway can be an exciting process, revealing as it does a captured moment in time when the foot of a human made contact with the ground. Tracks lead to a range of analytical questions (Fig. 2.3b), and there are four broad areas of inference that can be drawn from such discoveries: (1) the trackmaker, their pedal anatomy and inferences about size and body mass; (2) locomotion style and speed from the depth distribution which is assumed to be a proxy for pressure; and (3) the palaeobiology of the track assemblage. Different preservation conditions favour different types of inferences as illustrated in Fig. 2.5 and discussed below.

Anatomical Inferences

An individual track, or more reliably a population of morphologically similar tracks (Fig. 2.3b), preserves anatomical information about the trackmaker, such as the

shape of the foot and/or the number of digits. This information is inclusive of the soft tissue that surrounds the bones, material that is rarely preserved and yet essential to anatomical description and locomotory behaviour. A given animal may produce a range of different track topologies depending on functional interaction with the sediment and the sediment itself (Bennett et al. 2014). The next logical step is to name the trackmaker, although this is not always as simple as it sounds. Within the Plio-Pleistocene at least the starting point for such interpretation is the palaeontological record or a modern animal track guide. Over-reliance on the palaeontological record provides an ever-present risk of missing a species known only by its tracks at a given site. In a similar way, reliance on modern tracking guides or local/native trackers when dealing with Pleistocene track sites (Pastoors et al. 2015, 2016) assumes a similarity that is not always warranted between past and present communities. The tendency to fit tracks to a known template is also an ever-present risk. Good science comes from good building blocks forming safe foundations, and in the case of ichnology, this consists of good topological, quantitative, 3D descriptions of individual tracks and their topological variability as a population of tracks. This should occur independently of any assessment of the sedimentary facies and associated palaeontology (Fig. 2.1b).

Assuming the trackmaker can be deduced, the next stage is to consider what biometric inferences are possible for that given animal. Empirical relationships between foot size and height are well known for humans and some animals (Fig. 2.4). For example, Roberts et al. (2008) describe an elephant trackway dated to around 90 ka from Still Bay in South Africa in aeolinites. The tracks are attributed to the African elephant (*Loxodonta africana*), and, interestingly, Roberts et al. (2008) use the track dimensions to infer both shoulder heights and ages for the trackmakers using the empirical relationships of Western et al. (1983). There is good data about the ontology of African elephants (Western et al. 1983; Lee and Moss 1995; Shrader et al. 2006) allowing biometric data to be inferred. It is an approach that has been applied elsewhere to mammoth tracks in Canada (McNeil et al. 2005) and Miocene Proboscidea tracks in the United Arab Emirates (Bibi et al. 2012). The idea is based on fitting a growth curve such as a von Bertalanffy growth function, to available empirical data, despite the fact that the trackmaker's sex cannot normally be determined from a track alone and that the presence of sexual dimorphism complicates such inferences. To what extent this approach could be applied to other animals is uncertain but has the potential to be an interesting line for future research. It has been applied to dinosaur tracks where there are clear morphological variations with size (e.g. Avanzini and Lockley 2002), and some data on the ontology of ungulate tracks does exist (e.g. Miller et al. 1986; Musiba et al. 1997; Cumming and Cumming 2003; Stachurska et al. 2011; Parés-Casanova and Oosterlinck 2012a, b).

In terms of humans, there is a wealth of empirical relationships for different ethnic/racial groups which relate foot size to stature (and refs therein: Bennett and Morse 2014). The founding data is based on different measurement protocols and either 2D foot imprints or direct foot measurements. As a consequence the value of this huge body of data to fossil footprint studies is more limited than sometimes

