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Abstract	In this chapter we investigate the lower limb structural rigidity (using cross-sectional geometric properties of the diaphyseal midshaft) within a sample of 124 individuals from the Late Upper Paleolithic, Neolithic and Iron Age from Italy, Medieval Germany, and twenty-first Century Britain	

(long distance runners, field hockey players, and sedentary controls). Late Upper Paleolithic, Neolithic and Iron Age samples were settled in rugged areas, whereas the other samples inhabited plain areas. The aim of this study is to assess whether fibular diaphyseal properties reflect mobility patterns or terrain properties in past populations. Both fibular rigidity and relative fibular rigidity ratio (fibula/tibia) have been analyzed.

Results reveal that Late Upper Paleolithic, Neolithic and Iron Age samples show high fibular rigidity and have values of relative fibular rigidity that are most similar to modern hockey players. The relative fibular diaphyseal rigidity of hockey players has been previously explained as the consequence of their dynamic and repetitive change of direction. Late Upper Paleolithic and Neolithic individuals are thought to have been highly terrestrially mobile, while Iron Age people were probably fairly sedentary. However, all of the three groups lived in areas of uneven terrain. We concluded that fibular rigidity and relative fibular rigidity are influenced by factors that increase foot eversion/inversion such as frequent directional changes and uneven terrain. The results of this study suggest that inclusion of the fibula provides a valuable additional perspective that complements traditional predictions of mobility patterns based on the femur or the tibia alone.

Keywords
(separated by “-”)

Fibula - Tibia - Bioarchaeology - Cross-sectional geometry -
Terrain conformation

Chapter 6

The Importance of Considering Fibular Robusticity When Inferring the Mobility Patterns of Past Populations

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[AU1] Vitale S. Sparacello, Damiano Marchi, and Colin N. Shaw

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Abstract In this chapter we investigate the lower limb structural rigidity (using cross-sectional geometric properties of the diaphyseal midshaft) within a sample of 124 individuals from the Late Upper Paleolithic, Neolithic and Iron Age from Italy, Medieval Germany, and twenty-first Century Britain (long distance runners, field hockey players, and sedentary controls). Late Upper Paleolithic, Neolithic and Iron Age samples were settled in rugged areas, whereas the other samples inhabited plain areas. The aim of this study is to assess whether fibular diaphyseal properties reflect mobility patterns or terrain properties in past populations. Both fibular rigidity and relative fibular rigidity ratio (fibula/tibia) have been analyzed.

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24 uneven terrain. The results of this study suggest that inclusion of the fibula provides
25 a valuable additional perspective that complements traditional predictions of mobil-
26 ity patterns based on the femur or the tibia alone.

27 **Keywords** Fibula • Tibia • Bioarchaeology • Cross-sectional geometry • Terrain
28 conformation

29 **6.1 Introduction**

30 Although it constitutes one of the parameters that are most often investigated in
31 bioarchaeological research, mobility has not yet received a univocal definition. For
32 research aimed at the reconstruction of past activity patterns, mobility is usually
33 broadly defined as the habitual amount of traveling (either through walking or run-
34 ning) that characterized a population. However, it is difficult to numerically quan-
35 tify mobility in bioarchaeology, for example, through the reconstruction of home
36 ranges or trade networks. Qualitative assessments such as “high” or “low” mobility
37 are then usually used, and are linked to the logistic requirements of different subsis-
38 tence strategies (see Wescott 2014) based on ethnographic analogies.

39 Since walking and running are the main causes of anteroposterior (AP) repetitive
40 mechanical loading on lower limbs, the amount of physical activity associated with
41 traversing the landscape can be indirectly quantified through its effects on long bone
42 diaphyses. Research that has investigated the relationship between mobility and
43 long bone diaphyseal structure has generally considered the AP-oriented loads as
44 the main cause of lower limb loading (Ruff 1999, 2000a; Shaw and Stock 2009; see
45 Wescott 2014 and references therein). However, experimental and nonexperimental
46 studies conducted on mammals—including primates—have demonstrated that dif-
47 ferent “types” of mobility may considerably influence the amount of mediolateral-
48 oriented loads to which the lower limb is subjected (Carlson et al. 2005; Demes
49 et al. 2006; Carlson and Judex 2007; Marchi 2007; Marchi and Shaw 2011; Marchi
50 et al. 2011). Following these findings, here mobility is considered as having two
51 components, both of which influence lower limb morphology. The first component
52 is the amount of traveling that people undertake to have access to resources: this is
53 the traditional definition of mobility. The second component is the type of move-
54 ment, particularly focused on how movement influences mediolateral (ML) loading
55 (e.g., uphill/downhill and/or on even/uneven terrain). Untangling the concomitant
56 effect of the two components may improve the interpretation of lower limb skeletal
57 properties for behavioral reconstructions.

58 Cross-sectional geometry (CSG) is a biomechanical technique that studies
59 the plastic behavior of long bone diaphyses to adapt to mechanical loads (for
60 reviews, see Pearson and Lieberman 2004; Ruff et al. 2006b; and references
61 therein). Various bioarchaeological studies have described a correspondence
62 between femoral diaphyseal shape and levels of mobility dictated by subsis-
63 tence patterns. In particular, highly mobile hunter-gatherers generally show

[AU2] higher values of femoral shape ratios (I_x/I_y and I_{\max}/I_{\min})¹ than sedentary agriculturalists 64
 (e.g., Ruff and Hayes 1983; Ruff 1987, 1999; Larsen 1995; Stock and Pfeiffer 65
 2001; Holt 2003; Ruff et al. 2006a). 66

However, research suggests that distance traveled is not the sole agent of lower 67
 limb remodeling; other factors should be taken into account, and possibly factored out 68
 when comparing skeletal samples and inferring habitual behavior patterns (Ruff 1999, 69
 2000a; Sparacello and Marchi 2008). One of the confounding factors to consider 70
 when interpreting lower limb robusticity is the potential influence of topography. Ruff 71
 (1999) found that Native American groups characterized by different subsistence 72
 economies (preagricultural and agricultural, with assumed differences in patterns of 73
 mobility) were not differentiated in femoral diaphyseal robusticity. However, groups 74
 coming from more rugged areas showed significantly more robust femora. Based on 75
 these results, Ruff (2000a) proposed that once terrain is factored out, the influence of 76
 subsistence strategies on lower limb bone robusticity greatly declines. 77

