A Mechanical Analysis of Suspensory Locomotion in Primates and Other Mammals

by

Michael Constantine Granatosky

Department of Evolutionary Anthropology
Duke University

Date:_____
Approved:

_____
Daniel Schmitt, Supervisor

_____
Christine Wall

_____
Richard Kay

_____
Kenneth Glander

_____
Pierre Lemelin

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Evolutionary Anthropology in the Graduate School
of Duke University

2016

ABSTRACT

A Mechanical Analysis of Suspensory Locomotion in Primates and Other Mammals

by

Michael Constantine Granatosky

Department of Evolutionary Anthropology
Duke University

Date:_____
Approved:

_____
Daniel Schmitt, Supervisor

_____
Christine Wall

_____
Richard Kay

_____
Kenneth Glander

_____
Pierre Lemelin

An abstract of a dissertation submitted in partial
fulfillment of the requirements for the degree
of Doctor of Philosophy in the Department of
Evolutionary Anthropology in the Graduate School of
Duke University

2016

Copyright by
Michael Constantine Granatosky
2016

Abstract

For primates, and other arboreal mammals, adopting suspensory locomotion represents one of the strategies an animal can use to prevent toppling off a thin support during arboreal movement and foraging. While numerous studies have reported the incidence of suspensory locomotion in a broad phylogenetic sample of mammals, little research has explored what mechanical transitions must occur in order for an animal to successfully adopt suspensory locomotion. Additionally, many primate species are capable of adopting a highly specialized form of suspensory locomotion referred to as arm-swinging, but few scenarios have been posited to explain how arm-swinging initially evolved. This study takes a comparative experimental approach to explore the mechanics of below branch quadrupedal locomotion in primates and other mammals to determine whether above and below branch quadrupedal locomotion represent neuromuscular mirrors of each other, and whether the patterns below branch quadrupedal locomotion are similar across taxa. Also, this study explores whether the nature of the flexible coupling between the forelimb and hindlimb observed in primates is a uniquely primate feature, and investigates the possibility that this mechanism could be responsible for the evolution of arm-swinging.

To address these research goals, kinetic, kinematic, and spatiotemporal gait variables were collected from five species of primates (*Cebus capucinus*, *Daubentonia madagascariensis*, *Lemur catta*, *Propithecus coquereli*, and *Varecia variegata*) walking quadrupedally above and below branches. Data from these primate species were

compared to data collected from three species of non-primate mammals (*Choloepus didactylus*, *Pteropus vampyrus*, and *Desmodus rotundus*) and to three species of arm-swinging primates (*Hylobates moloch*, *Ateles fusciceps*, and *Pygathrix nemaeus*) to determine how varying forms of suspensory locomotion relate to each other and across taxa.

From the data collected in this study, it is evident the specialized gait characteristics present during above branch quadrupedal locomotion in primates are not observed when walking below branches. Instead, gait mechanics closely replicate the characteristic walking patterns of non-primate mammals, with the exception that primates demonstrate an altered limb loading pattern during below branch quadrupedal locomotion in which the forelimb becomes the primary propulsive and weight-bearing limb – a pattern similar to what is observed during arm-swinging. It is likely that below branch quadrupedal locomotion represents a "mechanical release" from the challenges of moving on top of thin arboreal supports. Additionally, it is possible that arm-swinging could have evolved from an anatomically-generalized arboreal primate with tendencies to forage and locomote below branches. During these suspensory bouts, weight would have been shifted away from the hindlimbs towards the forelimbs, and, as the frequency of these bouts increased, the reliance of the forelimbs for weight support would have also increased. This functional decoupling may have released the hindlimbs from their weight-bearing role during suspensory locomotion, and eventually, arm-swinging would have replaced below branch quadrupedal locomotion as the primary mode of suspensory

locomotion observed in some primate species. This study provides the first experimental evidence supporting the hypothetical link between below branch quadrupedal locomotion and arm-swinging in primates.

Dedication

This work is dedicated to Michael and Maria Granatosky. Thank for instilling within me the love of scientific exploration, and teaching me that all things are possible through education.

Contents

Abstract iv

List of Tables xii

List of Figures xiv

Acknowledgements xxix

1. Introduction 1

1.1 A mechanical definition of suspensory locomotion 7

1.2 Taxonomic diversity of suspensory locomotion in mammals 11

1.2.1 Marsupialia 13

1.2.2 Xenarthra 13

1.2.3 Dermoptera 15

1.2.4 Primates 15

1.2.5 Scandentia 20

1.2.6 Chiroptera 21

1.2.7 Carnivora 22

1.2.8 Rodentia 23

1.3 Postcranial morphology associated with suspensory locomotion 23

1.3.1 Manual and pedal phalangeal morphology 24

1.3.2 Forelimb morphology 26

1.3.3 Hindlimb morphology 32

1.3.4 Axial morphology 36

1.4 The evolutionary origins of suspensory locomotion 38

1.5 Mechanical strategies during suspensory locomotion 46

1.5.1 Center-of-mass movements 47

1.5.2 Kinetics 52

1.5.3 Kinematics 65

1.5.4 Footfall patterns and timing 71

1.6 Specific goals 77

1.7 Hypotheses and predictions 79

2. Materials and Methods 88

2.1 Subjects 88

2.1.1 Species profiles 90

2.2 Data Collection 96

2.2.1 Kinetics 102

2.2.2 Kinematics 107

2.2.3 Spatiotemporal gait variables 110

2.3 Data Analysis 112

2.3.1 An intraspecific comparison of the mechanics of above and below branch quadrupedal locomotion 113

2.3.2 An interspecific comparison of the mechanics of below branch quadrupedal locomotion 116

2.3.3 An interspecific comparison of the mechanics of below branch quadrupedal locomotion and arm-swinging 119

3. Results 122

3.1 An intraspecific comparison of the mechanics of above and below branch quadrupedal locomotion 122

3.1.1 Kinetics 122

3.1.2 Kinematics 148

3.1.3 Spatiotemporal gait variables 171

3.2 An interspecific comparison of the mechanics of below branch quadrupedal locomotion 183

3.2.1 Kinetics 183

3.2.2 Kinematics 231

3.2.3 Spatiotemporal gait variables 276

3.3 An interspecific comparison of the mechanics of below branch quadrupedal locomotion and arm-swinging 295

3.3.1 Kinetics 295

3.2.2 Kinematics 331

3.2.3 Spatiotemporal gait variables 354

4. Discussion 366

4.1 A mechanical and evolutionary interpretation of below branch quadrupedal locomotion in primates and non-primate mammals 368

4.1.1 A mechanical synthesis of below branch quadrupedal locomotion in primates and non-primate mammals 368

4.1.2 An evolutionary perspective of below branch quadrupedal locomotion in primates and non-primate mammals 395

4.2 A mechanical and evolutionary interpretation of arm-swinging in primates 397

4.2.1 A mechanical synthesis of arm-swinging in primates 397

4.2.2 An evolutionary perspective of arm-swinging in primates 403

Literature Cited 411

Biography 442

List of Tables

Table 1. The percentage of quadrupedal and bimanual suspensory locomotion observed in the locomotor repertoires of primates. 2

