Trabecular bone structure in forefoot and rearfoot endurance runners: Implications for interpreting fossil hominin morphology

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Introduction

Human endurance running (ER)- prolonged aerobic/submaximal running- is hypothesized to have first evolved with *H. erectus* (Bramble and Lieberman, 2004). Direct evidence of ER in hominins, and evidence of hominin footstrike patterns, is lacking. Forefoot striking (FFS), where the forefoot makes initial ground contact before the heel touches down, is thought to be the natural unshod condition (Lieberman et al., 2010), as opposed to rearfoot striking (RFS), where the heel makes initial contact. FFS generates a smoother ground reaction force curve (fig. 1 and 2), but Achilles tendon forces are 19% higher than in RFS (Kumala et al., 2013). Presumably, FFS places greater strain on the 1st metatarsal (due to forefoot impact) and greater strain on the calcaneus, which acts as a lever transmitting forces generated by the Achilles tendon.

Fig. 1: RFS ground reaction force

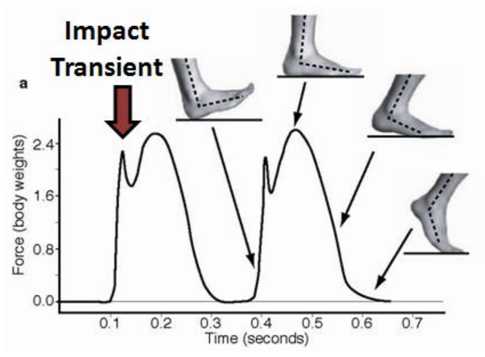
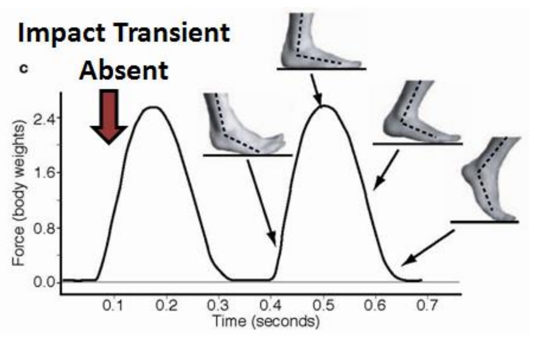


Fig. 2: FFS ground reaction force



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Currently no methodology exists to interpret hominin fossils for direct evidence of endurance running. The principle of bone functional adaptation (Wolff, 1892; Ruff et al., 2006), whereby bone remodels in response to strain, presents the possibility for inferring locomotor patterns from fossils, if the bone functional responses resultant from endurance running are identified. Long bone cross sectional geometry has proven useful in inferring locomotor patterns, and has recently been used to infer endurance running in fossil hominins (Shaw and Stock, 2013). Trabecular measures may be useful as well. Trabecular density, thickness and number are hypothesized to increase in response to loading in general (Pontzer et al., 2006; Joo et al., 2003) and to running specifically (Biewenner et al., 1996).

This study seeks to identify correlates in trabecular bone architecture in living subjects of known locomotor patterns in the calcaneus and 1st metatarsal. We test the following hypotheses:

1. **Runners display greater trabecular density, thickness, and number than non-runners (NR) in the calcaneus and 1st metatarsal due to the extreme forces generated during running.**
2. **FFS have more robust calcaneal trabecular architecture than RFS, likely due to increased Achilles tendon forces.**

Methods

- Subjects: 19 healthy males aged 20-41-- 6 FFS, 6 RFS, 1 mixed-footstrike runner, 6 NR
- Average weekly mileage for runners: 25-70 miles
- Five of the six NR either engage in rigorous physical activity on a regular basis or have a history of competitive sports during adolescence

Table 1: Participant Summary

	n	mean age	age SD	mean weight (lbs)	weight SD	mean years running	years running SD
FFS	6	26.5	4.7	155.2	8.4	10.0	5.1
RFS	6	36.2	4.4	165.3	12.0	9.2	6.0
NR	6	28.7	6.9	193.5	6.9	0.0	0.0

- Footstrike confirmed using high-speed motion capture
- Subjects landing on the middle third of the foot were classified as FFS
- High-resolution computed tomography scans: right 1st metatarsal and right calcaneus
- Region of interest in the calcaneus: 15mm inferior to the talo-calcaneal joint; 9mm stack of the entire medial-lateral width of the calcaneus; scans cropped to a 15mm region projecting distally from the calcaneal tuberosity to ensure analysis of a common region
- Region of interest in the 1st metatarsal: 5mm proximal to the medial-most projection of the metatarsal head; 9 mm stack

