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It's in the loop: shared sub-surface foot kinematics in birds and other dinosaurs shed light on a new dimension of fossil track diversity

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Abstract

The feet of ground-dwelling birds retain many features of their dinosaurian ancestry. Experiments with living species offer insights into the complex interplay among anatomy, kinematics, and substrate during the formation of Mesozoic footprints. However, a key aspect of the track-making process, sub-surface foot movement, is hindered by substrate opacity. Here, we use biplanar X-rays to image guineafowl walking through radiolucent substrates of different consistency (solid, dry granular, firm to semi-liquid muds). Despite substantial kinematic variation, the foot consistently moves in a looping pattern below ground. As the foot sinks and then withdraws, the claws of the three main toes create entry and exit paths in different locations. Sampling these paths at incremental horizons captures 2-D features just as fossil tracks do, allowing depth-based zones to be characterized by the presence and relative position of digit impressions. Examination of deep, penetrative tracks from the Early Jurassic confirms that bipeds had an equivalent looping response to soft substrates ~200 million years ago. Our integration of extant and extinct evidence demonstrates the influence of substrate properties on sinking depth and sub-surface foot motion, both of which are significant sources of track variation in the fossil record of dinosaurs.

1. Introduction

Fossil dinosaur tracks preserve unique evidence of locomotion in long-extinct species [1-4]. Rather than being perfect molds of static feet, track morphologies arise through the dynamic interplay of pedal anatomy, step kinematics, and substrate properties [5-10]. Ground-dwelling birds have proven to be excellent models for experimentally studying these interactions [11-19]. The functionally three-toed feet of many species closely resemble those of bipedal, non-avian dinosaurs [20-21], allowing the visible movements responsible for shallow tracks to be studied directly.

With each step, a dinosaur deformed not only the exposed air-sediment boundary, but a volume of substrate beneath [7,17,22-25]. Layered sediments, once lithified, can develop planes of weakness at multiple potential track surfaces below the originally exposed horizon [7,17,22,26-28]. In species with relatively narrow toes (theropods and small ornithopods), compliant substrates can flow around and over the foot, leaving only furrow-like seams marking its deep passage [14,27-32]. Such ‘penetrative tracks’ offer an excellent source of functional information [14,33-36], capturing foot movements throughout the track volume. Yet tracks on bedding planes sampled from within these depths can differ substantially [17,34,37-38], both from each other and from the foot that made them.

Herein, we quantify the three-dimensional (3-D) foot movements of a chicken-like bird (guineafowl) walking through a spectrum of deformable substrates. Following earlier studies of burrowing [39-45] and stepping [17,46-48], we use X-ray imaging to see through opaque ground. We emulate potential fossil track surfaces within each track volume by sampling guineafowl movement data at depth intervals, thereby identifying common patterns among the highly variable toe trajectories. Using this new perspective, we re-examine morphological variation among the classic Early Jurassic tracks of the Connecticut Valley [37-38,49-57] and discern previously unrecognized similarities with modern birds.

2. Material and Methods

(a) Animals, substrates, and recording

Biplanar X-ray data were collected from three adult Helmeted Guineafowl (*Numida meleagris*). All live animal experiments were conducted in accordance with the Institutional Animal Care and Use Committee of Brown University.

Dry and cohesive substrates were contained in a plastic trough filled to a depth of ~18 cm to form a trackway, which was enclosed by a clear acrylic tunnel. In lieu of sand, we used poppy seeds (*Papaver somniferum*) [17,58]. Artificial mud [10] was mixed from ~60 µm glass bubbles, ball clay, and water. Mud consistency was adjusted from very firm to semi-liquid by evaporating or adding water. For comparison, birds also walked across a stiff, non-deformable trackway.

Walking guineafowl were recorded at 250 fps by two X-ray and two standard light cameras (Fig. 1a, b), along with images for camera calibration and X-ray undistortion. One bird had ~2 mm disc-shaped lead markers fixed with cyanoacrylate beneath each claw (Fig. 1b).