Table 2. Animal subjects used in the study..... 89

Table 3: Limb loading data (mean ± standard deviation) and significance tests for above and below quadrupedal locomotion in four species of primates..... 123

Table 4. The timing of limb loading events throughout support phase (mean ± standard deviation) and significance tests observed during above and below branch quadrupedal locomotion in four species of primates. 125

Table 5: Mean and standard deviation values for kinematic gait variables collected during above and below branch quadrupedal locomotion in five species of primates..... 149

Table 6: Mean and standard deviation values for spatiotemporal gait variables collected during above and below branch quadrupedal locomotion in five species of primates. .. 172

Table 7: Limb loading data (mean ± standard deviation) and significance tests for below branch quadrupedal locomotion in primate and non-primate mammals. 184

Table 8: The timing of limb loading events throughout support phase (mean ± standard deviation) and significance tests observed during below branch quadrupedal locomotion in primate and non-primate mammals. 186

Table 9: Mean and standard deviation values for kinematic gait variables collected during above below branch quadrupedal locomotion in primate and non-primate mammals. .. 232

Table 10: Mean and standard deviation values for spatiotemporal gait variables collected during below branch quadrupedal locomotion in primate and non-primate mammals. . 277

Table 11. Limb loading data (mean ± standard deviation) for below branch quadrupedal locomotion and arm-swinging in primate and non-primate mammals. 296

Table 12: The timing of limb loading events throughout support phase (mean ± standard deviation) during below branch quadrupedal locomotion and arm-swinging in primate and non-primate mammals..... 297

Table 13: Mean and standard deviation values for kinematic gait variables collected during above below branch quadrupedal locomotion and arm-swinging in primate and non-primate mammals. 332

Table 14. Mean and standard deviation values for spatiotemporal gait variables collected during below branch quadrupedal locomotion and arm-swinging in primate and non-primate mammals. 355

List of Figures

Figure 1: Mammalian phylogeny (adapted from Springer et al., 2004) indicating the mammalian orders in which suspensory locomotion has evolved. 12

Figure 2: The various solutions to prevent toppling off a thin arboreal support. 41

Figure 3: Schematic diagram of force traces observed during suspensory locomotion. .. 54

Figure 4: Three locomotor characteristics that distinguish primates from other non-primate mammals. 58

Figure 5: Description and results of camera verification. 99

Figure 6: Representative force traces for *Lemur catta* during above branch quadrupedal locomotion. 128

Figure 7: Representative force traces for *Propithecus coquereli* during below branch quadrupedal locomotion. 129

Figure 8: Mean and standard deviation values of peak vertical forces in the forelimbs and hindlimbs in four species of primates. 130

Figure 9: Mean and standard deviation values of the first occurring horizontal peak force in the forelimbs and hindlimbs in four species of primates. 132

Figure 10: Mean and standard deviation values of the second occurring horizontal peak force in the forelimbs and hindlimbs in four species of primates. 133

Figure 11: Mean and standard deviation values of the net horizontal impulse in the forelimbs and hindlimbs in four species of primates. 135

Figure 12: Mean and standard deviation values of the first horizontal impulse in the forelimbs and hindlimbs in four species of primates. 137

Figure 13: Mean and standard deviation values of the second horizontal impulse in the forelimbs and hindlimbs in four species of primates. 138

Figure 14: Mean and standard deviation values of the medial peak in the forelimbs and hindlimbs in four species of primates. 140

Figure 15: Mean and standard deviation values of the lateral peak in the forelimbs and hindlimbs in four species of primates. 141

Figure 16: Mean and standard deviation values of the medial impulse in the forelimbs and hindlimbs in four species of primates. 142

Figure 17: Mean and standard deviation values of the lateral impulse in the forelimbs and hindlimbs in four species of primates. 143

Figure 18: Mean and standard deviation values of the mediolateral impulse in the forelimbs and hindlimbs in four species of primates. 144

Figure 19: The relationship between protraction to retraction ratio and net horizontal impulse during above branch quadrupedal locomotion in four primate species. 146

Figure 20: The relationship between protraction to retraction ratio and net horizontal impulse during below branch quadrupedal locomotion in four primate species. 147

Figure 21: Patterns of mean shoulder movement (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 153

Figure 22: Mean and standard deviation values of shoulder excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 154

Figure 23: Patterns of mean elbow movement (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 156

Figure 24: Mean and standard deviation values of elbow excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 157

Figure 25: Patterns of mean wrist movement (°) observed in two species of primate that use flexion/extension grasps during above branch quadrupedal locomotion. 159

Figure 26: Patterns of mean wrist movement (°) observed in five species of primate that use supinated hook grasps during above and below branch quadrupedal locomotion. .. 160

Figure 27: Mean and standard deviation values of wrist excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 161

Figure 28: Patterns of mean hip movement (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 163

Figure 29: Mean and standard deviation values of hip excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 164

Figure 30: Patterns of mean knee movement (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 166

Figure 31: Mean and standard deviation values of knee excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 167

Figure 32: Patterns of mean ankle movement (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 169

Figure 33: Mean and standard deviation values of ankle excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates..... 170

Figure 34: The relationship between log-transformed normalized speed and stride duration (sec) during above and below branch quadrupedal locomotion in five species of primates..... 174

Figure 35: The relationship between log-transformed normalized speed and stride distance (sec) during above and below branch quadrupedal locomotion in five species of primates..... 175

Figure 36: Forelimb duty factor (mean and standard deviation) during above and below branch quadrupedal locomotion in five species of primates..... 177

Figure 37: Hindlimb duty factor (mean and standard deviation) during above and below branch quadrupedal locomotion in five species of primates..... 178

Figure 38: Relative forelimb swing phase (mean and standard deviation) during above and below branch quadrupedal locomotion in five species of primates. 179

Figure 39: Relative hindlimb swing phase (mean and standard deviation) during above and below branch quadrupedal locomotion in five species of primates. 180

Figure 40: A modified “Hildebrand” plot (following the approach of Cartmill et al. 2002) displaying diagonality for multiple strides of each of the study species over hindlimb duty factor during above and below branch quadrupedal locomotion..... 182

Figure 41: Representative force traces for *Choloepus didactylus* during below branch quadrupedal locomotion..... 188

Figure 42: Mean and standard deviation values of peak vertical forces in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. 189

Figure 43: Multiple statistical comparisons between peak vertical forces in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. . 190

Figure 44: Multiple statistical comparisons between peak vertical forces in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. . 191

Figure 45: Multiple statistical comparisons between the timing of the peak vertical force in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 192

Figure 46: Mean and standard deviation values of first occurring horizontal peak in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion..... 195

Figure 47: Multiple statistical comparisons between the first occurring horizontal peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 196

Figure 48: Mean and standard deviation values of second occurring horizontal peak in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion..... 197

Figure 49: Multiple statistical comparisons between the second occurring horizontal peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 198

Figure 50: Multiple statistical comparisons between the second occurring horizontal peak in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 199

Figure 51: Multiple statistical comparisons between the timing of first occurring horizontal peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion..... 200

Figure 52: Multiple statistical comparisons between the timing of first occurring horizontal peak in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion..... 201

