

## Modern vertebrate tracks from Lake Manyara, Tanzania and their paleobiological implications

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**Abstract.**—We studied mammal and bird track formation at the northern edge of Lake Manyara, Tanzania, to develop models for interpreting fossil tracks and trackways. Lake Manyara is a closed-basin, alkaline lake in the East African Rift System. The area has a high vertebrate diversity, allowing us to investigate tracks in an environment similar to that of many ancient track-bearing sequences. Three study sites, two on mud flats adjacent to the lake margin and a third on a delta floodplain, provided contrasting environments in which to assess the types of biological data that can potentially be extracted from fossil trackways.

Our censuses of mammals and their tracks revealed that most species that occur within the study area leave a track record, and that common species leave abundant tracks, although numbers of trackways are not proportional to numbers of individuals. Logarithmic increases in track sampling area yield a linear increase in the proportion of both the medium and large-sized local mammals represented in a track record. Transect vs. area mapping methods produced different censusing results, probably because of differences in monitoring periods and areal coverage.

We developed a model of expected track production rates that incorporates activity budget and stride length data in addition to abundance data. By using these additional variables in a study of diurnal birds, we obtained a much better estimator relating track abundance to trackmaker abundance than that provided by census data alone. Proportions of different types of tracks predicted by the model differ significantly from the observed proportions, almost certainly because of microenvironmental differences between the censusing and track counting localities. Censuses of fossil tracks will be biased toward greater numbers of depositional-environment generalists and away from habitat-specific species.

Trackways of migratory animals were dominantly shoreline-parallel, whereas trackways of sedentary species were more variable. A strong shoreline-parallel environmental zonation at the Alkaline Flats site exerted an influence on trackmaker distribution patterns, initial track formation, and track preservation. Variations in habitat usage by different species, as well as species abundance and directionality of movement, were all important in determining the number of preservable tracks a species produced within a given environmental zone.

Fossil trackways are time-averaged, although over entirely different temporal scales than are bones. Unlike bones, tracks are not space-averaged. Therefore, wherever possible, fossil track and bone studies should be used to complement each other, as they provide fundamentally different pictures of paleocommunities. Tracks provide "snapshot" views of localized assemblages of organisms useful in reconstructing autecological relationships, whereas bones yield a broader image of a local fauna in which seasonal and microenvironmental variation are more commonly smoothed out.

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### Introduction

The study of fossil vertebrate tracks has expanded rapidly in recent years with the realization that valuable information about the biology of extinct organisms is bound up in their footprints (Farlow 1981; Leonardi 1981; Thulborn 1990; Lockley 1991a). Unlocking

that information, however, requires an understanding of what biologically significant signals are encoded in tracks when they are first formed, as well as how taphonomic biases affect tracks after they form. How precisely can habitat usage patterns be inferred from fossil trackways? What is the relation-

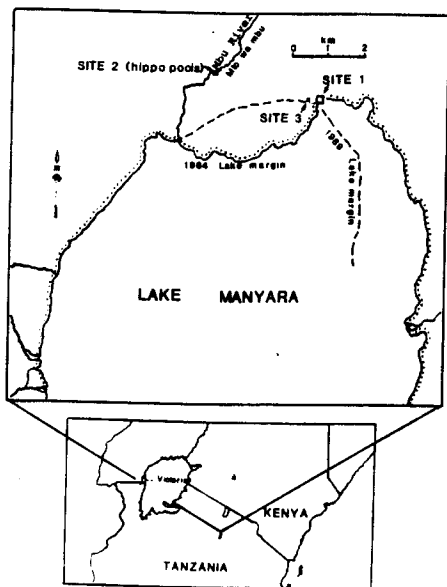


FIGURE 1. Location map for Lake Manyara and the three study sites. Site 1 is the Alkaline Flats site (the Manyara National Park Boundary runs N-S along the western edge of this site). Site 2 is the Hippo Pool site. Site 3 is the Bird Track site. Note shift in lake margin from 1964 topographic map location. Lake Manyara is a closed basin with widely fluctuating lake levels. In 1989 lake level was relatively high.

in preparation) consider the sedimentology and track taphonomy in the study area and use our findings to interpret several important fossil trackway sites. In this paper we use the term "track" for a single footprint and "trackway" for a series of tracks produced by a single moving animal.

### Study Area

Lake Manyara lies in the southern part of the Gregory Rift Valley in northern Tanzania (fig. 1). The lake lies in a half graben basin at 950 m elevation, bounded by the 300-m-high Mto Wa Mbu Fault scarp. The lake drains Precambrian metamorphic and Neogene sedimentary and volcanic bedrock.

The Lake Manyara area is tropical semiarid to semihumid. Rainfall varies greatly between 375–1250 mm/yr. There are two distinct rainy seasons (November–December and March–May) (Greenway and Vesey-Fitzgerald 1969). Two major perennial streams feed the lake, the Mbu River (referred to as the Simba River or Mto Wa Mbu on some maps) from the north, and the Makuyuni River from the east, as well as numerous other perennial and seasonal streams that drain the fault scarp to the west and the surrounding hinterland.

Lake Manyara is a shallow (3.9 m max. depth), closed-basin lake with a mean surface area for recent years of 470 km<sup>2</sup> (E. Molle personal communication 1989). The lake undergoes considerable areal expansion and contraction during the wet and dry seasons. Lake water is highly saline (conductivity 4000–100,000  $\mu\text{mho}/\text{cm}$ ) and alkaline (30–800 mEq/liter  $\text{CO}_3 + \text{HCO}_3$ , pH 9.8–10), with great seasonal and interannual variation in concentrations. The lake was relatively fresh during the study period, which followed the rainy season. Measured values of conductivity, alkalinity, and pH began at the low ends of these ranges and rose progressively through the dry season. The distribution of diverse plant communities around the lake margin is controlled by spring discharge, steep local topographic gradients, perennial rivers, and the fluctuating position of the lake margin. These communities include groundwater-riverine forests (partly closed canopy), *Acacia* woodlands, thicket woodlands, alkaline grass-

ship between animal abundance and track abundance in the area of track preservation (i.e., can tracks be used as a fossil census?)? How precisely can behavior be inferred from fossil trackways? To what extent are fossil trackways time-averaged and when do they indicate coexistence of species at the trackway site?

To address these questions about biological signals encoded in tracks and track taphonomy, we studied track formation and preservation at Lake Manyara, Tanzania. We chose Lake Manyara because of its abundant and diverse large vertebrate fauna as well as its geological similarity to numerous important fossil track sites: it is a saline closed-basin lake in an aggrading rift basin. This paper addresses only the biological information encoded in our Manyara track data. Two separate papers (Cohen et al. 1991; Lockley et al.

lands, *Cynodon* grasslands, and swamps (signifying fresh groundwater discharge [Greenway and Vesey-Fitzgerald 1969]). These varied habitats are largely responsible for the high vertebrate diversity in our study area.

### Study Sites

We chose three study sites, all 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. Two of the three sites straddle the strandline of late May through early July, 1989, and the third is located on a delta floodplain.

To make our results of more general significance for comparison with a variety of fossil track studies, we used the following criteria in locating our research sites:

1. Abundant bird and large mammal populations, both local and migratory.
2. Depositional substrates suitable for track formation. This criterion favored shoreline environments.
3. Suitable off-site locations for observing trackmaker abundance and activity (either distant with an unobstructed view or nearby with cover).
4. Variable habitats, with different substrate conditions and fauna.

The Alkaline Flats site (Site 1) is bordered on the west by Lake Manyara National Park and covers an area 250 m  $\times$  250 m (fig. 2). It is a featureless plain of exposed alkaline mud flats, alkaline grasslands (dominated by *Sporobolus spicatus*), and other emergent aquatic graminoids. The surficial sediments are mixtures of calcium carbonate and clastic muds, or calcium carbonate and sodium carbonate muds.

The Hippo Pool site (Site 2) lies 2 km to the west of Site 1, on the east bank of the Mbu River, a short distance upstream from the river mouth (fig. 3). This site (60 m  $\times$  100 m) is a freshwater, mixed fluvial-floodplain grassland/mud flat habitat. Surficial sediments here are clastic muds, with high organic content from mammal feces.

The Bird Track site (Site 3) is located 170 m west of Site 1 (fig. 1). The research area comprises a 50 m  $\times$  50 m bird observation study plot and two adjacent 1-m<sup>2</sup> track plots.

The site straddles the dry ground/wet grass/marsh ecotone, ensuring that we would encounter many bird species. The site is a mosaic of shallow (0–15 cm) ponds, exposed ground, and grass/sedge cover. During the course of the experiment, minor lake level fluctuations alternately exposed or flooded large portions of this study area.

### Methods

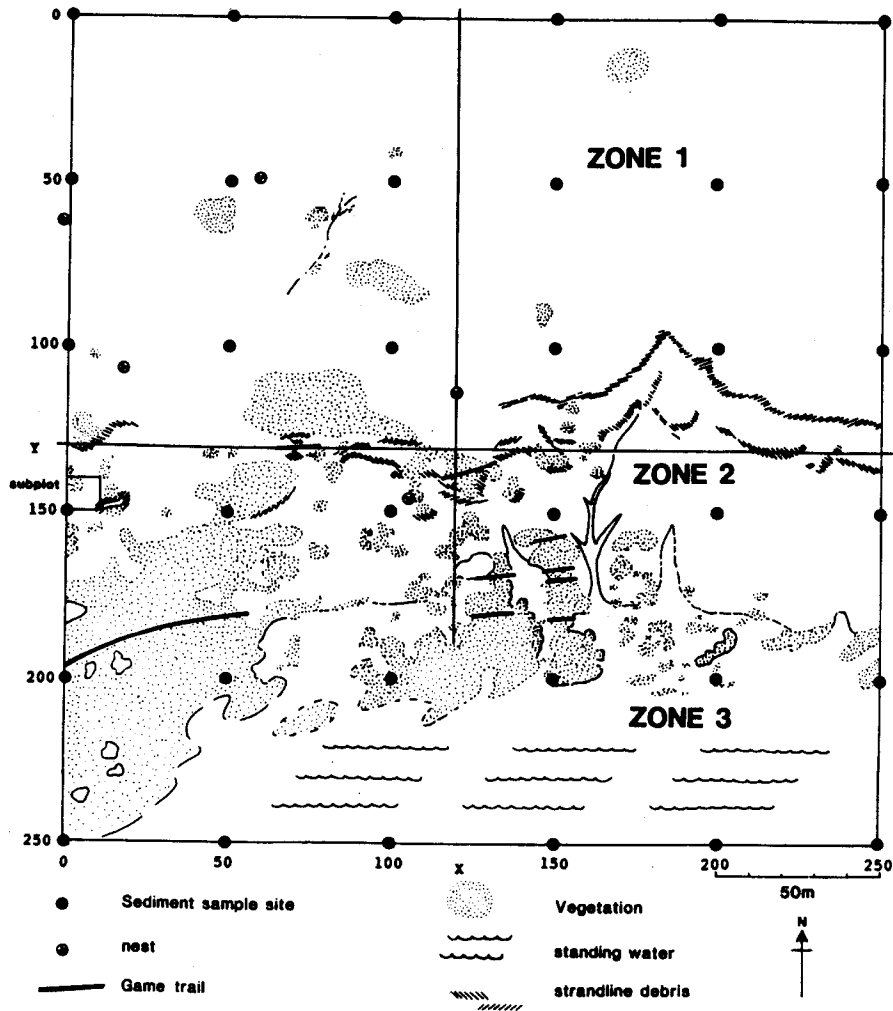
#### Site Surveys

We initially surveyed our study sites using a line and compass to generate E-W (X) and N-S (Y) baselines. We then mapped major physiographic features such as vegetation, open mud flat, standing water, and strandline accumulations onto these grids. These maps served as references for updates as the shoreline shifted position. We also used the same survey maps to compile site-wide trackway maps, and for locating a 10 m  $\times$  10 m subplot used for several experiments.

