

# Load Complexity Categories in Limb Bones: A Working Hypothesis for Bone Adaptation Studies

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**INTRODUCTION:** Bone adaptation studies often consider the load history of a region of a bone as the basis for identifying structural or material adaptations to the habitual (i.e., ‘typical/baseline’) loading environment and/or changes that occur in that environment. The load history of a bone region (e.g., mid diaphysis of a long bone) is often based on an averaged known, or presumed, strain distribution. Histomorphological (bone material) adaptations to the strain history of a bone region can manifest very differently as the complexity of habitual loading increases. Failure to recognize that there are gradations in the manifestations of a bone’s structural and material organization with respect to differences in habitual load history can lead to misinterpretations of the presence of characteristics presumed to represent adaptation (e.g., regional variations in distributions of secondary osteons, cortical thickness, and mineral content) vs. the absence of ‘expected’ adaptations. To help clarify the strengths and limitations of interpreting the habitual load history, or changes in this load history, for studies that draw comparisons between bones where load complexity might be confounding, we have devised a strategy that employs what we call ‘load complexity categories.’

**METHODS:** Four distinct load complexity categories were determined from published data of *in vivo* and *ex vivo* strain data (in some cases only indirect or finite element data were available) (see below for internet link to references). These four categories are currently based on neutral axis rotation during typical loadings of the bone region: (1) low complexity ( $\pm 10^\circ$ ), (2) intermediate complexity A ( $\pm 10$ - $20^\circ$ ), (3) intermediate complexity B ( $\pm 20$ - $45^\circ$ ), and (4) high complexity ( $>45^\circ$ ). Three researchers trained in biomechanics individually reviewed each study to determine the degree of NA rotation of the bones discussed in each study. We also included some studies that did not explicitly define neutral axis rotation, but contained sufficient strain gauge data that allowed for reasonable inference of what category the bone belonged in. For example, the human femur is a highly studied bone, but there is only one known study describing *in vivo* strain on the lateral cortex of the human proximal femur (Aamodt et al., 1997).

**RESULTS:** After extensive literature review and evaluation of relevant studies, 68 studies ranging across a wide variety of mammalian, avian, and reptilian species were placed into one of four load complexity categories (low, moderate A, moderate B, high). The results are shown below.

**DISCUSSION:** Load complexity categories have the potential to guide future bone adaptation research, clarify contradictions about strain-related bone adaptation, and elucidate relationships between bone material heterogeneities between bones and/or bone regions and local loading environments. It is important to emphasize, however, that this is a ‘working hypothesis’ and limitations include the paucity of *in vivo* strain data in anthropoid bones and the imperfect criteria used to designate the categories — defined by the magnitude of change in neutral axis location during habitual/controlled ambulation. Future studies on load complexity could use coefficients of variation in peak strains (Main & Biewener, 2004) or other measures of variation of the strain milieu to segregate bones into discrete load complexity categories. More research is needed to explore these or other criteria in order to advance the validity and utility of the load-complexity category as an important ‘working hypothesis.’ We recognize that less frequent natural gait-related activities can shift the neutral axis beyond the ‘habitual range’ and this, even if very brief, might be sufficient to evoke cortical bone adaptation that confounds attempts to make simple interpretations (Main, 2007; Moreno et al., 2008; Rubin et al., 2013). Our designation of “neutral axis regions” is also least rigorous in bones in the moderate-complexity categories (i.e., there is a greater potential for overlap in these bones with the other categories) (Skedros et al., 2006), which is the main reason why in our prior study we conducted our statistical analyses using data from the moderate A and B categories combined into one category. Rubin et al. (2013), Skedros et al. (2006), and Judex et al. (1997) discuss various problems with the assumption that characteristics of peak stresses or strains are important in causing regional variations in bone histomorphological adaptation.

**SIGNIFICANCE:** Load complexity categories have the potential to guide future bone adaptation research, clarify contradictions about strain-related bone adaptation, and elucidate relationships between bone material heterogeneities between bones and/or bone regions and local loading environments.