Figure 53: Multiple statistical comparisons between the timing of second occurring horizontal peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion..... 202

Figure 54: Multiple statistical comparisons between the timing of propulsive to braking transition in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 203

Figure 55: Multiple statistical comparisons between the timing of propulsive to braking transition in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 204

Figure 56: Mean and standard deviation values of the net horizontal impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. 206

Figure 57: Multiple statistical comparisons between the horizontal impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 207

Figure 58: Multiple statistical comparisons between the horizontal impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 208

Figure 59: Mean and standard deviation values of the first occurring horizontal impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. 210

Figure 60: Multiple statistical comparisons between the first occurring horizontal impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 211

Figure 61: Mean and standard deviation values of the second occurring horizontal impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. 212

Figure 62: Multiple statistical comparisons between the second occurring horizontal impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 213

Figure 63: Multiple statistical comparisons between the second occurring horizontal impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 214

Figure 64: Mean and standard deviation values of peak medial forces in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. 216

Figure 65: Multiple statistical comparisons between the medial peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 217

Figure 66: Mean and standard deviation values of lateral peak in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. 218

Figure 67: Multiple statistical comparisons between the lateral peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 219

Figure 68: Multiple statistical comparisons between the lateral peak in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 220

Figure 69: Mean and standard deviation values of the medial impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. 221

Figure 70: Multiple statistical comparisons between the medial impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. . 222

Figure 71: Multiple statistical comparisons between the medial impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. . 223

Figure 72: Mean and standard deviation values of the lateral impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. 224

Figure 73: Multiple statistical comparisons between the lateral impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. . 225

Figure 74: Multiple statistical comparisons between the lateral impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. . 226

Figure 75: Mean and standard deviation values of the mediolateral impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion..... 227

Figure 76: Multiple statistical comparisons between the mediolateral impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 228

Figure 77: Multiple statistical comparisons between the mediolateral impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 229

Figure 78: Multiple statistical comparisons between the timing of the lateral peak in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. 230

Figure 79: Patterns of mean shoulder movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals. 235

Figure 80: Multiple statistical comparisons between shoulder angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion. 236

Figure 81: Multiple statistical comparisons between shoulder angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. 237

Figure 82: Multiple statistical comparisons between shoulder angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. 238

Figure 83: Mean and standard deviation values of shoulder excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals..... 239

Figure 84: Multiple statistical comparisons between shoulder excursion in primate and non-primate mammals during below branch quadrupedal locomotion. 240

Figure 85: Patterns of mean elbow movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals. 242

Figure 86: Multiple statistical comparisons between elbow angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion..... 243

Figure 87: Multiple statistical comparisons between elbow angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. 244

Figure 88: Multiple statistical comparisons between elbow angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. 245

Figure 89: Mean and standard deviation values of elbow excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals..... 246

Figure 90: Multiple statistical comparisons between elbow excursion in primate and non-primate mammals during below branch quadrupedal locomotion..... 247

Figure 91: Patterns of mean wrist movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals..... 249

Figure 92: Multiple statistical comparisons between wrist angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion..... 250

Figure 93: Multiple statistical comparisons between wrist angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion..... 251

Figure 94: Multiple statistical comparisons between wrist angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. 252

Figure 95: Mean and standard deviation values of wrist excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals..... 253

Figure 96: Multiple statistical comparisons between wrist excursion in primate and non-primate mammals during below branch quadrupedal locomotion..... 254

Figure 97: Patterns of mean hip movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals..... 256

Figure 98: Multiple statistical comparisons between hip angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion..... 257

Figure 99: Multiple statistical comparisons between hip angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion..... 258

Figure 100: Multiple statistical comparisons between hip angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. 259

Figure 101: Mean and standard deviation values of hip excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals..... 260

Figure 102: Multiple statistical comparisons between hip excursion in primate and non-primate mammals during below branch quadrupedal locomotion..... 261

Figure 103: Patterns of mean knee movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals..... 263

Figure 104: Multiple statistical comparisons between knee angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion..... 264

Figure 105: Multiple statistical comparisons between knee angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. 265

Figure 106: Multiple statistical comparisons between knee angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. 266

Figure 107: Mean and standard deviation values of knee excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals..... 267

Figure 108: Multiple statistical comparisons between knee excursion in primate and non-primate mammals during below branch quadrupedal locomotion..... 268

Figure 109: Patterns of mean ankle movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals..... 270

Figure 110: Multiple statistical comparisons between ankle angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion. 271

Figure 111: Multiple statistical comparisons between ankle angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. 272

Figure 112: Multiple statistical comparisons between ankle angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. 273

Figure 113: Mean and standard deviation values of ankle excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals..... 274

Figure 114: Multiple statistical comparisons between ankle excursion in primate and non-primate mammals during below branch quadrupedal locomotion..... 275

Figure 115: The relationship between log-transformed normalized speed and stride duration (sec) during below branch quadrupedal locomotion in primate and non-primate mammals. 279

Figure 116: Multiple statistical comparisons between stride duration in primate and non-primate mammals during below branch quadrupedal locomotion..... 280

Figure 117: The relationship between log-transformed normalized speed and stride distance (m) during below branch quadrupedal locomotion in primate and non-primate mammals. 281

Figure 118: Multiple statistical comparisons between stride duration in primate and non-primate mammals during below branch quadrupedal locomotion. 282

Figure 119: Forelimb duty factor (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals. 284

Figure 120: Multiple statistical comparisons between forelimb duty factor in primate and non-primate mammals during below branch quadrupedal locomotion. 285

Figure 121: Hindlimb duty factor (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals. 286

Figure 122: Multiple statistical comparisons between hindlimb duty factor in primate and non-primate mammals during below branch quadrupedal locomotion. 287

Figure 123: Relative forelimb swing phase (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals. 288

Figure 124: Multiple statistical comparisons between hindlimb duty factor in primate and non-primate mammals during below branch quadrupedal locomotion. 289

Figure 125: Relative hindlimb swing phase (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals. 290

Figure 126: Multiple statistical comparisons between hindlimb duty factor in primate and non-primate mammals during below branch quadrupedal locomotion.. 291

Figure 127: A modified “Hildebrand” plot (following the approach of Cartmill et al., 2002) displaying diagonality for multiple strides of each of the study species over hindlimb duty factor during below branch quadrupedal locomotion..... 293

Figure 128: Multiple statistical comparisons between diagonality in primate and non-primate mammals during below branch quadrupedal locomotion..... 294

Figure 129: Representative forelimb force traces for *Choloepus didactylus* (A) and *Propithecus coquereli* (B) during below branch quadrupedal locomotion and *Pygathrix nemaeus* (C) during arm-swinging..... 299

Figure 130: Mean and standard deviation values of peak vertical forces in the forelimb of the study species during below branch quadrupedal locomotion and arm-swinging. 300

Figure 131: Multiple statistical comparisons between peak vertical forces in the forelimb of the study species during below branch quadrupedal locomotion and arm-swinging. 301

Figure 132: Multiple statistical comparisons between the timing of the peak vertical force in the forelimb if the study species during below branch quadrupedal locomotion and arm-swinging. 302

