# The “Shear Resistance-Priority Hypothesis”: A Means for Enhancing Understanding of Material Adaptations in Bones that Habitually Experience Complex Loading

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In anthropological studies of cortical bone adaptation in limb-bone diaphyses there is an unrecognized bias — the bones examined are often habitually/stereotypically subjected to complex loading. Consequently, bone matrix adaptations can be difficult to interpret because complex loading engenders prevalent/predominant shear strains. Of the three strain modes (shear, tension, and compression) shear is potentially most deleterious (bone is strongest and more resilient in compression). Non-uniform strain distributions in cortical bone, whether produced by bending or combined bending/torsion, are an essential consequence of a bone’s function because they are linked to predictability of load and nutrient delivery. One solution for the regional prevalence/predominance of tension and compression in generally exclusive regions in habitually bent bones is the formation of strain-mode-specific osteon morphotypes and/or predominant collagen fiber orientation (CFO). If, however, a bone is loaded primarily in torsion, then clear regional variations in histomorphological adaptations for these ‘conventional’ strain modes do not occur. This is because in limb-bone diaphysis loaded in habitual torsion there are no significant regional disparities in strain modes. The prevalent/predominant mode in torsion is shear; by the adult stage, the adaptation for this mode might be seen as relative greater uniformity in matrix organization when compared to bones that experience habitual bending with little torsion (e.g., CFO is relatively more uniform across the entire bone cross-section). Because this is not intuitive, we recommend considering the “shear resistance-priority hypothesis” (see figure at far LOWER RIGHT), which helps in understanding how a bone might adapt at the material level when the strain milieu has prevalent/predominant shear.

**Most anthropology studies use bones in “High Complexity Category”.**

## Habitual Load Complexity Categories Based on N.A. Rotation Criterion‡

| Complexity Category | Examples |
|---|---|
| **Low** (N.A.: <10° rotation) (Tension and compression minimally overlap; Shear is localized near N.A.) | **1. artiodactyl and perissodactyl calcanei** (Lanyon, 1974; Su et al.,1999)<br>**2. potoroo calcaneus** (Biewener et al., 1996)<br>**3. chicken metatarsus** (Judex et al.,1997; Skedros et al., 2003) |
| **Intermediate A** (N.A.: 10° - 20° rotation) | **4. dog, sheep and horse radii** (Carter et al., 1980; Coleman et al., 2002)<br>**5. macaque ulna** (Demes et al., 1998; Skedros et al., 2003) |
| **Intermediate B** (N.A.: 20° - 40° rotation) | **6. sheep metatarsal** (Lieberman et al., 2004)<br>**7. chimpanzee femoral neck** (Kalmey and Lovejoy, 2002; Skedros et al., 2008)<br>**8. immature turkey ulna** (Skedros and Hunt, 2004)<br>**9. horse third metacarpal** (Gross et al., 1992; Skedros et al., 1996)<br>**10. human tibia** (Lanyon et al., 1975; Burr et al., 1996; Milgrom et al., 2000; Peterman et al., 2001)<br>**11. human femur proximal diaphysis** (Skedros et al., 1999) |
| **High** (N.A.: >40° rotation) (Tension and compression overlap extensively; Shear is relatively more diffusely distributed across the cortex when compared to other categories.) | **12. goat radius** (Main and Biewener, 2004; Main, 2007; Moreno et al., 2008)<br>**13. mature turkey ulna** (Rubin and Lanyon, 1985; Skedros and Hunt, 2004)<br>**14. horse third metacarpal** (Skedros et al., 2006)<br>**15. human tibia (in some athletes)** (Lanyon et al., 1975; Burr et al., 1996; Milgrom et al., 2000; Peterman et al., 2001)<br>**16. human femur mid-diaphysis** (Cristofolini et al., 1996; Goldman et al., 2003; Drapeau and Streeter, 2006)<br>**17. sheep tibia** (Lanyon and Bourn, 1979; Lieberman et al., 2004)<br>**18. pigeon humerus** (Biewener and Dial, 1995)<br>**19. chimpanzee femoral neck** (Kalmey and Lovejoy 2002; Skedros et al., 2008)<br>**20. human femoral neck** (Pidaparti and Turner, 1997; Skedros et al., 1999; Skedros and Baucom, 2007)<br>**21. free-flying bat humerus** (Swartz et al., 1992)<br>**22. chicken femur** (Carrano and Biewener, 1999; Skedros, 2002)<br>**23. alligator femur** (Blob and Biewener, 1999; Lee, 2004)<br>**24. greyhound femur** (Szivek et al., 1992) |