Fig. 2.4 Stature and body mass inferences from footprints; **(a)** data from a beach showing variation in foot length due to intra-step variability. A total of 57 tracks were used and then boot-strapped to give the 2000 data points shown. The 95% confidence ellipse is shown by the dashed line; **(b)** stature estimates using a range of different published stature equations for a single Holocene trackway in Namibia $N = 77$. A fuller description of this analysis is provided in Bennett and Morse (2014); **(c)** foot length, stature and body mass estimates for a sample ($N = 234$) of 3D footprints for a Bournemouth University staff/students

assumed. The first issue is that foot length varies considerably along a trackway due to substrate, biomechanical inter-step variability and chance. Consider the data in Fig. 2.4a which shows the length variation of a single individual walking on a beach and the potential height variations obtained using a simple 15% foot length to stature ratio. Similarly for a fossil trackway, you don't normally know the ethnicity/race, sex or age of the trackmaker, and you are left to make a series of assumptions in selecting an empirical relationship to model stature from foot length, and this is even more problematic when dealing with extinct human ancestors. Figure 2.4b shows a series of height estimations made from the same trackway of 77 tracks in Namibia (Morse et al. 2013) using different empirical equations. They give a range of estimates which are generally higher than the more conservative 15% rule of Topinard (1877). While they give a greater sense of scientific rigour, this is perhaps an illusionary, and the results depend on the empirical relationship chosen (Fig. 2.4). Empirical relationships to body mass are available (Fig. 2.4), but they are much weaker than those for stature, and, while some more sophisticated modelling has been attempted (e.g. Dingwall et al. 2013; Masao et al. 2016), again the reliability of such estimates has to be questioned (Bennett and Morse 2014). Finally, while modest levels of sexual dimorphism are evident in human track length, it is possible to separate genders on the basis of track measurements within controlled populations (Bennett and Morse 2014). However, there are simply too many unknowns to do so in the fossil record. Where small adult tracks exist, it is perhaps possible to tentatively suggest that they may be those of women, but the possibility that they are adolescent males can never be ruled out definitively. Despite this, implicit and explicit gender assignment of footprints is common within the literature. The other issue to be considered is how representative are size estimates of a population as a whole. Sampling by substrate and sampling by activity are all issues that are relevant here (Kinahan 2013). The harsh reality is that unless a large number of tracks are present, clearly made by different individuals, it is hard to make reliable inferences. True demographic reconstructions from the basis of human footprints have yet to be attempted, not least because the number of sites where it can be applied is limited. In terms of track abundance, there is also a fine line between too many tracks leading to multiple partial impressions due to over-printing and too few to do anything other than to give data on an individual (Fig. 2.5).

Biomechanical Inferences

As the foot makes contact with the ground, if the shear strength of the substrate is exceeded, it will deform leaving a record of that interaction (Hatala et al. 2018). Implicit in all biomechanical inferences from tracks is the idea that distributions in depth across the surface of a track provide a measure of the plantar force applied by the foot in different locations and phase of stance. The experimental work of Bates et al. (2013) shows that there is greatest correlation between plantar pressures and depth for shallow tracks and that this relationship holds less for deeper examples.

Fig. 2.5 Factors that control the nature of an ichnosurface and its scientific value

Given that the preservation potential is greater for deeper tracks, this may limit biomechanical inferences from some types of fossil track site (Fig. 2.5). Speed estimates are possible using step and stride length records and the empirical relationships developed by Alexander (1984). Biomechanical inferences on hominin tracks have been extensive and fiercely debated (e.g. Meldrum et al. 2011; Bennett et al. 2016a, b; Hatala et al. 2016b) and, as such, are not considered further here.

Palaeobiological Inferences

Lockley (1986) argues that tracks provide palaeobiological data, ranging from the taxonomic identification of the trackmaker, placing them at given location and time, to providing information on faunal biodiversity where evidence of multiple trackmakers is present. This can be used to contribute data on the palaeogeographic range of a species, its demography and/or population dynamics. Interestingly, in contemporary environments track density maps are used to assess population numbers of specific species, most notably carnivores, and perform better than some other census methods (e.g. Prins and Reitsma 1989; Silveira et al. 2003; Gompper et al. 2006; Funston et al. 2010; Moreira et al. 2018). The problem with fossil tracks is one

cannot constrain the time interval over which tracks are preserved, and faunal sampling usually influences the results. This subject is explored further below.