Figure 133: Mean and standard deviation values of the first occurring horizontal peak in the forelimb of the study species during below branch quadrupedal locomotion and arm-swinging. 305

Figure 134: Mean and standard deviation values of the second occurring horizontal peak in the forelimb of the study species during below branch quadrupedal locomotion and arm-swinging. 306

Figure 135: Multiple statistical comparisons between the first occurring horizontal peak in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 307

Figure 136: Multiple statistical comparisons between the second occurring horizontal peak in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging..... 308

Figure 137: Multiple statistical comparisons between the timing of the first occurring horizontal peak in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 309

Figure 138: Multiple statistical comparisons between the timing of the second occurring horizontal peak in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 310

Figure 139: Multiple statistical comparisons between the timing of the propulsive to braking transition in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 311

Figure 140: Mean and standard deviation values of the net horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 313

Figure 141: Multiple statistical comparisons between the horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 314

Figure 142: Mean and standard deviation values of the first occurring horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 316

Figure 143: Mean and standard deviation values of the second occurring horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 317

Figure 144: Multiple statistical comparisons between the first occurring horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 318

Figure 145: Multiple statistical comparisons between the second occurring horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 319

Figure 146: Mean and standard deviation values of peak medial force in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 321

Figure 147: Multiple statistical comparisons between the medial peak force in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 322

Figure 148: Mean and standard deviation values of peak lateral force in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 323

Figure 149: Multiple statistical comparisons between the lateral peak force in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 324

Figure 150: Mean and standard deviation values of medial impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 325

Figure 151: Multiple statistical comparisons between the medial impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 326

Figure 152: Mean and standard deviation values of lateral impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 327

Figure 153: Multiple statistical comparisons between the lateral impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 328

Figure 154: Mean and standard deviation values of mediolateral impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 329

Figure 155: Multiple statistical comparisons between the mediolateral impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. 330

Figure 156: Patterns of mean shoulder movement (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species. 334

Figure 157: Multiple statistical comparisons between shoulder angle at touchdown in the study species during below branch quadrupedal locomotion and arm-swinging. 335

Figure 158: Multiple statistical comparisons between shoulder angle at mid-support in the study species during below branch quadrupedal locomotion and arm-swinging. 336

Figure 159: Multiple statistical comparisons between shoulder angle at the end of support phase in the study species during below branch quadrupedal locomotion and arm-swinging. 337

Figure 160: Mean and standard deviation values of shoulder excursion (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species. 338

Figure 161: Multiple statistical comparisons between shoulder excursion in the study species during below branch quadrupedal locomotion and arm-swinging. 339

Figure 162: Patterns of mean elbow movement (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species. 341

Figure 163: Multiple statistical comparisons between elbow angle at touchdown in the study species during below branch quadrupedal locomotion and arm-swinging. 342

Figure 164: Multiple statistical comparisons between elbow angle at mid-support in the study species during below branch quadrupedal locomotion and arm-swinging. 343

Figure 165: Multiple statistical comparisons between elbow angle at the end of support phase in the study species during below branch quadrupedal locomotion and arm-swinging. 344

Figure 166: Mean and standard deviation values of elbow excursion (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species..... 345

Figure 167: Multiple statistical comparisons between elbow excursion in the study species during below branch quadrupedal locomotion and arm-swinging.. 346

Figure 168: Patterns of mean wrist movement (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species. 348

Figure 169: Multiple statistical comparisons between wrist angle at touchdown in the study species during below branch quadrupedal locomotion and arm-swinging. 349

Figure 170: Multiple statistical comparisons between wrist angle at mid-support in the study species during below branch quadrupedal locomotion and arm-swinging. 350

Figure 171: Multiple statistical comparisons between wrist angle at the end of support phase in the study species during below branch quadrupedal locomotion and arm-swinging. 351

Figure 172: Mean and standard deviation values of wrist excursion (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species..... 352

Figure 173: Multiple statistical comparisons between wrist excursion in the study species during below branch quadrupedal locomotion and arm-swinging. 353

Figure 174: The relationship between log-transformed normalized speed and stride duration (sec) during below branch quadrupedal locomotion and arm-swinging in the study species. 357

Figure 175: Multiple statistical comparisons between stride duration in the study species in the study species during below branch quadrupedal locomotion and arm-swinging. 358

Figure 176: The relationship between log-transformed normalized speed and stride distance (m) during below branch quadrupedal locomotion and arm-swinging in the study species. 359

Figure 177: Multiple statistical comparisons between stride duration in primate and non-primate mammals during below branch quadrupedal locomotion. 360

Figure 178: Forelimb duty factor (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals. 362

Figure 179: Multiple statistical comparisons between forelimb duty factor in the study species during below branch quadrupedal locomotion and arm-swinging. 363

Figure 180: Relative forelimb swing phase (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals. 364

Figure 181: Multiple statistical comparisons between relative forelimb swing phase in the study species during below branch quadrupedal locomotion and arm-swinging. 365

Figure 182: A model explaining the differentiation of the propulsive and braking roles of the forelimbs and hindlimbs during (A) above and (B) below branch quadrupedal locomotion. 373

Figure 183: A model for understanding hypothetical center-of-mass (COM) movements during above and below branch quadrupedal locomotion. 388

Figure 184: Model of forelimb mechanics during below branch quadrupedal locomotion in various elbow joint angles from (A) flexed to (D) extended. 390

Figure 185: Arm-swinging in *Propithecus coquereli*. 406

Acknowledgements

The work presented in this dissertation marks the culmination of 22 years of continuous formal education. Throughout that time there have been countless individuals that have come into my life and made an important impact that has shaped who I am today. First among them is my graduate advisor, Dr. Daniel Schmitt, who has been an inspiration and unwavering form of support. From my first day of graduate school he has challenged me to always become better, and to never stop pushing forward the frontiers of science. His dedicated guidance and approach to mentoring has instilled in me a true passion for experimental research, and has provided me with the skills and confidence necessary to become an independent and productive researcher. Beyond this, he has been a role model for the person I hope to become. His dedication to his students, family, and all those that work around him is incredible. I know I can always go to him for advice, no matter what the subject, and for that, I am now, and will always, be grateful.

I also thank the rest of my committee for providing continual support throughout my graduate training. Dr. Christine Wall is the epitome of what a careful scientist should be, and has provided me with a wealth of knowledge beyond my area of study. She has inspired me to always keep learning, and to expand my area of expertise whenever possible. Dr. Richard Kay has provided me with an evolutionary perspective in all my thinking and has been a great source of fascinating discussion throughout my time at Duke. He has opened his home and lab to me over the years and for that I will be always be grateful. Dr. Kenneth Glander has been a tremendous help with work at the Duke

Lemur Center, and reminds of the importance of incorporating an ecological perspective in my thinking. Dr. Pierre Lemelin has been an amazing collaborator and mentor. His approach to asking important questions in functional morphology has shaped much of my thinking.

This work could not have been possible without the help and support of David Brewer, Dr. Erin Ehmke, Meg Dye, and the many other research technicians and animal trainers at the Duke Lemur Center. The data collected in this study required patience and support, and everyone at the Duke Lemur Center was so kind and accommodating. My work and time at the Duke Lemur Center has been nothing but an enjoyable experience, and has allowed me to appreciate the incredible range of behaviors present within living primates.