We established transects on the Alkaline Flats site (fig. 2) running roughly parallel to shore on the line Y = 130 m S and perpendicular to the shoreline on the X = 120 m E line (NW corner was X = 0, Y = 0). We used these lines to make daily census counts of trackmaker activity. The Y = 130 m S line was consistently wet enough during the study to record the prints of any vertebrates that crossed. The northern, dry portion of the N-S line (X = 120 m E) had to be raked daily to expose fresh sediment upon which tracks could register.

#### Animal Censusing and Trackway Observation

We censused mammals and birds on a daily, diurnal basis over a 1-month period, from late May to late June, 1989, at the three study sites to document the relationship between trackmaker abundance and track abundance. We initially identified both mammal and bird prints by sighting on the animals and observing the tracks immediately after the track was made. Operationally this proved more difficult with birds, because there were many similar-sized species producing similar tracks in a single area. We collected track size and



Lake Manyara : site 1

FIGURE 2. Environmental map for Lake Manyara Alkaline Flats site (=Site 1). Grid measures for the 250 × 250 m site referred to in text are measured from the northwest corner (X = E-W distance, Y = N-S distance). Zone 1 is the landward area of relatively dry sediments. Zone 2 is the strandline zone where sediment is saturated. Zone 3 is the subaqueous zone.

stride length measurements for all mammals frequenting the study sites. If we did not identify an animal actually making a track, we identified the track by referring to paws on skins at the Lake Manyara Museum, in-

formation in books, and previous personal experience with African mammal tracks.

*Animal Observation and Censusing: Alkaline Flats and Hippo Pool Sites.*—We monitored large mammal and bird activity in and near the

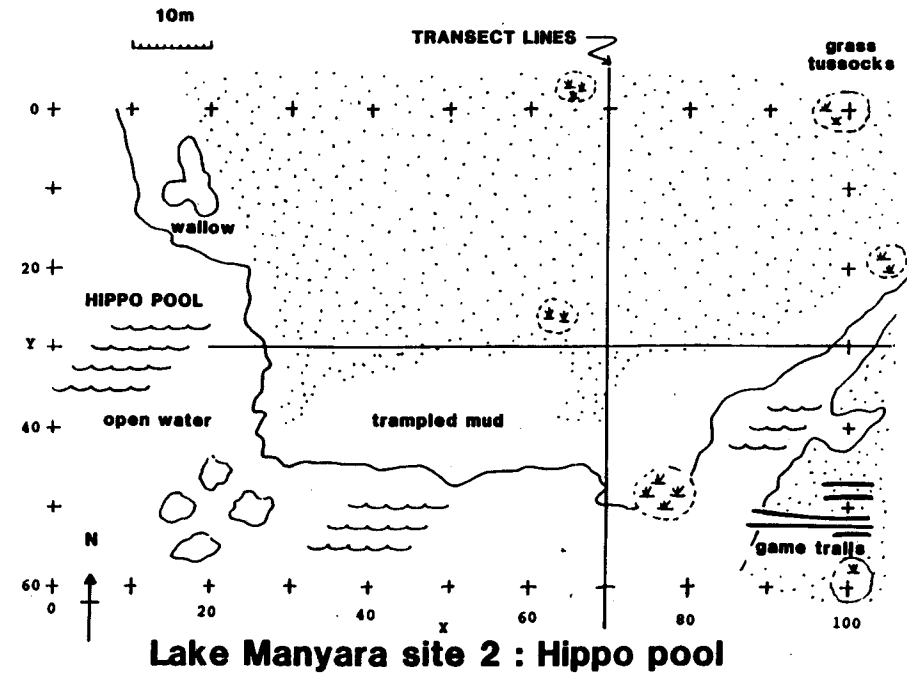


FIGURE 3. Environmental map for Lake Manyara Hippo Pool site (=Site 2). Grid measures for the 100 × 60 m site referred to in the text are measured from the northwest corner (X = E-W distance, Y = N-S distance).

study sites during the period of maximum daily diurnal activity (6:30–7:30 A.M.) each day of the study period (May 29–July 5, 1989). We minimized disturbance during censusing by using binoculars at a distance of several hundred meters. On arrival at our observation stations, we counted all the large mammals on the two sites or in the immediate vicinity. We also noted the appearance and disappearance of any other animals that ventured in or out of the study sites. Weather data (temperature, wind direction, wind speed, cloud cover) were routinely recorded at the same time to understand physical processes affecting track formation. Because of the considerable distance between the observation point and the edge of the Alkaline Flats site (830 m), we could not census birds there, but did count them at the Hippo Pool site.

*Footprint and Trackway Documentation: Alkaline Flats and Hippo Pool Sites.*—We used two

methods of mammal track censusing during our study: area mapping and transects. Mapping had the advantage of separating milling and directional travel behaviors but was labor intensive. Mapping was also impractical in heavily trampled areas because multiple, superimposed tracks were difficult to document graphically or quantitatively over a large area, and trackway dating on the mapped surface became increasingly difficult as tracks accumulated. The amount of effort therefore reduced the area that could be censused. While estimating the age of a given trackway was possible, locating all new trackways each day was not always possible. Directional biases were minimized, however, because a whole area was known.

Transect surveys allowed large areas that crossed several habitats to be sampled because only a narrow study strip was used. The width of the strip had to be chosen carefully

in reference to stride length to adequately survey very common trackmakers, while still detecting rarer trackmakers. A 1-m-wide swath was raked but the transect width within this swath was adjusted for each species to equal one half of the species' stride length. If the transect was raked out or the new tracks marked, it was easier to interpret the daily accumulation. This was possible because the study strip area was not large (1 m × 214 m).

We identified mammal trackways present at the beginning of the study to species and plotted them on the base maps and/or transect lines. We continuously updated the tracks map at the Alkaline Flats site. This method showed the exact configuration and orientation of all recognizable trackways over a given time period. Such maps facilitated comparison with existing site maps of fossil footprints. We used this additive mapping method for a limited time period (May 29–June 9), and in areas where recognizable tracks could be recorded.

We used transects to monitor both the Alkaline Flats and Hippo Pool sites. We monitored transects on arrival at the study sites each morning (about 7:30 A.M.). We counted fresh trackways and recorded their orientation. We marked the tracks by drawing a line through them, to prevent accidental rerecording at a later time. For track counts, we counted footprints if they occurred within one-half walking stride length of the south or west side of the transect lines (one half stride length for gazelles = 35 cm, wildebeests and other ungulate species = 55 cm [Halfpenny 1986]). By using one-half walking stride length, we could detect all walking animals without duplicating track counts of the same animal because, at least one set of prints must show within a half-stride length of the transect line. It was possible that galloping, trotting, or jumping animals could cross the transect width without leaving a track impression, thereby causing us to underestimate their abundance based only on track prints.

We counted trackways by species for the following: (1) relative abundance, (2) track accumulation rate, (3) new track density and areal extent, and (4) preferred orientation. We calculated relative abundance by making cu-

mulative counts of trackway abundances from both the Alkaline Flats site trackway maps and the daily transects across the Alkaline Flats and Hippo Pool sites.

We calculated trackway accumulation rates by species from the transects at the Alkaline Flats site. Accumulation rates for gazelle and wildebeest prints were collected from daily transect surveys (June 2–5) by dividing the total number of tracks on the transect by 4 days of accumulation. The accumulation rate in tracks per day was divided by the species strip-width times 214 m of effective transect survey distance to give tracks/m<sup>2</sup>/day. Information on track production rates is important for assessing the degree of time averaging represented in an analogous fossil trackway assemblage.

We also determined rates of trackway accumulation by daily mapping of a 10 m × 10 m plot with its SW corner located at X = 0 m, Y = 140 m (fig. 2). We placed each trackway on a map and checked the plot daily from May 29 to June 15. We recognized three categories for each trackway: identifiable to species, identifiable as a mammal trackway, and no longer identifiable as a discrete trackway. A trackway fell in the third category when gaps between recognizable footprints exceeded 50% of the trackway.

We calculated new track density (number of tracks/m<sup>2</sup>) and areal extent from a survey of the number of tracks occurring within the N–S and E–W transect strips on June 5. Our transects intersected both heavily and lightly used parts of the study area, thereby providing average-use data.

We determined the preferred orientation of trackways from the trackway maps and the transects at the Alkaline Flats site and analyzed these orientations using rose diagrams.

*Bird Censusing and Track Documentation: Bird Track Site.*—We established Site 3 (50 m × 50 m) to study bird activity and track formation at a closer range than was possible in either of the other sites. One of three observers alternated in monitoring bird activity continuously during daylight hours over a 23-day period. We used binoculars to observe from the same position (approx. 25 m north of the study plot) during the entire study. At this

distance, disturbance of the resident bird population was negligible. We censused the study plot by species every hour, on the hour, during daylight. We included only individuals within the flagged boundary at the start of counting in the census. We compiled activity budget data by counting the number of footsteps an individual bird of a particular species took over a 2-minute period (or until flight, whichever occurred first). We established an observation protocol to avoid excessive recounting of the same individual, or of more easily counted individuals (e.g., those which were asleep and not moving): we counted the individual of a given species that was nearest to a fixed point at the center of the study area, and then switched to other individuals progressively farther from the fixed point for subsequent counts. When a 2-minute count ended (or the bird flew), we recorded the time, species, duration of observation, and number of steps taken, and then chose a new individual (preferably of a different species) to be counted. We continued this procedure throughout the daylight hours, except for brief censusing and track-clearing interludes, or when no birds were on the study plot. We obtained between 20–60 observations (footsteps/minute) for each common species, for each 2-hour interval of daylight, from 6:00 A.M. to 6:00 P.M.

We inspected and counted two footprint plots for new tracks each day of the study, at varying times. All identifiable tracks were tabulated. In many cases, tracks from birds of similar stature could not be differentiated (e.g., stints and small plovers). We tabulated these tracks in "species groups," which formed our observed bird track production data set. We compared these data with a predicted species-group track production, generated from summed-averaged census and activity data from the members of that group in the data analysis (discussed in detail in the Bird Track site censusing section). After counting, we raked the plots smooth and re-wet them with approximately 1-cm-deep standing water to allow an entirely new set of impressions to form during the next 24-hour period. Counting and clearing of track plots took approximately 30 minutes. During this time birds

left the study plot and we did not resume counting for approximately 30 minutes thereafter, when bird activity had returned to normal. We altered the times of track-plot counting and clearing times to prevent a reduction in activity and inaccurate census counts for particular times of day.