Fig 3: Approx. calcaneus region of interest

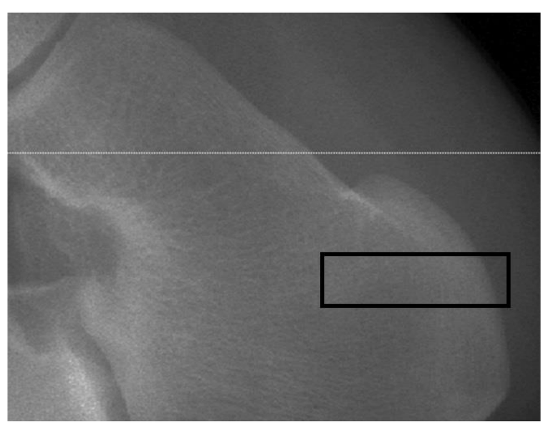


Fig 4: Approx. 1st metatarsal region of interest

- 10 variables of interest- 4 in the calcaneus and 6 in the 1st metatarsal
- Cortical bone variables were not included for the calcaneus due to calcification of the Achilles tendon insertion

Results

ANOVA (testgroup 1, left) and T-tests (testgroup 2, right) showed no significant differences between groups for any of the dependent variables. However, two variables hypothesized to be sensitive to loading (trabecular density and trabecular number, both in the calcaneus--highlighted with red text) were found to be moderately influenced by body weight. We plotted each of these variables against body mass (log transformed) and ran ANOVAs on the residuals to account for the effects of body weight.

