

ANTHROPOLOGY

Footprints preserve terminal Pleistocene hunt? Human-sloth interactions in North America

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Predator-prey interactions revealed by vertebrate trace fossils are extremely rare. We present footprint evidence from White Sands National Monument in New Mexico for the association of sloth and human trackways. Geologically, the sloth and human trackways were made contemporaneously, and the sloth trackways show evidence of evasion and defensive behavior when associated with human tracks. Behavioral inferences from these trackways indicate prey selection and suggest that humans were harassing, stalking, and/or hunting the now-extinct giant ground sloth in the terminal Pleistocene.

INTRODUCTION

Evidence of predation from vertebrate fossil tracks, whatever the age, is extremely rare (1, 2) and unknown for a human trackmaker. We present such an example from the terminal Pleistocene. Ichnofossils of extinct Rancholabrean fauna at White Sands National Monument (WHSA) in New Mexico comprise one of the largest concentrations of Cenozoic vertebrate tracks in North America (Fig. 1) (3). The tracks of interest here are visible only under specific moisture conditions (Fig. 2, A and B). As a consequence, we pioneered detection by aerial and geophysical survey, supplemented with excavation. These efforts revealed tracks and trackways of Proboscidea (mammoth), Folivora (ground sloth), Carnivore (canid and felid), and Artiodactyla (bovid and camelid). The tracks occur close to the surface of a playa (Alkali Flat) and are impressed into thinly bedded gypsiferous and siliciclastic muds and sands, which interdigitate laterally with organic-rich deposits (figs. S1 and S2). These sediments were deposited along the margins of Pleistocene Paleo-Lake Otero (4), located in the north-south trending Tularosa Basin. Wind erosion of the former lake floor excavated lacustrine and lake margin deposits to the level of the current playa and supplied sand to adjacent gypsum dunes (5). Here, we present the first well-documented co-association of unshod human tracks with those of extinct Pleistocene ground sloth in the Americas, and we infer behavioral implications from these contemporaneous tracks.

RESULTS

The study area (60,000 m²) is located on the western edge of Alkali Flat, adjacent to a 5-m escarpment that rises above the playa surface (Fig.

1 and fig. S1). The tracks appear in negative (depressed) relief and are infilled by reworked playa sediments. Deformation structures occur beneath most tracks (for example, small normal and listeric thrust faults, folds, boudins, diapirs, and fluid-escape fractures) and suggest variable substrate moisture conditions at the time of imprinting (fig. S2). Unlike modern tracks made on the playa, which erode quickly, the fossil tracks persist. Pore-water expulsion during compression, growth of gypsum cements, and the remains (in the form of salt and iron laminae) of algal mats all aid preservation (6).

The exact age of the track-making events remain unknown. Deposits enriched in organic detritus outcrop in the playa-margin escarpment, on the current playa surface, and below the surface exposed in the side-walls of tracks and shallow excavations. This sediment is frequently reworked into the material infilling the tracks, posing problems for dating. Radiocarbon dates for this organic sediment typically range from 20 to 33 thousand years (Ka) before present (BP) (dates are quoted uncalibrated, unless otherwise stated), and age profiles in shallow excavations show both vertical and lateral variability (fig. S2 and table S1). Sediments in the adjacent escarpment range from 33 to 10 Ka BP (fig. S1). The uppermost lacustrine beds of Paleo-Lake Otero have been dated to 15.56 Ka BP at two sites (4) and represent an approximate age for the commencement of deflation of Alkali Flat to the current level. Using summed radiocarbon dates for sloth extinction (7) and archaeological sites with established ages or time-diagnostic artifacts (8, 9), the density distribution overlap establishes a likely time for trackmaking (Fig. 3A). The most parsimonious interpretation of these data is that the tracks were made sometime before 10 Ka BP and after 15.56 Ka BP when the Paleo-Lake Otero lake bed began to erode (Fig. 3B). That period corresponds with a wetter climatic interval in the American Southwest (10) and coincides with the Clovis culture (11.05 to 10.8 Ka BP) (11), although most of the Paleoindian finds in the Tularosa Basin represent Folsom and more recent artifact styles (12).