Throughout the struggles of preparing a dissertation, I could not have come to this point without my Duke University family. I have had the opportunity to meet such amazing people over the last five years. Lisa Jones has been a constant source of clarity, and has been a true friend. She has made my time a Duke a great experience, and I cannot thank her enough for all the times she has gone above and beyond to help me. I would not have got through this without her. For all my academic big sisters in the Animal Locomotion Lab, thank you all so much. My thinking and work has matured considerably due to the support and constant discussions with Anne-Claire Fabre, Charlotte Miller, Roxanne Larsen, Karyne Rabey, and Angel Zeininger. I also thank all of my amazing friends that have been so patient and understanding throughout this whole

process. I could not have come to this point without the help of Lauren Gonzales, Christopher Krupenye, India Schneider-Crease, Gabriel Yapuncich, Emily Boehm, and Jackson Spradley. I hope that they all realize the impact they have had on my life, and I hope I can somehow repay the kindness they have shown me.

There are also so many others that have helped me throughout this process. First and foremost is Katie Overbey. Her love and support has been the most reassuring part of my life. I could not have gone through this process without her encouragement and advice. She has given me the confidence to be the best I can be, and has been a patient listener during all my crazy rants and monkey-talk. I cannot express enough how essential having Katie in my life has been, and I am looking forward to sharing many adventures with her as we share our future together.

I thank my parents, Maria and Mike Granatosky, for providing me with a great life and the confidence I need to accomplish whatever I want to do. They have shown me how incredible the natural world can be, and have always encouraged me to explore and learn as much as possible. I thank my brother, Coty Granatosky, for being my best friend, and a person I can always rely on. I am so proud of all his accomplishments, and can't wait for a lifetimes of free dental care.

Finally, I want to thank all the current and past members of the Tan and Sober Gentlemen and all our wonderful fans for five great years of music and mayhem. Working with Al Segars, Ben Noblit, John Thorp, Aaron Turney, Armando Alvarez, Alan Best, Dave DeHarde, Dan Ouimet, and Greyson Leybourne has been such an

enjoyable experience. Thanks to these gentlemen, I have got to explore all corners of the Triangle, and have made some great memories and truly fantastic music. I will miss playing music with all of you in the future.

This project was supported by the Leakey Foundation, the Force and Motion Foundation, the National Science Foundation's Graduate Research Fellowship Program, the Duke Lemur Center's Molly Glander Award, and Duke University.

1. Introduction

Suspensory positional behaviors (see definition in section 1.1) have evolved independently in at least 14 different mammalian clades (Fujiwara et al., 2011), and numerous times in living primates (Stern and Oxnard, 1973; Granatosky et al., 2016). All primates can, and do, adopt suspensory behaviors, but some groups emphasize these behaviors more effectively, or for longer periods of time than others (see Table 1; Stern and Oxnard, 1973). The shift to specialized suspensory locomotion, and the ability to use both above and below branch locomotion, is interpreted as a major transition during the evolution of primates, and is seen by many (Stern and Oxnard, 1973; Stern, 1975, 2000; Rose, 1983; Green and Alemseged, 2012; Churchill et al., 2013; Macias, 2015) as a likely precursor prior to the acquisition of bipedalism in early hominins (but see Lovejoy, 2009; Lovejoy et al., 2009a, b; White et al., 2009). Additionally, at least in respect to living and fossil apes, it remains unclear as to whether the acquisition of suspensory locomotion was a result of a single adaptive shift (Alba et al., 2015), or the result of multiple, independent evolutionary events (Larson, 1998). Because of the critical importance of the evolution of suspensory postures in primate and human history, numerous scenarios have been proposed about both the development of these postures and their significance. Yet none of those scenarios have ever been tested experimentally in a broad mammalian sample, nor have the deep underlying mechanics (force distribution and limb movements) been compared across animals that are capable of adopting suspensory movement. The goal of this study is to fill this gap.

Table 1. The proportion of quadrupedal and bimanual suspensory locomotion observed in the locomotor repertoires of primates

Family	Species	Source	Captive (C)/wild (W)	Quadrupedal suspension (%)	Bimanual suspension (%)
Galagidae	*Galago senegalensis*	(Gebo, 1987)	C	2	1
	Galago demidoff	(Gebo, 1987)	C	6	0.5
Lorisidae	*Perodicticus potto*	(Gebo, 1987)	C	22	0.5
	Nycticebus coucang	(Gebo, 1987)	C	29	0.020
	Nycticebus coucang	(Glassman and Wells, 1984)	C	0.5	
	Loris tardigradus	(Gebo, 1987)	C	29.5	0.5
Cheirogaleidae	*Mirza coquereli*	(Gebo, 1987)	C	23	0.5
	Microcebus murinus	(Gebo, 1987)	C	5	0.5
	Cheirogaleus medius	(Gebo, 1987)	C	11	0.5
	Cheirogaleus major	(Gebo, 1987)	C	7	0.5
Daubentoniidae	*Daubentonia madagascariensis*	(Curtis and Feistner, 1994)	C	2	
Indriidae	*Propithecus verreauxi*	(Gebo, 1987)	C	5	10
Lemuridae	*Varecia variegata variegata*	(Gebo, 1987)	C	11	0.5
	Varecia variegata rubra	(Gebo, 1987)	C	14	1
	Lemur catta	(Gebo, 1987)	C	4	1
	Hapalemur griseus	(Gebo, 1987)	C	3	0.5
	Eulemur rubriventer	(Tilden, 1990)	C	0.9	0.1
	Eulemur mongoz	(Gebo, 1987)	C	8	1
	Eulemur macaco	(Gebo, 1987)	C	6	4

	Eulemur fulvus	(Gebo, 1987)	C	9	0.1
	Eulemur coronatus	(Gebo, 1987)	C	2	0.1
Tarsiidae	*Tarsius syrichta*	(Gebo, 1987)	C	8	
Atelidae	*Lagothrix lagothricha*	(Cant et al., 2001, 2003)	W	0.1	11
	Ateles paniscus	(Youlatos, 2002)	W	3.1	32.1
	Ateles paniscus	(Mittermeier, 1978)	W		38.6
	Ateles paniscus	(Fleagle and Mittermeier, 1980)	W		38.6
	Ateles geoffroyi	(Fontaine, 1990)	W	0.5	21.8
	Ateles geoffroyi	(Johnson and Shapiro, 1998)	W		37.5
	Ateles geoffroyi	(Mittermeier, 1978)	W		26
	Ateles geoffroyi	(Cant, 1986)	W		25
	Ateles belzebuth	(Cant et al., 2001, 2003)	W	3.1	20
	Alouatta seniculus	(Youlatos, 1998)	W	1.3	
	Alouatta pigra	(Cant, 1986)	W	0.5	
	Alouatta palliata	(Gebo, 1992)	W	2	0.5
	Alouatta palliata	(Johnson and Shapiro, 1998)	W		20
Callitrichidae	*Leontopithecus rosalia*	(Rosenberger and Stafford, 1994)	C	9	
Cebidae	*Saimiri oerstedii*	(Johnson and Shapiro, 1998)	W		1.1
	Saimiri boliviensis	(Fontaine, 1990)	W		1.6
	Cebus capucinus	(Gebo, 1992)	W	0.5	1
	Cebus capucinus	(Johnson and Shapiro, 1998)	W		6.4