## Results

### Animal Censusing and Trackway Observations

*Relationships between Animal and Track Censuses.*—Table 1 lists the types of mammals and birds and identifiable tracks observed at the Alkaline Flats and Hippo Pool sites. For the fourteen species of mammals we recorded at the Alkaline Flats site, six (43%) were recorded both in censuses and as tracks, three (21%) were recorded only in censuses, and five (36%) only as tracks. For the eight mammal species observed on the Hippo Pool site, four (50%) were recorded both in censuses and as tracks, two (25%) were recorded only in censuses, and two (25%) only as tracks. We observed three additional species of mammals near the Hippo Pool site but did not see their tracks on the site. Mammals that we recorded from censuses but not tracks are either infrequent visitors to the specific habitats enclosed in the sites or moved through the sites in areas that were not receptive to track formation. Mammals recorded from tracks but not censuses were largely nocturnal species.

Paleobiologists can take heart from the fact that nine of twelve species of large mammals (>50 kg) and twelve of eighteen species of medium and large mammals (>2 kg) known to inhabit the Alkaline Flats area from wild-life records were recorded in our track counts. Furthermore, individuals of the species for which we recorded tracks at the Alkaline Flats site make up over 96% of the total census sightings for this area (table 2). Considering the likelihood that not all species identified as "in the area" by the Wildlife Department were actually resident during our study, the tracks we observed give a good picture of the local large mammal fauna present. This suggests that ancient track sites that cover comparable areas (50,000 m<sup>2</sup> subaerial) and formed

TABLE 1. Mammal and bird species observed active or from tracks at the Alkaline Flats and Hippo Pool sites. \* indicates that the animal or its tracks were observed in areas adjacent to the study sites. An "X" indicates that the species was observed, a "0" indicates that the species was not observed.

Species	Alkaline Flats site		Hippo Pool site	
	Active	Tracks	Active	Tracks
<b>Mammals</b>				
<b>Herbivores/omnivores</b>				
Hippopotamus, <i>Hippopotamus amphibius</i>	X	X	X	X
Wildebeest, <i>Conochastes taurinus</i>	X	X	X	X
Buffalo, <i>Syncerus caffer</i>	X	X	X	X
Burchell's zebra, <i>Equus burchelli</i>	X	X	X	X
Thomson's gazelle, <i>Gazella thomsoni</i>	X	X	0	0
Maasai giraffe, <i>Giraffa camelopardalis</i>	X	0	X	0
Warthog, <i>Phacocoerus aethiopicus</i>	X	0	0	0
Olive baboon,* <i>Papio anubis</i>	X	0	0	0
Impala,* <i>Aepyceros melampus</i>	0	0	X	0
Waterbuck,* <i>Kobus ellipsiprymnus</i>	0	0	X	0
Abyssinian hare, <i>Lepus habessinicus</i>	0	X	0	0
<b>Carnivores</b>				
Lion, <i>Panthera leo</i>	0	X	0	0
Black-backed jackal, <i>Canis mesomelas</i>	X	X	0	X
Spotted hyena, <i>Crocuta crocuta</i>	0	X	0	X
Marsh mongoose, <i>Antilax paludinosus</i>	0	X	X	X
Dwarf mongoose, <i>Hellgale parula</i>	0	X	0	0
Clawless otter,* <i>Aonyx capensis</i>	0	0	0	X
<b>Birds</b>				
White-necked cormorant, <i>Phalacrocorax carbo</i>	0	0	X	?
Sacred ibis, <i>Threskiornis aethiopicus</i>	X	X	X	0
Glossy ibis, <i>Plegadis falcinellus</i>	0	0	X	0
Little egret, <i>Egretta garzetta</i>	X	X	0	0
Cattle egret, <i>Ardeola ibis</i>	0	0	X	0
Grey heron, <i>Ardea cinerea</i>	0	0	X	0
Goliath heron, <i>Ardea goliath</i>	X	X	X	0
Maribou stork, <i>Leptotilos orumeniferus</i>	0	0	X	0
Yellow-billed stork, <i>Ibis ibis</i>	0	0	X	0
Lesser flamingo, <i>Phoenicopterus minor</i>	X	0	X	0
Crowned crane, <i>Balaerica pavonina</i>	0	0	X	0
African spoonbill, <i>Platalea alba</i>	0	0	X	0
Pink-backed pelican, <i>Pelecanus rufescens</i>	0	0	X	?
White pelican, <i>Pelecanus oncorotalus</i>	0	0	X	?
Red-billed duck, <i>Anas erythrorhynchus</i>	X	?	0	0
Knob-billed duck, <i>Sarkidornis melanotus</i>	0	0	X	0
White-faced tree duck, <i>Dendrocygna viduata</i>	0	0	X	0
Cape teal, <i>Anas capensis</i>	X	?	0	0
Egyptian goose, <i>Alpochen aegyptica</i>	X	X	X	X
Grey-headed gull, <i>Larus cirrocephalus</i>	X	0	X	0
Augur buzzard, <i>Buteo rufofuscus</i>	X	0	0	0
Fish eagle, <i>Haliaeetus vocifer</i>	0	0	X	0
Spotted stone curlew, <i>Burhinus capensis</i>	0	0	X	0
Kittlitz's plover, <i>Charadrius pecuarius</i>	X	X	X	0
Blacksmith plover, <i>Vanellus armatus</i>	X	X	X	0
Little stint, <i>Calidris minuta</i>	X	?	0	0
Wood sandpiper, <i>Tringa glareola</i>	X	?	0	0
Blackwinged stilt, <i>Himantopus himantopus</i>	X	?	0	0
African jacana, <i>Actophilornis africanus</i>	0	0	X	0

under similar conditions (i.e., marginal to a relatively calm water body whose level fluctuates over similar amplitudes) are also likely to capture a good presence-absence picture of the local fauna. Not surprisingly, the small-

er study areas (Hippo Pool site, 10 m × 10 m transect area, and Bird Track site) record a much less complete picture of the local fauna (fig. 4). Cumulatively, the data show a weak species-area effect with larger species equally

or better represented than medium-sized ones. Smaller ancient trackway sites (<1000 m<sup>2</sup>) are unlikely to register the majority of species inhabiting an area. As this is the first study of its type, it is not possible at present to assess the general applicability of these findings to the entire spectrum of fossil trackway environments of deposition.

We compared the transect and mapping methods for ability to detect animals and for utility as counting methods for fossil trackways. Because the transect width was adjusted by species to half of the stride length, each animal crossing the transect can be expected to leave two footprints on average if there is a perfect record of animals moving over the transect. On June 2, 1989, we counted 57 gazelle and 34 wildebeest tracks on the Y = 130 m transect. By dividing the numbers of tracks by two and rounding up to the nearest whole number, it appears that a maximum of 29 gazelle and 17 wildebeest crossed the transect on that day. The number represents a maximum because animals may recross the transect. On the same day, 28 new gazelle and 11 new wildebeest trails were independently mapped on the entire Alkaline Flats area, suggesting that at least one gazelle and six wildebeest did recross the transect on that day. By following the trails where they went off the transect onto the mapped area, we identified 15 wildebeest tracks that were made by animals walking on courses roughly parallel to the transect. This number accounts for much of the discrepancy between the transect and trail counting methods ( $(34 - 15)/2 = 9.5$ , rounded up to ten animals). Thus the total

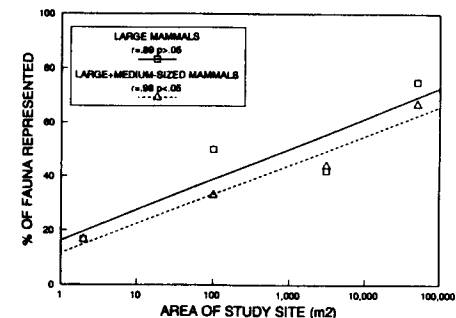


FIGURE 4. Proportion of local fauna represented by tracks in various sized trackway sites. Information on local fauna was obtained from interviews with game scouts and park officials.

map count provided a more complete census of the animals present than the transect track count. Where feasible, and where censusing is the goal, fossil trackway counts by areal mapping are preferable to those by transect.

The wildebeest were on the map area during the night of June 1-2, so we could not census them while they were there. However, on June 2 as we drove to the Alkaline Flats site, we observed 30 gazelle on the map area. The 28 trails on the transect underestimated the number of animals by at least two.

There was no statistically significant correlation between the number of new trails on the Alkaline Flats and the number of mammals observed during the morning census at the Alkaline Flats over the 2-week period (May 29-June 13, Pearson correlation coefficient  $p > 0.05$ ). Neither the 1-hour observation period at daybreak nor observation upon

TABLE 2. Mammal frequencies (%) in visual census, total trackway census and transect censuses for Alkaline Flats site.

Species	Visual observation	Total trackways	E-W transect	N-S transect
Thomson's gazelle	29	19.0	79.9	79.3
Wildebeest	51	49.5	10	18.1
Zebra	16	2.8	0	0
Hippopotamus	<1	20.8	8.5	2.1
Buffalo	<1	2.8	0	0
Giraffe	1	0	0	0
Warthog	2	0	0	0
Spotted hyena	0	1.9	0	0
Black-backed jackal	0.3	1.9	1.5	0.5
Mongoose	0	0.9	0	0
Lion	0	0.5	0	0

TABLE 3. Rates of trackway accumulation at the Alkaline Flats site (trackways/m<sup>2</sup>/day).

Species	10 × 10 m (100 m <sup>2</sup> ) plot	E-W transect	N-S transect
Hyena	0.0016	ND	ND
Gazelle	0.0111	0.0489	0.1274
Wildebeest	0.0033	0.0062	0.0274
Hippopotamus	0.0033	0.0052	0.0034
Jackal	ND	0.0009	0.0008
Snake	ND	0.0003	ND
Fishermen	0.0044	ND	ND

\* ND, not determined.

our arrival at the sites at other times accurately predicted the number of tracks or trackways that were laid down during a 24-hour period.

We attribute the lack of correlation between census observations and track counts of large mammals to our short observation period (only 1 hour per day) and to the animals' nocturnal activity. Observations from June 2 suggest that it is possible to census the number of animals from their trails. However, we would need to do observations over 24-hour periods using night-vision spotting scopes to establish the relationship of large mammals present to track and trackway counts. At Lake Manyara, hippopotamus, hyenas, and lions were rarely observed on the Alkaline Flats site, even though their tracks record their presence (abundantly in the case of hippopotamus).