(b) Point tracking, animation, and depth sampling

3-D toe coordinates for the marked individual were extracted in XMALab [59-60]. and animated in Maya 2020 (Autodesk Inc., San Rafael, CA, USA). For the unmarked birds, point rotoscoping [47] was done in Maya using virtual camera calibrations and undistorted video from XMALab. 58 trials of birds walking on deformable substrates were analyzed, yielding 81 subsurface steps (Table 1). CT-based bone models were animated for several trials using a combination of marker-based X-ray Reconstruction of Moving Morphology [61] and Scientific Rotoscoping [59].

		number of trials analyzed				number of complete steps analyzed			
individual	tracking method	solid	dry granular	muds	total	solid	dry granular	muds	total
6	rotoscoping	6	2	16	24	10	4	22	36
7	marker-based	5	12	17	34	8	16	23	47
8	rotoscoping	5	11	0	16	8	16	0	24
		16	25	33	74	26	36	45	107

Table 1. Overview of analyzed guineafowl data.

The paths of the three main toes (II-IV) were visualized in Maya by connecting their claw locations at each frame into motion trails (Fig. 1c). Substrate contact for digit III was identified from standard video, thereby setting the initial height of the substrate surface. To sample sub-surface motion trails in the vertical dimension (equivalent to bedding planes spanning the track volume), we extracted the coordinates at which each claw passed down (entry) or up (exit) through depth horizons set at 5 mm increments. At each increment, the 2-D horizontal position of the claws were used to calculate three variables: ‘digit III offset,’ defined as the difference in entry and exit of the middle toe, measured along the direction of travel; ‘digit II-IV width,’ measured as the distance between the side toes, for both entry and exit pairs; and, “digit representation,” simply the presence or absence of each toe at each increment. Sample horizons and variable graphs were plotted in R [62].

(e) Fossil specimens

All fossil specimens included in this study are housed in the Beneski Museum of Natural History at Amherst College, Amherst, MA, USA and designated ACM-ICH.

For more information, see Supplemental information.

2. Results

(a) Guineafowl sub-surface foot kinematics

Across trials, guineafowl slowed down, sped up, and paused frequently. Such non-steady locomotion provided a broad sampling of kinematic variation from the three individuals. Normal striding steps were by far the most common, although a few trials included non-alternation. Guineafowl sank to a wide range of depths (1.15 – 13.13 cm), penetrating deepest in semi-liquid muds.

As characterized by the paths of the three main toes, sinking and withdrawal exhibited consistent patterns. A lateral view of digit III, which forms the central axis of the tridactyl foot, is exemplary. Unlike its V-shaped path above solid surfaces, digit III always followed a loop below ground (Fig. 1d). Plotting digit III offset (Fig. 1e) reveals a consistent relationship between entry and exit, despite step by step variation in angle of entry, specific loop shape, and maximum depth. Digit III's arc-like withdrawal typically crossed from behind entry (negative) to in front of entry (positive) prior to removal. As the foot sank, digits II and IV remained widely spread until they reached their maximum depth. Upon withdrawal, the side toes collapsed towards digit III throughout their arcing ascent (Fig. 1f, g). The combination of anterior-posterior looping and transverse collapse indicates that the three main claws crossed through all horizons above their maximum depth twice, but in different locations (Fig. 1h). Such dissimilar entry and exit paths were found on all deformable substrates.

(b) Depth zones and fossil tracks

The common sub-surface motion pattern among guineafowl steps allows depth-based zones to be characterized by digit representation, digit III offset, and digit exit conformation, (Fig. 1h, Table 2). In Zone 1 (Fig. 1h, 0-1 cm), the adducted claws exit in front of their entry, often moving horizontally. In Zones 2 and 3, digit III offset is negative (Fig. 1h, 3-13 cm). All three toes are tightly converged when passing back up through Zone 2, but exit separately in Zone 3. The deepest zone can be further subdivided by the number of main toes represented: all three (3a), only two (3b), or just digit III (3a).