Diaphyseal cross-sectional robusticity may therefore be influenced by both the 78
 activity performed and the topography upon which the activity is performed. Further 79
 support to this hypothesis came from the comparison of two groups that adopted dif- 80
 ferent subsistence economies (herding and fishing-agriculture, respectively) settled 81
 in the same rugged area (Sparacello and Marchi 2008). Despite differences in pre- 82
 sumed mobility levels, comparisons did not reveal significant differences in femoral 83
 robusticity, but showed significant differences in diaphyseal shape (I_x/I_y). This was 84
 interpreted as reflecting the influence of mobility levels and terrain properties on 85
 femoral midshaft robusticity and shape. The high femoral robusticity of both sam- 86
 ples was interpreted as dictated by terrain ruggedness. The more elliptical diaphyseal 87
 shape (greater I_x/I_y ratios) of the Neolithic sample was interpreted as a consequence 88
 of higher mobility levels (Sparacello and Marchi 2008). A similar pattern was 89
 observed for the tibia in a comparison among several groups that adopted different 90
 subsistence economies (hunter-gatherers and herders) who had settled in both plain 91
 and mountainous regions (Sparacello et al. 2008). These results suggest that, when 92
 comparing groups dwelling in areas with similar topographies, different subsistence 93
 economies seem to generate less dramatic differences in lower limb robusticity. 94

Differently from the femur, there is not consistent correspondence between 95
 tibial shape (as revealed by I_{\max}/I_{\min} ratio) and mobility patterns (cf. Stock and 96
 Pfeiffer 2001; Holt 2003; Marchi 2008; Marchi et al. 2011). A comparison of 97
 upper and lower limb CSG properties in Andaman Islanders and Later Stone 98
 Age southern African foragers (Stock and Pfeiffer 2001) showed that 99
 Andamanese people had significantly more robust upper limbs than Later Stone 100
 Age people. Andamanese people incorporated a significant degree of marine 101
 mobility into their behavioral pattern that included swimming and canoe pad- 102
 dling, which probably led to this result. Later Stone Age people were highly 103
 mobile terrestrial hunter-gatherers and were characterized by significantly more 104

¹ I_x is the AP bending rigidity; I_y is the ML bending rigidity; I_{\max} is the maximum moment of area; and I_{\min} is the minimum moment of area of a bone at a cross section (Ruff and Hayes 1983). Femoral I_x/I_y is normally referred to as a mobility index.

105 robust lower limbs, and more AP-strengthened femoral cross sections. However,
106 Later Stone Age people did not display statistically significant differences
107 (more) in platycnemic tibiae relative to the Andamanese people. It therefore
108 appears that femoral cross-sectional shape shows a more strict correspondence
109 with inferred mobility levels than the tibia. A similar pattern was observed in
110 European skeletal samples ranging from the Early Upper Paleolithic to the
111 Bronze Age (Holt 2003; Sládek et al. 2006a, b; Marchi 2008; Marchi et al. 2011;
112 see also Pearson et al. 2014, for an analysis of the weak correlation between
113 femoral and tibial shape indices).

114 In a study of the associated influence of activity, climate, and mechanical con-
115 straints for tissue economy in the lower limb, Stock (2006) found that tibial diaphy-
116 seal robusticity was less correlated than femoral diaphyseal robusticity with climate
117 and body shape, and showed less inherent variance in the samples. Stock (2006)
118 concluded that the strongest morphological correlates of terrestrial mobility are
119 femoral cross-sectional shape and tibial diaphyseal robusticity. A recent study on
120 modern athletes and a bioarchaeological sample also found a good correspondence
121 between tibial robusticity (relative to humeral robusticity) and mobility patterns
122 (Shaw and Stock 2013).

123 Recently, Shaw and Stock (2009) compared three modern human samples: cross-
124 country runners, field hockey players, and sedentary controls. Results revealed that
125 the two highly mobile athlete samples had significantly more robust tibiae com-
126 pared to controls. Further, diaphyseal shape differences between runners and hockey
127 players were significant, with runners showing higher values (more elliptical diaphy-
128 seal cross sections). This result was interpreted as reflecting a greater degree of
129 AP-oriented bending stress in runners—whose mode of locomotion was mainly
130 linear—compared to field hockey players who performed frequent changes of direc-
131 tion (Spencer et al. 2004, and references therein). The results of Shaw and Stock
132 (2009) suggest that tibial diaphyseal robusticity provides information about the
133 level of mobility, while tibial cross-sectional shape is more informative about the
134 directionality of loading.

135 Despite the abundance of work focused on the relationship between bone struc-
136 ture and mobility, the fibula has been often overlooked in anthropological studies
137 because most of the body weight is supported by the tibia (Marchi and Shaw 2011
138 and references therein). Moreover, in bioarchaeological skeletal samples the fibula
139 is less frequently found intact compared to the tibia. Nevertheless, the fibula may
140 provide valuable information on mobility patterns. Studies on living hominoids
141 have demonstrated that the relative fibular diaphyseal robusticity (tibia/fibula) cor-
142 responds with variation in locomotor patterns (Marchi 2007). Specifically, primarily
143 arboreal hominoids possess a relatively more robust fibula compared to primarily
144 terrestrial hominoids. These differences have been interpreted as a likely conse-
145 quence of a more mobile fibula (Barnett and Napier 1953) and more adducted
146 hindlimb position in the former (Carlson et al. 2005), which is necessary for travel
147 in arboreal environments.