	Cebus apella	(Fleagle and Mittermeier, 1980)	W	1	
Pitheciidae	*Pithecia pithecia*	(Fleagle and Mittermeier, 1980)	W		5
Cercopithecidae	*Trachypithecus leucocephalus*	(Xiong et al., 2009)	W		0.2
	Trachypithecus francoisi	(Xiong et al., 2009)	W		2.1
	Pygathrix nemaeus	(Wright et al., 2008)	C		46
	Pygathrix cinerea	(Wright et al., 2008)	C		56
	Presbytis siamensis	(Fleagle, 2013)	W		5
	Presbytis melalophos	(Fleagle, 1978)	W		3.4
	Colobus guereza	(Gebo and Chapman, 1995)	W	0.5	0.5
	Colobus guereza	(Rose, 1978)	W		0.1
	Colobus badius	(Gebo and Chapman, 1995)	W	0.5	3
	Colobus badius	(McGraw, 1998)	W		3.9
	Cercopithecus mitis	(Gebo and Chapman, 1995)	W	0.3	0.3
	Cercopithecus diana	(McGraw, 1998)	W		0.1
	Cercopithecus ascanius	(Gebo and Chapman, 1995)	W		0.5
	Cercocebus albigena	(Gebo and Chapman, 1995)	W		0.5
Hylobatidae	*Symphalangus syndactylus*	(Chivers, 1972)	W		80
	Symphalangus syndactylus	(Fleagle, 1976)	W		37.9

	Nomascus nasutus	(Fan et al., 2013)	W		59.6
	Hylobates pileatus	(Srikosamatara, 1984)	W		84.4
	Hylobates lar	(Fleagle, 1976)	W		56
	Hylobates lar	(Fleagle, 1980)	W		51.2
	Hylobates agilis	(Gittins, 1983)	W		66.3
	Hylobates agilis	(Cannon and Leighton, 1994)	W		48
Hominidae	*Pongo pygmaeus*	(Manduell et al., 2011)	W	1.1	47
	Pongo pygmaeus	(Cant, 1987b)	W	1	11
	Pongo pygmaeus	(Sugardjito, 1982)	W		21
	Pongo pygmaeus	(Sugardjito and van Hooff, 1986)	W		19.8
	Pongo abelii	(Thorpe and Crompton, 2006)	W	26	16
	Pan troglodytes	(Sarringhaus et al., 2014)	W		6
	Pan troglodytes	(Doran and Hunt, 1996)	W		1.3
	Pan troglodytes	(Doran and Hunt, 1996)	W		0.8
	Pan troglodytes	(Hunt, 1991)	W		0.5
	Pan troglodytes	(Hunt, 1992)	W		0. 2
	Pan troglodytes	(Doran and Hunt, 1996)	W		0. 2
	Pan paniscus	(Susman, 1984)	W		21
	Pan paniscus	(Susman et al., 1980)	W		15
	Gorilla gorilla	(Doran and Hunt, 1996)	W		0.1

This study takes a comparative approach to anatomical and behavioral changes that are associated with the transition from arboreal quadrupedalism to suspensory locomotion. Specifically, kinetic, kinematic, and spatiotemporal gait data were collected from a broad phylogenetic sample of primate and non-primate mammals walking quadrupedally both above and below an instrumented runway. Below branch quadrupedal locomotion is an understudied form of suspensory locomotion that requires very few anatomical modifications, and therefore, most primates are capable of moving in this manner. In this study, data from both above and below branch walking was compared with data from specialized arm-swinging primates in order to answer the following research questions:

(1) Do primates adopt differing mechanical strategies when switching from above to below branch quadrupedal locomotion, or simply modify the existing gait patterns?

(2) Do primates and non-primate mammals utilize the same mechanical strategies during below branch quadrupedalism, or are different species capable of adopting differing mechanical strategies?

(3) Does below branch walking bear greater similarities to above branch walking or more specialized forms of suspensory locomotion (i.e., arm-swinging)?

Data from this study provides insight into an essential, but understudied, evolutionary transition within our own clade and more broadly aid in our understanding

of how animals deal with the mechanical demands of switching from one form of locomotion to another.

There is currently no clear consensus on what features (anatomical or mechanical) species that use suspensory locomotion have in common. This introduction surveys suspensory locomotion from a neontological perspective and addresses such topics as the mechanical definition of suspensory locomotion, the taxonomic diversity of suspensory locomotion, anatomical features associated with suspensory locomotion, current theories about the origins of suspensory locomotion, and experimental studies on suspensory locomotion. The goal of this introduction is to identify themes and patterns about suspensory locomotion to determine what is currently known and unknown about this form of locomotion.

1.1 A mechanical definition of suspensory locomotion

Perhaps the most difficult aspect of discussing suspensory locomotion is the nebulous terminology that is currently used to describe this form of movement. It is important to first outline differences between postural, locomotor, and positional behaviors. A locomotor behavior is one where animal moves its center of mass (COM) over distance, whereas a postural behavior is one where the COM moves very little, or not at all (Johnson, 2012). The combination of the postural and locomotor behaviors is defined as positional behaviors (Prost, 1965).

For most, images of suspensory locomotion are centered on what is commonly referred to as arm-swinging, a form of forward progression in which the animal hangs below the support and the forelimbs bear most of the weight. Arm-swinging may be

associated with prehensile tail use in the New World atelines (Turnquist, 1975; Swartz, 1989; Hunt, 1991; Hunt et al., 1996; Turnquist et al., 1999; Bertram, 2004; Schmitt et al., 2005). The issue with this common definition is that it excludes species that utilize below branch quadrupedal locomotion, which is a form of suspensory locomotion in which both the forelimbs and hindlimbs are used in some combination, the torso is pronograde, and the limbs are loaded in tension (Cant, 1986; Ishida et al., 1990; Hunt et al., 1996; Bergeson, 1998). Many studies have identified the problems with these definitions of suspensory locomotion; to find a more unifying terminology, many have sought a mechanical definition that applies to all suspensory positional behaviors.

