

Modern Vertebrate Track Taphonomy at Lake Manyara, Tanzania

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Fossil vertebrate tracks have a potential for providing valuable paleobiologic data to complement investigations of body fossils. Before tracks can be used for this purpose, it is critical to establish precisely what biologically significant signals are encoded in them. It is equally important to know how those signals are affected by the environmental conditions existing at the time and site of track formation and the subsequent taphonomic processes affecting the track. We studied modern tracks at Lake Manyara, Tanzania, to document the environmental and taphonomic controls on track preservation. This closed basin, saline lake closely resembles the depositional setting of many ancient track-bearing strata.

Two study sites (an alkaline mudflat and a delta floodplain) were established to monitor substrate conditions and physicochemical/biological processes of importance to track formation, preservation and survivorship probability. Physicochemical factors of importance to tracks included substrate composition and texture, daily wave and seiche reworking, seasonal lake level fluctuations, groundwater table fluctuations, surficial drying, wind deflation and salt crust development. Textural, compositional and moisture content differences between sites regulate the probability of initial track registration and depth of penetration. The various flooding and drying phenomena also generate cycles of track reworking and cracking and stimulate invertebrate bioturbation. Salt crusts on the Alkaline Flats strongly influenced the distribution and preservational quality of smaller tracks. Biological

factors included both invertebrate (insect) bioturbation and secondary vertebrate trampling. Surficial turnover rates were estimated at 0.5–1 cm/yr (locally up to 20 cm/yr) for invertebrates and 2.5–3.7 cm/yr for vertebrates.

Track and trackway survivorship was monitored both qualitatively (to document the sequence of track deterioration) and quantitatively (to determine rates of deterioration). A systematic and direct relationship exists between track survivorship and distance of the track from shoreline. Nearshore track assemblages persist over time periods measured in hours whereas at distances of >100 m inland, tracks may persist for months. This results both directly from wetting/drying cycles and indirectly from induced invertebrate bioturbation. An abrupt threshold of increased bird track survivorship correlates with the landward limit of significant nightly groundwater discharge.

A strong shoreline-parallel zonation of environmental variation correlates with differences in track preservation style. Zone 1, a landward zone of dry, salt encrusted sediments, is dominated by large ungulate tracks which are deformed primarily by baking, cracking and deflation. Tracks here have low probabilities of initial formation but high survivorship. Zone 2, a strandline zone of saturated sediments, contains a mix of large and small mammal and bird tracks. Tracks formed here display the best morphologic definition. Both track formation and reworking rates are higher here than in zone 1. Zone 3 is a subaqueous zone where liquefaction and increasing water depth again limit tracks to those of larger mammals and prevent good track definition. Shoreline parallel tapho-

onomic zonation of tracks should be useful in defining paleoenvironments for ancient track sequences.

Preburial track survivorship can be modelled as the interaction between three variables: 1) strain susceptibility of a substrate prior to track formation; 2) track loading stress; and 3) secondary reworking rate. Survivorship isograds (surfaces of equal survivorship probability) can then be plotted in this 3-D space to investigate their relative importance for track preservation. Apparently thresholds or discontinuities exist in track preservation space, where isograds are bunched together. These correlate with points along environmental gradients where extremely rapid transitions in track taphofacies occur. Time averaging is important in the formation of track assemblages but operates over a much briefer time scale than for body fossils. By quantifying the shapes of survivorship isograds ichnologists will ultimately be able to directly estimate trackmaker mass and velocity, substrate compactibility and water content at the time of track formation, as well as quantify time averaging of track assemblages.

INTRODUCTION

Ancient trackways* form an important part of the fossil record. They have a potential for providing paleontologists with a wealth of information about the paleobiology of extinct organisms and the environments in which they lived. However, before this record can be either accurately or thoroughly read, paleontologists need a much better understanding of how trackways enter the fossil record. What types of biologically significant information are encoded in individual tracks and trackways? What taphonomic biases exist in the initial formation and subsequent preservation of tracks that might affect their distribution as fossils? What is the relationship between depositional environment and track preservation? Does the probability of track preservation vary gradually between adjacent environments or are there thresholds of rapidly changing preservation probabilities? One promising avenue into these problems of trackway interpretation is through experimental research. The formation and preservation of tracks can be simulated under either controlled conditions (as for example, in experiments by Padian and Olsen, 1984) or under field-actualistic conditions. Both approaches can provide valuable and complementary information.

This is an actualistic study of animal tracks. Our goals were to determine how animal tracks and trackways are formed, preserved and degraded under natural conditions for comparison with fossil track assemblages in the geologic record and to develop a semiquantitative model of preburial trackway preservation. To achieve this we needed to know what physical, chemical and biological factors regulate the initial formation and subsequent degradation

or preservation of tracks. How do differences in substrate composition and water content serve to modify initial track impression depths and subsequent infilling or preservation? What is the relative importance of such diverse factors as wave reworking and bioturbation in destroying tracks? Additionally, we wanted to know the rates at which these various factors operate and how both factors and rates might vary between subenvironments. For example, what are the survivorship probabilities of tracks in lake-margin settings? How and why do they vary along a shoreline-normal transect? Additional parts of this study, to be published elsewhere, will also consider the biological signal encoded in tracks and the direct use of our Lake Manyara data in analyzing fossil trackway sites.

An exploratory investigation such as this is best conducted where environmental and biological conditions closely mimic those of ancient track-bearing strata. As numerous fossil track-bearing horizons are located in ancient lake margin strata, within aggrading, closed depositional basins, we decided to concentrate on a modern, hydrologically-closed lake margin environment where trackmakers are both numerous and diverse and sediments are currently accumulating. Few areas meeting all these criteria exist today outside Africa. Lake Manyara, Tanzania, was chosen for this initial study because it meets all of these criteria. First, its northern and western lake margins support large populations of wild animals that have not had their habitats destroyed or excessively modified by agricultural development. Second, the lake shore sediments provide a suitable receptive substrate for track formation. Finally, the geological setting is one in which track-bearing sediments are potentially fossilizable.

Study Area Setting

Lake Manyara is situated in northern Tanzania, in the southern portion of the Gregory Rift Valley (Fig. 1). It lies at 950 m elevation in a half graben basin, bounded to the west by the Mto Wa Mbu Fault scarp that rises another 300 m above the lake level. The lake's drainage basin comprises a combination of Precambrian metamorphic and Neogene sedimentary and volcanic rocks.

The lake basin has a semiarid to semihumid, tropical climate (rainfall varies greatly between 375–1250 mm/yr) with two distinct rainy seasons (November–December and March–May) (Greenway and Vesey-Fitzgerald, 1969). The lake is fed by the Mbu River (referred to as the Simba R. or Mto Wa Mbu on some maps) which enters from the north, the Makuyuni River entering from the east and numerous other perennial and seasonal streams that drain the fault scarp to the west, and the surrounding hinterland.

Lake Manyara itself is a medium sized (470 km²), shallow (3.9 m maximum depth), topographically closed basin lake. It undergoes considerable areal expansion and contraction during the wet and dry seasons. Not surprisingly, lake water chemistry is highly variable from year to year. The lake is normally highly saline (conductivity 4000–100,000 $\mu\text{mho/cm}$) and alkaline (30–800 meq/l $\text{CO}_3 + \text{HCO}_3$, pH 9.8–10). During the study period however, the lake was

* The terms *tracks* and *trackways* are used throughout this paper with distinct meanings. *Tracks* refers to individual footprints, whereas *trackways* refers to entire paths of footprints.

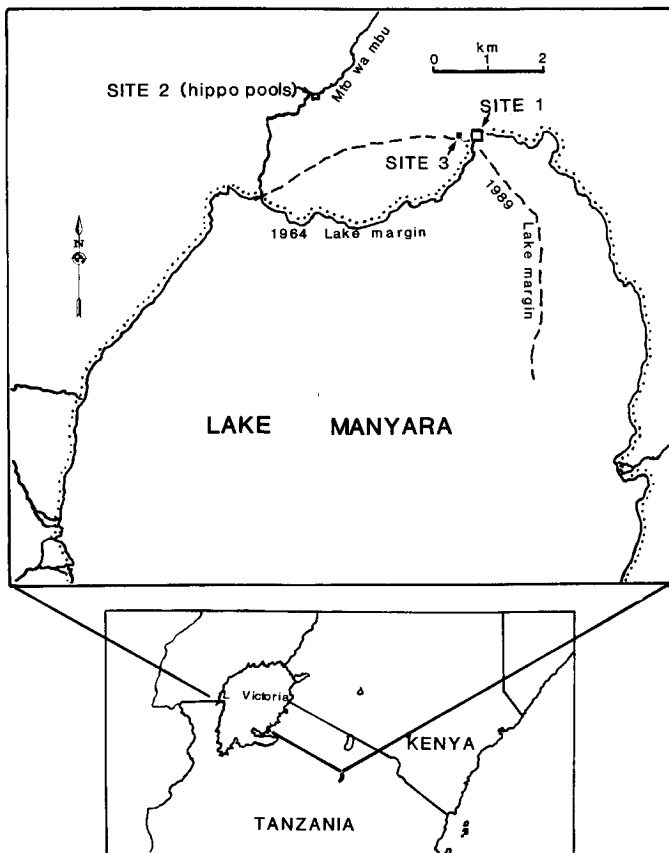


FIGURE 1—Location map for Lake Manyara and the two study sites. Site 1 is the Alkaline Flats Site. Site 2 is the Hippo Pool Site. Note shift in lake margin from 1964 topographic map location. Lake Manyara is a closed basin with widely fluctuating lake levels. In 1989 lake level was relatively high.

relatively fresh (immediately following the end of the rainy season) and measured values were at the low ends of these ranges, rising continuously as the dry season progressed.

Study Sites

Specific study sites were chosen on the basis of several criteria:

- 1) Presence of local or migratory bird and large mammal populations.
- 2) Presence of substrates suitable for track formation. This constraint favored selection of a shoreline environment, where there was a relatively abrupt transition from emergent dry or moist substrates to wet and/or submerged substrates.
- 3) Presence of a suitable off-site location (either distant with an unobstructed view or nearby with cover) for making regular observations of trackmakers.
- 4) Presence of variable environmental and sedimentologic settings, where substrate conditions and the local animal communities would differ between sites. Our intent was to make our results of more general significance and

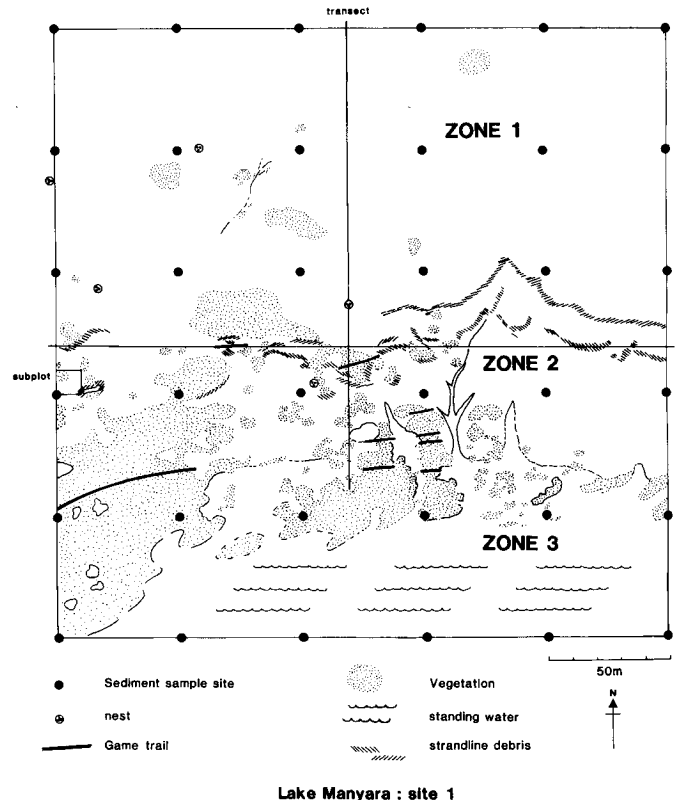


FIGURE 2—Environmental map for Lake Manyara Alkaline Flats Site (Site #1). Grid measures for the 250 m × 250 m site referred to in text are measured from the Northwest corner (X = E-W distance, Y = N-S distance). The 10 m × 10 m subplot, shoreline parallel (Y = 130 m) and shoreline normal (X = 120 m) transects are also shown.

provide some ideas about track formation and preservation in contrasting environments.