Table 2: CT scan results

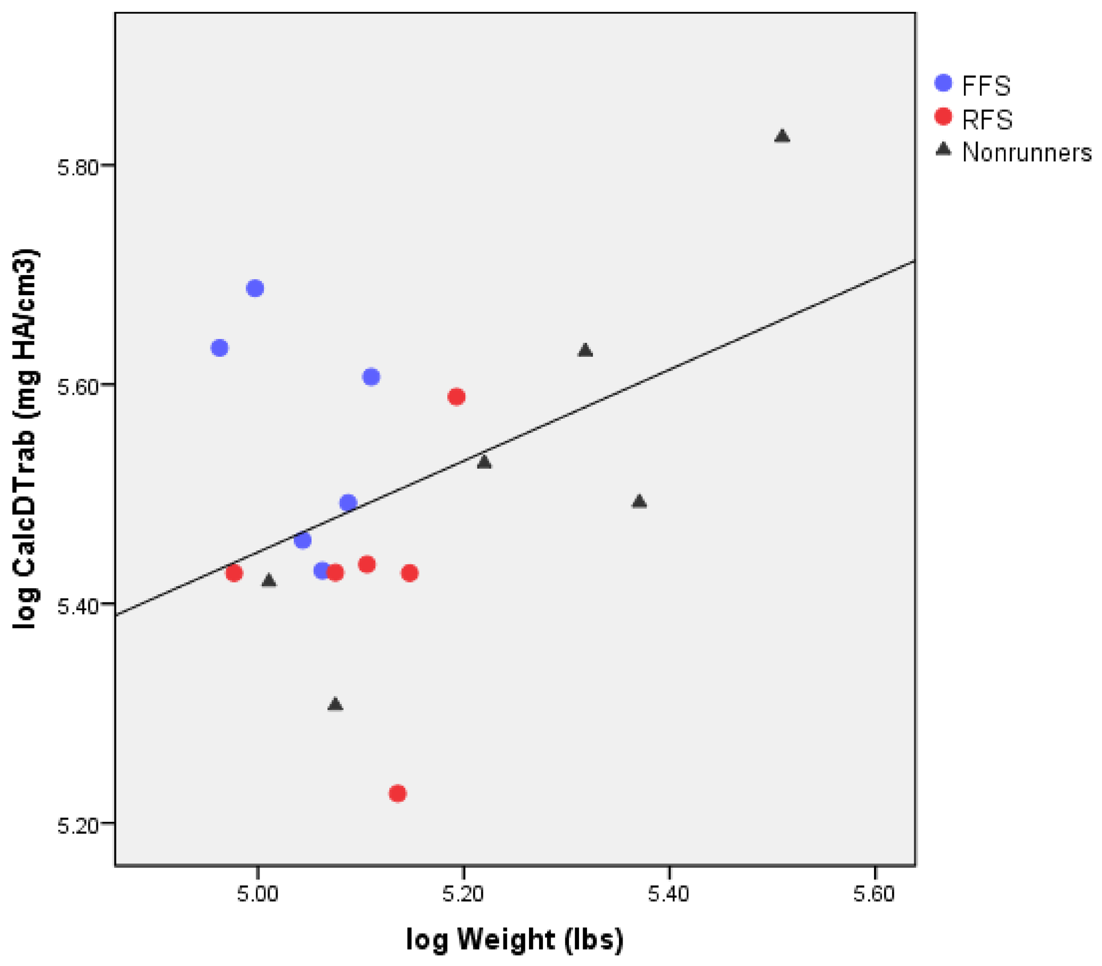
Testgroup1: FFS vs. RFS vs. Nonrunners

	FFS mean (n=6)	SD	RFS mean (n=6)	SD	NR mean (n=6)	SD	p
Calcaneus							
Trabecular density (mg HA/cm3)	258.8	27.3	227.7	25.7	256.8	47.7	0.26
Trabecular number (1/mm)	3.35	0.32	3.42	0.21	3.52	0.21	0.529
Avg. trabecular thickness (mm)	0.065	0.005	0.055	0.005	0.061	0.011	0.144
Avg. trabecular spacing (mm)	0.236	0.287	0.238	0.018	0.225	0.021	0.569
1st Metatarsal	FFS mean (n=5)	SD	RFS mean (n=4)	SD	NR mean (n=5)	SD	p
Trabecular density (mg HA/cm3)	247.8	40.7	260.0	43.9	233.7	51.3	0.697
Trabecular number (1/mm)	1.58	0.40	1.77	0.32	163.80	0.38	0.767
Avg. trabecular thickness (mm)	0.137	0.036	0.124	0.009	0.121	0.020	0.585
Avg. trabecular spacing (mm)	0.535	0.168	0.459	0.104	0.526	0.185	0.754
Compact bone density (mg HA/cm3)	743.8	66.0	801.8	56.4	798.8	93.8	0.433
Cortical thickness (mm)	0.86	0.20	1.16	0.04	1.04	0.34	0.198

Testgroup2: Runners vs. Nonrunners

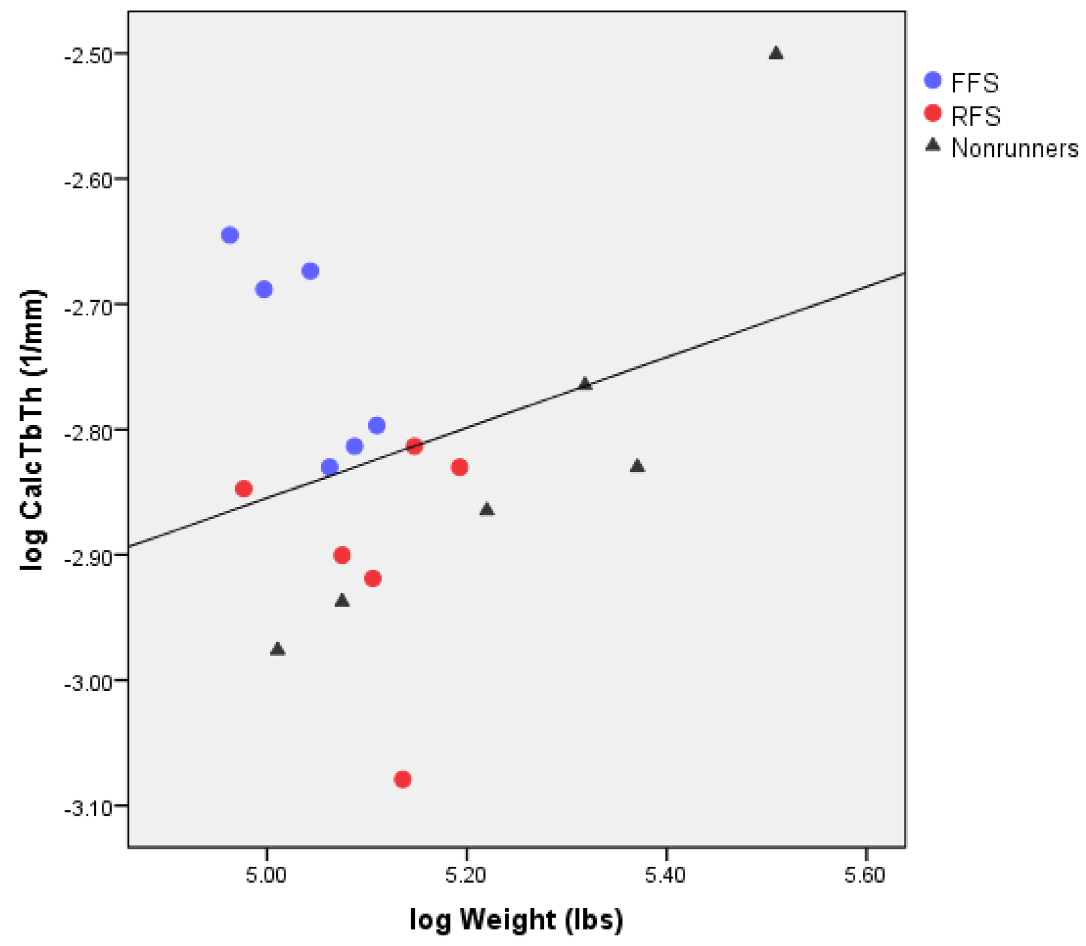
	Runner mean (n=13)	SD	Nonrunner mean (n=6)	SD	p
Calcaneus					
Trabecular density (mg HA/cm3)	242.4	28.9	256.8	47.7	0.425
Trabecular number (1/mm)	3.37	0.25	3.52	0.21	0.247
Avg. trabecular thickness (mm)	0.060	0.007	0.061	0.011	0.84
Avg. trabecular spacing (mm)	0.238	0.222	0.225	0.021	0.231
1st Metatarsal	Runner mean (n=13)	SD	Nonrunner mean (n=6)	SD	p
Trabecular density (mg HA/cm3)	254.0	37.7	233.7	51.3	0.398
Trabecular number (1/mm)	1.63	0.36	1.64	0.38	0.965
Avg. trabecular thickness (mm)	0.134	0.277	0.121	0.020	0.359
Avg. trabecular spacing (mm)	0.510	0.136	0.526	0.185	0.858
Compact bone density (mg HA/cm3)	776.8	65.9	798.8	93.8	0.604
Cortical thickness (mm)	1.01	0.21	1.04	0.34	0.812