Stern and Oxnard (1973) proposed that all suspensory positional behaviors are united by a common limb loading pattern in which the forelimbs and/or hindlimbs are loaded in uni-axial tension rather than compression. However, they see this as an approximation since they have no direct data on limb loading patterns during suspensory locomotion. This definition alludes to an important mechanical situation that differs drastically from the limb loading behavior of most other forms of locomotion (Kimura et al., 1979; Reynolds, 1985a, b; Demes et al., 1994; Schmitt and Lemelin, 2002, 2004; Schmitt and Hanna, 2004). Tensile loading on the limbs, when it is a dominant part of the loading environment, is thought to result in profound changes to the overall intrinsic and structural properties of the bones allowing them to become thinner, longer, and materially more compliant (Swartz, 1990; Skedros et al., 1994, 1996, 2004; Rein et al., 2015). To explore the claim that suspensory locomotion is defined by “limbs in tension” (Stern and Oxnard, 1973), Swartz et al. (1989) collected strain data from the long bones of the

forelimb (humerus, radius, and ulna) to determine intrinsic strain patterns during arm-swinging in a freely moving gibbon. From this data it was determined that strain patterns were not evenly distributed throughout the forelimb, and while ulna and portions of the radius did experience tensile loading, the humerus experienced net compressive loading due to muscular contraction from powerful flexors. This finding makes a simple definition of "limbs in tension" problematic as it indicates only the direction of the pull of the body and not actual loading specifically. Perhaps a more general definition of "limbs under reduced compressive loading" may be more accurate (Carlson and Patel, 2006; Patel and Carlson, 2008). This more general approach is also too simplistic and difficult to apply because of the need to determine if the bone is actually under reduced compressive loading. There are many ways an animal can reduce compressive loading without adopting what is traditionally considered suspensory behaviors (Reynolds, 1985a; Demes et al., 1994; Schmitt, 1999; Schmitt and Lemelin, 2002).

For many types of locomotion, the use of mechanical analogies has proven effective as a means of translating complex mechanics into understandable concepts. In numerous studies, suspensory movement is often described and discussed as a movement analogous to a simple pendulum (Avis, 1962; Erikson, 1963; Fleagle, 1974; Andrews and Groves, 1976; Swartz, 1989; Swartz et al., 1989; Turnquist et al., 1999; Chang et al., 2000; Bertram and Chang, 2001; Usherwood, 2003; Bertram, 2004; Nyakatura and Andrada, 2012; Granatosky, 2015). When examined in more detail however, this analogy weakens (Bertram, 2004), and many suspensory animals modify pendular movements through kinematic mechanisms in order to "smooth-out" COM movements (Fleagle,

1974; Bertram et al., 1999; Bertram and Chang, 2001; Usherwood, 2003; Bertram, 2004). This process is considered an important adjustment required during brachiation in order to reduce mechanical energy loss due to collisions that occur as a result of discontinuity in COM path (Bertram et al., 1999; Bertram and Chang, 2001; Bertram, 2004). Additionally, data on the COM movements in sloths reveal that that these animals do not use pendular motion during below branch quadrupedal locomotion. Nyakatura and Andrada (2012) demonstrate that sloths actively slow themselves down throughout the stride, and subsequently use shoulder retraction and elbow flexion to propel themselves prior to swing phase. This active perturbation of pendular motion in sloths is thought to be a mechanism to ensure deliberate limb placement and cryptic movements necessary for the unique locomotor niche observed in living sloths (Nyakatura, 2011; Nyakatura and Andrada, 2012). It remains unclear as to whether this type of movement is present for all species during below branch quadrupedal locomotion, or whether the sloth is unusual in this regard.

It is obvious, that determining a single mechanical definition for suspensory locomotion is quite difficult. Current definitions based on “limbs in tension” and/or simple pendular motion do not properly describe the mechanics that occur during suspensory locomotion or exclude certain types of suspensory locomotion altogether. To rectify this problem, Granatosky et al. (2016) proposed that suspensory locomotion should be defined as any form of forward or backward progression in which the animal’s COM is positioned beneath the support. This definition is inclusive of many forms locomotion without specifically invoking patterns of limb loading and COM movements.

Additionally, it speaks to the biomechanical challenge of gravity acting on the animal by pulling the COM away from the support. In order to avoid falling, animals must either evolve beneficial anatomical features (see section 1.3), or adjust themselves through behavioral mechanisms. By using a definition that speaks to the biomechanical challenges, rather than particular solutions (either anatomical or behavioral), allows a broader appreciation of the number of different strategies that have arisen in order to deal with the stresses and mechanical challenges associated with moving below branches.

1.2 Taxonomic diversity of suspensory locomotion in mammals

Suspensory locomotion has evolved in at least nine of the major mammalian radiations (i.e., Marsupialia, Xenarthra, Pholidota, Dermoptera, Primates, Scandentia, Rodentia, Carnivora, and Chiroptera) (Figure 1). For certain taxonomic groups (i.e., Primates), locomotor profiles documenting the percentage of certain locomotor modes observed within species have been quite extensive, and this type of data allows us to obtain a detailed understanding of those species locomotor repertoires. For most other mammalian groups, data documenting locomotor profiles are minimal or absent, and inferences about locomotion are primarily based on anecdotal reports rather than specific observations. This introduction will discuss, to whatever extent possible, the frequency and nature of suspensory locomotion in the major mammalian orders.