**Track Abundance, Areal Coverage, and Accumulation Rates.**—Estimates of track production rates are essential for calculating the degree of time-averaging represented in fossil track sites and for making inferences about the relationship between numbers of individual trackmakers passing through a site and numbers of preserved tracks. We analyzed production of tracks (individual prints) and trackways (trails of many prints) and report them separately here. An estimated 117,000 gazelle tracks and 422,000 wildebeest tracks existed on the mapped area on June 2. These estimates were based on initial surveys of transects running N-S and E-W across the Alkaline Flats grid that was above water line. Track density averaged 2.34/m<sup>2</sup> for gazelle and 8.44/m<sup>2</sup> for wildebeest. Gazelle densities in the study area were relatively constant,

averaging 13.1 ± 6.6 resident gazelle in the mapped area, as observed in our daily censuses, with a maximum of 27 individuals seen at any one time. Wildebeest densities were more erratic (22.9 ± 44.1) with one exceptionally large herd (May 29, estimated at 165 animals) probably responsible for most of the recorded track density.

Tracks accumulated on the Y = 130 m transect at the rates of 0.26 and 0.08 tracks/m<sup>2</sup>/day for gazelles and wildebeest, respectively. The estimate of accumulation rate for wildebeest does not include the herd observed on May 29, but was based only on new tracks made after the herd passed.

Because we sampled a small area, our measures of accumulation rate on the 10 m × 10 m subplot (within the Alkaline Flats site) were lower than on the transect. Accumulation rates on transects varied 150-fold from a low of 0.0008 tracks/m<sup>2</sup>/day for jackals to a high of 0.1274 tracks/m<sup>2</sup>/day for gazelles (table 3). The greater accumulation rates of gazelle and wildebeest on the N-S transect reflected their movements parallel to the shore, closer to grass meadows and away from the mud flats. High accumulation rates of hippopotamus on the E-W transect also reflected shore-parallel movements but restricted to the near-water zone.

We used accumulation rates to estimate the number of days that were required for tracks to accumulate to the number in the initial survey on June 2. For gazelle, nine days would have been required (2.34 tracks/m<sup>2</sup> divided by 0.26 tracks/m<sup>2</sup>/day), and for wildebeest, 105.5 days would have been required (8.44 tracks/m<sup>2</sup> divided by 0.08 tracks/m<sup>2</sup>/day). The estimate for wildebeest is inflated because a herd passed through the area immediately before census. At the time of the census, the number of gazelle tracks was more representative of a small group passing through, (although gazelle were observed at other times to exhibit herding behavior in larger groups within the mapped area). Our observations suggest that dense trackway assemblages in the fossil record may occasionally form as a result of the movement through the track site of abnormally large concentrations of animals, whose numbers do not accurately re-

fect resident population sizes. However, for two species at a track site with equal mean densities over time, but where one species occurs sporadically (high variance in numbers of individuals, as with the wildebeest) and one occurs continuously, the preservation of tracks of the low variance species will be favored. Assuming that the probability of preservation of the track surface at any given time is either equal or varies stochastically, then fossil track counts from two such species are likely to suggest that the continuously resident (low variance) species is more abundant.

Since the state of tracks on the ground is constantly deteriorating, the number of days needed to accumulate tracks can be considered a turnover rate and also an indirect estimate of survivorship. For gazelle for example, we have previously estimated mean track survivorship to be 9 days, but we don't yet have a good estimate of the variance around this mean (Cohen et al. 1991); that would require long-term studies that account for variables such as frequency of herding behavior, average herd size, lake level, and weather. However, survivorship of Alkaline Flats tracks is normally expressed in days (Cohen et al. 1991). As figure 5 illustrates, track deterioration is often related to specific physical events (in this case, periodic seiche surges that wash away the tracks). Burial and preservation of the figure 5 trackway plot on any given day would result in an extremely short-term view of the faunal composition of this site.

**Relative Abundance of Trackways—Mapping Method.**—We mapped a total of 215 recognizable mammalian trackway segments at the Alkaline Flats site (fig. 6). Of these, 205 (95%) were herbivore (ungulate) trackways and 11 (5%) were carnivore trackways. The proportion of carnivore trackways is considerably higher than the number of carnivores tallied in the censuses (<1%), which probably reflects both a higher proportion of carnivore activity at night and higher activity levels among carnivores than herbivores.

**Relative Abundance of Trackways—Transect and Subplot Methods.**—We estimated the relative abundance of mammalian trackmakers

from cumulative daily counts of new trackways that crossed the E-W and N-S transect lines at the Alkaline Flats and Hippo Pool sites (fig. 7). These relative abundances provided census data (comparable to that obtained from the Alkaline Flats site map, see below), which could be used to assess the usefulness of transect censuses at fossil footprint sites.

Both of the Alkaline Flats transect censuses resulted in identical rank abundances of Thomson's gazelle, wildebeest, and hippopotamus. Jackals were the only other mammalian trackmaker recorded. Hippos were better represented on the lake-parallel transect and less presented on the lake-perpendicular transect, possibly reflecting their normal night-time grazing pattern parallel to the shoreline.

At the Hippo Pool site, hippopotamus trackways dominated in similar proportions on both the E-W and N-S transect lines. Wildebeest and buffalo trackways made up the remainder of the ungulate track census with additional records for carnivores (mongoose, jackal, and hyena). Rank-order correlation between the E-W and N-S transects was not significant ( $p > 0.05$ ), primarily because of a greater representation of buffalo tracks and fewer mongoose tracks on the E-W transect. The former may be attributable to a greater frequency of buffalo movement across, rather than parallel to, the Mbu River, following the primary game corridor in the area.

The E-W and N-S transect data from each site were largely consistent in their relative abundance estimates. Minor differences, such as the decreased number of hippopotamus trackways at the Alkaline Flats site, may have resulted from the fact that the shorter N-S transect line did not extend into the zone of dense hippo tracks. Similarly, at the Hippo Pool site, the N-S transect line was shorter than the E-W line and it extended into the zone where most of the small carnivore tracks were recorded. This accounted for the smaller sample size and the higher proportion of recorded carnivore trackways.

We compared the relative abundance of trackways recorded by the cumulative mapping and by the cumulative transect census

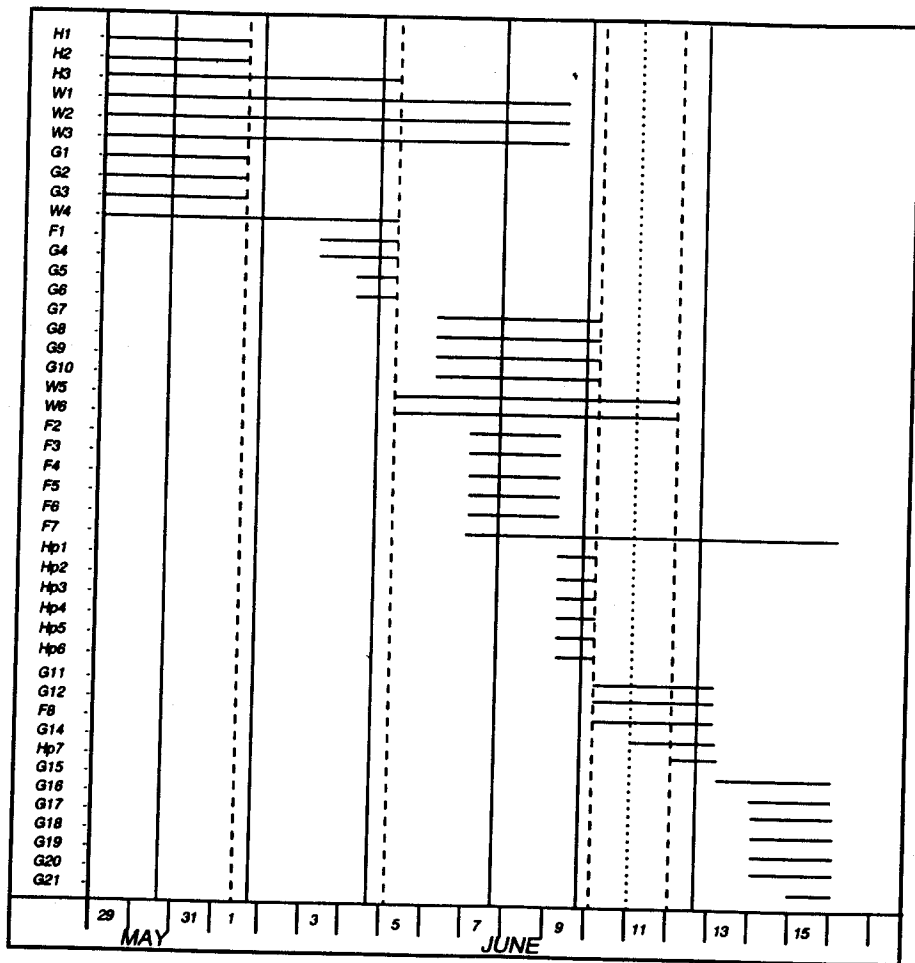


FIGURE 5. Duration of tracks on the  $10 \times 10$  m<sup>2</sup> trackway plot. The broken vertical line was a weak event that did not completely erase tracks: it simply made them considerably fainter. H, hyena; W, wildebeest; G, gazelle; F, fishermen; Hp, hippopotamus.

methods at the Alkaline Flats site. The cumulative mapping census data (fig. 6) indicate a higher proportion of wildebeest trackways but this is explained in part by the longer monitoring period. Early in the mapping period a herd of 165 wildebeest crossed the area. Both census methods indicate that wildebeest, Thomson's gazelle, and hippopotamus were the three dominant ungulates and that

carnivores represented a small proportion of the trackmakers.

**Trackway Orientations—Mapping Method.**—Orientations for wildebeest, hippopotamus, and Thomson's gazelle trackways from the Alkaline Flats site are illustrated in figures 8–10. Orientations of trackways of other less abundant or smaller species (zebra, buffalo, carnivores, and birds) are shown in figure 11,

but we excluded them from the statistical analysis because of small sample sizes.

Wildebeest trackways showed a strong preferred orientation towards the WNW, with a minor secondary trend in the opposite direction (ESE). This trend broadly parallels the shoreline and the Tarangire (Kwakuchinga) Game Corridor in the region of the site. It is clear from the trackway map (fig. 8) that wildebeest trackways frequently occur in parallel or subparallel groups, reflecting commonly observed gregarious behavior during progression. Trackways were mainly straight or slightly curved away from the lake to continue along the Tarangire Corridor.

Hippopotamus trackways indicate a predominant E–W bimodal trend, but there is notable evidence of movement in other directions also (fig. 9). Many hippo trackways are sinuous or meandering, so we determined orientations as the mean bearing between the beginning and end of an observed trackway segment. Among hippo trackways, there are few parallel or subparallel groupings indicative of group travel. The orientation patterns again appear to indicate shore-parallel movement, modified by individual movement that is more variable than for wildebeest. Such trends probably reflect browsing behavior in the site area.

Thomson's gazelle trackways have a N–S bimodal trend (fig. 10), with movement in several other directions. There are few trackways in the sparsely vegetated eastern half of the Alkaline Flats site. Therefore, the rose diagram largely reflects recognizable trackway orientations in the western half of the site.