Using guineafowl sub-surface kinematics as a reference, we are now able to confirm the presence of comparable looping and depth zones in fossil penetrative tracks from Lower Jurassic strata of the Connecticut Valley (Fig. 2). Single slabs exposing penetrative tracks on both surfaces (Fig. 2b, c) support depth-based predictions of digit representation, anterior-posterior digit III offset, and digit exit conformation. Such patterns are particularly well-displayed when track volumes are split into multi-slabs. A five-slab specimen exposing track surfaces across Zones 2 and 3 preserves not only evidence of looping, but also allows specific details of digit III loop expansion and contraction to be distinguished (Fig. 2d).

Zone	digit representation	digit III offset	digit exit conformation
1	II - IV	exit in front	three converged
2	II - IV	exit behind	three converged
3a	II - IV	exit behind	three separate
3b	II + III or III + IV	exit behind	two separate
3c	III	exit behind	single

Table 2. Summary of depth zones.

Discussion

(a) Impact on track diversity and interpretation

Documentation of sub-surface looping in guineafowl walking through a wide variety of substrates offers a new perspective on the tracks of extinct bipeds. If dinosaurs responded to deformable ground similarly, we expected that the claws of the three main toes would have likewise passed through most surfaces twice—once going down and once coming back up—in different locations. Treatments of the Early Jurassic fauna of the Connecticut Valley [37-38,49-51,56,63-64] do not recognize any evidence of withdrawal. Yet armed with an improved search image, we have identified distinctly separate entry and exit features in hundreds of fossil footprints (sampled in Fig 2). Once penetrative tracks are understood as slices through a disturbed volume of sediment, their true nature becomes apparent. Such surfaces do not represent anatomy per se, but rather the collapsed seams left behind by toes punching, slashing, scraping, and ascending into and out of each potential track horizon on their looping paths.

A shared kinematic response to deformable substrates does not, however, mean that movements were tightly stereotyped. X-ray imaging allows us to measure guineafowl inter-step variation directly (Fig. 1e, g). In extinct dinosaur tracks, such kinematic variation must be inferred from its morphological consequences. For example, Connecticut Valley tracks assignable to Zone 2 reveal a wide range of loop-related disparity (Fig. 2e). Some preserve toe withdrawal back up through the entry furrow of digit III (Zone 2, left), others near the confluence of the digital furrows (Zone 2, middle), and yet others at the very rear of the track (Zone 2, right). Workers have attributed such a diverse array of shapes to multiple taxonomic groups (lizards, thin-toed birds, reptiles of uncertain affinity, and vertebrates of unknown class [38,50]). Yet despite their distinctive forms and deviation from known dinosaurian pedal anatomies, we propose that this diversity of penetrative tracks could all have been created by small theropods and/or ornithopods.

(b) Foot function in birds and other dinosaurs

Evidence of sub-surface looping in ~200 million-year-old fossils supports the hypothesis of functional continuity among tridactyl feet of birds and other bipedal dinosaurs when walking through deformable substrates. Although sub-surface looping has been previously reported in several dinosaur tracks [65-67], loops are ubiquitous and often of substantial magnitude in these Early Jurassic penetrative specimens. Our kinematic perspective offers a fresh viewpoint on depth-based track variation. Rather than being incomplete molds beneath the surface [38,68], substrate-modulated foot motion is intimately accountable for these disparate tracks. Perhaps the enduring success of the dinosaurian tridactyl foot design can be attributed, at least in part, to its ability to provide a stable base when spread, yet collapse to facilitate extraction from deformable substrates.