Inferences from track assemblage with respect to the behavioural ecology of trackmakers, such as the composition of herds, tendency toward gregarious habits and even prey-predator relationships, are, in theory, possible. Martin and Pyenson (2005) argue that trackways contain evidence of an array of behaviours, such as shifts in speed and direction, lateral movements, obstacle avoidance as well as gregarious movements. Ostrom (1972) and several others have used directional data of dinosaur trackways, for example, to argue for gregarious behaviour, while Bibi et al. (2012) argued for evidence of social structure in Miocene Proboscidea in the United Arab Emirates on the basis of trackway patterns. Working at Ileret (Kenya) track site, Roach et al. (2016, 2018) argued that hominin tracks show similar states of deterioration and typically do not cross-cut one another and as such can be considered at best to be contemporaneous and at worst penecontemporaneous. They suggest that the parallel hominin trackways (1.5 Ma), with individual tracks of similar size, indicate that the trackmakers moved as part of male hunting groups (see also Hatala et al. 2016a, 2017). Altamura et al. (2018) point to the co-association of child tracks with stone tools and the remains of a butchered hippo carcass from which they infer a more pastoral scene in which young children are present (0.7 Ma) and presumably learning. Perhaps one of the best examples, however, of behavioural inference is provided by Bustos et al. (2018). In this work they show that the tortuosity of trackways made by extinct giant ground sloth from the terminal Pleistocene increases in the presence of human trackmakers. In fact the trackways show evidence of evasion with sudden changes in direction and speed. Bustos et al. (2018) suggest that human hunters were stalking and harassing sloth, presumably as part of a hunting strategy. The higher the density of tracks and the more extensive they are in space, the greater the potential to infer palaeobiological information (Fig. 2.5).

Critical to all these inferences are two fundamental questions which are referenced in passing in most track-based publications but rarely developed in detail. They are issues of faunal sampling and of demonstrating co-association within a track assemblage. Both issues are underpinned by the geological context of the site and are explored further here due to the fundamental importance of these issues.

Faunal Sampling

Essentially this distils down to the question that troubles all palaeontological studies eventually, which is to what extent does a proxy count, for example, of the number of bones or tracks mirror the original faunal population from which they are derived, in terms of composition and abundance, and to what degree do taphonomic processes distort this reflection? In the context of tracks, these issues were explored in the seminal papers by Cohen et al. (1991, 1993) which provide one of the few

Table 2.2 Factors influencing track survivorship after Cohen et al. (1993)

Substrate susceptibility (strain)	Track loading (stress)	Secondary reworking rates
Sediment properties (texture, sorting, bulk density, organic content)	Pedal anatomy and animal body mass (mass/shape/force)	Vertebrate trampling/foraging (+)
Water content (+/–)	Biomechanics (including manus vs pes variations)	Invertebrate bioturbation (+)
Degree of cementation inclusive of salts and algal mats (–)	Kinematics (e.g. direction, acceleration and deceleration)	Surface disturbance such as waves, run-off, deflation, desiccation (+)
		Algal stabilisation/cementation (–)
		Salt blooms (–/+)
		Surface desiccation (–/+)
		Burial (–)

The positive and negative signs refer to the direction of a potential influence. These three grouped variables are plotted on ternary diagrams in Fig. 2.6

modern analogue studies (neoichnology) relevant to the interpretation of Plio-Pleistocene track sites.

Cohen et al. (1993) recognise three basic variables at play in track preservation (summarised in Table 2.2), namely, (1) animal load (force/area) (2) sediment susceptibility (strain/stress) and (3) secondary reworking. These three summary variables are not completely independent of one another. For example, a surface with a high susceptibility to deformation will also be one that is easily reworked. However, it does provide a means of exploring the interplay of these variables in track formation and the immediate taphonomy of those tracks. Here we conceptualised these variables on a ternary diagram to define a track-forming window for a given animal (load), at a specific time and place (Fig. 2.6). It defines the Goldilocks track-forming zone, as modelled numerically by Falkingham et al. (2011). These variables and the track-forming windows they define vary spatially across a site such as a lake margin, or river, and temporally, as pore water and surface water conditions change over time. The track-forming window, present at one location and moment in time, samples the fauna that passes; too little fauna and it won’t be sampled, too much and it will not be preserved at all due to self-inflicted bioturbation (Fig. 2.5). Take the example shown in Fig. 2.7, which shows a hypothetical model based on a lake or river margin. Rainfall events are linked to rises in water level, and track preservation occurs primarily during falls in water levels when the maximum printable surface is revealed. Animals are not continuously present but visit periodically, as indicated by the green bars. For tracks to be preserved, there need animals to be coincident with a track-forming window. The site is effectively trackmaker limited, and the tracks preserved do not reflect the whole faunal community, simply part of it (Fig. 2.7).