Our trackway orientation data mirror our prior knowledge about the behavior and habitat preferences for the major trackmakers. This provides strong support for the idea that valuable paleobiological information can be gleaned from analyzing fossil trackway orientations relative to each other and to paleoenvironmental gradients.

**Bird Track Site Census and Track Observations.**—Bird census data are presented in table 4. We recorded 25 species of birds in the study plot over a 23-day period. Some species, such

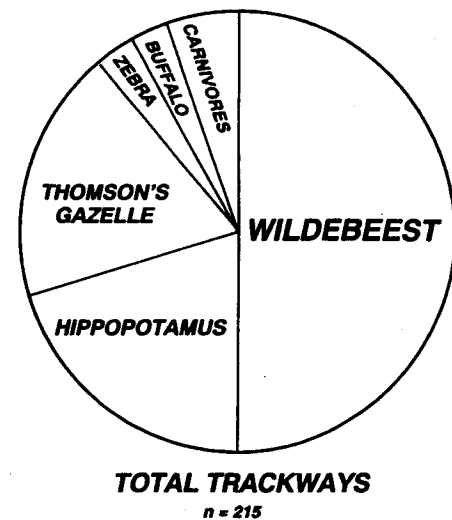


FIGURE 6. Total number of trackways counted on the Alkaline Flats site. Species proportions are as follows (in order of decreasing relative abundance): wildebeest, 49.5%; hippopotamus, 20.8%; Thomson's gazelle, 19.0%; zebra, 2.8%; buffalo, 2.8%; all carnivores, 5.2% (includes hyena, 1.9%; jackal, 1.9%; mongoose, 0.9%; lion, 0.5%).

as *Charadrius pecuarius* (Kittlitz's plover) are abundant at all times of the day. Others, such as *Calidris minuta* (little stint) and *Tringa glareola* (wood sandpiper), leave the area in the later afternoon and return to it the following morning.

Six species of birds (fig. 12) were sufficiently common during all time intervals to establish complete activity budgets. Mean activity rates (expressed as numbers of steps per minute) had extremely high variances, because during any 2-minute observation period most birds were either resting (0 steps/minute) or continuously active. Activity budgets for all common bird species showed a maximum of walking/running activity during the early morning, with a rapid dropoff toward midday. Some species (*Calidris minuta* and *Himantopus himantopus* [the black-winged stilt]) became progressively more inactive in the later afternoon, whereas others (e.g., *Charadrius pecuarius* and *Alpochen aegyptica* [the Egyptian goose]) displayed a slight increase in activity

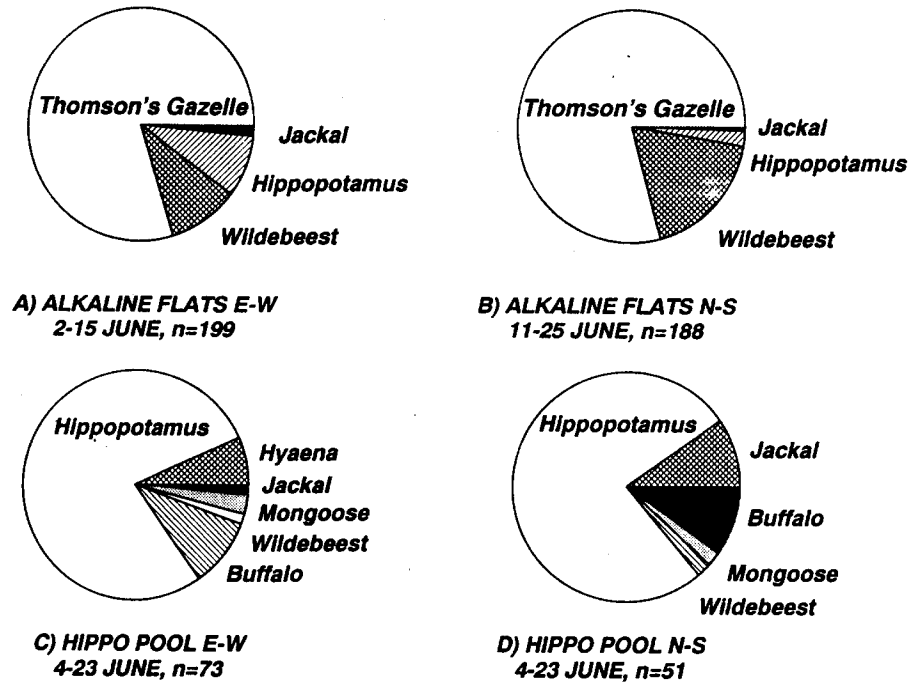


FIGURE 7. Cumulative daily trackway counts for Alkaline Flats and Hippo Pool sites, E-W and N-S transects. In order of decreasing relative abundances the values are: A. Alkaline Flats, E-W. Thomson's Gazelle, 79.9%; wildebeest, 10%; hippopotamus, 8.5%; jackal, 1.5%. B. Alkaline Flats, N-S. Thomson's Gazelle, 79.3%; wildebeest, 18.1%; hippopotamus, 2.1%; jackal, 0.5%. C. Hippo Pool, E-W. Hippopotamus, 78%; buffalo, 9.6%; wildebeest, 6.8%; mongoose, 2.7%; jackal, 1.4%; hyena, 1.4%. D. Hippo Pool, N-S. Hippopotamus, 76%; wildebeest, 9.8%; mongoose, 9.8%; buffalo, 2%; jackal, 2%.

in late afternoon, as the air temperature cooled.

The number of footsteps ( $F$ ) taken by all the individuals of a bird species per day on the study plot is equivalent to the mean number of individuals present ( $n$ ) over the course of the day multiplied by their mean activity rate ( $r$  = footsteps per unit time) over the same period, multiplied by the duration of activity ( $t$ ), as shown in equation (1):

$$F = nrt. \quad (1)$$

$F$  also represents the theoretical maximum number of tracks produced per day by these birds over their entire activity range. The actual production of tracks ( $P$ ) will then be a function of  $F$  times some probability of preservation ( $k$ ) that is dependent upon the na-

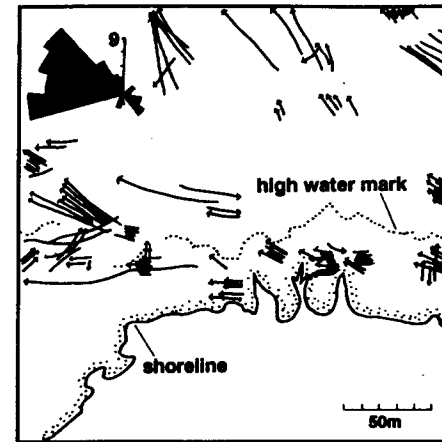
ture of the substrate/organism interaction, given in equation (2):

$$P = kF. \quad (2)$$

Track production per unit area ( $E$ ) by the same species will then be determined by  $P$  as well as the animal's stride length ( $l$ ) as in equation (3):

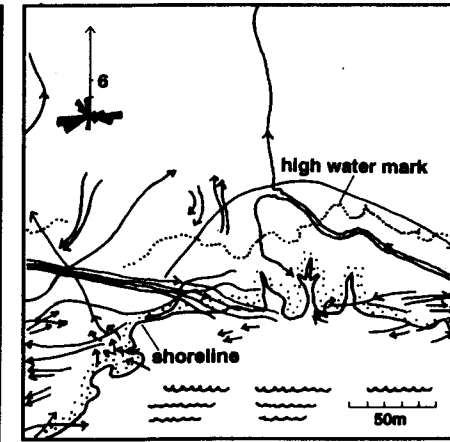
$$E = kP/l^2. \quad (3)$$

In practice  $P$  cannot be calculated directly, since one cannot collect activity and census data continuously. However, an estimator of  $P$ , determined as a summation of mean activity rate measured over representative time intervals multiplied by mean numbers of individuals present during a representative series of time intervals, may provide an ade-



TOTAL WILDEBEEST TRACKWAYS

FIGURE 8. Recognizable wildebeest trackways and trackway orientations at the Alkaline Flats site produced during study interval. The scale bar refers to the number of measured trackways.



TOTAL HIPPOPOTAMUS TRACKWAYS

FIGURE 9. Recognizable hippopotamus trackways and trackway orientations at the Alkaline Flats site produced during study interval.

quate substitute, assuming that the rates and numbers of individuals present does not vary greatly during each summed interval. This is given in the equation

$$P = \Sigma(\bar{r}^* \bar{n}). \quad (4)$$

For the data collection methods used in this study then,

$$P = \Sigma_i(\bar{r}^* \bar{n}) * 120, \quad (5)$$

where  $\Sigma_i$  is the summation of 2-hour time periods 1-6 comprising the daylight activity hours (e.g., 6:00-8:00 A.M., 8:00-10:00 A.M.),  $\bar{r}$  is the mean stride rate per minute for animals of the species during that time of day and  $\bar{n}$  the mean abundance in the study area of that species at that time of day. Then

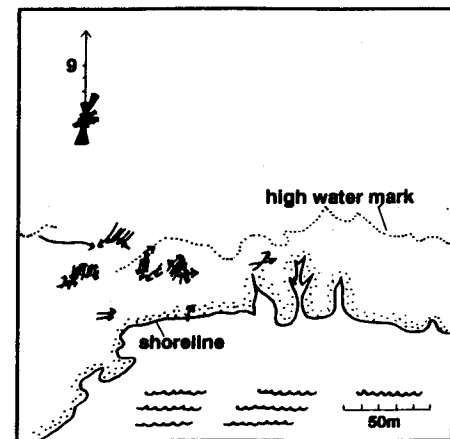
$$E = k \Sigma_i(\bar{r}^* \bar{n}) / l^2. \quad (6)$$

If individual tracks could be unambiguously associated with their trackmakers, we could test this model directly against an observed set of tracks produced in the same area. Unfortunately, as mentioned earlier, some species of birds produce tracks which are essentially indistinguishable. Therefore, to test a censusing model of track production we

must combine species which produce virtually identical tracks into species groups.

$$E = k \Sigma_i ( (\Sigma_j (\bar{r}^* \bar{n}_j)) / l^2, \quad (7)$$

where  $\Sigma_j$  is the summation of all summed track



TOTAL THOMSON'S GAZELLE TRACKWAYS

FIGURE 10. Recognizable Thomson's gazelle trackways and trackway orientations at the Alkaline Flats site produced during study interval.



TABLE 4. Census data for species observed at the Bird Track site. Values given are the mean numbers of individuals of each species observed during all censuses made for each two-hour time period, during the interval June 21, 1989-July 5, 1989. Many of the species are organized by "species groups." A species group is a cluster of species, all of which produce tracks that cannot be differentiated. The term has no taxonomic significance.