Two study sites were chosen, both located on the north shore of Lake Manyara, south of the village of Mto Wa Mbu, on the eastern perimeter of Lake Manyara National Park. One of the sites straddled the strandline, as it was situated in late May through early July of 1989, and the second was located on a delta floodplain.

The Alkaline Flats Site (Site #1) is bordered on the west by Lake Manyara National Park boundary markers (making relocation simple) and covers a 250 m × 250 m area (Fig. 2). It consists of a topographically featureless plain, covered by a mix of exposed alkaline mud flats, alkaline grasslands (dominated by *Sporobolus spicatus*) and other emergent aquatic graminoids. Surficial sediments consist of alkaline soils, carbonate/clastic muds (a mixture of micrite and gastropod fragments) and mixed Ca and Na carbonate muds.

The Hippo Pool Site (Site #2) is about 2 km to the west of Site #1, on the east bank of the Mbu River, covering an area of 60 m × 100 m (Fig. 3). Situated a short distance upstream from the river mouth, it represents a fresh water, mixed fluvial-floodplain grassland/mudflat habitat which is clearly different from the alkaline-saline lacustrine hab-

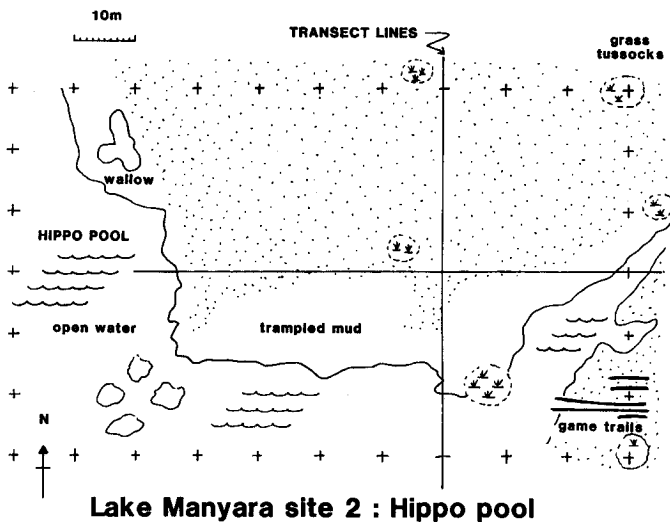


FIGURE 3—Environmental map for Lake Manyara Hippo Pool Site (Site 2). Grid measures for the 100 m × 60 m site referred to in the text are measured from the Northwest corner (X = E-W distance, Y = N-S distance).

itat of the main site. Surficial sediments here are clastic (clay-rich) muds, with a high organic content from mammal feces.

METHODS

Site Surveys

Study sites were laid out and flagged on coordinate grids with E-W (X) and N-S (Y) baselines (Figs. 2 and 3). Within the sites, the main physiographic features such as vegetation, open mudflat, standing water and strandline accumulations were initially mapped onto a base map. These maps served as references for updates as the shoreline shifted position and were used as a basis for compiling site-wide trackway maps. They also provided a grid for locating specific smaller study plots and transects used for monitoring various experiments, including a 10 × 10 m subplot and both shoreline parallel (E-W, Y = 130 m) and shoreline normal (N-S, X = 120 m) transect lines.

Monitoring Of Substrate Dynamics

A variety of biological and environmental variables having a bearing on track impression and preservation were monitored or measured within the study sites (Fig. 4). Surficial sediment samples were collected at 50 m (Alkaline Flats Site) or 10 m (Hippo Pool Site) grid intervals for routine granulometric (sieve + sedigraph), insoluble residue and mineralogic analyses. Sediment samples from the same localities were also collected over a very brief (<1 hr) morning interval on several occasions for soil moisture determinations. At the Alkaline Flats Site, salt crust compression ridge heights, spacing and percentage cover were also measured. Salt crusts were absent from the Hippo Pool Site.

Shoreline position was routinely monitored, being re-mapped following major shoreline excursions. Water table height was routinely measured in four test pits dug perpendicular to shoreline across the Alkaline Flats Site surface at 0 m, 50 m, 100 m and 150 m along the X = 0 m baseline.

Vertebrate trampling can cause extensive reworking of lake margin sediments. To estimate trampling and resultant sediment turnover rates we measured mean track size and mean track compression depth data for each common species: this allowed us to determine the average volume of sediment disturbed or overturned per track per species. These values were then multiplied by track production rate data obtained within the 10 × 10 m subplot and along the X = 120 m and Y = 130 m transects (Lockley et al., pers. comm.) to estimate mean surficial reworking rates.

Burrowing invertebrates also play a major role in the reworking of lake margin sediments at Lake Manyara. Invertebrate bioturbation of trackway substrates was investigated through a series of experiments monitoring burrow castings production rates. Six pairs of 1 m² study plots were laid out at the Alkaline Flats Site within the shore parallel zone where castings commonly occur. Plots were sited along the X = 198–199 m strip at the following coordinates: Y = 90 m, 99 m, 110 m, 125 m, 142 m, and 152 m. No insect castings piles had been observed landward of the 90 m position prior to the start of the experiment and the study area was partly flooded lakewards of 152 m at the start of the experiment.

At each site fresh castings piles were counted, removed, air dried and weighed on a daily or more frequent basis, over the course of 8 days. The total castings volume generated in a plot was then averaged over the plot area, to calculate a minimum rate of surficial sediment turnover. Over the course of several days the plots were monitored more than once per day to determine the timing of castings production. One plot of each pair was designated “dry” and was left undisturbed after collection of the castings. A second, designated “wet,” was flooded with approximately 10 l of water each day, to determine if additional surface water flooding would stimulate enhanced burrowing.

Track Survivorship Study Methods

Two approaches were used in this study to estimate the preservation potential of individual tracks *prior* to burial. First, individual trackways were monitored qualitatively for several weeks after formation, to understand specific mechanisms of track deterioration under differing environmental conditions. Second, quantitative track survivorship studies were conducted to determine average rates of track destruction.

Qualitative Track Deterioration

Three Alkaline Flats Site mammal trackways, two from hippopotami and a third from a marsh mongoose, were monitored. Trackways were chosen to provide data on both

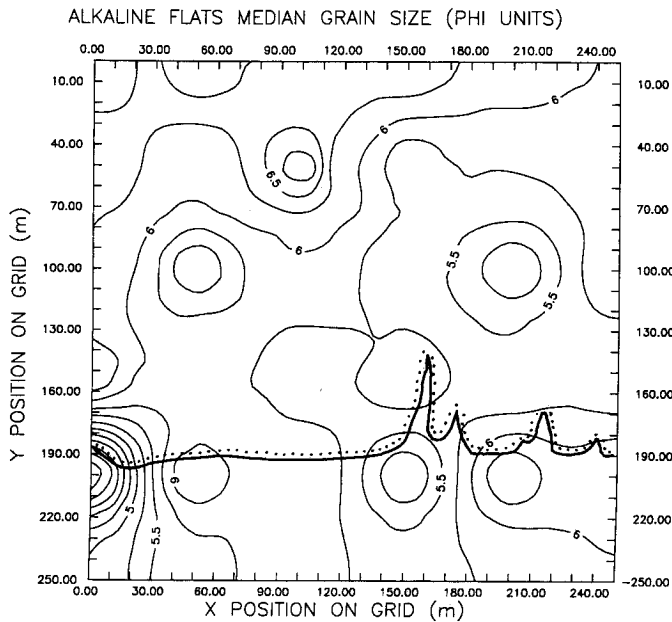


FIGURE 4—Median grain size (ϕ units) contour map for the Alkaline Flats Site. Heavy solid + dotted line indicates shoreline position of 21 June, 1989 (dots on landward side).

small and large track degradation, at locations both near and far from the shoreline. The first hippopotamus trackway was located relatively close to the waterline (X = 3 m, Y = 107 m to X = 10 m, Y = 151 m, walking lakeward), whereas the second was located in the landward portion of the site (X = 10 m, Y = 0 m to X = 37 m, Y = 60 m, walking lakeward). The mongoose trackway was located close to the waterline (X = 55 m, Y = 160 m to X = 57 m, Y = 160 m, walking east). All three trackways ran across both open salt flat and *Sporobolus* covered areas. Small mammal tracks could not be impressed in the landward portion of the Alkaline Flats Site, because of low water content. Consequently, no mongoose trackway is available for direct comparison with the landward hippopotamus trackway.

All trackways were monitored daily from the morning following their formation (all were produced during the night of June 5/6) for a period of 3 weeks. Each trackway was inspected for qualitative evidence of infilling and deterioration. Individual tracks within each trackway were marked, measured for maximum impression depth and photographed daily, at the same time and under similar lighting conditions.

Quantitative Track and Trackway Survivorship

Mammal track survivorship was determined from individually marked prints of different species. At the Alkaline Flats Site, we monitored 3 gazelle trackways including 50 tracks, 4 wildebeest trackways including 50 tracks, 1 zebra trackway including 20 tracks, 1 lion trackway including 30 tracks, 1 hippopotamus trackway in-

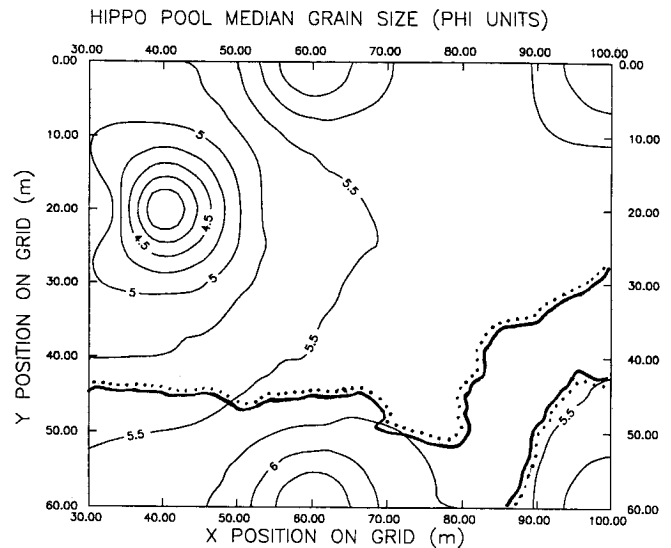


FIGURE 5—Median grain size (ϕ units) contour map for the Hippo Pool Site. Heavy solid + dotted line indicates shoreline position for early June 1989 (dots on landward side).

cluding 25 tracks, and 1 hyaena trackway including 15 tracks. At the Hippo Pool Site, we monitored 2 hippopotamus trackways including 20 prints and 1 wildebeest trackway including five prints. Trackway survivorship was calculated for the trackways crossing a 10 × 10 m² plot at the Alkaline Flats Site (Fig. 2). Survivorship was calculated both for the time trackways were identifiable to species and for the time they were only identifiable as trackways (with no individual track clear enough to identify species).

Bird track survivorship studies were performed on the same experimental study plots as the insect bioturbation experiments, after the latter experiments were completed. All 2 m² plot areas were cleared, smoothed and watered prior to beginning the study. The plots were left unattended for 12 hours to allow birds to walk over them without interference. At the end of this time, all complete tracks were counted and marked within each study plot by circling and by having a single small pin inserted at the intersection of the digit impressions. Tracks were differentiated into small tracks (produced by several species of smaller plovers which are practically indistinguishable on the basis of their tracks) and large tracks (almost exclusively from blacksmith plovers).