Complexity Category	Examples	Complexity Category	Examples
(Based on N.A. rotation during middle portion of typical load phase.)		(Based on N.A. rotation during middle portion of typical load phase.)	
<b>Low</b> (N.A.: $<10^\circ$ rotation) (Tension and compression minimally overlap; Shear is localized near N.A.)	<b>1. artiodactyl and perissodactyl calcanei</b> (Lanyon, 1974; Su et al., 1999; Skedros et al., 2019) <b>2. potoroo calcaneus</b> (Biewener et al., 1996) <b>3. chicken tarsometatarsus (TMT) *</b> (Judex et al., 1997; Skedros et al., 2003a) <b>4. iguana tibia &amp; femur</b> (Blob and Biewener, 2001) <b>5. alligator tibia</b> (Blob and Biewener, 2001)	<b>High</b> (N.A.: $>45^\circ$ rotation) (Tension and compression overlap extensively; Shear is relatively more diffusely distributed across the cortex when compared to other categories.)	<b>25. human tibia (in some athletes) §</b> (Lanyon et al., 1975; Burr et al., 1996; Milgrom et al., 2000; Peterman et al., 2001; Yang et al., 2014) <b>26. human femur mid-diaphysis §</b> (Duda et al., 1998; Goldman et al., 2003; Drapeau and Streeter, 2006; Edwards et al., 2008) <b>27. human femoral neck</b> (Pidaparti and Turner, 1997; Skedros et al., 1999; Skedros and Baucom, 2007; Edwards et al., 2008) <b>28. chimpanzee femoral neck §</b> (Kalmey and Lovejoy 2002; Skedros et al., 2008) <b>29. dog femur mid-diaphysis</b> (Schatzker 1980; Szivek et al., 1992; Shahar et al., 2003) <b>30. horse third metacarpal §</b> (Skedros et al., 2006; Rubin et al., 2013) <b>31. goat radius §, **</b> (Main and Biewener, 2004; Main, 2007; Moreno et al., 2008) <b>32. sheep tibia</b> (Lanyon and Bourn, 1979; Lieberman et al., 2004; Gautier et al., 2000) <b>33. free-flying bat humerus</b> (Swartz et al., 1992; Swartz and Middleton, 2008; Skedros and Douré, 2019) <b>34. mature turkey ulna §</b> (Rubin and Lanyon, 1985; Skedros and Hunt, 2004) <b>35. emu femur and tibiotarsus</b> (Main and Biewener, 2007) <b>36. pigeon humerus</b> (Biewener and Dial, 1995; Skedros and Douré, 2019) <b>37. chicken femur</b> (Carrano and Biewener, 1999; Skedros, 2002) <b>38. alligator femur</b> (Blob and Biewener, 1999; Blob and Biewener, 2001; Lee, 2004)
<b>Moderate A</b> (N.A.: $10^\circ$ - $20^\circ$ rotation)	<b>6. dog, sheep and horse radii §, **</b> (Carter et al., 1980; Lanyon et al., 1982; Coleman et al., 2002; Takano et al., 1999) <b>7. dog ulna</b> (Carter et al., 1980) <b>8. macaque ulna</b> (Demes et al., 1998; Skedros et al., 2003a) <b>9. macaque tibia</b> (Demes et al., 2001) <b>10. river cooter turtle femur</b> (Butcher and Blob, 2008; Aiello et al., 2013)		
<b>Moderate B</b> (N.A.: $20^\circ$ - $45^\circ$ rotation)	<b>11. human fibula</b> (Lambert, 1971; Thomas et al., 1995; Weaver and Skedros, 2016) <b>12. human tibia §</b> (Lanyon et al., 1975; Burr et al., 1996; Milgrom et al., 2000; Peterman et al., 2001; Yang et al., 2014) <b>13. human femur proximal diaphysis §</b> (Cochran et al., 1980; Aamodt et al., 1997; Skedros et al., 1999; Skedros and Baucom, 2007; Skedros et al., 2012) <b>14. chimpanzee femoral neck §</b> (Kalmey and Lovejoy, 2002; Skedros et al., 2008) <b>15. dog tibia</b> (Bouvier and Hylander, 1984) <b>16. dog proximal femur</b> (Page et al., 1993; Shahar et al., 2003) <b>17. horse third metacarpal §</b> (Gross et al., 1992; Skedros et al., 1996) <b>18. sheep metatarsal</b> (Lieberman et al., 2004) <b>19. opossum femur</b> (Butcher et al. 2011; Gosnell et al., 2011) <b>20. armadillo femur</b> (Copplow et al., 2015) <b>21. bat metacarpal</b> (Swartz and Middleton, 2008; Skedros and Douré, 2019) <b>22. immature turkey ulna §</b> (Skedros and Hunt, 2004) <b>23. chicken tibiotarsus</b> (Biewener et al., 1986; Biewener and Bertram 1993; Vitiennes et al., 2023) <b>24. tegu lizard femur</b> (Sheffield et al., 2011)		

‡ These studies, despite not reporting neutral axis rotation, contain strain gauge and other types of data that allow for reasonable inference as to what category they belong.

§ (with color highlight) These are bones or bone regions that are in more than one category because of, for example, differences caused by habitual activity changes during ontogeny (e.g., domesticated turkey ulna), habit (e.g., goat vs. sheep radius, \*\*), or volitional activity (e.g., humans or racing horses).

\* Generally high shear strains can confound these categorizations in some cases (e.g., chicken TMT). This might also help explain why the human femoral neck is in the high complexity category (Skedros et al. 2023a).

**References:** A complete list can be found at: <https://teambone.com/themes/>.