Species	Observational interval							Grand total or mean (SD)
	6:00-8:00 A.M. (12)	8:00-10:00 A.M. (19)	10:00-12:00 A.M. (14)	12:00-2:00 P.M. (21)	2:00-4:00 P.M. (19)	4:00-6:00 P.M. (16)		
<b>Small plovers/sandpipers</b>								
Little stint, <i>Calidris minuta</i>	2.3	6.0	5.4	10.1	9.9	9.3	7.6	
Kittlitz's plover, <i>Charadrius pecuarius</i>	8.3	5	8.1	7.8	9.6	6.8	7.5	
Wood sandpiper, <i>Tringa glareola</i>	0.0	2.1	3.5	7.7	2.5	0.3	3.2	
Chestnut-banded plover, <i>Charadrius tenuis</i>	0.3	0.5	0.4	0.2	0.6	0.2	0.4	
Three-banded plover, <i>Charadrius tricollaris</i>	0.0	0.1	0.0	0.0	0.1	0.0	0.0	
Ducks/teals								
Cape teal, <i>Anas capensis</i>	2.3	0.9	0.2	0.4	1.7	1.8	1.2	
Red-billed duck, <i>Anas erythrorhynchos</i>	0.3	0.8	1.0	1.3	0.3	0.2	0.7	
Hottentot teal, <i>Anas hottentota</i>	0.0	0.0	0.9	0.1	0.7	1.0	0.4	
Fulvous tree duck, <i>Dendrocygna bicolor</i>	0.0	0.1	0.0	0.0	0.0	0.0	0.0	
Avocets/stilts								
Black-winged stilt, <i>Himantopus himantopus</i>	1.8	1.1	1.9	2.1	2.7	1.0	1.8	
Avocet, <i>Recurvirostra americana</i>	0.1	0.1	0.1	0.0	0.2	0.1	0.1	
<b>Other species (not lumped in species groups)</b>								
Egyptian goose, <i>Alpochen aegyptica</i>	4.7	2.1	0.6	4.0	4.0	1.9	2.9	
Blacksmith plover, <i>Vanellus armatus</i>	1.0	1.2	0.9	1.3	0.9	0.6	1.0	
Sacred ibis, <i>Threskiornis aethiopicus</i>	0.3	0.0	0.0	0.4	0.5	1.1	0.4	
White-winged black tern, <i>Chlidonias leucopetra</i>	0.0	0.1	1.6	0.1	0.0	0.1	0.3	
Pratincole, <i>Glareola pratincola</i>	0.0	0.0	0.2	0.3	0.3	0.1	0.2	
Grey-headed gull, <i>Larus cirrocephalus</i>	0.6	0.3	0.0	0.1	0.1	0.0	0.1	
Little egret, <i>Egretta garzetta</i>	0.0	0.0	0.0	0.4	0.3	0.0	0.1	
Black heron, <i>Egretta ardesiaca</i>	0.3	0.2	0.0	0.2	0.0	0.0	0.1	
Lesser flamingo, <i>Phoenicopterus minor</i>	0.0	0.0	0.0	0.1	0.3	0.0	0.1	
Spotted stone curlew, <i>Burhinus capensis</i>	0.0	0.0	0.4	0.0	0.2	0.0	0.1	
Painted snipe, <i>Rostratula benghalensis</i>	0.2	0.2	0.0	0.0	0.0	0.2	0.1	
Yellow-billed stork, <i>Ibis ibis</i>	0.0	0.0	0.1	0.0	0.0	0.3	0.0	
Rufous sparrow, <i>Pseudonigrita motientis</i>	0.1	0.1	0.0	0.0	0.0	0.0	0.0	
Glossy ibis, <i>Plegadis falcinellus</i>	0.0	0.0	0.0	0.1	0.1	0.0	0.0	

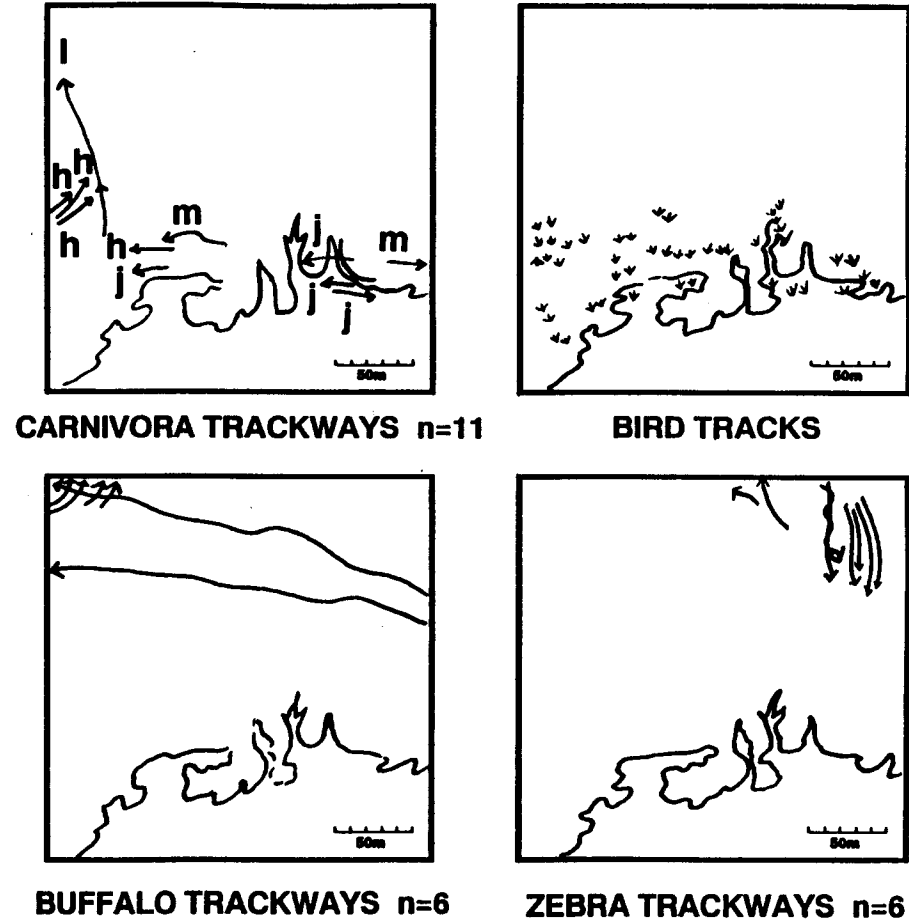


FIGURE 11. Recognizable trackways for other species. Carnivore symbols are h, hyena; l, lion; j, jackal; m, mongoose. Bird track production was not monitored continuously at the Alkaline Flats site and only representative trackways are shown, (all within environmental Zone 2).

productions by species  $i$ ,  $j$ , and  $k$  is a constant relating the production over the entire study area to the size of the track plot where tracks are actually counted. An expected percentage ( $E_A$ ) of the total number of tracks in the track plot then is simply

$$E_A(\%) = \frac{\sum_i (\sum_j (\bar{r}_j \cdot \bar{n}_j)) / P^2}{\sum_A (\sum_i (\sum_j (\bar{r}_j \cdot \bar{n}_j)) / P^2)} \quad (8)$$

where  $A \dots n$  represent all the species groups present. This value can be compared with the

observed proportions of tracks measured in the footprint plots.

Table 5 shows results of the cumulative footprint plot counts and their percentages. We tallied nine track types representing a minimum of six bird and three mammal species over the study period. All of the bird tracks observed were from species which were commonly seen on the study plot. We measured mean stride lengths for 15 trackways for each of three species (Kittlitz's plover, the

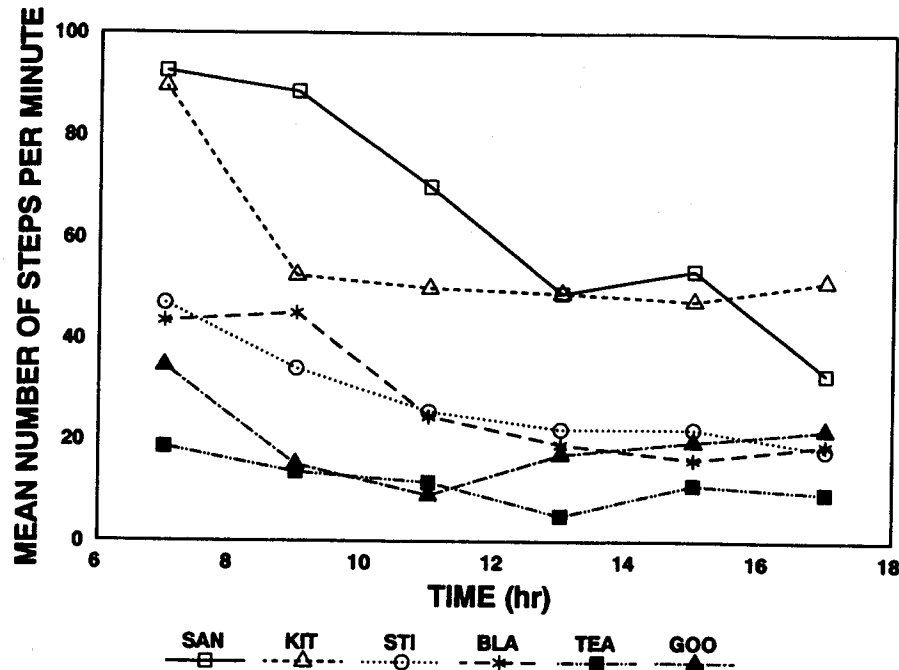


FIGURE 12. Activity budget summary for six species of common birds at the Bird Track site. SAN, Wood sandpiper; KIT, Kittlitz's plover; STI, Black-winged stilt; BLA, Blacksmith Plover; TEA, Cape Teal; GOO, Egyptian goose. The graph illustrates the mean number of steps taken per minute by individuals of each species for six 2-hour time intervals (e.g., 6:00-8:00 A.M., 8:00-10:00 A.M.) during daylight hours.

Egyptian goose and the Blacksmith plover). We estimated mean stride lengths of the remaining species by combining field observations with leg length from museum specimens.

Expected vs. observed percentages of tracks from five common species groups (small plovers

and sandpipers, ducks and teals, avocets and stilts, Egyptian geese, and Blacksmith plovers) and their rank orders are shown in table 6. These groups include all species that were abundant enough on the study plot to establish statistically meaningful activity budgets. The observed values in table 6 are

TABLE 5. Cumulative track counts from bird footprint plots at the Bird Track site. A total of 1532 tracks was counted during the study period of which 1486 were from birds.

Birds species "group"	Number of tracks	Total (%)	Total bird tracks (%)
Small plovers/sandpipers	1328	86.7	89.4
Blacksmith plover	76	5.0	5.1
Egyptian goose	30	2.0	2.0
Avocet/stilt	27	1.8	1.8
Ibis	13	0.8	0.9
Duck/teal	12	0.8	0.8
Mammals			
Black-backed jackal	26	1.7	—
Thomson's gazelle	17	1.1	—
Hippopotamus	3	0.2	—

TABLE 6. Bird Track site observed vs. expected track production data. Expected values are calculated using both data normalized for activity budget and stride length (Expected, #, %, and rank) and based on non-normalized raw census data (Expected-census only). Observed values are actual numbers of tracks counted on track plots.