Survivorship plots were visited daily for the first week following the start of the experiment, to determine the proportion of original tracks which were still visible. During the second week of the study, when rates of change on remaining tracks had significantly decreased, the plots were visited less frequently. The criteria used for "visibility" was necessarily subjective. A track was considered "visible" only if all three digits were still clearly demarcated. Since a variety of observational and lighting biases might make a track invisible at one time and then visible later, our track counting was done by a single analyst, at a single

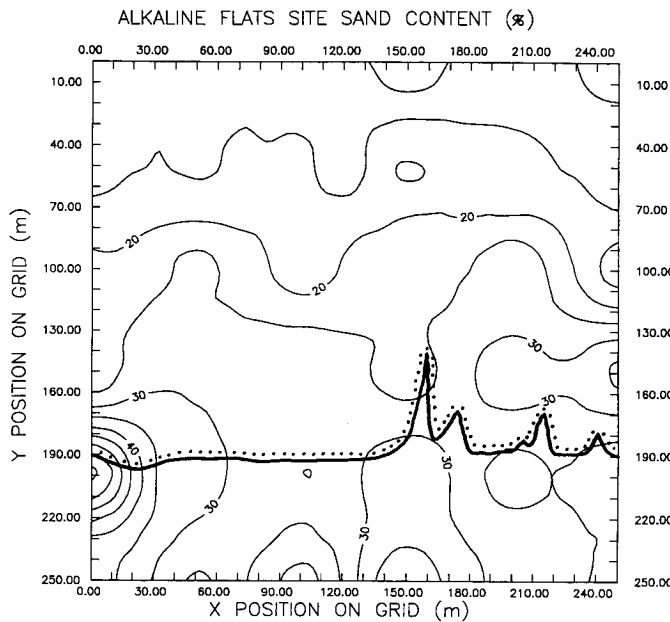


FIGURE 6—Sand Content (coarser than 4.25ϕ) contour map (%) for the Alkaline Flats Site.

time of day and, as much as possible, under equivalent lighting conditions. Secondary counts were made on some days to determine if higher rates of track destruction were related to specific daily events, such as the daily invertebrate bioturbation cycle (discussed below). Once a track was considered invisible ("dead" in terms of survivorship) it was marked with a second pin. In this fashion, "dead" tracks could not confuse us by coming back to life under later, more favorable lighting conditions. The cause of "death" for each individual track was also recorded (flooding inundation, insect bioturbation, secondary trampling, surface deformation caused by salt crystallization or indeterminate fading). The experiment was allowed to run for two weeks.

RESULTS

Substrate Dynamics

The substrates of the Lake Manyara study sites are highly dynamic environments, altered on a daily basis by a variety of short-term, physical, chemical and biological processes. Many of these processes are interactive and all have a direct impact on both the receptivity of the surface to forming track impressions as well as their short term preservation probability. All serve to modify the sediment surface following initial track formation; all influence both the destruction rate of preformed tracks and the susceptibility of the surface to the formation of new impressions.

Physical Factors

Substrates at both the Alkaline Flats and Hippo Pools Sites are dominantly fine-grained (muddy or sandy silts,

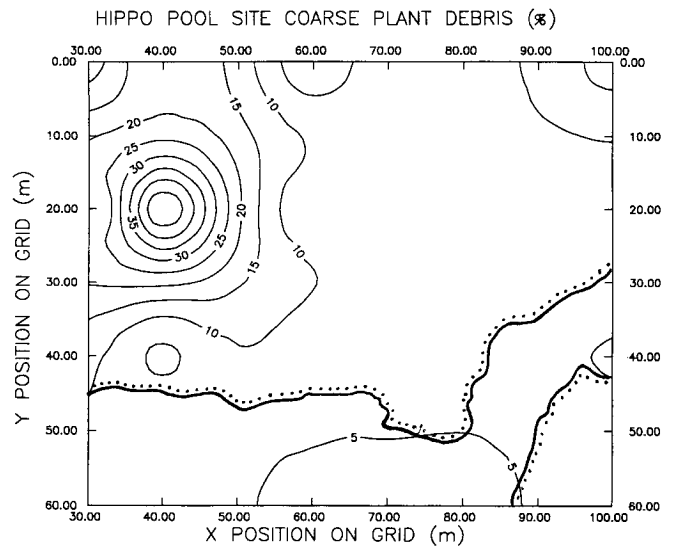


FIGURE 7—Coarse Plant Debris Content (Plant Debris coarser than 4.25ϕ) contour map (%) for the Hippo Pool Site.

Figs. 4 and 5). At the Alkaline Flats, there is a weak trend towards increasing median grain size near the shoreline. Sand content is highest (30–50%) in the higher energy shoreline environment, decreasing from this zone in the landward and (to a lesser degree) lakeward directions. Hippo Pool Site substrates are, overall, slightly coarser grained than those of the Alkaline Flats. Textural differences within the Hippo Pool Site are more difficult to interpret, since most of the coarser fraction is trampled and disseminated plant debris. Some of the increase in coarse fraction content in the northwestern part of the site may also be attributable to fluvial transport (Figs. 6, 7, 8).

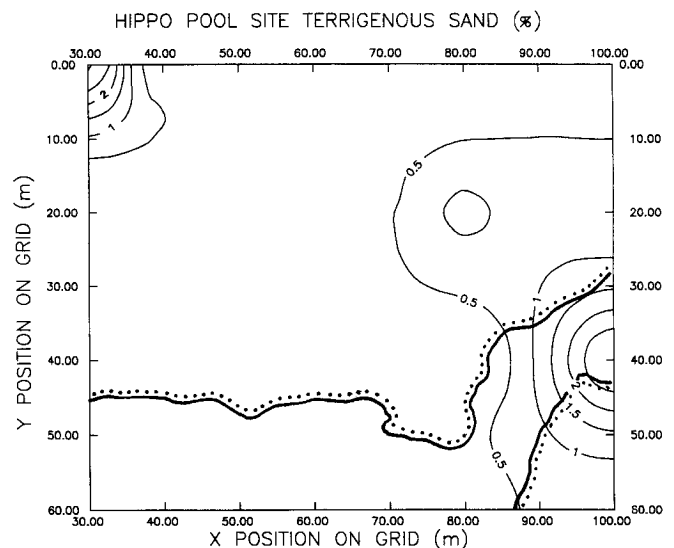


FIGURE 8—Terrigenous Sand Content (coarser than 4.25ϕ) contour map (%) for the Hippo Pool Site.

ALKALINE FLATS NONBIOGENIC CARBONATE SAND (ϕ)

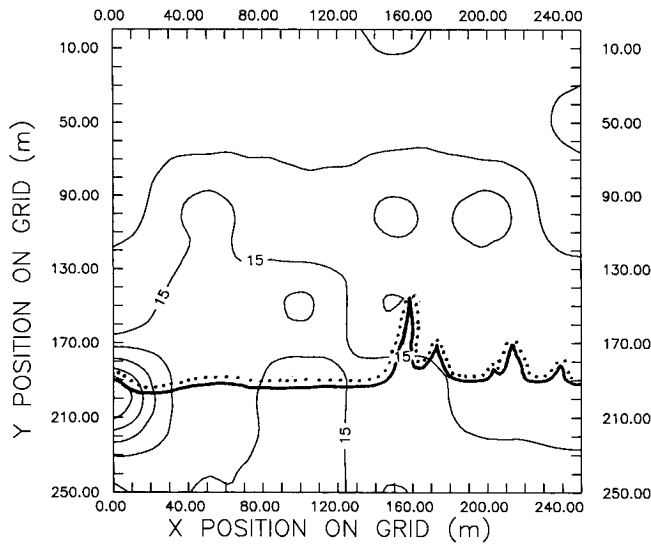


FIGURE 9—Nonbiogenic Carbonate Sand Content (coarser than 4.25 ϕ) contour map (%) for the Alkaline Flats Site.

Alkaline Flats substrates are dominated by a mix of carbonate (both Ca and Na) silt and terrigenous clays. Nonbiogenic (grapestone, ooid and aggregate) and biogenic (ostracode, gastropod and *Chara*) carbonate sands are also major components of the sediment mass, both displaying moderate increases in proportion in the lakeward direction (Figs. 9 and 10). In many places (particularly near the lake margin), these carbonates have experienced early, surficial cementation, producing local hardgrounds.

ALKALINE FLATS BIOGENIC CARBONATE SAND (ϕ)

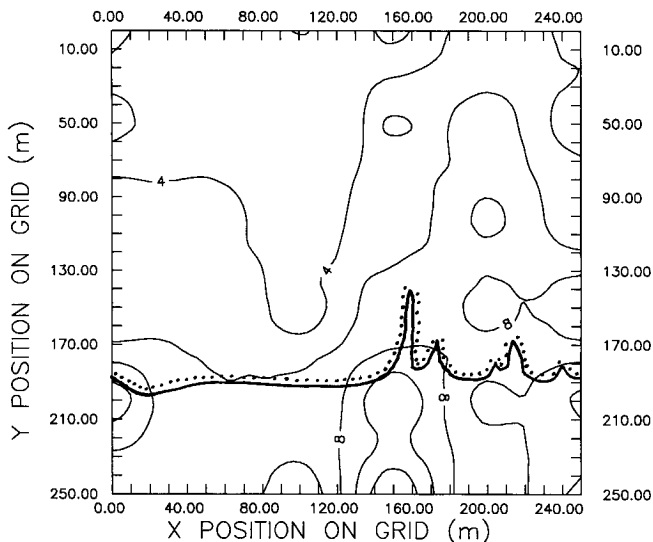


FIGURE 10—Biogenic Carbonate Sand Content (ostracodes, gastropods and *Chara*-coarser than 4.25 ϕ) contour map (%) for the Alkaline Flats Site.

ALKALINE FLATS SITE COARSE PLANT DEBRIS (ϕ)

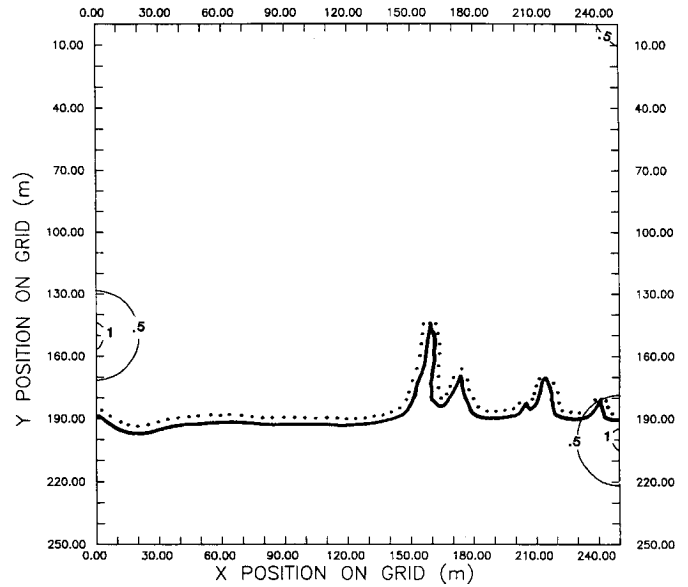


FIGURE 11—Coarse Plant Debris Content (coarser than 4.25 ϕ) contour map (%) for the Alkaline Flats Site.

Additionally, fish bone often comprises a significant fraction of the nearshore sandy samples. By contrast, coarse plant debris and terrigenous sands make up an insignificant fraction of the Alkaline Flats sediment mass (Figs. 11 and 12).

Hippo Pool substrates are quite different from the Alkaline Flats, reflecting their floodplain origins. The fine fraction predominantly comprises terrigenous silt and clay

ALKALINE FLATS SITE TERRIGENOUS SAND (ϕ)

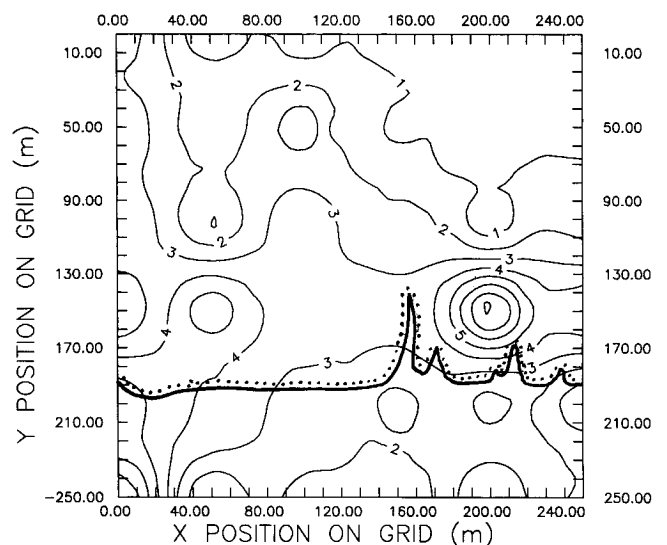


FIGURE 12—Terrigenous Sand Content (coarser than 4.25 ϕ) contour map (%) for the Alkaline Flats Site.