The site consists of more than a hundred sloth and human tracks (figs. S3 to S9 and table S2). Sloth tracks are readily distinguished from human tracks based on their elongated kidney-shaped tracks and claw marks. Sloth tracks vary from 30 to 50 mm deep, 300 to 560 mm long, and 100 to 350 mm wide (13–15). The sloth tracks show evidence of eversion, consistent with biomechanics of the ground sloth (16). Mixtures analysis of the length of unexcavated sloth tracks ($L/W < 0.7$; $n = 251$; fig. S10) reveals three groups with means of 401, 492, and 595 mm,

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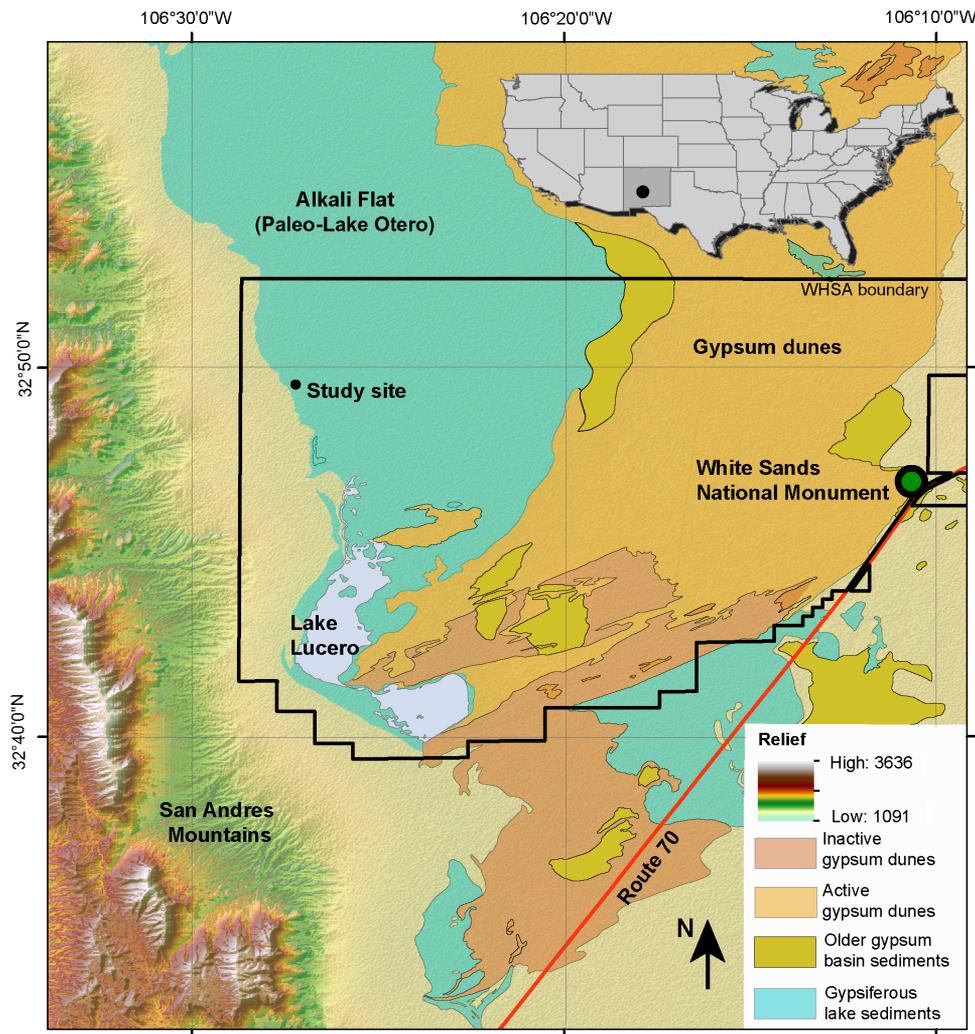


Fig. 1. Map showing WNSA, Alkali Flat, and the study site. Digital elevation model is from the Shuttle Radar Topography Mission 1-arc sec data with the surficial geology taken from U.S. Geographical Survey maps.

suggesting several individuals of varying age or sex, if sexual dimorphism existed. Although Megalonychidae (*Megalonyx*), Nothrotheriidae (*Nothrotheriops*), and Mylodontidae (*Paramylodon*) occur in New Mexico, only the latter two genera are known from late Pleistocene faunas. Both *Nothrotheriops* and *Paramylodon* have been identified from bone fossils in the vicinity of Paleo-Lake Otero. Although insufficient ground sloth track data exist to identify the taxon of the trackmaker, both genera have a pedolateral foot, which would produce a shape similar to the WNSA tracks (17).