Species "group"	Expected (#, %, rank)	Expected-census only (#, %, rank)	Observed (#, %, rank)
Small plovers	1305, 88.1, 1	1027, 65.82, 1	1328, 90.2, 1
Ducks/teals	79, 5.4, 2	127, 8.15, 3	12, 0.8, 5
Egyptian goose	46, 3.1, 3	160, 10.25, 2	30, 2.0, 3
Avocet/stilt	21, 1.4, 4	103, 6.59, 4	26, 1.8, 4
Blacksmith plover	21, 1.4, 4	55, 3.52, 5	76, 5.1, 2

the actual proportions of tracks produced by each species group. We derived the expected percentages from the previously discussed censusing model (eq. 8), using the census data from table 4, the activity budget data from figure 12 and measured mean stride lengths for members of each species group. We summed the expected percentages for all species within each species group to obtain the expected percentage for each group as a whole. We also calculated an alternative set of expected proportions of tracks using only the species proportion data derived from summations of the hourly census data for all birds within a species group (i.e., without correcting the bird census counts for activity patterns or stride length as is done in eq. 8). These alternative expected values are given in table 6 as "Expected-census only."

An initial examination of the observed and expected data shows that the model predicts the rank and frequency of the most common type of track, the small plover species group, relatively well. It also reasonably estimates the Egyptian goose and avocets/stilts groups. However, both the  $\chi^2$  ( $p < 0.001$ ) and rank-order correlation tests ( $p > 0.05$ ) show that the differences between expected and observed data are unlikely to be caused by chance alone. We observed behaviors that explain this result. The deviation between the expected and observed percentages and ordering of tracks results from the reversal in rank and proportion of the Blacksmith plover and duck/teal groups. Our model predicts that duck/teal tracks should rank second in track abundance (5.4%) based on their census counts, activity patterns, and stride lengths, and that Blacksmith plovers should rank last (tied with avocets/stilts). Observed track counts are just the reverse of this expectation.

Blacksmith plovers primarily forage and display in exposed or extremely shallow (water depth  $< 1$  cm) grassy areas. In contrast, the species of ducks and teals observed in our study area spent most of their time walking or wading in the open water areas of the shallow pond adjacent to the study plot. The footprint plot was located in a small exposed patch surrounded by grasses on the margin of the pond, ideal for plovers, but we could not flood areas near the footprint plot deeper than 1 cm, so the ducks were not drawn to that site. This produced an inherent but essentially unavoidable microhabitat bias between our footprint and study plots. At the end of the study we had hoped to collect footprint data from the activity plot after the lake level had dropped sufficiently to expose the plot's surface, thereby allowing us to count all of the tracks preserved in the precise area where activity rates and abundances were measured. Unfortunately, an unexpected brief lake surge (caused by a seiche) erased the footprints just before a final track census could be made.

Although our model does not account for the microhabitat-induced differences between observed and expected values, it does provide a more realistic explanation for the observed track proportions than a simple comparison of proportionate census data. Census data alone grossly underestimates the track frequency of small, highly active species, while overestimating the track frequency of larger, more slowly moving birds, such as the Egyptian goose. The  $\chi^2$  (goodness-of-fit) using the model which incorporates census, activity data, and stride length to derive expected values ( $\chi^2 = 208.05$ ) is considerably better than the goodness-of-fit for expected values derived from census data alone ( $\chi^2 = 363.42$ ). This shows that calculating original

animal abundance from fossil tracks by taking into consideration numbers of tracks as well as stride length and activity budget estimates will produce a better estimate than by using numbers of tracks alone. Track counts alone cannot be taken as proxy censuses of the relative proportions of species inhabiting a trackway. However, if we also have measures of microhabitat variation, activity, and stride length, we may be able to approximate original species abundances by accounting for the biases between trackmakers and track frequencies.

### Discussion

Paleobiologists have attempted to address three major ecological issues using fossil tracks and trackways (Thulborn 1990 and references therein):

1. How precisely can habitat usage patterns be inferred from fossil tracks?
2. How precisely can behavior be inferred from fossil tracks?
3. To what extent can fossil tracks be used in estimating abundances (either absolute or relative) of particular species?

Our Lake Manyara study provides insights into all three of these questions, and also allows us to begin asking important questions about the comparative utility of tracks vs. bones in paleoecological investigations.

### Habitat Usage

Three ecological attributes of animals determine the likelihood of track preservation: habitat usage, behavioral patterns, and abundance. Vertebrates can be categorized as to type of potential trackmaker based on their habitat usage with respect to a specific trackway site (table 7). Chronic trackmakers are present almost daily on the site, either singly or in groups. Such animals may be specific to a particular microhabitat within the track site or occur throughout the site. Sporadic trackmakers visit the site in small groups but are absent for several days at a time. Episodic trackmakers are those that visit the site in large numbers, again on an erratic but frequent basis. Habitat-specific trackmakers may occur frequently near the preservation site, but because of their preference for another

habitat, their tracks are seldom found on the preservation site. Rare trackmakers are those which occur very infrequently at the preservation site. Morphological characteristics of a potential trackmaker can also determine their probability of leaving a track record. For example, soft-footed trackmakers may be present on a track site on a daily basis but, because of their foot morphology and/or low weight, their tracks may fail to register deeply enough to form preservable tracks. Note that these categories are not mutually exclusive. The reduced probability of both habitat-specific and soft-footed animals leaving tracks automatically biases any census of a preservation site toward species in the other categories. Tracks of animals that readily cross depositional environmental boundaries are favored in the fossil record. Conversely, species which are "locally" abundant but which avoid commonly preserved depositional environments are likely to be excluded from the fossil track record. In our study, there were seven common mammal species that we observed as close as 200 m from the Alkaline Flat site, but which were never observed (nor their tracks recorded) on the study grid.

The classification of trackmakers is different for each habitat. For example, lake shore, savanna, and light woodland have different habitat-specific visitors. A small pond or stream in a dry habitat may record the tracks of species specific to the dry habitat (e.g., savanna) even though that species' tracks will not be detected in a nearby mud flat lacking vegetation or cover. This was certainly true at Lake Manyara for the habitat-specific trackmakers: warthogs, impala, baboon, vervet monkeys, and waterbuck. These species would be chronic trackmakers along a savanna game trail, but not in the expanse of mud flats adjacent to their habitat. The fossil track record is almost certainly biased toward common species that are chronic to depositional environments with high preservation probability.

The lake margin at Lake Manyara displays a strong shoreline-normal environmental zonation, which regulates animal distribution patterns, initial trackway formation, and subsequent preservation (Cohen et al. 1991). This

TABLE 7. Classification of mammalian trackmakers reflecting their habitat usage at a specific preservation site and morphology. Examples are from field work at the Alkaline Flats site located in the greater Lake Manyara region. All species mentioned were observed within 5 km of the study sites.

Category	Examples
Chronic (typically on-site)	Gazelle
Sporadic (typically on-site)	Wildebeest, hippopotamus, buffalo, mongoose, jackal, hyena, lion
Episodic (typically on-site)	Wildebeest, zebra
Habitat-specific (typically off-site)	Warthog, impala, baboon, other monkeys, waterbuck
Rare (typically off-site)	Giraffe, elephant
Soft footed (on or off site)	Hare

zonation is not static, as boundaries migrate seasonally with lake level fluctuations. Zonation is most evident at the Alkaline Flats site which, by virtue of its size, encompasses the largest intrasite variation. The Alkaline Flats site was strongly differentiated into three environmental zones, in terms of track type and recognizable trackway patterns (fig. 2):

Zone 1. A landward zone of relatively dry sediments, where the track record is dominated by large ungulates.

Zone 2. A strandline zone where sediment is saturated, and tracks of smaller birds and mammals are abundant in addition to tracks of larger mammals.

Zone 3. A subaqueous zone where, because of water depth and liquefaction processes, smaller animals are either excluded or their tracks are erased, and the track record is again dominated by larger mammals.

Shoreline position exerts a stronger influence on the distribution of animal activity than any other environmental factor. The trackway distribution patterns we noted cannot be attributed solely to differential preservation biases. Some ungulates, like the Thomson's gazelle, appeared to range freely across all three zones, whereas the semi-aquatic hippopotamus ranged mainly in Zones 2 and 3. 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. Some smaller terrestrial mammals (e.g., baboons and warthogs) confined themselves to the landward side of Zone 1 and never left recognizable tracks in the study area. Our detailed studies at the Bird Site (where the same environmental zones exist) showed that foraging patterns for many species of small animals (particularly birds) are

tightly constrained, even within our zonal categories. Many common bird species of Zone 2 and Zone 3 (e.g., flamingoes) were never seen in Zone 1 even though the distances separating zones are only tens of meters. Other species, such as the Blacksmith plover, were found over a much wider range of habitats. For animals with restricted environmental preferences, track abundance patterns are tightly linked to microhabitat differences, often at levels of resolution even finer than our three environmental zones. Minor differences in both water depth (e.g., 1 vs. 2 cm depth) or percentage of dry land regulate the foraging patterns of many bird species (and therefore their track distribution patterns), particularly on the diffuse land-water ecotone that commonly occurs on the margins of saline lakes. Because minor water-depth differences have a particular impact on a smaller bird's ability to forage, the smaller species are, as a group, more localized by these spatial differences than larger species. Birds of all sizes with specialized foraging requirements are also limited in the same fashion. This suggests that track distribution patterns at the lake margin for smaller and more feeding-specialized bird species may be more patchy than for larger species and those with more catholic feeding habits.

These results have two major implications for the fossil record. First, ichnofacies can be characterized by trackways that are environment-specific. Such ichnofacies can be used to identify the position of fossil track formation with respect to shoreline. Second, these results show the difficulty of interpreting fossil abundances for habitat-specific species. Among smaller bird and mammal tracks, for example, only those formed by species

inhabiting Zone 2 are likely to fossilize. Conversely, very large animals appear to be less sensitive to these microhabitat differences. Their tracks are less likely to be restricted to narrow environmental zones, and abundance patterns inferred from their fossil tracks are probably more useful than those of smaller animals. This sensitivity has already been recognized by Scrivner and Bottjer (1986) in their analysis of Cenozoic bird tracks from Death Valley. Paleobiologists studying fossil tracks should recognize that if bird tracks are employed to estimate relative abundances of species, such estimates will likely provide censuses only of localized habitat usage rather than of regional abundance. Individual bird species, being mostly small and habitat-restricted, are always unlikely to leave behind fossil tracks, except under exceptional circumstances of preservation. Conversely, the tracks of larger mammals (or dinosaurs), with habitat requirements at a different scale may provide a less localized picture of abundance ratios.

#### Behavioral Patterns

For on-site trackmakers, behavioral patterns (movements and activities) also determine trackway abundance, location, and preservation potential. Movement patterns strongly influence the formation of trackways. Track orientations at Lake Manyara are bimodal, most being either shore-parallel or shore-perpendicular. Several species showed shore-parallel movement both near (Zone 2) and far (Zone 3) from the shoreline. Near-shoreline species, such as the hippopotamus, tend to move in the water or just above the water line near the strand line. Because this zone is very wet, tracks readily register.