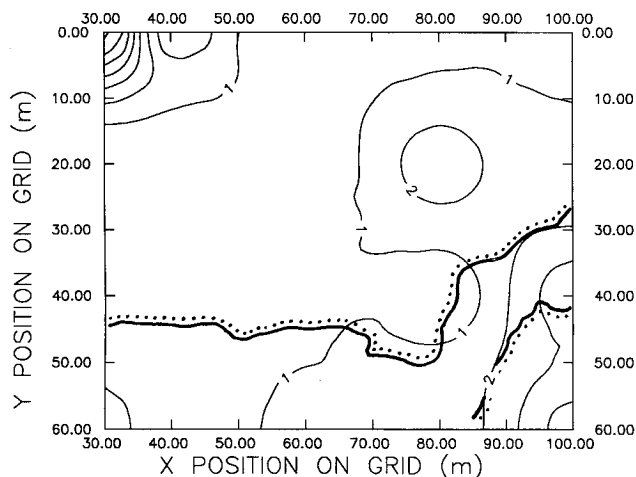
HIPPO POOL SITE BIOGENIC CARBONATE SAND (ϕ)

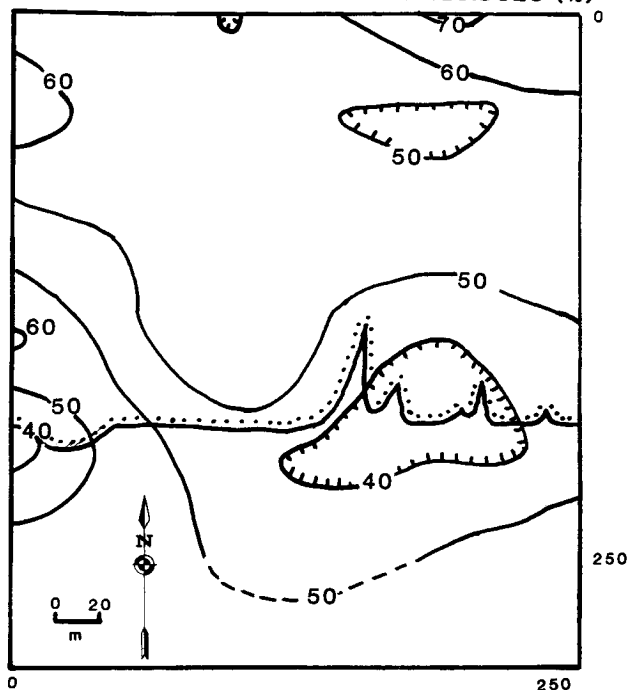
FIGURE 13—Biogenic Carbonate Sand Content (coarser than 4.25 ϕ) contour map (%) for the Hippo Pool Site.

and finely disseminated organic matter (both transported and autochthonous). The abundance of plant debris is illustrated in Figure 7 (coarse fraction only). Most of this coarse material appears to be trampled and disseminated herbivore feces. The increase towards the Mbu River (to the west) probably reflects a greater amount of hippopotamus activity in that area. In contrast, biogenic carbonates (dominantly ostracodes with occasional gastropods) are uncommon in the Hippo Pool Site samples (Fig. 13), and nonbiogenic carbonates are absent. Low values of terrigenous sands at the Hippo Pool Site (Fig. 8) suggest that seasonal flooding events over this floodplain do not carry significant amounts of overbank sands.

Insoluble residue analyses illustrate the marked compositional difference between the Alkaline Flats (carbonate rich) and Hippo Pools (carbonate poor) Sites (Fig. 14). At the Alkaline Flats Site there is a weak trend of increased carbonate concentrations (i.e., lower insoluble residue fraction) towards the lake margin, probably reflecting the great increase in abundance of lacustrine mollusc and ostracode shells in the sediment. No such trend is observed at the Hippo Pool Site, where carbonate concentrations (principally supplied from land snail shells) are uniformly low.

Textural and compositional differences between the two sites have an important bearing on the differential probability of track formation. Carbonate and terrigenous silts of the Alkaline Flats Site display high rates of strain per unit stress when wet and compressed by an animal (discounting those silts which have been previously cemented); rheologically they behave in a relatively inelastic fashion. This in turn produces relatively deep and "permanent" compressions. This pattern is even more accentuated in terrigenous clays observed along floodplains outside of our main study areas. In contrast, the Hippo Pool Site organic-rich sediments are less compactible and behave more elastically, rebounding when compressed and thus producing shallower and less durable tracks.

ALKALINE FLATS SITE INSOLUBLE RESIDUES (%)



HIPPO POOL SITE INSOLUBLE RESIDUES (%)

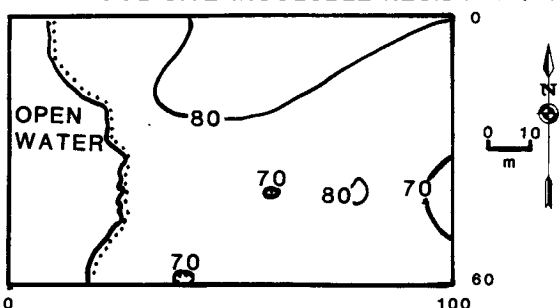


FIGURE 14—Insoluble residues (in 10% HCl) contour map (%) for the Alkaline Flats and Hippo Pool Sites.

In vertical profiles (derived from shallow trenches), both sites are relatively homogeneous, with little obvious bedding or sedimentary structure (this was the result of extremely high rates of bioturbation relative to sedimentation, although no absolute dates or sediment accumulation rates are available for either site at present). The Alkaline Flats Site displays a noticeable coarsening upward trend in the upper meter of sediment (e.g., 1.5% to 25% sand in one trench at X = 0 m, Y = 100 m). However, all the sediments are, nonetheless, homogeneous sandy muds or muds; thus, buried tracks, even if well preserved, cannot be recognized as such in cross sectional view because of a lack of stratification. Clearly, substrate heterogeneity and the development of well defined bedding planes are important criteria for track visibility. Near the end of our field season we identified a site, several kilometers from our 1989 sites, where strong vertical lithologic contrasts

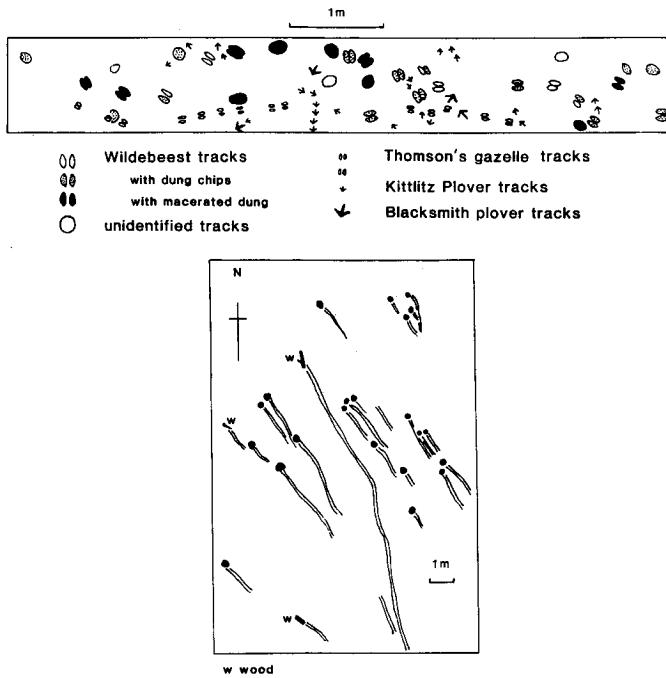


FIGURE 15—A) Map of dung ball accumulation within a small zone 2 area of the Alkaline Flats Site. B) Tool mark tracks created by the movement of dung balls and driftwood (w) during a seiche. The lake is towards the bottom (S) of the figure.

do allow tracks to be recognized when buried. We propose to continue our studies on short-term preservation at that locality or at another where stratification of the sediments is equally well developed.

Oscillatory wave activity along the extremely low gradient lake margin of Lake Manyara is normally insufficient to rework sediments significantly. However, at the end of the rainy season (May–June), the lake level of Manyara undergoes a discontinuous fall caused by decreasing precipitation/evaporation ratios in the lake basin. Superimposed on this seasonal decline are shorter-term excursions, of as much as 20 cm and at rates of up to 1.5 cm/hr, caused by water pileups along the lakeshore mudflat (between zones 1 and 2) from discontinuous SSE-SSW onshore breezes and the movement of surficial seiches. At the Alkaline Flats Site, this translates into lateral transgressions and regressions of 50–80 m.

Rapid lake level excursions serve alternately to inundate and expose the lake margin, in turn leading to the possibility either of reworking and infilling of tracks (stimulated by lake-level rise) or of track drying and cracking (during lake-level fall). Because they represent low spots on an otherwise near featureless topography, Manyara tracks serve as ready traps for suspended sediments and organic debris following flood events, a phenomenon previously noted for fossil tracks by Laporte and Behrensmeyer (1980), Lockley (1989) and Allen (1989). This is particularly evident for larger tracks, such as those of hippos, which effectively baffle minor wave reworking. Figure 15a shows

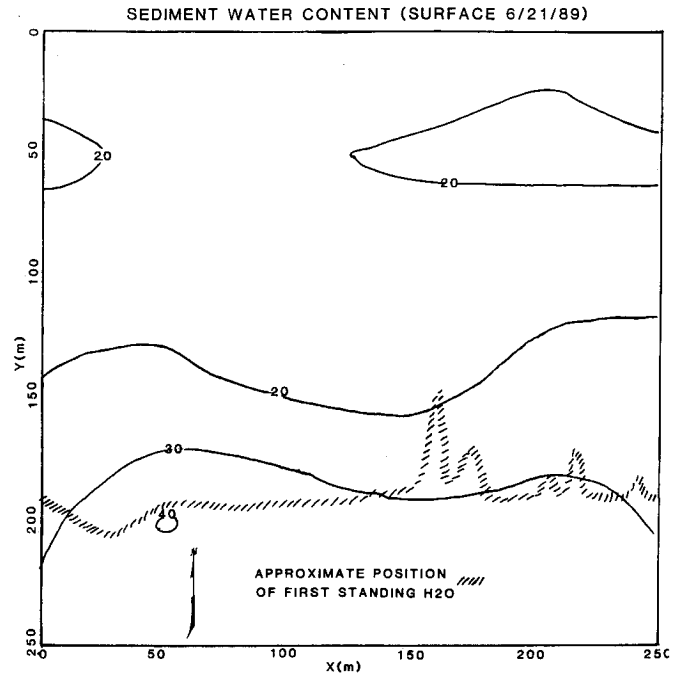


FIGURE 16—Sediment moisture content at midday (June 21, 1989) for the Alkaline Flats Site.

the distribution of dung balls and other light debris across one 1 m × 7 m lake margin strip of the Alkaline Flats Site following a flood event. Figure 15b shows the prominent tool marks created by dung and wood driven onshore during a seiche. Stronger seiches will also introduce denser debris, including mollusc shell fragments into the track depressions. Larger fragments frequently produce tool marks across the mudflat surface. Under conditions of rapid drying and consolidation, such events may be adequate to visibly preserve tracks in the inundated zone, since the infilling is texturally quite distinct from the surrounding substrate. For example, for five wildebeest track infillings in the same area, large mammal dung represented between 3–50% of the track infilling by weight.

Very short-term lake level rise and fall also serves to shift the location of bird activity for species which are sensitive to microhabitat variations (a common characteristic across the dry ground-submerged ground ecotone). Flooding remobilizes a surface for the trampling and destruction of old tracks and renewed track production.