148 Marchi and Shaw (2011) analyzed fibular robusticity and tibio-fibular ratios in
149 university varsity athletes and controls, in order to assess whether fibular properties

are influenced by the intensity and type of mobility (i.e., straight line movement or with frequent changes of direction). Results showed a trend of increased fibular diaphyseal robusticity from controls to runners to field hockey players, with a significant difference ($P < 0.05$) between field hockey players and controls. Moreover, relative fibular robusticity (fibula/tibia ratio) was significantly greater in hockey players compared to runners. The authors concluded that fibular robusticity and relative fibula/tibia robusticity may reflect adaptation to patterns of mobility that incorporate high degrees of foot eversion and inversion. In field hockey players, foot eversion/inversion is likely to have been caused by constant and abrupt changes of direction. When studying mobility patterns in bioarchaeological research, frequent foot eversion and inversion may have been caused by mobility in highly uneven terrains. Comparison of Italian Neolithic and Iron Age skeletal series from individuals dwelling in mountainous terrains versus medieval and modern samples seems to provide support for this interpretation (Marchi et al. 2011; see also Higgins 2014, who found a similar effect of terrain properties on ML bending of bovid metacarp1).

In another study, Rantalainen et al. (2010) investigated the influence of locomotor patterns on tibial and fibular rigidity. The authors found that the repetitive loadings associated with running appear to primarily influence tibial robusticity. According to their model, runners would show low levels of relative fibular robusticity. This prediction was empirically supported by the results of Marchi and Shaw (2011). By contrast, Rantalainen et al. (2010) suggested that high impact activities involving jumping influence the mechanical strength of both the tibia and the fibula. The authors concluded that although the tibia and the fibula are spatially close, they experience substantially different loading environments. Analyzing both the fibula and the tibia may therefore help in obtaining a more thorough understanding of mobility patterns.

In the present study we analyze tibial and fibular diaphyseal robusticity, and tibio-fibular ratios within bioarchaeological and modern skeletal samples. The samples are characterized by different levels of mobility: in the bioarchaeological samples, mobility is inferred from archaeological evidence and femoral shape indices, while modern samples include varsity athletes and sedentary controls (Shaw and Stock 2009; Marchi and Shaw 2011). Three bioarchaeological samples come from mountainous areas, while one bioarchaeological sample and the modern samples come from areas associated with relatively flat terrain (see below). The aim of this research is to assess whether fibular CSG properties can successfully be integrated with the information drawn from femoral and tibial data to provide a more accurate reconstruction of mobility levels and types in bioarchaeological populations. In particular, the presence of samples characterized by varying degrees of mobility coming from both relatively flat and rugged areas gives the opportunity to untangle the possible concomitant influence of mobility and terrain properties on the tibio-fibular complex. On the basis of the above research on tibial and fibular robusticity, we hypothesize that tibial robusticity will be influenced by both mobility levels and terrain ruggedness, while fibular robusticity and relative fibular proportions will mainly reflect foot eversion/inversion, associated with the terrain ruggedness. In particular, we hypothesize that (1) when comparing groups dwelling in areas with

195 similar terrain properties, tibial diaphyseal robusticity will be higher in more mobile
 196 groups; (2) when comparing groups with similar levels of mobility, tibial diaphyseal
 197 robusticity will be higher in groups settled in mountainous (more rugged) terrain;
 198 and (3) when fibular diaphyseal robusticity and the fibula/tibia robusticity ratio will
 199 be higher in skeletal series drawn from more mountainous/uneven areas, indepen-
 200 dent of mobility levels.

201 **6.2 Materials and Methods**

202 **6.2.1 The Sample**

203 The skeletal series analyzed here include four bioarchaeological and three modern
 204 samples. Only male individuals were included in this study, given that, cross-
 205 culturally, most of the mobility-oriented activities were performed by males, at least
 206 beginning with the Neolithic (Ehrenberg 1989). Bioarchaeological skeletal series
 207 include 7 Late Upper Paleolithic, 15 Neolithic, 33 Iron Age, and 14 medieval indi-
 208 viduals (Table 6.1). Mobility levels for these samples are presumed based on archae-
 209 ological information and ethnographic analogy with modern or recent groups (e.g.,
 210 Hudson and Hudson 1980; Kelly 1983, 1995; Larsen 1995; Carlson et al. 2007).

211 The Late Upper Paleolithic sample (12,000–10,000 BP) (Alessio et al. 1967;
 212 Martini et al. 2004; Paoli et al. 1980) consists of individuals from the sites of Arene
 213 Candide (Liguria, Northwestern Italy) and Romito (Calabria, Southern Italy).

t1.1 **Table 6.1** Bioarchaeological skeletal samples composition

t1.2	Period	N	Necropolis	Terrain	Subsistence	Mobility level
t1.3	Late Upper	7	Arene Candide 2, 4, 5, 10	Mountainous	Hunting	High
t1.4	Paleolithic		Romito 3, 7, 8			
t1.5	Neolithic	15	Arene Candide 2 Tinè, E VI,	Mountainous	Herding	High
t1.6			7, 8, IX, XIII			
t1.7			Arma dell' Aquila II			
t1.8			Bergeggi 2, 3			
t1.9			Boragni 2			
t1.10			Pollera 10, 13, 30, 32, 6246			
t1.11	Iron Age	35	Alfedena 1, 4, 5, 6, 9, 18, 19,	Mountainous	Agriculture-	Moderate-Low
t1.12			21, 40, 41, 53, 66, 67, 68,		herding	
t1.13			73, 82, 83, 84, 88, 89, 90,			
t1.14			91, 97, 98, 102, 105, 109,			
t1.15			114, 115, 116, 119, 121,			
t1.16			126, 130, 132			
t1.17	Medieval	14	Neuburg 24, B21, B26, 61,	Plain	Agriculture	Low
t1.18			65_57, 75, 80, 101_73,			
t1.19			109, 111, 167, 175, 176,			
t1.20			189			

Subsistence for these peoples was based on hunting mid-sized ungulates such as red deer, roe deer, and ibex (Mussi 2001; Martini et al. 2009), an activity pattern that required a high level of mobility (Kelly 1983, 1995).