The corollary to the track-forming window is the surface relaxation time. That is, the time it takes for the surface structure (i.e. track topology) to decay through surface reworking, whether due to bioturbation or by surface processes, along with

Fig. 2.6 Track-forming window as defined by the interplay of animal load, substrate reworking and substrate susceptibility. Different animals have different track-forming windows. For example, compare (b) to (c) while track-forming windows may vary through time, as shown in (c)

sediment plasticity during enhanced moisture or brecciation caused by desiccation. Brecciation of desiccated tracks was documented in modern analogue studies from Amboseli (Kenya) by Bennett and Morse (2014) and is discussed by Cohen et al. (1993). There are factors which can delay relaxation, such as the growth of algal mats, associated sediment trapping (Marty et al. 2009) and cementation by salts. The distribution of track-forming windows will vary spatially around a given environment. On the margins of the saline Lake Manyara (alkaline flats) in Tanzania, Cohen et al. (1991, 1993) recognised three ichnological zones:

- **Zone One:** This was an onshore zone where the sediment is dry at the surface and subject to salt blooms and associated deflation. Insect bioturbation is limited, and biotic reworking is achieved by animal trampling. While groundwater fluctuations do occur, the surface is sufficiently firm to only take the tracks of the

Fig. 2.7 Hypothetical model of a lake or river margin. For tracks to be preserved as shown on the right, animals need to be coincident with a track-forming window. The isolated tracks shown are associated with occasional preservation during water level rises, while the broader ichnosurfaces are revealed during water-level regression

heaviest animals when groundwater rises. Desiccation often renders tracks indistinct, and they are infilled by breccia and wind-blown mud. Long-term survivorship of tracks can be high.

- **Zone Two:** This is the shore zone where sediments are usually wet and salt crusts are minimal. Insect bioturbation is pronounced, as is animal reworking, groundwater fluctuations and shore face reworking. The soft sediment in this zone is ideal for the preservation of small mammals and birds in conjunction with larger ones, but survivorship, and therefore preservation potential, is far less.
- **Zone Three:** This is the subaqueous zone where the sediment is saturated and often, as a consequence, unstable. Larger animals may leave abundant tracks in this zone, but they quickly become indistinct and have low survivorship potential.

The way in which animals traverse these zones, and thereby leave their tracks, depends in part on water quality. In the case of Lake Manyara, most of the trackways follow the shoreline due to its salinity. No animals drink here. At less saline lakes, animal trackways may be more perpendicular to the shore, and carnivores (including humans) may adopt a more shore-parallel strategy in order to intersect prey (Roach et al. 2016). The point here is that each zone has different track-capturing properties and will sample the fauna differently, and different zones also have different preservation potentials. Clearly the deeper tracks in Zone One may have greater preservation potential than those in Zone Three. Small mammals and birds, for example, may be under-represented in some faunal samples.

Animal behaviour in each of these zones may also be relevant; one animal repeatedly walking in a small area can generate a lot of tracks! Cohen et al. (1993) make a distinction between faunal estimates based on milling and directional behaviour, tracks left by the former greatly inflate animal abundances, and they suggest that randomly orientated tracks should be avoided in making abundance estimates. Similarly, game trails may be recognisable at some sites, but because of their composite nature, they speak only to the presence of multiple animals, not to the exact number, even if individual ichnotaxa can be discerned (e.g. Ashley and

Liutkus 2003). In terms of broad time-averaged faunal assessment, the risk of sampling across diachronous surfaces is unlikely to be a significant issue, unless we are dealing with large time intervals; after all, skeletal and tool assemblages are time-averaged phenomena. However, demonstrating co-association is an issue for inferences around behavioural ecology.