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Figure Legends

Figure 1. Sub-surface foot kinematics through a volume of substrate. Synchronized standard (a) and X-ray (b) video frames of a guineafowl walking through a dry granular substrate. Toes and markers are clearly revealed sub-surface (inset). c) Oblique view of digit claw marker motion trails for one step through dry grains. d) Lateral view of a sample of digit III motion trails on several deformable substrates (colored lines; thin = entry, bold = exit) and one solid substrate (black line). Digit III offset (e) measured at 5 mm depth horizons (horizontal lines), are plotted for 81 steps from all three individuals. f) Anterior view of claw motion trails showing the toes widely spread when sinking (thin), and smoothly collapsing upon withdrawal (bold). g) Digit II-IV width are plotted from 49 steps of two individuals (equal scales in d-g). h) Selected horizons for the green step (d-g) showing changing locations of claw entry (filled circles) and exit (open circles). The looping entry (thin) and exit (bold) path of digit III is indicated by a dashed line. Division of this track volume into zones (gray bars). Vertical and horizontal scales in (d-g) shown by axes in (e). Tick marks in (h) equal 1 cm. For foot animations, see supplemental video.

Figure 2. Exit features and depth zone attribution in Early Jurassic fossil tracks. a) Digit tip impression identification on entry (small circles) and exit (large circle) on one surface of ACM-ICH 37/24. b) A penetrated slab (ACM-ICH 39/8) from high in the volume reveals three elongate Zone 1 tracks on its upper surface and furrowed, Zone 2 tracks on its lower surface (mirrored). c) A penetrated slab (ACM-ICH 31/50) from low in the volume reveals a scrape-like, Zone 3a track with separate exits on its upper surface; only digit III reached its lower, Zone 3c surface (mirrored). d) A five-slab specimen (ACM-ICH 34/33) preserves the down and forward

penetration of the foot, followed by its looping withdrawal. Note changes in track morphology with depth. Dashed line indicates the entry (thin) and exit (bold) paths of digit III. e) Tracings of 19 Early Jurassic track surfaces displaying inter- and intra-zone diversity (ACM-ICH specimen numbers shown below). Exit features (black arrows) vary widely in location along the lengths of the tracks (see Fig. S1 for specimen photos and entry/exit overlays). Scale bars equal 5 cm.

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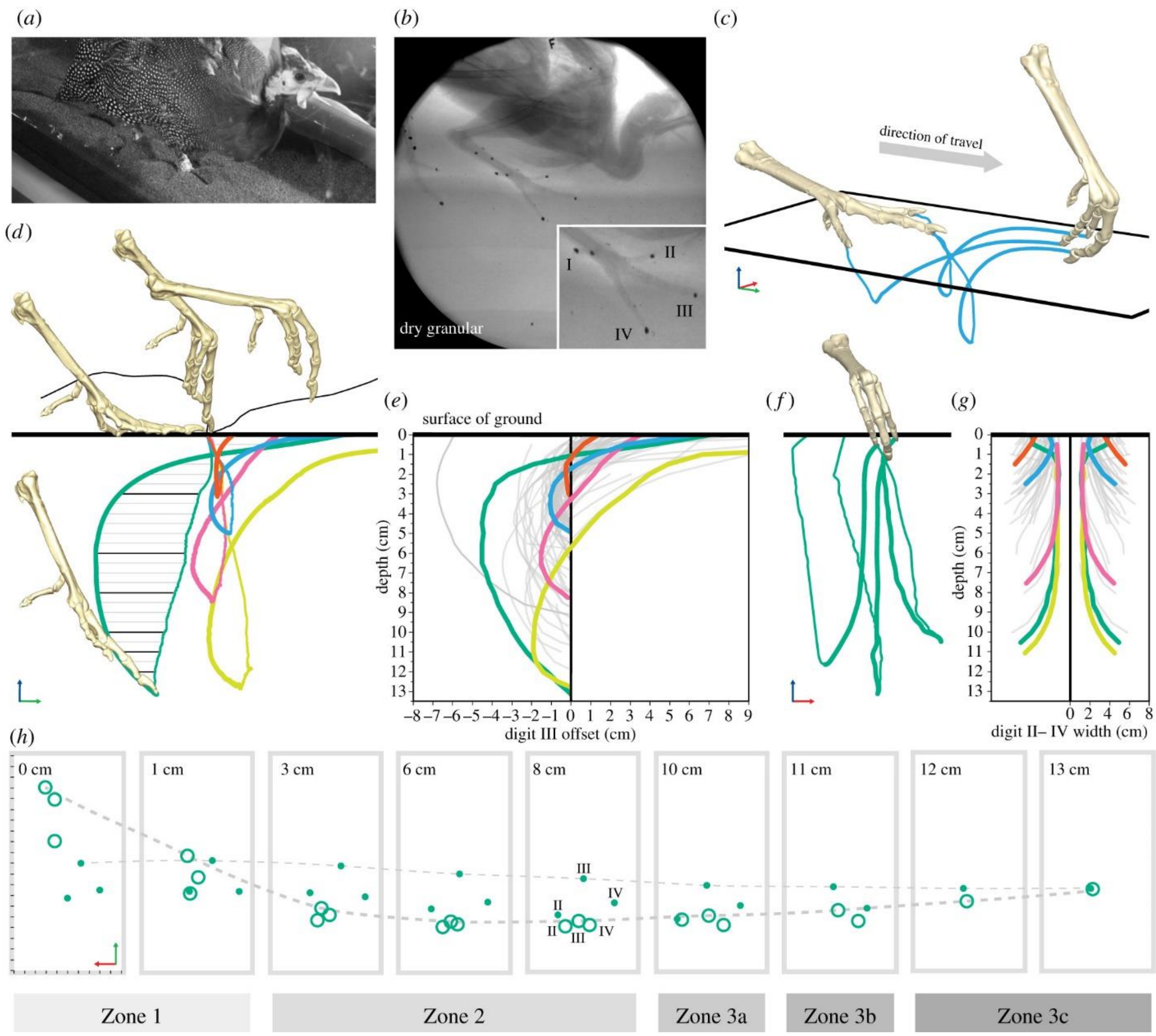