Neolithic individuals date to 6,000–5,500 BP (Maggi 1997) and were unearthed from a series of neighboring caves including Arene Candide (Liguria, Northwestern Italy). The main subsistence activity for Neolithic people was sheep herding, although agriculture played a minor role (Marchi et al. 2006, 2011, and references therein). In general, pastoral systems rely on both seasonal movements among various pasture zones (ranging from 20 to more than 300 km), as well as daily dispersal from encampments (Niamir-Fuller 1999). Herder mobility is predicated on the availability of pasture and water. For example, in arid areas cattle herders may walk 8–9 km per day (Coppolillo 2000; Turner and Hiernaux 2002) and, during the dry season, up to 17 km per day (Adriansen and Nielsen 2005). Therefore, the most mobile herders perform both high logistic and high residential mobility. This level of mobility overlaps with that of modern hunter-gatherers (Kelly 1983, 1995; Marlowe 2005). The Ligurian Neolithic people were part of a small-scale transhumance system in a region that virtually lacked pastures (Marchi et al. 2006, 2011), a subsistence strategy that likely required logistic mobility. High mobility of the Ligurian Neolithic people was supported by previous analysis performed on their femoral CSG (Marchi et al. 2006).

Iron Age individuals date back to 2,600–2,400 BP and were unearthed from the necropolis of Alfedena in Abruzzo (central Italy). The economy at Alfedena was based on agriculture, while a small subset of the population was involved in herding. This subsistence strategy would have required lower population level mobility levels (Sparacello et al. 2011). Accordingly, the Iron Age sample is associated with a relatively circular femoral shape.

Medieval individuals (1,300 BP) were mainly agriculturalists (Marchi 2007; Benjamin Höke, pers. comm.) and were unearthed from the necropolis of Neuburg in Bavaria (Southern Germany). Historical studies indicate that early medieval peasants had little or no opportunity for residential mobility and lived the majority of their lives close to the field (Le Goff 1988, 1990). Furthermore, previous comparisons of hunter-gatherer and agricultural skeletal remains suggest decreased levels of mobility in agricultural populations (Larsen 1995; Ruff et al. 2006a).

The modern samples include 15 field-hockey players, 15 cross-country runners, and 21 sedentary control individuals (Shaw and Stock 2009). Two additional individuals practicing rugby were included in the field hockey players' sample, given the similarity of the movements involved in the two sports (Marchi and Shaw 2011). The two athlete samples are characterized by high levels of mobility. However, in general, runners travel in a relatively straight-ahead direction, while hockey players perform frequent and abrupt changes of direction (Shaw and Stock 2009; Marchi and Shaw 2011).

Bioarchaeological samples come from areas that are easy to categorize topographically, being either flat or fairly rugged. Modern samples performed their sports in mainly flat terrain. However, we (Sparacello et al. 2008) developed a protocol to assess terrain ruggedness in an objective way using the freeware program

259 Google Earth™. A circle with a diameter of 5 km is drawn, with the archaeological
260 site at the center. An altimetry profile is calculated using a function of Google
261 Earth™ for the four paths drawn along the directions N-S, E-W, NW-SE, SW-NE of
262 the circle (Sparacello et al. 2008). The altimetry profile provides the sum of the
263 elevation gain and loss along the path. We consider the average of this value among
264 the four paths as an effective measure of terrain ruggedness. In fact, the value pro-
265 vides a standardized assessment of the amount of vertical traveling (either uphill or
266 downhill) imposed by traversing a landscape. Moreover, the value is not dependent
267 on the altitude of the starting point. After testing the method on several landscapes,
268 it was decided to consider “flat” terrain as having an average value between 0 and
269 500 m for the sum of elevation gain and loss. “Moderately hilly” was defined as a
270 sum between 500 and 1,000 m; “hilly-mountainous” as a sum between 1,000 and
271 1,500 m. Finally, we consider “mountainous” territory to have a sum above 1,500 m.
272 For example, the Black Hills in Wyoming (United States) and the iconic landscape
273 of the Tuscany hills (Italy) both average ~1,000 m, while the Himalayan village of
274 Chukhung, Nepal, at the fringes of Mount Everest, averages 2,512 m. Using this
275 method, the site of Neuburg falls in the “flat” category, averaging 202.5 m, while
276 Alfedena (average 1,580 m), Arene Candide (average 1,868 m), and Romito (aver-
277 age 1,875 m) fall in the “mountainous” category.

278 6.2.2 Methods

279 Cross-sectional properties were calculated at 50 % bone length, using three differ-
280 ent methods: (1) polysiloxane molds and measurements of biplanar radiographs of
281 the diaphysis for the Late Upper Paleolithic sample and the majority of the Ligurian
282 Neolithic sample (O’Neill and Ruff 2004); (2) polysiloxane molds of the cortical
283 contour and regression equations for some Ligurian Neolithic individuals and the
284 Iron Age sample (Sparacello and Pearson 2010); (3) pQCT scans for the modern
285 athlete and control samples (Shaw and Stock 2009). Previous research has demon-
286 strated the compatibility of results obtained using different techniques (Stock 2002;
287 Stock and Shaw 2007; Sparacello and Pearson 2010; Davies et al. 2012). For the
288 first two methods, dry bones were positioned following Ruff (2002) and Marchi
289 (2007); for the third method, limbs of the living individuals were held in place
290 using purpose-designed clamping devices as described in Shaw and Stock (2009).

291 The cross-sectional variable Z_p (section modulus) is used here to evaluate overall
292 bone rigidity in both the tibia and the fibula. Z_p is calculated by raising the polar
293 second moment of area (J) to the power of 0.73 (Ruff 1995, 2000b). Mechanical
294 loading of long bones is a function of physical activity, bone length, and body mass
295 (Ruff 2000b). Thus, to identify behaviorally significant differences in robusticity, it
296 is necessary to control for the effects of body size. Z_p was scaled for body size by
297 dividing it by bone mechanical length and body mass (Ruff 2000a, b). Body mass was
298 calculated from femoral head superoinferior (SI) diameter by averaging the values
299 obtained using equations in Grine et al. (1995), McHenry (1992), and Ruff et al. (1991).

[AU3]

Diaphyseal shape in CSG refers to the ratios of second moment of areas (SMAs), which are proportional to bending rigidity. For the tibia, I_{\max}/I_{\min} (ratio of the maximum and minimum SMA) was used, while for the femur, I_x/I_y (ratio of SMAs calculated about ML and AP planes) was used. Relative fibular robusticity was calculated as $100 \times (J \text{ fibula} / J \text{ tibia})$. Shape indices and relative fibular robusticity are derived from unstandardized data.