Fig. 5: Calcaneus Trabecular Density



- FFS displayed greater trabecular density (mean=258.8) than RFS (mean=227.7) and NR (mean=256.8). See table 2.
- Body weight was significantly predictive of trabecular density (p=.036). NR trabecular density appeared to be more closely associated with body weight than either FFS or RFS (fig. 5).
- A plot of trabecular thickness vs. body weight (fig. 5) shows FFS clustered near and above the best-fit line and RFS clustered near or below the line. NR values more closely followed the linear trend.
- Post hoc analysis of the residuals of body weight vs. trabecular density indicate that the difference in trabecular density between FFS and RFS approaches statistical significance (p=.085). FFS are statistically indistinguishable from NR (p=.244) and RFS are indistinguishable from NR (p=.804).

Fig. 6: Calcaneus Trabecular Thickness



- FFS displayed greater trabecular thickness (mean=.065) than RFS (mean=.055) and NR (mean=.061). See table 2.
- Body weight was not significantly predictive of trabecular thickness (p=.112). However, NR trabecular thickness appears to be more closely associated with body weight than either FFS or RFS (fig. 6).
- A plot of trabecular thickness vs. body weight (fig. 6) shows FFS clustered near and above the best-fit line and RFS clustered near or below the line. NR values more closely followed the linear trend.
- Post hoc analysis of the residuals of body weight vs. trabecular thickness indicate that the difference in trabecular thickness between FFS and RFS is statistically significant (p=.031) and the difference between FFS and NR approaches statistical significance (p=.091). RFS and NR are statistically indistinguishable (p=.832).

Conclusions

- Near the calcaneal tuberosity, FFS display higher trabecular density than RFS, and thicker trabeculae than either RFS or NR, likely a remodeling response to high Achilles tendon forces.
- In the absence of a repetitive, high-strain loading regime, trabecular density and trabecular thickness near the calcaneal tuberosity of NR seems strongly influenced by body weight.
- These differences suggest the possibility for inferring locomotor patterns from the proximal region of hominin fossil calcanei. However, if hominins ran with a RFS pattern, the proximal calcaneus may not be a useful diagnostic, as it seems to reflect Achilles tendon forces rather than impact forces.
- Trabecular and cortical bone in the region of the 1st metatarsal that we sampled—just proximal to the metatarsal head– does not appear to be highly malleable to forces generated during running, at least not to a degree that allows for locomotor inference. This is surprising, given the high strain experienced by this bone during the late stance and toe-off phases of the gait cycle. The 5th metatarsal, often the first point of contact in FFS, may yield useful information.

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