Figure 1. Sub-surface foot kinematics through a volume of substrate. Synchronized standard (a) and X-ray (b) video frames of a guineafowl walking through a dry granular substrate. Toes and markers are clearly revealed sub-surface (inset). c) Oblique view of digit claw marker motion trails for one step through dry grains. (d) Lateral view of a sample of digit III motion trails on several deformable substrates (coloured lines; thin = entry, bold = exit) and one solid substrate (black line). Digit III offset (e) measured at 5 mm depth horizons (horizontal lines in (d)) and are plotted for 81 steps from all three individuals. (f) Anterior view of claw motion trails showing the toes widely spread when sinking (thin), and smoothly collapsing upon withdrawal (bold). (g) Digit II–IV width are plotted from 49 steps of two individuals (equal scales in d–g). (h) Selected horizons for the green step (d–g) showing changing locations of claw entry (filled circles) and exit (open circles). The looping entry (thin) and exit (bold) path of digit III is indicated by a dashed line. Grey bars indicate zones for this track volume. Vertical and horizontal scales in (d–g) shown by axes in (e) and (g). Tick marks in (h) equal 1 cm. For foot animations, see electronic supplementary material, video.

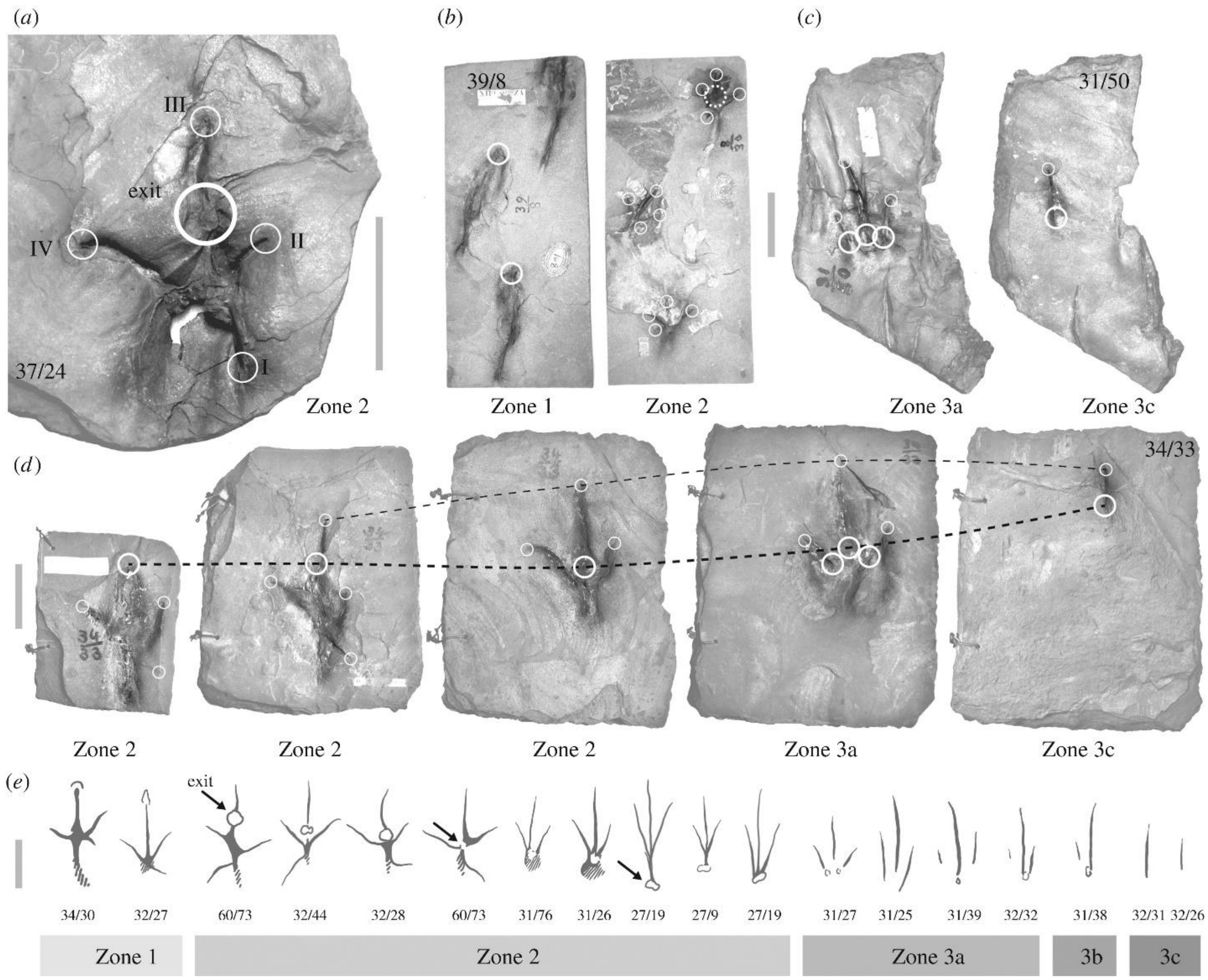

Figure 2. Exit features and depth zone attribution in Early Jurassic fossil tracks. (a) Digit tip impression identification on entry (small circles) and exit (large circle) on one surface of ACM-ICH 37/24. (b) A penetrated slab (ACM-ICH 39/8) from high in the volume reveals three elongate Zone 1 tracks on its upper surface and furrowed, Zone 2 tracks on its lower surface (mirrored). (c) A penetrated slab (ACM-ICH 31/50) from low in the volume reveals a scrape-like, Zone 3a track with separate exits on its upper surface; only digit III reached its lower, Zone 3c surface (mirrored). (d) A five-slab specimen (ACM-ICH 34/33) preserves the down and forward penetration of the foot, followed by its looping withdrawal. Note changes in track morphology with depth. Dashed line indicates the entry (thin) and exit (bold) paths of digit III. (e) Tracings of 19 Early Jurassic track surfaces displaying inter- and intra-zone diversity (ACM-ICH specimen numbers shown below). Exit features (black arrows) vary widely in location along the lengths of the tracks (see electronic supplementary material, figure S1 for specimen photos and entry/exit overlays). Scale bars equal 5 cm.