Statistical analysis consisted of a one-way ANOVA for each variable considered in this study, and both Fisher LSD and Tukey HSD post-hoc tests. Using Fisher LSD with seven groups increases the risk of Type I errors, because it does not correct for multiple comparisons. Tukey HSD corrects for multiple comparisons, but given the small sample size of several samples included here, this test may be too restrictive for the purposes of this study. We present results for both tests and base our discussion on the LSD test. However, we note instances for which LSD and HSD tests provide different results. In those cases, results should be further verified using a larger sample size. All statistical analyses were carried out with STATISTICA 10 (Statsoft Inc. 2011).

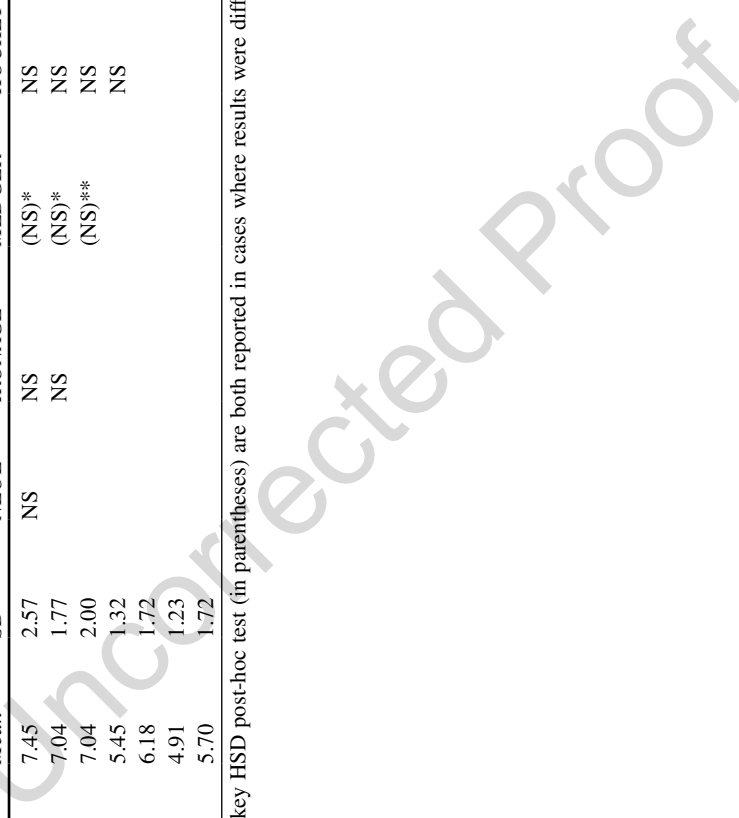
6.3 Results

Table 6.2 shows the mean, standard deviations, Fisher LSD, and Tukey HSD post-hoc results for comparisons of femoral, tibial, and fibular CSG variables. Figure 6.1 displays the femoral shape index (I_x/I_y) of those bioarchaeological samples for which the femur was available (Late Upper Paleolithic, Neolithic, and Iron Age). The Late Upper Paleolithic and Neolithic samples show midshaft femora that are more elliptical and AP oriented, while the Iron Age sample displays significantly more circular sections (Fig. 6.1 and Table 6.2).

Figure 6.2 displays variation in tibial Z_p across all samples. Tibial Z_p is higher in the bioarchaeological samples settled in mountainous areas (Late Upper Paleolithic, Neolithic, and Iron Age samples) when compared with the sedentary sample settled in a flat terrain (medieval individuals). However, only the comparison between the Neolithic and medieval sample is significant after correcting for multiple comparisons. Within the samples settled in a rugged terrain, the less mobile Iron Age individuals have the lowest average value of tibial Z_p , and the difference is significant when compared with Neolithic individuals. Late Upper Paleolithic, Neolithic, and Iron Age individuals are not significantly different from runners (which have the highest values among modern samples) and have significantly higher tibial Z_p than the sedentary control sample (Table 6.2).

Figure 6.3 displays variation in tibial shape (I_{\max}/I_{\min}). Tibial shape reveals a diachronic decreasing trend from the Late Upper Paleolithic sample to the medieval sample, and all pairwise comparisons are significant according to LSD post-hoc analyses, but not according to the Tukey HSD post-hoc analyses (Table 6.2). When compared with the modern athlete samples, the Late Upper Paleolithic sample shows a significantly higher shape index than runners, while the Neolithic and

12.28	RUNNERS	15	11.13	2.61										NS
12.29	CONTROL	21	10.1	2.23										
12.30	<i>(J Tibula/J Tibia) × 100</i>													
12.31	LUP	7	7.45	2.57	NS	NS	(NS)*	NS	NS	(NS)*	(NS)*	(NS)*	(NS)*	(NS)*
12.32	NEOL	15	7.04	1.77	NS	NS	(NS)*	NS	NS	(NS)*	(NS)*	(NS)*	(NS)*	(NS)*
12.33	IRONAGE	21	7.04	2.00			(NS)**	NS	NS	(NS)**	(NS)**	(NS)**	(NS)**	(NS)**
12.34	MEDGER	14	5.45	1.32										
12.35	HOCKEY	17	6.18	1.72										
12.36	RUNNERS	15	4.91	1.23										NS
12.37	CONTROL	21	5.70	1.72										(NS)*
12.38	*Fisher LSD post-hoc test and Tukey HSD post-hoc test (in parentheses) are both reported in cases where results were different. NS nonsignificant; * <i>p</i> <0.05;													
12.39	*** <i>p</i> <0.001; **** <i>p</i> <0.001													