Shore-parallel trackways were produced by migratory mammals moving from one area to another. The Tarangire-Kwa Kuchinga Game Corridor runs southeast to northwest along the east side of Lake Manyara from Tarangire National Park to the greater Serengeti region. Giraffe and wildebeest were observed traveling through the corridor landward of Lake Manyara. However, giraffe did not come close enough to the lake to leave tracks on the study site. Different grid or transect orientations are

needed to detect directional movement patterns (see "Abundance" below). Censuses derived from exposed fossil trackways will be negatively biased by directional movement patterns relative to milling movement patterns. Determining the location of water bodies or even migration routes is important in identifying such biases.

Less frequently, animals moved perpendicular to the shoreline. We recorded trackways from zebra making infrequent visits to the lake. On another occasion we recorded tracks of a hippopotamus that lost a territorial battle on our grid and retreated to the forest. Shore-perpendicular movements might result from animals coming to drink, although this is unlikely at Lake Manyara because the lake is highly saline. This highlights the important differences likely between the fossil track record of saline vs. freshwater lake margins. Animals will approach the margin of a lake to drink, forage, or pass by (or, in the case of carnivores, to hunt herbivores doing any of the above). As a lake becomes progressively more saline, first drinking and then herbivorous foraging are eliminated as options. The fossil track record of saline-hyper-saline lake margins is therefore likely to be dominated by migratory animals and benthos/plankton-feeding waders.

Mammals exhibited two patterns of movement: directional and milling. Travel across the site is directional movement. This makes long, linear trackways. Milling patterns are harder to decipher because they turn back and recross themselves many times. Milling was associated with bedding sites, scent and scat marking stations, and feeding at patches of vegetation. Tracks left by large milling animals greatly inflate estimates of animal abundance. Censuses of fossil trackways should avoid counts of randomly oriented tracks, which could have been made by milling animals.

Bird trackways cannot be readily interpreted in terms of directionality. Almost all bird movements that we observed were related to intraspecific interactions or feeding, and thus would be characterized by a milling type of trackway. Aggressive, territorial interaction between small to medium-sized

plowers and some feeding paths by geese or larger wading birds may produce trackways with some sense of directionality. However, these rarely exceed 10–20 meters in length before a change in direction or flight.

#### Abundance

To what extent are track or trackway counts proxy censuses of species abundance? Most animals that were common on the track sites were also well represented by tracks. However, as we have shown, track counts can be heavily biased by habitat uses and behavioral patterns. Before paleobiologists attempt to use track counts to make statements about relative abundances of species, it is important to answer two related questions: (1) When are such counts justified?, and (2) What is the best method for estimating fossil track frequency for this purpose?

Track counts are justified when the intent of the investigator is to obtain a semi-quantitative picture of the proportions of organisms inhabiting the track site itself at the time of track production. Given the habitat-specificity problems and the short time duration sampled by tracks, it is probably not appropriate to extrapolate either spatially or temporally beyond the track site. Extrapolation of track data to a regional or broader temporal scale is only justifiable if multiple track sites from the area are available for study. Even when this is the case, the investigator must carefully consider the potential biases in the record caused by differences in preservation probability between environments, animal size, and foot characteristics.

Once a decision to census fossil tracks has been made, a censusing method must be chosen. Transect and mapping methods produce somewhat different pictures of the mammal fauna. The transect method proved to be sensitive to directional movements. Transects perpendicular to the shoreline detected trackways running parallel to the shoreline but missed those running perpendicular to the shoreline. These transects also undercounted the number of hippopotamuses coming on shore because these excursions only ran short distances parallel to the shore. Transects parallel and close to the strandline detected most

on-shore movements of hippopotamuses, but missed the shore-parallel movements of buffalo entirely. The mapping method detected a larger proportion of the species present, but may be more biased in estimating relative species proportions, favoring more active species. The method should be determined by the objectives of the investigation. Where behavior and track-orientation data are paramount or time is limited, transects are preferable. Alternatively, one should map entire bedding planes when information about relative numbers of individuals is required. When abundance estimates must be made from fossils of animals that are invariably milling, they should be made on track counts rather than trackway counts and should incorporate activity and stride-length estimates. By incorporating measurements of stride length (obtained directly from the track surface) and estimates of activity (obtained by analogy with phylogenetically or morphologically similar organisms), semiquantitative (i.e., rank abundance) estimates of the proportions of species that produced the fossil tracks can be obtained.

Opportunities exist to apply both map area and transect methods of censusing to fossil track-bearing surfaces. However, while every track may be mapped on an area survey, many exposures simply are not extensive enough to provide a complete picture of the site. At Lake Manyara a track-bearing surface of approximately 1000 m<sup>2</sup> would be required to register 50% of the resident large-mammal fauna. Relatively few fossil track sites are this large. Note for instance the small area crossed by carnivores (Fig. 11). Often, small exposed areas are equivalent to transects. In attempting to apply either map or transect methods in marginal lacustrine, fluvial, or marine deposits, it is critical to determine the position of shoreline at the time of track formation to understand the relative orientation of a transect and the directional biases associated with it.

#### Time Averaging in the Fossil Track and Fossil Bone Records

Fossil track accumulations, like fossil bone accumulations, do not represent instantane-

TABLE 8. Estimates of mammalian community composition based on track records for six dates on the  $10 \times 10$  m ( $100 \text{ m}^2$ ) plot. Unidentifiable tracks produce an underestimate for a given date. Dates and individual counts by species correspond to figure 5. Number in parentheses after species names corresponds to the number of individuals observed crossing the grid.

Track types	Dates (1989)					
	5/30	6/1	6/4	6/7	6/9	6/12
Unidentifiable	0	2	2	5	0	5
Hyena (3)	3	1	1	0	0	0
Wildebeest (6)	4	4	4	5	2	0
Gazelle (21)	3	0	3	4	4	3
Humans (8)	0	0	1	6	1	2
Hippopotamus (7)	0	0	0	0	6	1
Underestimate*	0	29	22	25	0	55

\* Percent of numbers produced by unidentifiable tracks.

ous events. Track-bearing surfaces are cumulative pictures formed over some period in time, which varies by species and microhabitat. The record cannot be treated simply as a cumulative picture of populations because different turnover rates of trackways will bias both absolute and relative estimates of numbers of individuals. A long turnover time for a given track-bearing surface will tend to inflate abundance estimates but at the same time smooth out seasonal differences in track site use by different animals. To understand the magnitude of this effect, consider samples taken from the  $10 \text{ m} \times 10 \text{ m}$  subplot at eight points in time (table 8). Each of the eight estimates yields a different picture of the mammal community composition that might be preserved under rapid burial conditions. The persistent effect of long lasting wildebeest tracks is obvious, especially when compared to the short duration for gazelle tracks.

The degree of time averaging in a track assemblage is very short, measurable in days to weeks, rather than months to years as with most bones (Behrensmeier et al. 1979). Furthermore, since tracks normally cannot be transported, they are not spatially averaged at all (fig. 13). Where trackways cover enormous areas (megatracksites confined to single bedding planes and formed along broad transgressive surfaces, *sensu* Lockley 1991b), they provide a much broader spatial picture of a fauna and are formed over a much longer time interval than smaller sites, reflecting the

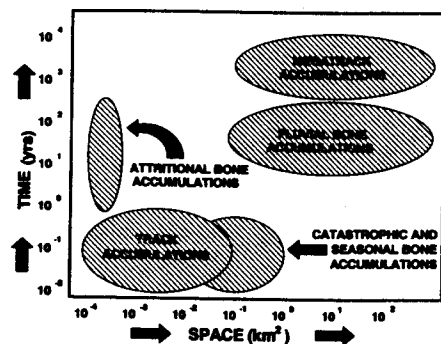


FIGURE 13. Model of time- and space-averaging of track and bone assemblages. Precise positions of the edges of the fields are unknown; the intention of the diagram is to present the approximate positions of each field and their relationship to each other.

diachroneity of the bedding plane over long distances (Lockley 1992; Lockley et al. 1992a). Fossil tracks and bones provide fundamentally different types of information about paleocommunities and it serves little purpose to compare them in terms of which provides a "better" picture of community composition. Fossil tracks are a precise record of a fauna and the behaviors of its component species over a very short time and limited to the immediate track site. In contrast, bones provide a more generalized picture of a community, which informs us about a wider range of organisms, including many living away from the burial site, but which cannot provide details of which species actually occupied the site. Ideally we want to incorporate both into a paleocommunity analysis but, unfortunately, tracks and bones from the same sites have rarely been studied together. In cases where both tracks and bones have been studied together (e.g., the Laetoli Beds of northern Tanzania [Leakey et al. 1976; Leakey and Hay 1979], the Koobi Fora Formation of northern Kenya [Laporte and Behrensmeier 1980], the Chinle Group of western North America [Lockley et al. 1992b,c] and see Schult and Farrow [1992] for a general review), the potential for interpreting fossil community structure is greatly enhanced. In such circumstances behavioral data (derived from tracks),

local and regional faunal data (derived from tracks and bones), and environmental data (derived from the encasing sediments) can be combined to provide a much more complete picture of how members of a fossil community associated with each other and over what spatial scales such associations occurred. For example, Lockley et al. (1992c) recently demonstrated from trackways that prosauropods were a significant component of Lake Triassic communities in western North America, despite the fact that prosauropods had not been documented previously as body fossils from these same strata. Similarly, Schult and Farrow (1992) have shown that for smaller vertebrates, combining track and bone assemblage data produces a much more complete picture of the Laetoli Formation fauna than either data set produces alone.

### Conclusions

Our study of modern tracks and trackways at Lake Manyara demonstrates the rich variety of paleobiological information potentially extractable from tracks. We have delimited the types of information that can and can't be reasonably inferred from fossil tracks. Fossil track sites faithfully reflect the chronic fauna of the track site, but are much less reliable indicators of habitat-specific elements of the fauna. The utility of paleocommunity inferences derived from trackway sites is directly related to the outcrop area covered by the site. Small sites ( $<10^3 \text{ m}^2$ ) are unlikely to provide a very complete picture of the local fauna. The faithfulness of the fossil track record to the local fauna will also be highly dependent on the habitat complexity around the environment of deposition and the degree to which elements of that complexity are preserved in the deposit. In contrast, large ( $>10^4 \text{ m}^2$ ) fossil trackway sites can provide detailed information on animal behavior and precise habitat inferences from ichnofacies analysis. If one has prior knowledge of behavior, one can calculate qualitative or even semiquantitative estimates of relative proportions of common animal species from their tracks.

Track records are fundamentally different from bone records. A synthesis of the two types of analysis could lead to important new

understandings of trophic structure among dinosaurs or behavior in early mammals. Achieving this synthesis will require a clear understanding of both the strengths and limitations of these two types of data. Our study identifies these possibilities for tracks in a single depositional system but did not address the preservation of bones from this same site. Future investigations should address the complementarity of bone and track records in other settings where tracks are likely to be preserved.

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