Barefoot human tracks at WNSA are typical in morphology to those associated with soft, compliant substrates (Fig. 2, D and F to H) (18, 19). Foot length analysis of both excavated and unexcavated human tracks suggests multiple individuals of varying age or sex (fig. S10 and table S2). A number of human footprints (>10) are superimposed into sloth tracks. The human footprints share the same long-axis orientation and occur inside the sloth track outline, indicating that the human trackmaker was walking intentionally within the sloth track. These steps required the person to adjust her/his normal stride to accommodate the longer stride of the sloth, which typically showed tracks spaced 0.8 and 1.1 m apart. Two superimposed sets of deformation and fluid-escape

structures exist (fig. S2): The initial set associated with the sloth track and the subsequent deformation structures from the human heel strike. Similar pore-water conditions existed during both track-making events. No expulsion of sediment or ponded water (that is, ejecta or wash/scour structures) resulted from the human foot strike, and little or no sediment lies between the two plantar surfaces. This relationship suggests that the sloth tracks remained unfilled, either by water or by sediment, when the human followed.

The sloth trackways show several circular (and elliptical) track patterns that have never been reported (Fig. 2C and figs. S3 and S11). They consist of one or more deformed pes tracks surrounded by a circle of irregular impressions, which show evidence of manus claw marks (Fig. 2I). The manus impressions are distinctive, 120 to 140 mm long, with pointed termini at both the distal and proximal ends, showing evidence of one or more claw scrapes (figs. S8L and S9, A, D, and F). The pes impressions at the center of these circular patterns are irregular and in some cases circular (figs. S8J and S9E), and they appear to represent heel or pivot traces (fig. S13). In one case, a line of human toe impressions leads to the circle center, suggesting that someone approached on raised toes (fig. S11). In another, an adult human track occurs in the middle of



Fig. 2. Trackways and prints at WHSA. (A and B) Unexcavated sloth track. The track outlines are only visible during specific moisture conditions. (C) Flailing circle made by a sloth reaching forward with its forelimbs and leaving knuckle and claw impressions. (D) Human unshod right foot, unexcavated, and 30 mm below current surface. (E) Superimposed human and sloth track. (F to H) Unshod human feet. (I) Sloth pes track. (J and K) Human tracks superimposed in sloth tracks, indicating contemporaneity. (L and M) Manus claw impression of a sloth.

one circle (fig. S11). These structures occur both independently and in association with overlapped human-sloth trackways. Sloth trackways show sharp changes in the direction of travel. These inflections are associated with concentrations of human tracks (fig. S3). In the

absence of human tracks, sloth trackways progress in a straight or curvilinear fashion. Measures of tortuosity (20) confirm this (fig. S12).

We have evidence for: (i) sloth and human tracks in close spatial association, (ii) superimposed human and sloth tracks with geological