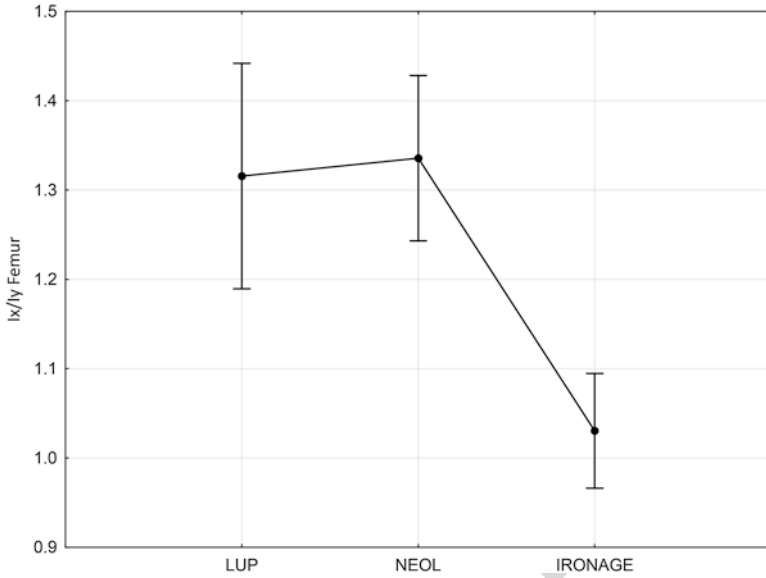


Fig. 6.1 Femoral shape index I_x/I_y . I_x =anteroposterior bending rigidity; and I_y =mediolateral bending rigidity. *LUP* Late Upper Paleolithic, *NEOL* Neolithic, *IRONAGE* Iron Age

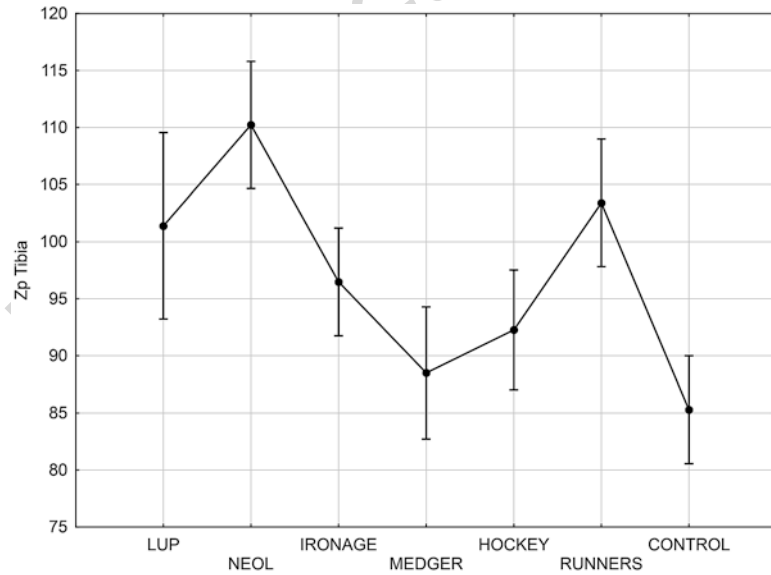


Fig. 6.2 Tibial section modulus Z_p : size-standardized diaphyseal torsional rigidity. *LUP* Late Upper Paleolithic, *NEOL* Neolithic, *IRONAGE* Iron Age, *MEDGER* Medieval, *HOCKEY* field hockey players, *RUNNERS*, cross-country runners, *CONTROL* sedentary control

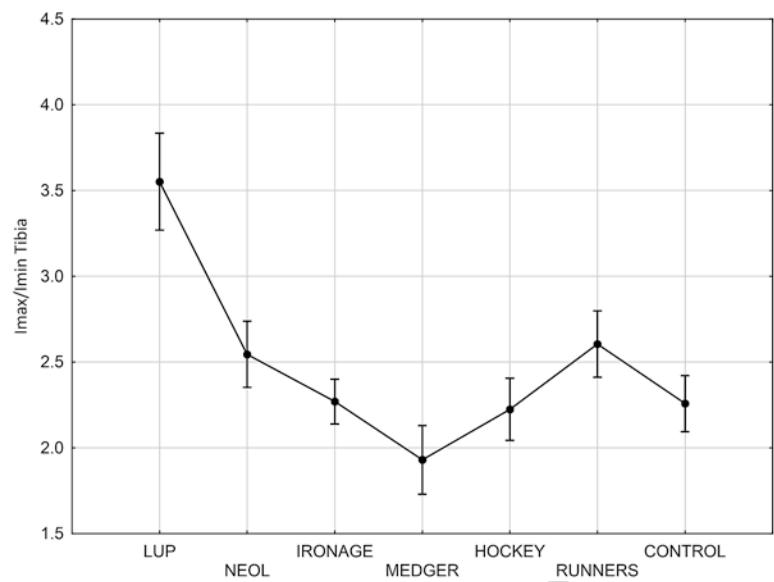


Fig. 6.3 Tibial shape index I_{max}/I_{min} : I_{max} =maximum bending rigidity; I_{min} =minimum bending rigidity. *LUP* Late Upper Paleolithic, *NEOL* Neolithic, *IRONAGE* Iron Age, *MEDGER* Medieval, *HOCKEY* field hockey players, *RUNNERS* cross-country runners, *CONTROL* sedentary control

runner samples show comparable values. Iron Age individuals have a shape index that is comparable with hockey players and the control sample.

Figure 6.4 displays variations in fibular Z_p . As seen for tibial Z_p , within bioarchaeological samples, fibular Z_p of the samples settled in mountainous areas (Late Upper Paleolithic, Neolithic, and Iron Age) is significantly higher than values in the sedentary control sample and those settled in flat terrain (medieval sample). These results are still significant after correcting for multiple comparisons with the Tukey HSD test. The bioarchaeological samples settled in mountainous areas also display higher values of fibular Z_p than most of the modern samples. After correcting for multiple comparisons by using the Tukey HSD test, comparisons of the Late Upper Paleolithic and Iron Age samples with hockey players and runners are not significant at the 0.05 level. Among the samples settled in rugged terrains, the less mobile Iron Age individuals display the lowest average fibular Z_p , but differences from other samples settled in rugged terrains are not statistically significant.

Figure 6.5 displays variations in relative fibular rigidity [$100 \times (\text{fibula } J / \text{tibia } J)$]. All of the bioarchaeological samples settled in mountainous areas (Late Upper Paleolithic, Neolithic, and Iron Age samples) have a relatively more robust fibula when compared to the medieval, runner, and control samples. However, after correcting for multiple comparisons, the same groups show a significantly higher value of relative fibular rigidity only in comparison to runners. No significant difference is present when compared with hockey players. Finally, no differences in relative fibular robusticity are present within samples settled in a rugged terrain.