Saturation of lake margin sediments by both surface and groundwater is an important factor both in disaggregating sediment (making it more amenable to track impression) and in mobilizing secondary insect activity. Like lake level, groundwater level also fluctuates on varying time scales. In the early morning, the groundwater table reaches its highest level of the day through an excess of capillary recharge over evaporation during the night. Levels of soil moisture then decrease until the late afternoon, when the process reverses itself. Water table monitoring in these pits demonstrates that a nightly rise in water table of up

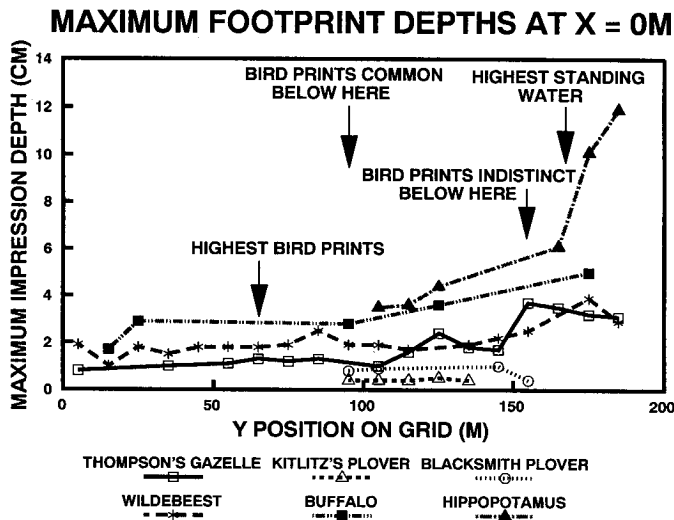


FIGURE 17—Maximum impression depths in cm (over 10 m N-S (=Y position) increments) for tracks for selected species of mammals and birds along the X = 0 m gridline at the Alkaline Flats Site. Shoreline was at approximately Y = 190 m at X = 50 m at the time the study was done.

to 4 cm (presumably stimulated by lowered night-time evaporation rates) is superimposed on the longer term seasonal decline and seiche-induced fluctuations observed during May and June. In the shoreline area, the nightly change translates into a zone 12–16 m wide, where surface standing water can accumulate and then evaporate on a daily basis. However, footprint impression and accumulation is affected by soil moisture fluctuations in a much wider zone than this since subsurface moisture increases stimulate insect bioturbation activity (discussed below).

Figure 16 illustrates the surface soil moisture content at midday (June 21, 1989) at Alkaline Flats Site. There is a real but erratic increase in soil moisture content towards the lake margin. The erratic increase results from textural and cementation differences in soils (particularly around rooted areas) and slight topographic irregularities as one moves lakewards.

Soil dampening has a profound effect both on the formation of subsequent footprints and on the destruction of previously produced ones. Transects of maximum track penetration depths (by species) across the Alkaline Flats Site area, taken perpendicular to lake shore, show a general (though not continuous) increase in depth with increasing water content (Fig. 17). In the immediate region of nightly shoreline fluctuation, however, the maximum impression depths increase dramatically. The trend towards increased track depth with proximity to the water line breaks down where soils have been weakly cemented.

Impression depths vary greatly, dependent on variations in compactibility related to sediment composition, in adsorption capacity for water and in texture. This variation was made evident by comparisons between the low-moderately compactible organic-rich muds of the Hippo Pools Site, the moderately compactible carbonate-rich muds of

the Alkaline Flats Site and the highly compactible terrigenous clays found on the outer fan-deltas of Lake Manyara National Park (outside of our study areas). For example, for uncemented sediments with similar water contents (30–40%), wildebeest track depths averaged 3 cm depth at the Hippo Pools, 4 cm at the Alkaline Flats and 10 cm in the terrigenous clays of the fan deltas.

In areas where the Alkaline Flats Site sediments are partially cemented, even high water content (>30%) does not allow significant sediment deformation during loading. For mixed, partially cemented sediments at the Alkaline Flats Site, there was no correlation (Pearson Product Moment Correlation, $p \gg .1$) between water content and impression depth for hippos walking across mixed cemented and uncemented surfaces. In contrast, on the organic-rich, uncemented sediments at the Hippo Pool Site there is an excellent ($p < .01$) and strong relationship between sediment water content and track impression depth for hippos.

Wind deflection provides a minor mechanism in regulating trackway preservation at Lake Manyara. Tracks impressed in evaporites (or tracks which have been secondarily encrusted in salts) lose their detail and definition, in part through salts and other dust being blown out of the tracks. This process went to completion only in areas where wetting was followed by complete drying over several days. It was normally, therefore, restricted to the upper parts of the Alkaline Flats Site, well away from the then-current lake margin (our Zone 1 discussed below).

Chemical Factors

The development of halite and sodium carbonate crusts on the lake margin mud flats of Lake Manyara is an important process, both in controlling the distribution of new impressions and stabilizing ones previously formed. Most of the exposed lake margin mudflats possess a cracked microtopography, with abundant salt compression ridges. The vertical relief of these compression ridges defines a minimum size of visible track impressions. Small tracks (of birds or small mammals for example) cannot be preserved in areas of high relief. Similarly, the thickness of the salt crust, by creating a rigid pavement for animals to walk over, is closely correlated with the minimum size of track impressions. Evaporite crusts are similar to coarse grained sandy substrates in not accepting small prints or details of prints. The salt encrusted tracks of the Alkaline Flats Site, for example, are incapable of capturing fine details like the webbing ridge impressions from wading birds, whereas at the Hippo Pool Site, stream inflow prevents salt crusts from forming and track impressions are more detailed.

Evaporite ridges and mudcracks can be observed up to several hundred meters away from the lake margin; they reach their greatest thickness and abundance in the zone spanned by the Alkaline Flats Site (between 50–150 m from shore). Figures 18, 19 and 20 show the distribution of maximum compression ridge height, crust thickness and percentage of ground surface area covered by compression

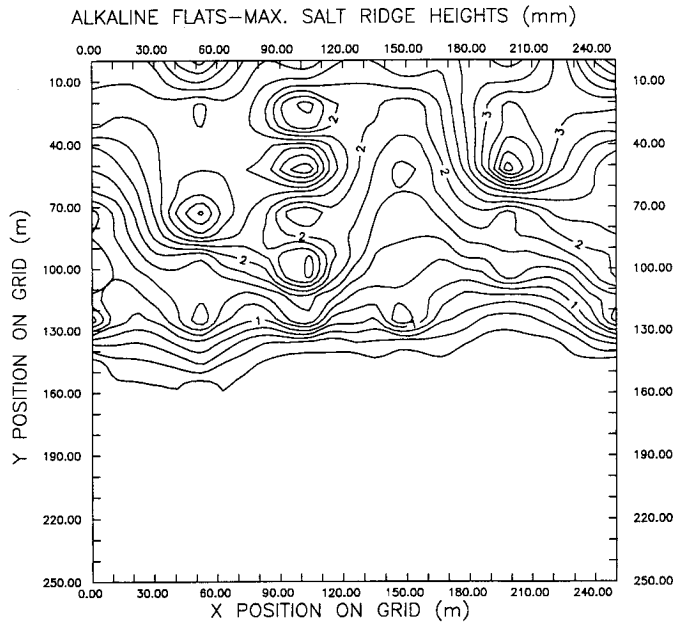


FIGURE 18—Maximum salt compression ridge heights (over 25 m N-S (=Y position) increments) in cm for the Alkaline Flats Site.

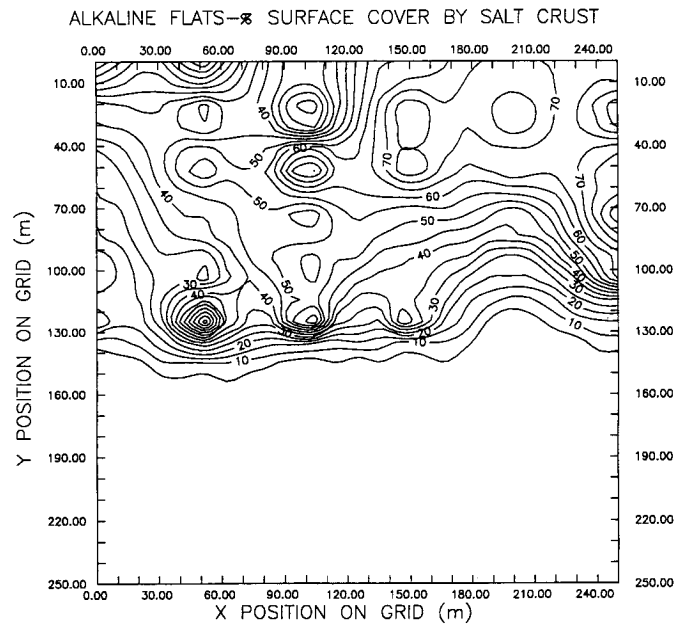


FIGURE 20—Percentage of substrate covered by salt compression ridges at the Alkaline Flats Site.

ridges at the Alkaline Flats Site. The values show great scatter, though there is a general tendency towards thinner crusts and lower compression ridge heights moving from land towards the lake margin. In the zone of occasional lakewater wetting and active recharge of groundwater to the surface sediments, the salts are flushed off the surface regularly. In the landward portions of the Alkaline Flats Site, most tracks are infilled by thick salt crusts since they

are the primary depressions on an otherwise extremely flat surface. These tracks are dominantly large and poorly defined, resulting from salt crystallization, trampling, deflation and mud cracking.

Closer to the water line, and particularly in the 20–40 m wide strip nearest the water line, the percentage of ground covered by compression ridges declines noticeably. This zone, not surprisingly, is the region where the proportion of smaller tracks (particularly from birds) reaches a maximum. Salts which do accumulate in these tracks are more regularly and rapidly flushed out. This enhances the possible, preservable detail of the tracks at the expense of increasing their likelihood of destruction from disaggregation (see track survivorship below).

Biological Factors

Destruction of previously formed tracks by trampling was a nearly continuous process at both the Alkaline Flats and Hippo Pool Sites. Extremely high track production rates for large mammals at Lake Manyara, measured by Cohen et al. (1990) and Lockley et al. (pers. comm.), indicate that tracks have a strong likelihood of destruction in this fashion. For example, an estimated 117,000 tracks of gazelle and 422,000 tracks of wildebeest existed on the Alkaline Flats Site grid on June 2. Based on our studies on the Y = 130 m transect, new gazelle and wildebeest tracks were forming in this area at rates of 0.26 and 0.08/m²/day, and in the process destroying numerous, previously formed tracks. During our study period, mean surficial reworking rates from vertebrate trampling within the onshore, near-shoreline region of the Alkaline Flats site varied between 100–150 g sediment (dry wt.)/m²/day, or approximately 2.5–3.5 cm/year.

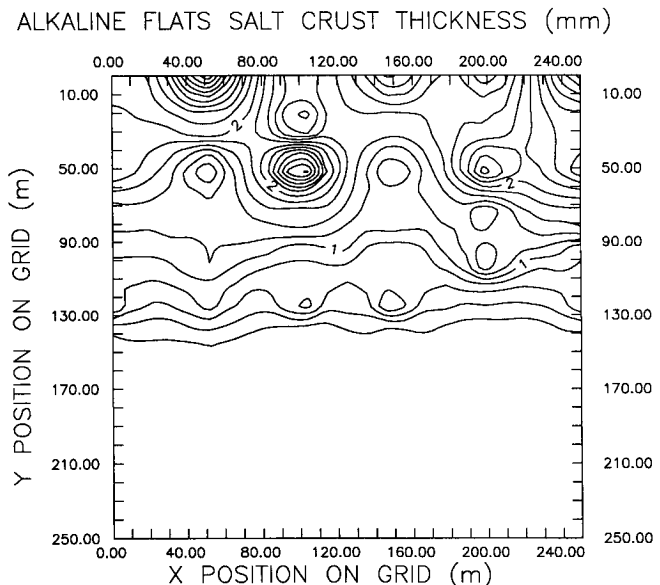


FIGURE 19—Mean salt crust thicknesses (over 25 m N-S (=Y position) increments) in cm for the Alkaline Flats Site.

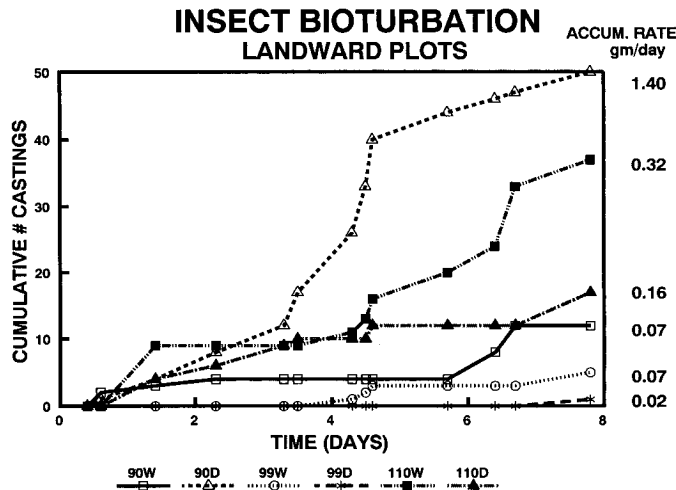


FIGURE 21—Insect bioturbation at the Alkaline Flats Site, for study plots away from the lake. Cumulative # castings is the number of castings piles produced during the experiment (6/12/89–6/20/89). Accum. rate is the mean accumulation rate of castings (in gm/day) for each study plot over the duration of the study. Numbers (90W, 90D etc. refer to the site localities of the experiment, in Y distance from the baseline (i.e., larger numbers are closer to the lake shore), and whether the plot was artificially wetted (W) each day or left dry (D), with only groundwater moistening.