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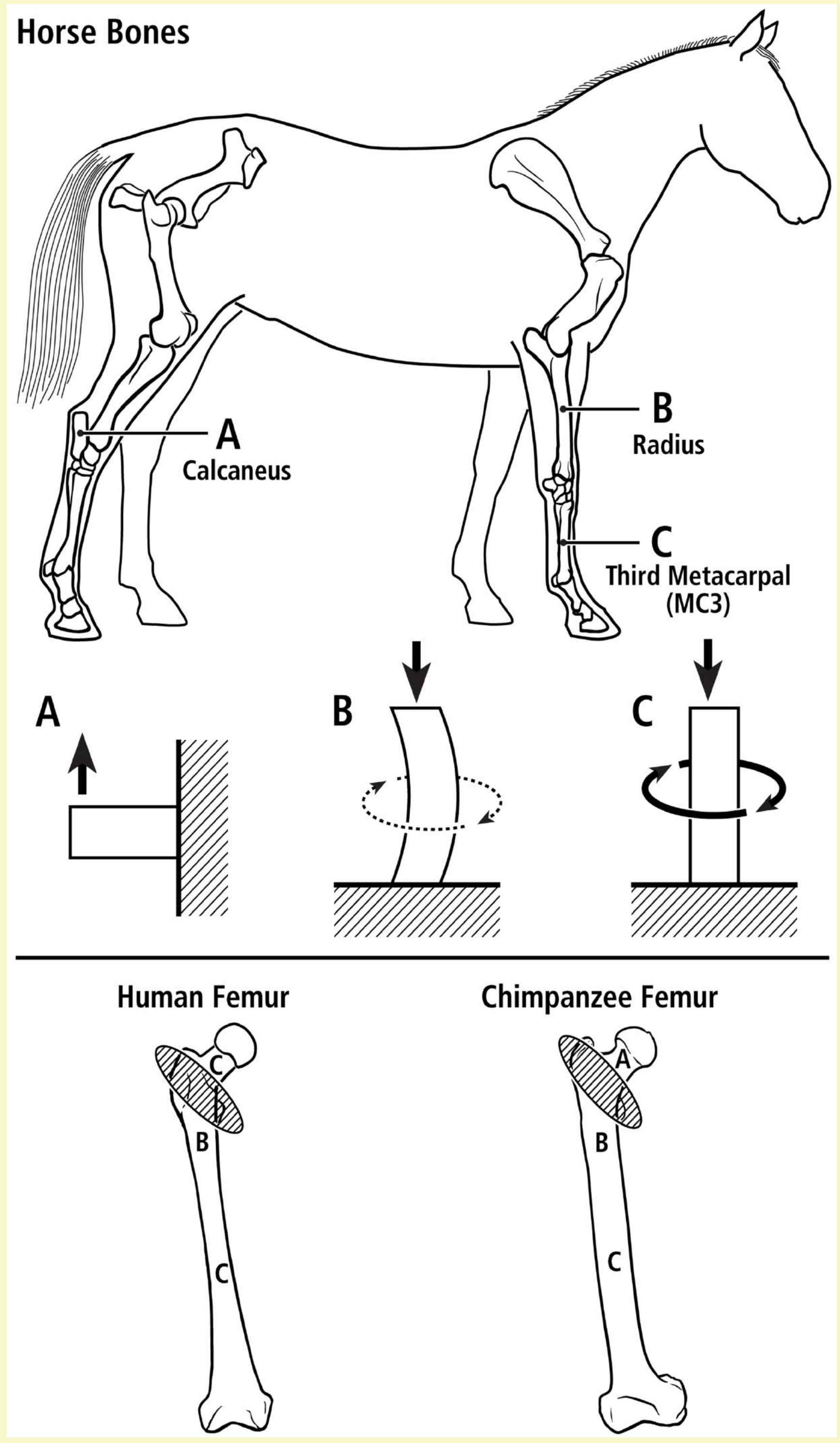
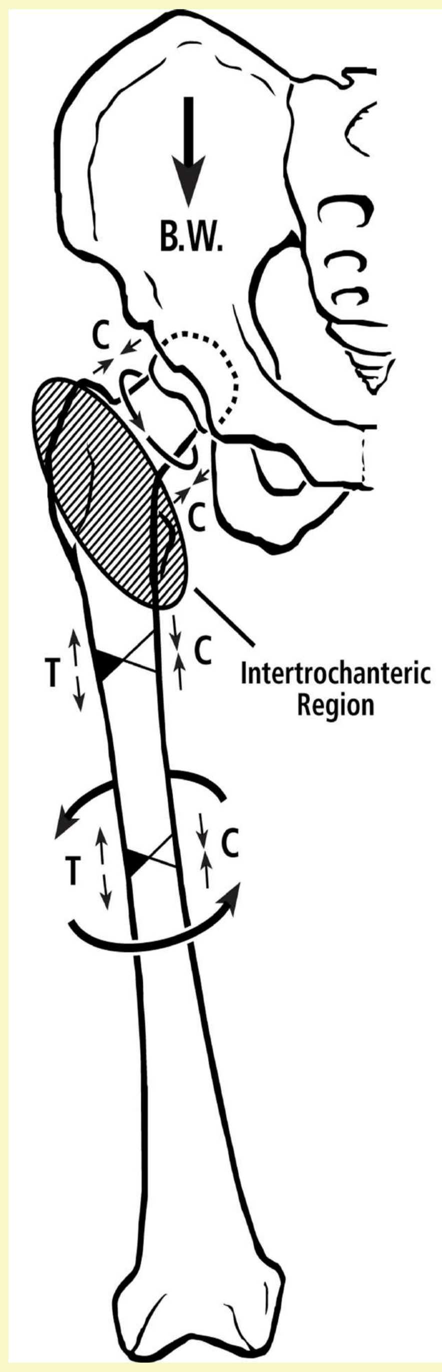
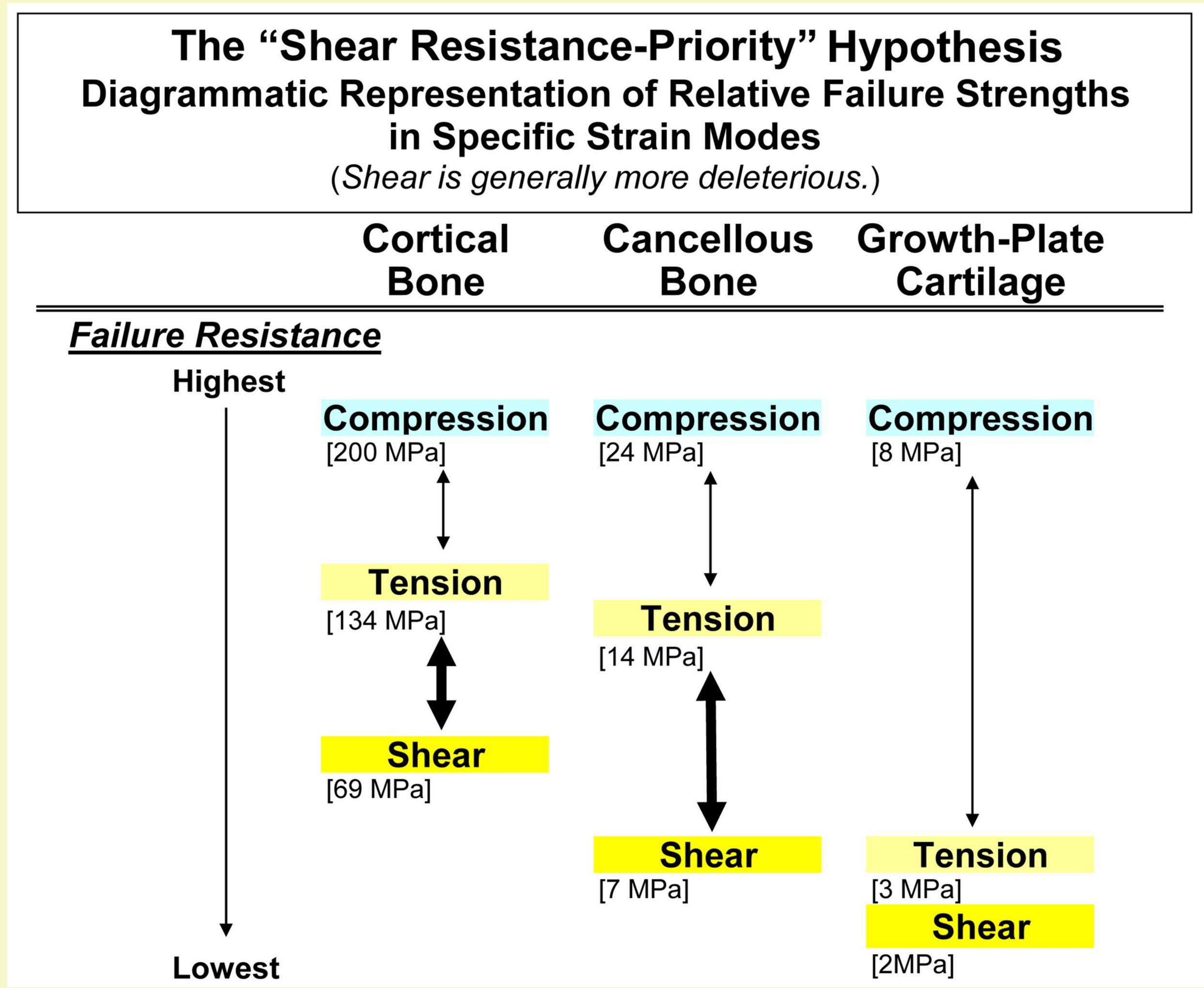
‡ The criterion used to designate these categories is the magnitude of the rotation of neutral axis (**N.A.**) during middle portion of stance phase. As shown by the **double-headed arrows**, this criterion can place some bone regions or closely related bones in different habitual load-complexity categories; for example: (1) sheep and goat radii, (2) human proximal femoral diaphysis and mid-diaphysis, and (3) immature and mature turkey ulnae. In some cases the bone can be placed into a different category if there are differences in habitual load complexity as a result of physical activity (e.g., increased torsion in human tibiae of individuals who regularly participate in twisting/turning sports). This possibility is usually seen in primates; more specifically, is almost always secondary to human volition (e.g., sports training) or human intervention (e.g., horse or greyhound dog racing). Additional discussion of the strengths and limitations of these categories can be found in Skedros (2012).




At **LEFT** top are bones of an adult horse showing a spectrum from low to high complexity loading, respectively: calcaneus (A), radius (B), and third metatarsal (MC3) (C). The drawings are simplified renditions showing: (A) the calcaneus as a cantilevered beam, (B) the radius as a curved beam with longitudinal loading; the curvature accentuates bending. Torsion (dotted line) is also present but is less than the torsion in the MC3 (solid circular line in C), and (C) the MC3 with off-axis longitudinal loading producing bending and torsion, the latter being greater than in the other two bones. At the **LOWER LEFT** and at **RIGHT** are the hypothesized multidomains for a human and chimpanzee femur.

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