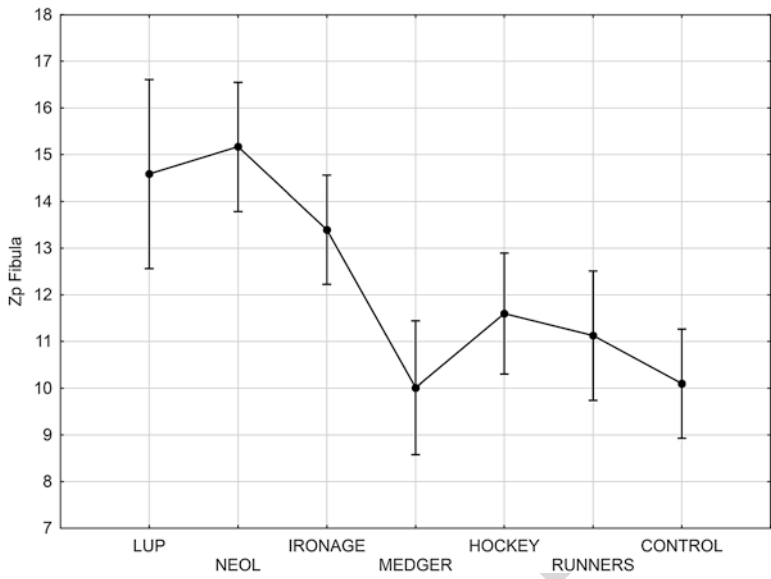


Fig. 6.4 Fibular section modulus Z_p : size-standardized diaphyseal torsional rigidity. *LUP* Late Upper Paleolithic, *NEOL* Neolithic, *IRONAGE* Iron Age, *MEDGER* Medieval, *HOCKEY* field hockey players, *RUNNERS* cross-country runners, *CONTROL* sedentary control

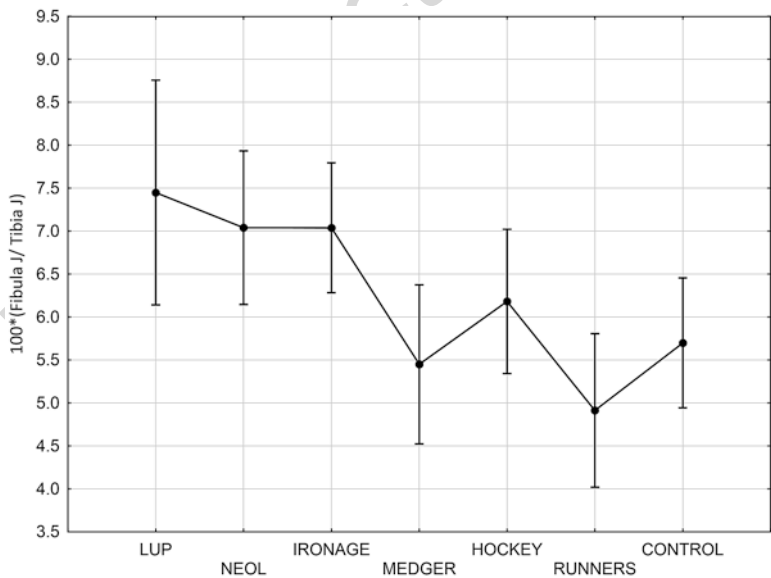


Fig. 6.5 Fibular relative robusticity: ratio between fibular J (polar moment of area) and tibial J. *LUP* Late Upper Paleolithic, *NEOL* Neolithic, *IRONAGE* Iron Age, *MEDGER* Medieval, *HOCKEY* field hockey players, *RUNNERS* cross-country runners, *CONTROL* sedentary control

6.4 Discussion and Conclusion

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The purpose of this research was to investigate the concomitant effects of mobility level and mobility type on lower limb mechanical properties, and in particular, fibular robusticity and tibio-fibular robusticity ratios. We compared bioarchaeological and modern samples, each with different levels of mobility (known or inferred on the basis of subsistence), and with or without factors influencing ML loadings (sport-induced changes in direction or terrain ruggedness). Overall, the results suggest that including the fibula in bioarchaeological behavioral reconstruction may provide insights on the “type” of mobility performed.

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Femoral shape indices could be calculated for Late Upper Paleolithic, Neolithic, and Iron Age individuals and confirm the expectations based on previous research: Late Upper Paleolithic and Neolithic individuals show similarly elliptical and AP-oriented femoral midshaft cross sections that are likely the result of high mobility levels, while Iron Age people display a significantly more circular midshaft shape. This finding is in agreement with Ruff’s work (1999, 2000a), which concluded that femoral shape indices are good indicators of mobility levels after terrain is factored out. Tibial cross-sectional properties provide a less clear correspondence with mobility levels. Given the same terrain, tibial Z_p is generally higher in more mobile groups, as evidenced by the comparison between Neolithic and Iron Age individuals, and between modern athletes and controls. However, if mobility was the only factor responsible for tibial diaphyseal robusticity, we would expect the Late Upper Paleolithic individuals to be significantly more robust than Iron Age individuals and that Iron Age individuals should not be significantly more robust than medieval individuals. Instead, we did not find any significant difference between Late Upper Paleolithic and Iron Age individuals, while the latter showed significantly more robust tibiae than medieval individuals (although the comparison is nonsignificant after correcting for multiple comparisons). For the comparison between Late Upper Paleolithic and Iron Age samples, the small sample size of the Late Upper Paleolithic sample could have played a role. We propose that terrain plays a major role in determining tibial diaphyseal robusticity. As Ruff (1999, 2000a) suggested for the femur, when comparing groups settled in similar terrains, the influence of different mobility levels seems to decline. This would also explain why the Iron Age individuals, who we assume were not very mobile but were settled in a mountainous area, show tibial Z_p values significantly higher than medieval individuals and sedentary modern controls, and comparable with the ones shown by hockey players.