Several unidentified species of beetles, earwigs and spiders are commonly found forming shallow (0–10 cm deep) burrows on the exposed mudflats of the Alkaline Flats Site. This burrowing generates piles of sediment castings which accumulate at burrow openings. Burrows were also observed at the Hippo Pool Site, produced by several species of ants. Burrowing degrades tracks in two ways. First, intensive burrowing below or around a track rapidly undermines it, causing caving and eventual obliteration of the track. Second, castings produced during burrowing can secondarily infill previously formed tracks. This type of burial is also a destructive process, since the castings have a similar texture and composition as the substrate.

Burrowing activity is not uniform across the study areas. Some areas near the daily water line at the Alkaline Flats Site undergo significantly greater amounts of bioturbation than other areas further inland, based upon amount of castings present on the ground surface.

In a lakeward direction, there was a dramatic increase in both the rate of arthropod burrow castings production (from 0 to approximately 400 castings/day/m²) and the castings mass land volume accumulation rates (essentially the surficial sediment turnover rate from arthropod activity, from 0 to over 40 g/m²/day, Figs. 21 and 22). For plots closer to the lakeshore (152 m and 142 m), wetting was significantly and consistently associated with enhanced burrowing rates. At plot 90 m, the reverse trend was observed; however, the results from that site were highly biased by a small number of consistently formed and very large castings piles. At other plots, the addition of water to the surface was associated with ambiguous results.

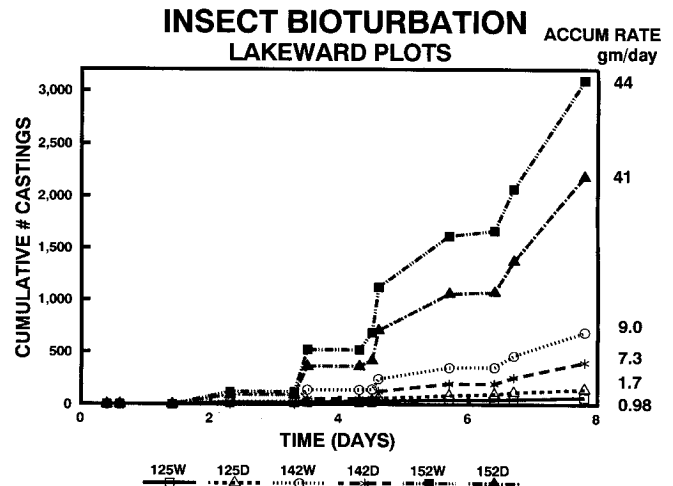


FIGURE 22—Insect bioturbation at the Alkaline Flats Site for plots close to the lake. Cumulative # castings is the number of castings piles produced during the experiment (6/12/89–6/20/89). Accum. rate is the mean accumulation rate of castings (in gm/day) for each study plot over the duration of the study. Numbers (90W, 90D, etc. refer to the site localities of the experiment, in Y distance (m) from the baseline (i.e., larger numbers are closer to the lake shore), and whether the plot was artificially wetted (W) each day or left dry (D), with only groundwater moistening. At the time of the study, the water line was at Y = 162 m.

The rates of castings production measured here would produce minimum average surficial turnover rates of between 0.5–1 cm/year, across the portion of the Alkaline Flats Site within 30 m of the shoreline (zone 2 discussed below). However, because burrow systems are patchily distributed, they may locally produce surficial turnover rates as high as 20 cm/year.

Perhaps the most important result of the study comes from the timing of castings production. On those days for which multiple castings collections were made, a consistent pattern of rapid castings production in the late morning–early afternoon was found to be followed by a hiatus in activity for the remainder of the day. Times of intense activity correspond with the periods when surficial sediments are drying out most rapidly, following nightly wetting.

Track And Trackway Survivorship

Qualitative Monitoring

Qualitative monitoring of individual tracks over the course of several weeks at the Alkaline Flats Site illustrated the basic sequences of track degradation. The mongoose trackway at X = 55–57 m, Y = 160 m deteriorated rapidly after initial formation because of soil mobilization caused by dampening and insect bioturbation. After 24 hours, the trackway as a whole was no longer readily visible. On a single, better preserved print the individual digits were all still visible but only the larger claw impressions (1 and 3) remained. After 72 hours and three

complete natural cycles of soil wetting/insect bioturbation, only a vague impression of the best print remained. The ridge between the 3rd and 4th digits could still be seen, but most of the remainder of the track had been reworked by burrowing and casting production.

The hippopotamus trackway, which lay in a similar position with respect to shoreline ($X = 3\text{--}10\text{ m}$, $Y = 107\text{--}151\text{ m}$), was also subject to reworking by bioturbation in its lakeward portion. However, the impact of insect reworking on these more deeply impressed tracks was less significant than for the mongoose tracks. The lakeward portion of the trackway was mostly destroyed over the two week study period, mainly by vertebrate trampling. Insect bioturbation served mostly to obscure the details of individual tracks, such as toe prints. This occurred within a few days on the more lakeward tracks but became much less noticeable in the landward direction. A representative individual print at $X = 3\text{ m}$, $Y = 110\text{ m}$, outside the zone of strong nightly rewetting and abundant insect bioturbation degraded in a quite different manner from the more lakeward prints. Within 12 hours of formation, the moist print surfaces began to shrink and crack from drying. This initial baking and deformation of the track surface did not obscure the toe impressions; moreover, it significantly slowed the rate of subsequent deterioration. Salt crusts began to form noticeably in individual tracks in the $Y = 100\text{ m--}110\text{ m}$ area after about 80 hr; by this time the individual toe impressions had become indistinct. After six days the digit impressions in the $X = 3\text{ m}$, $Y = 110\text{ m}$ print had become difficult to see because of repeated surface cracking, though the maximum track impression depth had remained essentially constant. An abrupt seiche event on the seventh night destroyed the remaining toe impressions and allowed a reactivation of surficial mudcracking the following day. Following this event, the direction in which the animal was walking could no longer be inferred from most individual tracks. During the second and third week no further destructive events occurred, but the prints gradually became more indistinct by deflation until only the bidirectional orientation of the trackway could be discerned.

Quantitative Survivorship

Survivorship curves for the Alkaline Flats and Hippo Pools mammal tracks are shown in Figures 23 and 24. Curves are constructed assuming the presence of 100 tracks at the beginning of each experiment. At the Alkaline Flats Site, track loss rates varied from a low of 1.6 tracks/day (calculated over 12 days) for zebra tracks in a salt crust to 83.5 tracks in a single day for hyaena tracks erased by lake water during a seiche. Direct estimates of survivorship for tracks vary from 1 to 20 days, with some tracks, for example zebra, not disappearing during the entire study. Track survival typically averaged about five to six days, but was dependent on the moisture content and substrate constituents, as well as trackmaker loading stress (Halfpenny et al., pers. comm.). In wet areas, track survival averaged two to six days, while in dry areas survival averaged to six to 12 days. The turnover rate for gazelle tracks

on the entire grid suggests that track survival for a lake shore including wet and dry areas averages 9 days for the small gazelle. Tracks gradually disappeared due to gravitational settling of soil and from wind erosion. Often a trackway did not lose tracks for several days. Disappearance rates increased from salt crusted muds, through partially cemented muds and low water content muds, to high water content muds. Disappearance rates were generally slower for large mammals than small mammals. Single events, including invertebrate bioturbation, trampling by mammals and seiches, often caused dramatic decreases in survivorship. However, tracks that became sun-baked into a crust (e.g., Fig. 23, lion and zebra) had high survivorship rates until destroyed by specific events. These tracks provide better candidates for fossilization.

Survivorship rates were considerably lower at the wetter Hippo Site than the Alkali Flats, disappearance rates varying from 25 to 50 tracks/day. Most tracks at the Hippo Site were destroyed by the seiche which occurred on the night of June 11. Other causes of track loss included the flow of wet mud and trampling by other mammals, especially hippopotamus. No tracks survived longer than five days providing a very short window for fossilization in this type of setting.

A systematic and direct relationship exists between bird track survivorship and distance of the track from the shoreline (Figs. 25 and 26). At the 152 m plot, the nearest plot to the shoreline, some track destruction occurred almost daily, caused primarily by groundwater discharge and infilling from insect castings. The survivorship curves, rather than declining continuously, tended to plateau, with sporadic, but larger magnitude destructive events destroying a large proportion of the tracks. At greater distances from the shoreline, flooding events, and the bioturbation they induced, became less frequent phenomena. Secondary vertebrate trampling, surface deformation caused by salt crystallization and fading were relatively uncommon causes of track disappearance in comparison with flooding and invertebrate bioturbation. The latter two causes were entirely restricted to the 90 m and 99 m plots, where complete daily drying and wind deflation occurred.

This general pattern of increasing survivorship away from the shoreline and a dichotomy in mode of track destruction was observed among both large and small tracks. The only systematic difference observed between large and small bird track preservation was a slight increase in the incidence of "plateauing" of the survivorship curves among the large bird tracks. This may reflect a higher threshold of destructiveness required from any given event before any large tracks are destroyed (relative to small tracks).

We calculated a D_{50} (duration of 50% print survivorship) curve for the combined small/large bird track data sets, plotting D_{50} vs. distance from shoreline (Fig. 27). This data suggests that track destruction rates increase gradually as one moves away from the shoreline, until approximately 100 m from shore (the 90 m--99 m plot transition), where survivorship increases dramatically. Interestingly, this zone of rapidly changing survivorship corresponds both to the zone below which nightly groundwater seepage surface dis-