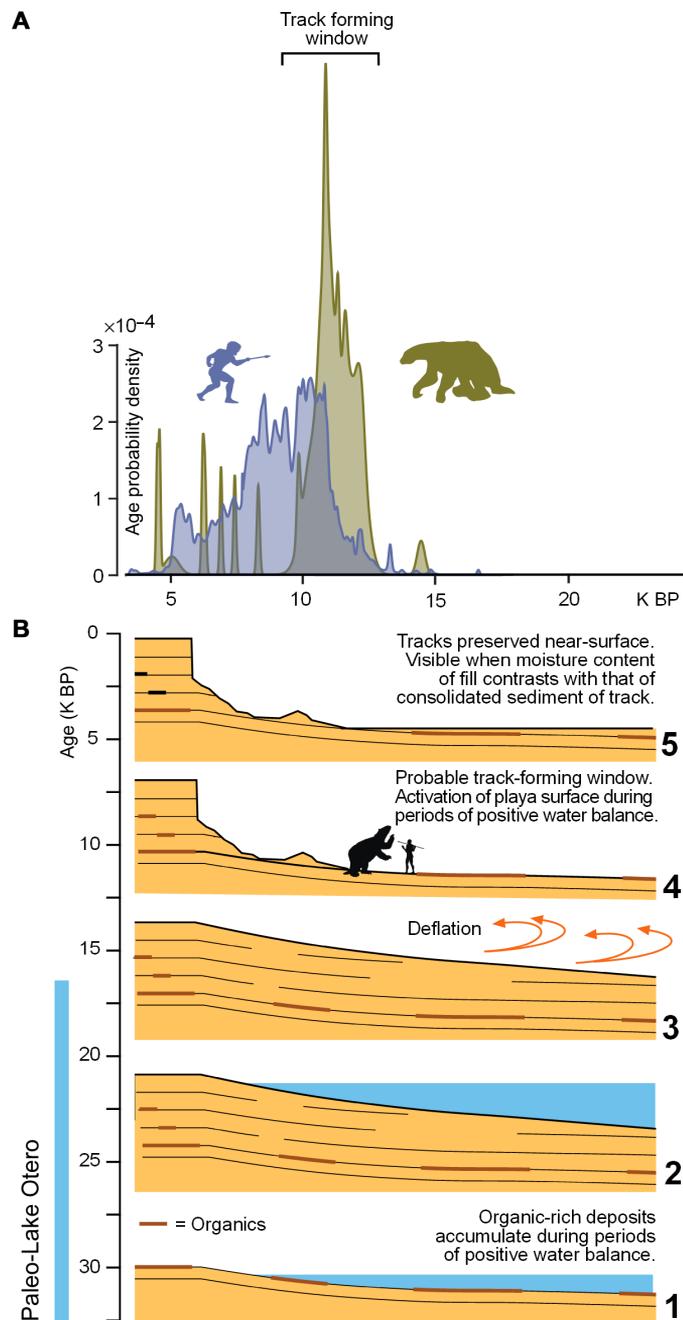


Fig. 3. WSHA chronology. (A) Summed probability density curves for extinction dates for ground sloth (8) and dates of human occupations in Southwestern United States (9, 10). Track creation probably occurred in the overlap. (B) Sequence of events on Alkali Flat.

evidence that suggests temporal association, (iii) increased sloth trackway tortuosity related to the presence of human tracks, and (iv) unusual circular sloth trackways. The challenge at any track site is to demonstrate contemporaneity of the ichnites. There are two key tests for contemporaneity (21): (i) Geologically, tracks must crosscut and be superimposed with no evidence of a temporal break, and the associated sedimentological conditions should remain constant for both track-forming events; and (ii) if animals were on the landscape at the same moment, then their tracks should show interaction. The evidence meets both tests. The sloth

tracks were open and unfilled with water and/or sediment when the human trackmaker followed, and the alignment was perfect. Pore-water conditions demonstrate constancy during both track-forming episodes, evidenced by the deformation structures present. In terms of the second test, the tortuosity of sloth trackways increases when human tracks are present, with sharp direction changes that suggest evasion (21). In addition, the circular sloth trackways are consistent with defensive behaviors in which sloths reared on their hindlimbs, freeing their forelimbs for defense. We termed these structures “flailing circles.” To be clear, the human-sloth interactions are not limited to one sloth trackway (or track size) but to several. It is, however, difficult to say definitively whether the sloths were traveling as a group and therefore were being collectively harassed or whether these features represent successive harassment events. The co-location of these trackways favors the former, in which case the results have implications for the social behavior of sloths.

We argue that the tracks evidence temporal and spatial associations of sloths and humans and infer that humans actively stalked and/or harassed sloths, if not hunted them. The absence of a carcass is not surprising for several reasons. The vast majority of hunts by modern hunter-gatherers are unsuccessful (for example, 94% for Hadza) (22). Sloths are so densely muscled that an outright kill is unlikely. Even if the hunt had been successful and the animal had died in the study area, the wetting and drying cycles and high pH rapidly degrade bones; thus, preservation of bones in the terminal Pleistocene therefore remains improbable. In terms of alternative explanations, it is possible that the human trackmaker was simply stepping in the sloth footsteps to follow a preexisting path in soft terrain. We dismiss this interpretation because the step length results in a long and uncomfortable human stride. The estimated stature of the human trackmaker (1.4 m; Tracks TE-A-44, -45, and -46; table S2) yields a stride of 0.6 m, contrasted with the sloth stride of 0.8 to 1.1 m. It is possible that the behavior was playful, but human interactions with sloths are probably better interpreted in the context of stalking and/or hunting. Sloths would have been formidable prey. Their strong arms and sharp claws gave them a lethal reach and clear advantage in close-quarter encounters.

DISCUSSION

Reported here is the first well-documented association of human and sloth trackways in the Americas. Inference from the interaction of the two species suggests that these trackways provide evidence of humans harassing/stalking potentially lethal sloths (23) by choice, presumably in an attempt at predation (24). This conclusion is consistent with subsistence strategies used by hunter-gatherers throughout the Americas during the terminal Pleistocene. During a time of climate change, predation (successful or not) may have contributed to the sloth’s extinction in North America. The site is extraordinary in the ichnological record because it demonstrates a predator-prey interaction. Furthermore, although the tracks at WSHA and similar playa sites in North America are visible only at certain times, we believe that the high track density and spatial scale allow behavioral information to be revealed for the first time. This geological archive has the potential to revolutionize understanding of the behavioral ecology and interaction of humans and megafauna.