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Previous research hypothesized that tibial shape may be influenced by both mobility level (increasing AP bending rigidity, and thus I_{max}) and frequent inversion/eversion of the foot caused by frequent changes of direction or terrain unevenness (increasing the ML bending rigidity, and thus I_{min}) (Marchi et al. 2011; see also Higgins 2014, for a comparable result in bovid metacarpals). Taking into account the influence of both mobility and terrain conformation on tibial shape, we would predict that, when comparing groups settled in areas with similar topographies, more mobile groups will show higher shape indices (less circular diaphyseal cross sections). Our results partially support these expectations, but some pairwise differences

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407 are difficult to explain in this framework and call for more investigation on the
408 reliability of tibial shape as an indicator of mobility levels. Within groups settled in
409 a mountainous terrain, the more mobile Late Upper Paleolithic and Neolithic indi-
410 viduals show a higher shape index than Iron Age individuals. However, Late Upper
411 Paleolithic individuals have extremely platycnemic tibiae (Fig. 6.3); if tibial shape
412 was strictly correlated with mobility, this would signal that these individuals were
413 much more mobile than Neolithic individuals. Although this explanation may be
414 possible, the signal should have been similar when comparing femoral shape and
415 tibial robusticity. Even more problematic is the result of comparisons involving
416 medieval and control individuals. It is difficult to imagine a more sedentary lifestyle
417 than the one performed by modern college students who work out less than one hour
418 a week (Shaw and Stock 2009). The medieval agricultural lifestyle required at least
419 some degree of mobility due to farming activities. Yet, medieval individuals show
420 significantly less elliptical tibial cross-sectional shape than control individuals. Both
421 samples dwelled on flat terrain, which excludes the possibility that the higher shape
422 in medieval individuals is due to traversing rugged terrains. It is more likely that, as
423 Stock (2006) suggested, tibial shape is influenced by factors in addition to mobility
424 and terrain, causing the extreme values found here in Late Upper Paleolithic and
425 medieval German individuals (Fig. 6.3).

426 Mobility as generally implied in bioarchaeological studies, i.e., the amount of
427 traveling due to subsistence activities, is probably only one of the factors that char-
428 acterize lower limb robusticity and shape. The type of substratum, different inten-
429 sity and repetitiveness of activity, and the linearity or nonlinearity of the movement
430 should be taken into account when analyzing mobility (Carlson and Judex 2007;
431 Shaw and Stock 2009; Carlson 2014). For the Late Upper Paleolithic and medieval
432 samples, activities such as long distance running or plowing, or other factors hith-
433 erto not investigated, may have had an influence on shaping lower limb properties.
434 However, it is difficult to incorporate information on the type of movements per-
435 formed by past populations for subsistence tasks. It appears that the inclusion of the
436 fibula in the study of lower limb bone structure can provide useful insights when
437 developing behavioral interpretations in bioarchaeological contexts.

438 While tibial Z_p is significantly higher in the Neolithic sample when compared
439 with the Iron Age sample (a difference that we interpreted as due to different levels
440 of mobility in similar terrains), the groups settled in mountainous areas show more
441 robust fibula compared with non-mountainous samples, regardless of the assumed
442 level of mobility (although some of the pairwise comparisons would not be signifi-
443 cant after correcting for multiple comparisons). Furthermore, while runners have
444 the highest tibial rigidity among modern samples (Fig. 6.2), no significant differ-
445 ence in fibular robusticity is present among modern groups, and the highest value is
446 displayed by hockey players (Fig. 6.4). Fibular Z_p appears, therefore, not signifi-
447 cantly influenced by the level of mobility, but mainly correlated with terrain proper-
448 ties and with sport-dictated frequent changes of direction.

449 The pattern described above for fibular diaphyseal rigidity is more apparent
450 when considering the ratio between fibular and tibial diaphyseal rigidity. All the
451 groups settled in a mountainous terrain show significantly higher fibula/tibia ratios

than all other groups (with the exception of hockey players). This ratio appears not to be influenced by mobility levels given equivalent terrain conditions. In fact, Late Upper Paleolithic, Neolithic, and Iron Age individuals display similar values, and also medieval, modern runners, and control individuals are not significantly different from each other. Hockey players show the highest fibula/tibia ratio among groups settled in plain areas, and the result is significant when compared to the ratio of runners. It therefore appears that what drives the increase in relative (to the tibia) fibular robusticity may be either terrain ruggedness or sport-related abrupt changes of direction, i.e., activities that have in common high levels of foot eversion/inversion. It should be noted, however, that after correcting for multiple comparisons the bioarchaeological samples settled in mountainous areas show significantly higher fibula/tibia ratios only in comparison to runners, whose ratio is low due to high tibial robusticity (Fig. 6.2). This calls for further verification of the results found here using a larger sample size.

The above results suggest a clear and coherent correspondence between fibular cross-sectional properties, relative fibular proportions, and factors increasing the frequency of foot eversion/inversion, such as frequent and abrupt changes of direction (Marchi and Shaw 2011) and traveling on uneven surfaces (Marchi et al. 2011). Rugged terrain may also increase fibular loading using a different mechanism than increasing the frequency of foot eversion/inversion: traveling downhill on particularly rugged terrain may increase the frequency of high-impact ground reaction forces that enhance fibular robusticity compared to traveling on level rugged terrain (Rantalainen et al. 2010). The apparent specificity of the response of the tibio-fibular complex should be further verified through experimental studies and larger sample sizes. However, the study of the tibio-fibular complex in bioarchaeology may integrate additional inferences about past population mobility. For example, in areas with mixed relief, with plains and mountains, a robust fibula with a high fibula/tibia ratio may indicate a preferential subsistence-related exploitation of mountainous areas. The same properties can be used to assess degree of exploitation of inland resources by coastal hunter-gatherers, provided that the inland region is mountainous.

Femoral shape and, to a lesser extent, tibial robusticity are integral to inferences of mobility patterns in past populations. Results presented here suggest that fibular analyses also have the potential to improve these inferences by providing anatomical information that may reflect variation in loading directionality and ankle mobility.

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Queries	Details Required	Author's Response
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AU3	The citation "Ruff, 2000" has been changed to "Ruff 2000a, 2000b". Please check if appropriate.	
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Uncorrected Proof