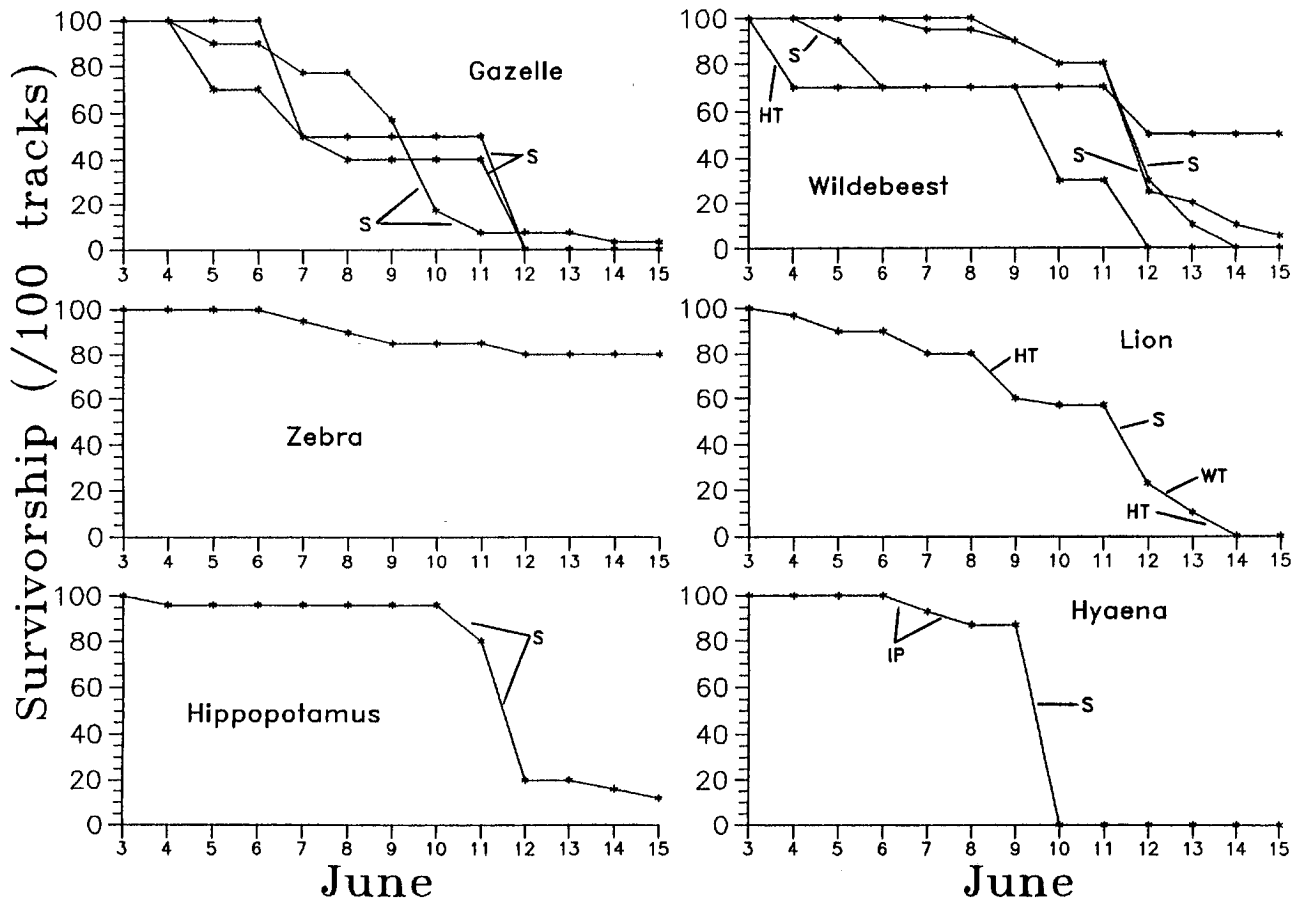


FIGURE 23—Track survivorship curves for six species of mammals at the Alkaline Flats. Survivorship curves are constructed assuming the presence of 100 tracks at the beginning of each experiment. Where tracks disappeared from causes other than fading, the reason for the loss is indicated: hippopotamus trampling (HT), wildebeest trampling (WT), insect bioturbation (IP), seiche or surge events (S), and mudflow mobilization (MF).

charge occurs, and below which bird track impressions become common. Landward from this zone, bird tracks have a lowered probability of initial formation, but a higher probability of short term preservation once formed.

Trackway Survival

Trackway survival was calculated from a 10 m × 10 m plot and ranged from one day (hippopotamus) for those immediately erased by seiche events to eleven days (wildebeest) (Table 1). The short interval between seiche events (3.6 ± 1.14 d), caused a low survivorship of trackways in this high water content mud site. Wildebeest produced the deepest and sharpest prints; their trackways survived the longest time. The tracks of hyaena and hippopotamus were relatively wide and shallow, and corresponding trackway survival was relatively short. Tracks from gazelle were small and disappeared quickly. Gazelle trackways persisted, identifiable as trackways, up to 1.58 times longer than it was possible to identify the species that made them. In contrast, larger mammal trackways (hippos, wildebeest)

in wet areas outside of the 10 m × 10 m plot remained visible for between 30 to 50× longer than the time period for which their identification to species was possible.

DISCUSSION

Our study suggests that the preservation of animal tracks in the fossil record is strongly dependent on the taphonomic processes which occur following registration of the track. These processes also may be related to variations in microenvironment. The lake margin at Lake Manyara displays a strong environmental zonation normal to the shoreline. This correlates with microhabitat variation, animal distribution patterns, initial trackway formation and subsequent preservation patterns. This zonation is not static; boundaries migrate seasonally with lake level fluctuations and daily with water table and seiche fluctuations. Zonation is most evident at the Alkaline Flats Site which, by virtue of its size, encompasses the largest amount of intrasite variation. The Alkaline Flats Site was strongly dif-

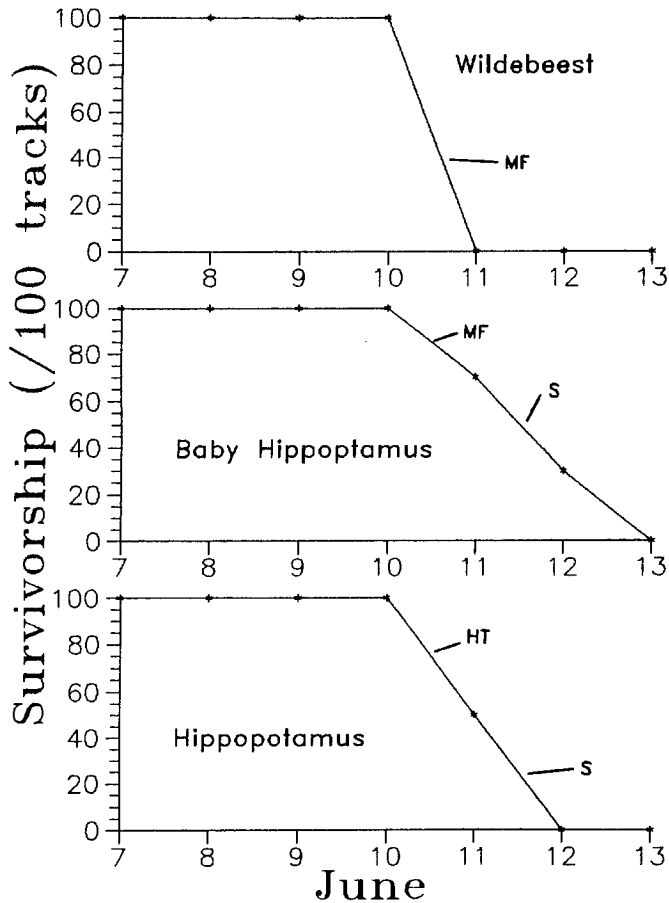


FIGURE 24—Track survivorship curves for two mammal species at the Hippo Pool site. Survivorship curves are constructed assuming the presence of 100 tracks at the beginning of each experiment. Where tracks disappeared from causes other than fading, the reason for the loss is indicated: hippopotamus trampling (HT), wildebeest trampling (WT), insect bioturbation (IP), seiche or surge events (S), and mudflow mobilization (MF).

ferentiated into three environmental zones, in terms of track type and recognizable trackway patterns (Fig. 2):

- 1) A landward zone of relatively dry sediments, where the track record is dominated by large ungulates.
- 2) A strandline zone where sediment is saturated, and tracks of smaller birds and mammals are abundant, in addition to larger mammals.
- 3) A subaqueous zone where, because of liquefaction processes, the track record is again dominated by larger mammals.

The shoreline significantly controls the distribution of animal activity; the trackway distribution patterns we have noted cannot be attributed solely to differential preservation biases. For example, certain large terrestrial animals, particularly buffalo and zebra, appeared to show a preference for zone 1 and the shoreward side of the study area, at least throughout the study period, whereas baboons and warthogs confined themselves to the landward

TRACK SURVIVORSHIP - LARGE BIRDS

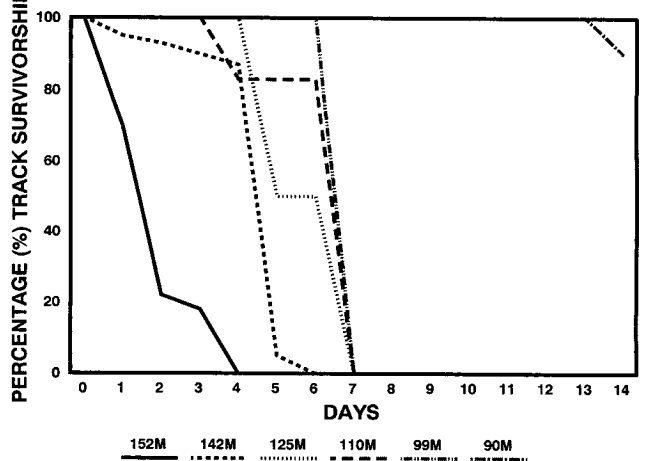


FIGURE 25—Bird track survivorship for larger bird prints (primarily Blacksmith plovers). The six study plots shown are numbered by distance from the Y = 0 baseline, along an X = 198–199 m strip, arranged from furthest (90 m) to nearest (152 m) to the lakeshore. Standing water was at Y = 162 m during the study. Experiment was conducted from 6/20/89 to 7/4/89.

side of zone 1, and never left tracks we could recognize in the study area.

Taphonomy

The environmental zonation of the Alkaline Flats Site also provides a useful model for examining short-term track/trackway taphonomic differences across environmental

TRACK SURVIVORSHIP - SMALL BIRDS

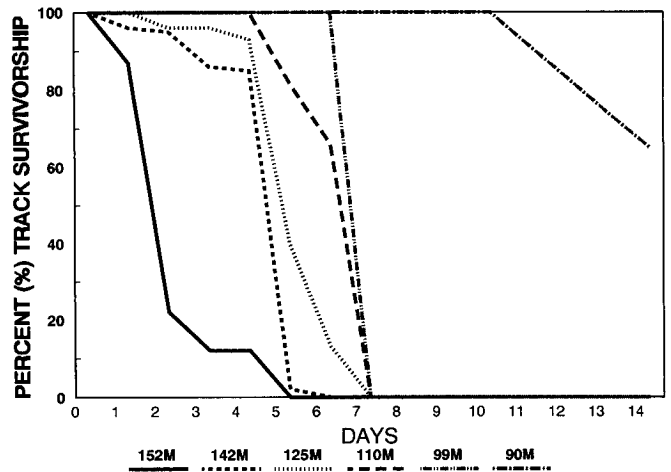


FIGURE 26—Bird track survivorship for smaller bird prints (primarily Kittlitz's plovers). The six study plots shown are numbered by distance from the Y = 0 baseline, along an X = 198–199 m strip, arranged from furthest (90 m) to nearest (152 m) to the lakeshore. Standing water was at Y = 162 m during the study. Experiment was conducted from 6/20/89 to 7/4/89.

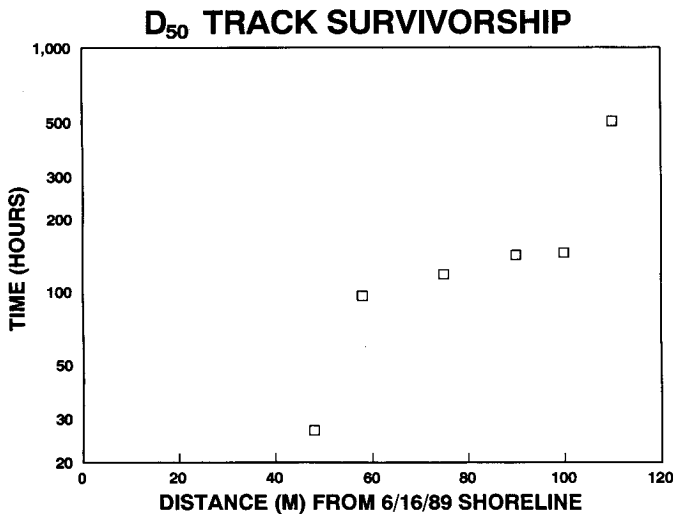


FIGURE 27— D_{50} duration for bird track survivorship. The time required for 50% of the tracks measured at the 90–152 m study plots at the Alkaline Flats Site to disappear from view, as a function of distance from shoreline.

gradients. In a taphofacies context, the three environmental zones discussed earlier can be distinguished as follows:

ZONE 1) This is the onshore zone, where mudflat sediments are comparatively dry, subject to the formation of relatively thick evaporite crusts and wind deflation. Within this zone, near-surficial groundwater fluctuations and insect bioturbation are limited. The major biotic reworking is caused by heavy vertebrate trampling. These factors combine to ensure that only the tracks of large mammals (mainly ungulates) are preserved within this zone. Tracks in this zone tend to deform through baking and subsequent cracking and are typically indistinct. Though their initial formation is relatively unlikely, once formed they have high survivorship probabilities, since reworking probabilities are low. As drying progressed during our study, a fine dust developed here which recorded minute details in tracks. In one instance, the development of the dust allowed the detection of hares, the tracks of which were not detected until late in the study (one piece of scat had been observed earlier on the Alkaline Flats grid). The dust, however, was not a good medium for long-term track preservation and prints would disappear if the wind blew.