Problems of Co-association

That a track assemblage was imprinted in close temporal association is an assumption that is implicit at most footprints sites but one which should, in truth, be demonstrated every time. We can explore some of the issues by theoretically modelling lake-level fluctuations around a lake such as Lake Manyara. Figure 2.8 shows a water-level curve, deduced from a stacked sequence of lithofacies, with tracked surfaces marking lake-level regressions. Lake regressions create the maximum spatial track-forming window; transgressions will tend to erode tracks, as shore process advances over an area and may compress the space for track-forming zones. This may correspond, however, to different rates of regression, when the data is re-plotted with time as the vertical (Fig. 2.8). Only one of the ichnosurfaces shown is isochronous, being associated with a rapid fall in lake levels, while the others record diachronous assemblages. On the margins of this hypothetical water body, the rates of sedimentation and therefore track burial will likely vary seasonally, and multiple track-forming windows may become superimposed (Fig. 2.9). We can develop the model first presented in Fig. 2.7 to explore this further, although in this case animal abundance is continuous (i.e. track formation is window limited). In the first

Fig. 2.8 Hypothetical model of lake-level fluctuations around a lake or river margin with available trackmakers. The lithofacies associated with such a scenario is indicated on the left. These are likely to be fining-upward sequences, associated with the transgressions, with tracks on the unconformities associated with regression. When time is substituted for depth on the right, the importance of a rapid fall in water level in creating an isochronous faunal track sample is indicated

Fig. 2.9 Three hypothetical scenarios around the margin of a lake or river, with a link between rainfall and water level. Animals are present throughout the time shown, and we assume that the optimum track-forming window occurs during a lake-level fall and that with exposure, the tracks degrade through desiccation and brecciation; (a) in this scenario only the deepest tracks (Zone One) will be preserved; (b) in this scenario the three track-forming windows are essentially superimposed on one another to form a diachronous assemblage; (c) finally, in this scenario, the rising lake level is assumed to be associated with sedimentation, and the tracks become more separated. With greater rates of sedimentation, separation between the track-forming surfaces will increase. The presence of isolated tracks represents the possibility of deeper tracks being preserved during a transgressive episode. Note the use of window limited and trackmaker limited in Fig. 2.7

scenario, periodic water-level highs are separated by desiccation events, leading to a tracked assemblage dominated by desiccation, in which only the deepest tracks, associated with the heaviest animals, are preserved, and then only poorly (Fig. 2.9a). In scenario two, we have shorter periods of desiccation between track-forming windows, but little sedimentation and the resulting tracks are superimposed one into the other, such that the surface is really a composite of several track-forming windows. This is typical, for example, of some of the assemblages at Illet. Only in the third scenario, where rising water levels and associated sedimentation are assumed, do we get tracked surfaces that separate out one from another and verge

toward being isochronous (Fig. 2.9c). Only on these types of surfaces is there potential to deduce behavioural interactions.

Co-association is usually argued for on the basis of cross-cutting relationships between different trackways and on similar levels of track freshness. That is, tracks which show a similar degree of degradation are assumed to be penecontemporaneous, especially if they are associated similar deformation structures (i.e. rim and sub-track structures) indicating similar pore water conditions. The ever-present risk is that a track-forming surface may have been reactivated several times. These models demonstrate that, in truth, there is no simple answer to the issue of co-association, other than care is needed when making such assumptions. These assumptions need to be justified and explained more clearly than is often the case in the literature. Ultimately the only way of demonstrating true co-association is to look for evidence of behavioural interaction between one or more trackmakers (e.g. Bustos et al. 2018). If two animals were present on the landscape at the same point and moment in time, there should be some interaction, either active (i.e. prey-predator) or passive (i.e. scenting or avoiding via trackway adjustment).

Conclusions

The study of human ichnology, along with other associated animals, is rapidly advancing with the discovery of new sites. The advent of 3D digital capture allows increasing research sophistication with quantitative hypothesis-led testing. There is much to do to replace the assertion-based approaches of the past with data-driven observations and inferences. In this review, we have explored some of the issues associated with the ichnological pipeline from data collection to the inferences that can be made, advocating throughout for the power of 3D digital data capture and analyses. In the later part of the review, we have emphasised the importance of geological context to the interpretation of track-based assemblages, and to assumptions of co-association, and around issues of faunal sampling. There is greater rigour needed here in ichnological research, and we would argue that the geological context of an assemblage is critical to its interpretation, regardless of the level of sophistication of the tools used to document it.

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