MATERIAL AND METHODS

In accordance with the Archaeological Resources Protection Act and Paleontological Resources Preservation Act, which empower the National Park Service (NPS) to omit disclosure of specific information

pertaining to the location of archeological and paleontological resources to help preserve them, the exact latitude and longitude of the sites reported here are withheld. Interested parties may apply to the NPS at WHSA for further details. The study area was selected for its concentration of what are known colloquially as “ghost tracks”; that is, tracks that are visible only under specific moisture conditions. The site was gridded into 5-m squares, and all tracks were mapped and measured. Shallow excavations were dug, and available sections were described (figs. S1 and S2). A camera elevated on a 5-m pole was used to create an orthorectified map in Esri ArcMap (fig. S3). Individual tracks were selected for excavation along some trackways and digitally captured via photogrammetry using DigTrace (www.digtrace.co.uk). Locations of the excavated tracks are shown in fig. S4, three-dimensional (3D) models of most of these tracks are presented in figs. S5 to S9, and track measurements and interpretations are given in table S2. Larger orthorectified mosaics and digital elevation models were created in Agisoft Pro (www.agisoft.com/). Because excavation was destructive, the excavated tracks were also cast in plaster; these casts are held by the NPS at WHSA. Radiocarbon and optically stimulated luminescence (OSL) dates are presented in table S1. The stratigraphy of the bluff adjacent to the track site is based on unpublished work conducted by B. Fenerty and V. Holliday at the University of Arizona (fig. S1).

The summed probability curves in Fig. 3A were generated in MATLAB using a Parzen density estimator function. Figure S12 shows the excavated and unexcavated track lengths subjected to a mixtures analysis to identify component populations. Using the paleontological software package PAST (25), the normality of the data was confirmed [$n = 328$, Shapiro-Wilk $W = 0.9498$, P (normal) < 0.001]. The Akaike information criterion (AIC) is calculated with a small-sample correction

$$AIC = 2k - 2\ln L + (2k(k+1))/(n-k-1) \quad (1)$$

where k is the number of parameters, n is the number of data points, and L is the likelihood of the model given the data. A minimum AIC value indicates the most likely number of groups the data represent. Individual data were assigned to groups with a maximum likelihood approach. Ten repetitions were calculated to ensure reliable identification of footprints into groups.

Making biometric inferences from tracks can be difficult (18). For stature, foot-length ratio based on Native Americans was used (26). That ratio was averaged across all tribes and both sexes (foot length as a percentage of stature, 14.9). Stature estimates were made for excavated tracks only. Age estimations for excavated human tracks were based on data from the UMTRI/CPSC Child Anthropometry Study (27). Excavated track lengths for human tracks showed a bimodal association, probably representing adolescents and adults (fig. S10). This age distribution may not, however, represent the actual population present. The unexcavated track measurements were evaluated; tracks with L/W ratios less than 0.7 were included, and tracks with lengths greater than 300 mm were excluded. Mixtures analysis reveals four components that suggest a greater age range (fig. S10).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/4/eaar7621/DC1>

fig. S1. Bluff section on the western edge of Alkali Flat adjacent to the study site.

fig. S2. Cross sections through tracks and geotrenches.

fig. S3. Map of part of the study site.

fig. S4. Map of excavated tracks in part of the study site.

fig. S5. Orthorectified mosaic of part of the study site.

fig. S6. 3D point cloud models of excavated human tracks.

fig. S7. 3D point cloud models of excavated tracks.

fig. S8. 3D point cloud models of excavated tracks.

fig. S9. 3D point cloud models of excavated tracks.

fig. S10. Size and age estimations for excavated and unexcavated elongated tracks at and in the vicinity of the study site.

fig. S11. (A) Orthorectified mosaic of part of the study site showing two “flailing circles” as well as sloth and human composite tracks. (B) Interpretation of trackway trajectories are based on ghost and excavated tracks.

fig. S12. Tortuosity of sloth tracks in presence/absence of human tracks.

table S1. Radiocarbon and OSL dates from WHSA.

table S2. Measurements and interpretations of excavated tracks at WHSA.

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D.B., V.T.H., B.F., B.D.A., D.W.L., and D.O. contributed insight into archeological context of the discoveries. M.R.B. and D.B. completed most of the analyses presented in the paper. D.A.R. and M.B. conceived and conducted the tortuosity analysis. H.G.M. provided insight into extinct sloth behavior, and S.C.R. provided insights into human hunting practice. P.W. and V.L.S. provided knowledge of vertebrate ichnology. All authors contributed to writing and critique of the paper. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors. 3D models of selected tracks are available on MorphoSource (morphosource.org).

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