ZONE 2) This is the strandline zone, where sediment is saturated, wind deflation is minimized and evaporite crusts are thin or absent. In this zone of significant near-surficial groundwater fluctuations, on-shore seiche events, vertebrate trampling and insect bioturbation are extremely important in short-term track reworking. The textural characteristics (finer grained, because of the absence of salt crusts) and absence of secondary track-cracking, make this zone conducive to the formation of abundant bird tracks and small mammal tracks, with considerable preserved detail, in conjunction with larger mammal tracks. However, track survivorship is lower here than in Zone 1 because of higher rates of secondary reworking.

TABLE 1—Survivorship of trackways on the 10×10 m (100 m^2) trackway plot (d). The ratio column refers to the ratio of the duration of the trackway to the duration of the time identifiable to species.

Species	Identifiable to species \bar{x} (SD)	Identifiable as trackways \bar{x} (SD)	Ratio
Hyaena	3.0 (1.00)	4.3 (2.31)	1.43
Wildebeest	5.7 (1.63)	9.0 (2.19)	1.58
Hippopotamus	1.0	1.0	1.00
Gazelle	2.0 (1.26)	2.6 (0.99)	1.30
Human	2.0 (0.53)	3.0 (2.45)	1.50

ZONE 3) This is the subaqueous zone where the sediment is soupy and not subject to the formation of evaporite crusts, deflation or insect bioturbation. In this zone, tracks are formed rapidly and are abundant but poorly defined because of continuous track-edge caving and infilling. Tracks of smaller animals are unlikely to be preserved here. Trampling, particularly by hippopotamus, is also an important agent of track destruction. Detail in track preservation is variable but generally inferior to that observed in Zone 1 and Zone 2. Track survivorship is low, since most sediments in this zone are completely unconsolidated (apart from previously cemented hard-grounds).

This broad zonation into differential track preservation zones within a site where substrate composition is relatively homogeneous has important implications. The first is that the water content of the sediment, and hence the shoreline, are of primary importance in the preservation of tracks. This provides a strong bias in favor of recognition, and ultimately preservation, of large tracks in all three zones, since impression depths (essentially equivalent to sediment strain) correlate with loading when all other factors remain equal. Small tracks are only well-preserved in the relatively narrow Zone 2. This implies also that small tracks may be particularly sensitive paleoindicators of a narrow lake margin parallel strip, wherever the appropriate water saturation conditions existed for their formation (cf. Lockley and Conrad, 1989).

In addition to environmental zonation within sites, substrate variations both within and between sites play a major role in initial track impression. These compositional, textural and cementational variations combine with water content to determine a potential strain for a sediment mass for a given loading stress applied by an animal moving over a site.

Clearly, numerous factors combined to influence short term (i.e., pre-burial) track survivorship. However, these can be combined into three major classes listed in Table 2. Strain Susceptibility (% Strain/Unit Stress of substrate) encompasses those environmental/substrate factors which exist at the track site prior to deformation. Each of these factors affects the total amount of retained, nonelastic strain (i.e., deformational shortening) which the track-

TABLE 2—Factors influencing short term survivorship of tracks. Pluses (+) indicate factors which enhance secondary reworking (reducing survivorship), whereas minuses (–) reduce the likelihood of secondary reworking (thereby increasing survivorship).

Strain susceptibility factors	Track loading stress factors	Secondary reworking rate factors
*Water content	*Trackmaker mass, foot size and shape	*Secondary vert. trampling (+)
*Sediment composition	*Differential loading (front vs. hind limbs)	*Insect bioturbation (+)
*Sediment texture	*Trackmaker acceleration at impact	*Physical disturbance (+)
*Sediment fabric		a) Waves
*Degree of cementation		b) Wind deflation
		c) Surface cracking
		*Surficial drying (+ or –)
		*Cementation (–)

bearing surface will display with a given stress. Because this composite variable is in large part a function of sediment water content, a given locality may vary greatly along this axis. Track Loading Stress (Impact Force/Unit Area) encompasses those factors affecting the impact of the trackmaker upon the substrate. Like strain susceptibility, track loading stress can vary greatly for a given animal-sediment interaction, depending on the velocity and trajectory of the trackmaker with respect to the substrate. Secondary Reworking Rate (Surficial Sediment Transport, both from and within a track measured in mass/area/unit time) encompasses those factors which are operative from the moment of track formation until initial burial, and include factors which act to both enhance (+) or reduce (–) the likelihood of track destruction through reworking. Some processes such as sun baking may cause prints to last very long periods, much longer than our study.

By combining these factors into three classes, it is possible graphically to investigate their combined effects on pre-burial track survivorship. Figure 28 illustrates a three dimensional contour plot of survivorship isograds (surfaces of equal survivorship probability). Note that because degree of cementation factors in both the Strain Susceptibility and Secondary Reworking variables, they are not perfectly independent and orthogonal. Nested zones of increasing survivorship are equated with higher substrate strain susceptibility and track loading stresses and lower secondary reworking rates. For example, a set of tracks produced along a trajectory through a single dimension of this diagram will yield a highly predictable set of results. For example, by holding strain susceptibility and reworking rate constant, there will be a direct relationship between trackmaking stress and survivorship probability. This would occur in a situation where an animal has changed its speed while moving across a substrate with uniform sediment, water content and reworking characteristics. Allowing two variables to change produces a less predictable

result. For instance, a wildebeest moving perpendicular to shoreline from zone 1 to zone 3 at the Alkaline Flats Site at a constant pace will produce a series of tracks which have a horizontal trajectory through survivorship "space" shown in Figure 28 (i.e., perpendicular to the track loading stress axis). Because track loading stress in this simplistic case is kept invariant, whether the animal's tracks are increasing or decreasing in survivorship probability is dependent on the precise shape of the survivorship probability function (i.e., the shapes of the series of nested envelopes $N..jN$, shown on the diagram). Obviously, if the animal changes speed or pattern of motion, its trackway trajectory will also vary in the vertical dimension, making a prediction of survivorship even more difficult. One very important implication of this model is that two animals of differing size moving together across a surface (i.e., two parallel horizontal lines on the graph) may produce tracks with very different survivorship probability paths, depending on the shape complexity of the survivorship isograds. Similarly, an individual animal moving at a constant pace can produce tracks with very different survivorship probability paths, if the survivorship isograd surfaces have complex shapes in the secondary reworking or strain susceptibility planes.

The track survivorship data we have collected to date, when examined in the context of our animal activity, sedimentologic and reworking data, does suggest certain things about the nature of the isograd surfaces. First and perhaps most interesting is the indication that thresholds or discontinuities exist in track preservation (i.e., that isograds are "bunched up" in certain parts of survivorship probability space). There are certain points along various quantitative environmental gradients where extremely rapid transitions in track survivorship occur; these correlate with sharp breaks in track taphofacies. A good example of this is the extremely abrupt increase in survivorship associated with relatively minor changes in sediment moisture content at the boundary between zones 1 and 2 (compare Figs.

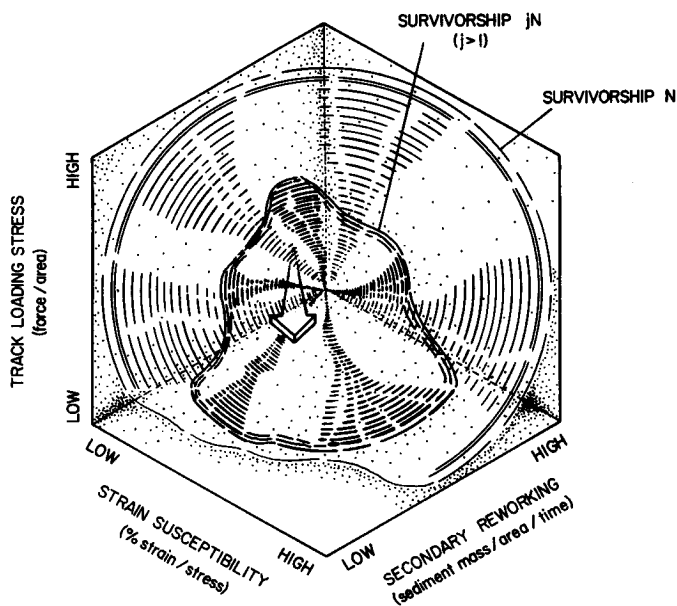


FIGURE 28—Three dimensional model of principal factors affecting short term (i.e., pre-burial) track preservation. Numerous factors affecting tracks can be distilled into three quantifiable axes. Within this 3-D space surfaces of equal survivorship (two of which are illustrated here) can be plotted. The surface labeled SURVIVORSHIP N, lies behind the surface SURVIVORSHIP jN , where N refers to an average survivorship duration (in units of time) and $jN > N$. Both surfaces are asymptotic to all three axes of the 3-space. A single organism moving across an environmental gradient can produce a series of tracks which will penetrate across numerous survivorship isograds (shown by the arrow), yielding a trackway which has differential likelihood of preservation in different areas. The same is true for different sized animals (or the same animal moving with different speed) across the same area.

2, 17, 27). The proximate causes of most of the track destruction within Zone 2 were abrupt (surficially instantaneous) events relating to inundation or trampling. In contrast, track degradation in Zone 3 is a much more gradual process (i.e., survivorship isograds are more evenly spaced along the secondary reworking axis).

This model provides a valuable framework through which future track preservation studies might be channeled, since all four variables can be measured quantitatively and their interactions predicted. Once the shape of these isograds is established, the model will have great utility in interpreting the fossil track record. It will provide constraints on trackmaker mass and velocity and direct estimates of substrate compactibility, and water content at the time of trackway impression. It will also allow predictions of the degree of time averaging represented by specific trackway sites.

Within relatively small areas, both track formation probability and survivorship can vary dramatically in very short distances and over very short time intervals. It is useful to visualize these differences in terms of "windows of preservation." A particular set of tracks within a limited area of track-bearing surface has a relatively brief (and,

in principal, measurable) period of time in which to be both formed and buried; after that time, the tracks will be destroyed. These windows are measurable in terms of days (shoreline/Zones 1 or 2 equivalent) to months (Zone 3) but are certainly of shorter duration than the period over which body fossils (bones, for example) might accumulate. Trackway-bearing surfaces are time-averaged, but over shorter-time scales than bone accumulations. Most tracks form near some kind of shoreline where sediment accumulation rates tend to be highly erratic. Thus the track record of a given land surface is normally wiped clean numerous times (and for many environments, in essentially instantaneous events) before a preservation event can occur. Because of the time scale of trackway time-averaging, this would be true even in areas of (geologically speaking) rapid vertical aggradation (e.g., several mm/yr). The nature of the preservational event thus becomes of primary importance in determining how time-averaged a picture of an area's fauna the trackway surface is providing. For example, if the preservation events in a stratigraphic sequence are primarily the result of predictable seasonal flooding, then areas with short preservation windows will contain tracks reflecting animal activity of a potentially highly seasonal nature. In contrast, the same burial event covering a spot with a longer preservation window, might give a more time-variable picture of the local fauna.

In this study we have concentrated on pre-burial processes affecting track preservation. This was a necessary limitation imposed by our specific study sites which had homogeneous sediments displaying little of the internal stratification required for observing buried tracks in unconsolidated sediments. However no sharp dividing line exists between pre- and post burial preservation. The timing, frequency and nature (e.g., catastrophic vs. gradual) of burial events will determine the likelihood of a trackway with a given preservational window being initially preserved in a stratigraphic sequence. At Lake Manyara there are some localities, such as along the fan deltas of the western lake margin, where sediment aggradation rates are high enough to bury tracks rapidly relative to their rate of surficial reworking. Other areas with lower rates of sediment input, like our study sites, have relatively slow rates of vertical aggradation compared with their reworking rates and a concomitantly lower probability of burial. Longer term post-burial events with a bearing on preservation (secondary exhumation and erosion, compaction, diagenetic alteration) are also largely site-dependent, although the "site" context becomes more geological rather than ecological. Thus our next goal is to investigate track burial processes at Lake Manyara at a site where internal stratification can be readily observed and buried tracks exhumed.

We are extremely optimistic that future analog studies will further refine some of the issues raised by this study. We hope to look at new problems which this study did not address, such as short-term post-burial preservation of tracks. In developing this first study, our major goal was to define the initial direction of a rigorous, quantitative

study of trackway formation and preservation. The Lake Manyara study, however, represents only one of many possible locations and strategies for such research. We encourage other workers on fossil trackways to join us in this task, to elevate the study of fossil trackways from an anecdotal to an analytical science.

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