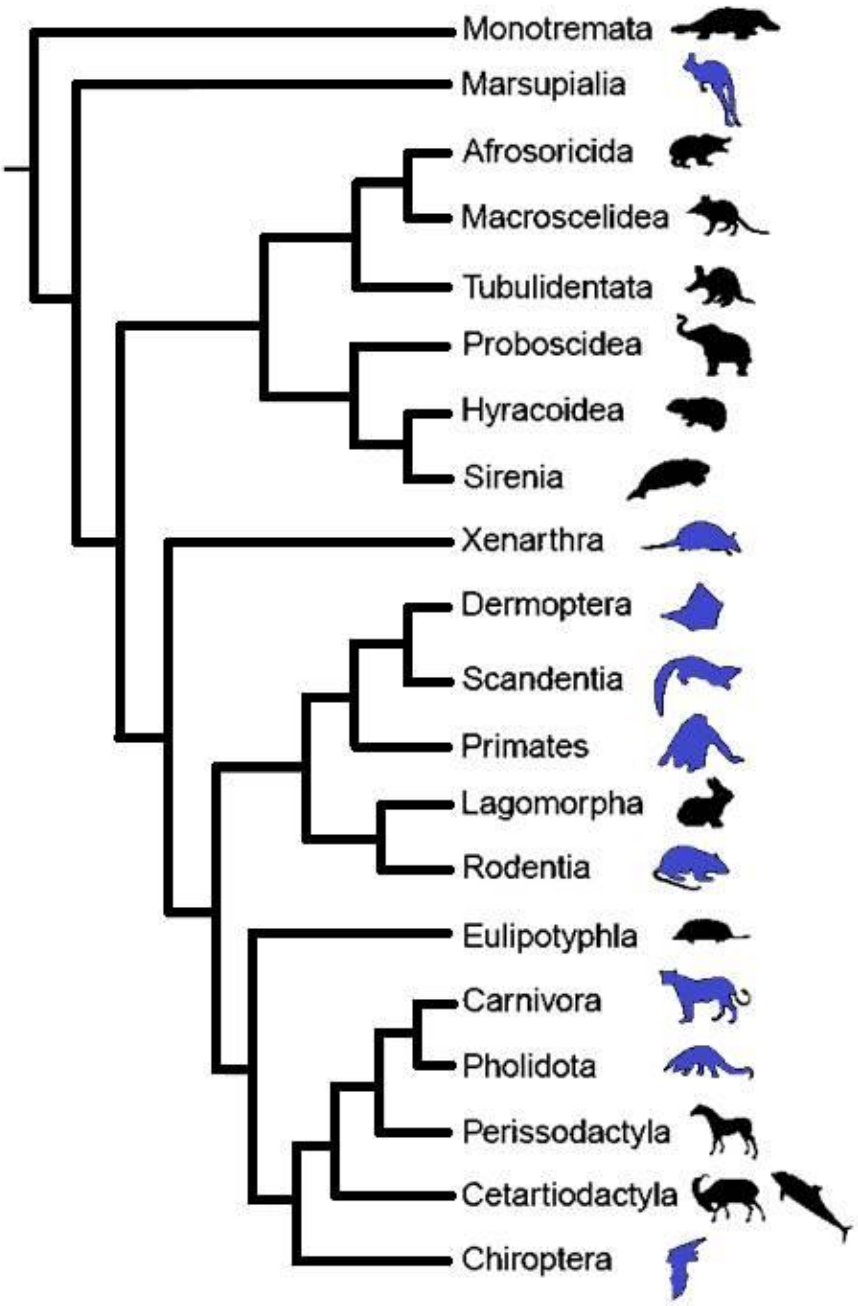

Figure 1: Mammalian phylogeny (adapted from Springer et al., 2004) indicating the mammalian orders in which suspensory locomotion has evolved. Orders illustrated in blue indicate that suspensory locomotion is present.

1.2.1 Marsupialia

Despite the numerous studies that have posited marsupials as an important model for the study of primate locomotor origins, little information is available on the locomotor behaviors of this group beyond gross categorization (e.g., terrestrial, arboreal, semi-arboreal). Without detailed locomotor profiles it is difficult to determine the importance and use of suspensory locomotion within the extant marsupials. It is assumed that most marsupials, with the exception of highly terrestrial species (e.g., macropods and dasyuromorphs), can adopt suspensory positional behaviors, but only three studies (Russell, 1986; Rasmussen, 1990; Dalloz et al., 2012) have actually provided detailed locomotor profiles of marsupials, and of those only Russell (1986) and Rasmussen (1990) documented the presence of any suspensory movement. Based on the anatomy of certain marsupials, it is likely that suspensory locomotion is far more common (Argot, 2001; Grand and Barboza, 2001; Kirk et al., 2008; Granatosky et al., 2014a; b).

1.2.2 Xenarthra

The xenarthrans are well known for their propensity for suspensory locomotion (with the exception of *Myrmecophaga tridactyla* and the dasypodids). While both *Tamandua* (the lesser anteater) and *Cyclopes* (the silky anteater) use suspensory locomotion during their normal locomotor behavior (Taylor, 1978, 1985), the sloths [*Choloepus* (two-toed sloths) and *Bradypus* (three-toed sloths)] are the exemplars of below branch walking. Considerable work has gone into understanding the evolutionary history behind how suspensory locomotion evolved in these species (Nyakatura, 2011; Grass, 2014).

It has long been assumed that based on the anatomical and biomechanical similarities between *Choloepus* and *Bradypus* that these species share a close taxonomic affiliation, but recent genetic evidence demonstrate that these species are only distantly related. Phylogenetic restructuring place *Bradypus* as either the sister taxon to all other extinct and extant sloths (Gaudin, 2004), or associated with the extinct megatheriid sloths (Greenwood et al., 2001). *Choloepus* is considered a member of the Megalonychidae, a group consisting primarily of the extinct "ground-sloths" of North America (McDonald and De Iuliis, 2008). Regardless of the exact taxonomic position of these species, none of the known fossil sloths show any anatomical indication of suspensory locomotion (McDonald and De Iuliis, 2008; Nyakatura, 2011; Grass, 2014). Therefore, it is most parsimonious to assume that *Bradypus* and *Choloepus* evolved obligate suspensory locomotion convergently. The exact mechanism for how this remarkable example of convergence occurred is still largely unknown, but Nyakatura (2011) suggested that the fossorial adaptations (i.e., strong forelimb flexor musculature and strong claws) present in the last common ancestors of sloths pre-adapted extant sloths for suspensory locomotion. Additionally, current reconstructions of many of the smaller fossil sloth species suggest a semi-arboreal lifestyle (White, 1993; Toledo et al., 2012). Suspensory positional behaviors in relatively large-bodied taxa negate the need to balance above branches, and are thought to be more energy efficient (Grand, 1972; Cartmill, 1985). The generally lower metabolic rates of xenarthrans (Nagy and Montgomery, 1980; Robinson and Redford, 1986) would have favored suspensory positional behaviors, and this need for

energy efficiency is thought to account for the convergence in modern sloths (Nyakatura, 2011).

1.2.3 Dermoptera

The dermopterans (flying lemurs/colugos) are Southeast Asian arboreal mammals characterized by large patagiums used for gliding between gaps in the canopy (Byrnes et al., 2008, 2011a; b). It is assumed that because of this large gliding membrane these animals are limited to suspensory locomotion and vertical climbing when not gliding, as upright quadrupedal locomotion is ungainly and awkward. Despite the numerous morphological studies that have used dermopterans to inform behavioral reconstructions of fossil taxa (Beard, 1989; Sargis, 2001a; Kirk et al., 2008; Granatosky et al., 2014b), incredibly little is known about the non-gliding locomotor behavior of these species. Dzulhelmi and Abdullah (2009) created an ethogram noting numerus aspects of dermopteran behavior, and while suspensory locomotion was recorded, no quantitative measures were presented to elucidate the relative importance of suspension within the overall behavioral repertoire. Fujiwara et al. (2011) compared static levels of elbow flexion in dermopterans and compared these to other species that utilize below branch quadrupedal locomotion (*Choloepus*, *Nycticebus*, and *Pteropus*), and from this data determined that dermopterans, like other below branch quadrupeds, demonstrate angles that maximize moment-arms during suspensory positional behaviors.

1.2.4 Primates

Of all the mammalian groups, primate locomotor behavior has been the most thoroughly studied and recorded. This level of detail allows us to understand more fully

what species are using suspensory locomotion, and whether taxonomic patterns are present. Suspensory positional behaviors are commonly discussed in concert with the hominoids, atelines, and to some extent the Asian colobines, but it should be noted that all primates can, and do, engage is suspensory locomotion, although some groups emphasize these behaviors more effectively, or for longer periods of time (Stern and Oxnard, 1973; Table 1). One group commonly ignored in terms of suspensory locomotion are the strepsirrhines (but see Ishida et al., 1990; Jouffroy and Petter, 1990; Jouffroy and Stern, 1990). While suspensory postural behaviors like vertical clinging and hindlimb suspension are commonly observed amongst the strepsirrhines, locomotor behaviors like inverted walking and bimanual progression are much more uncommon. These behaviors have generally been observed in *Loris*, *Nycticebus*, *Propithecus*, *Varecia*, *Lemur*, *Mirza coquereli*, *Daubentonia madagascariensis*, and *Cheirogaleus medius* (Table 1).

Perhaps no strepsirrhines are more well-known for suspensory locomotion than the subfossil sloth lemurs *Palaeopropithecus*, *Babakotia*, and *Mesopropithecus*. These animals were endemic to Madagascar, and persisted late into the Holocene (Godfrey and Jungers, 2003). Molecular evidence suggests that this group shared a close phylogenetic relationship with extant indriids (Yoder et al., 1999; Karanth et al., 2005; Orlando et al., 2008). Along with an extensive collection of skulls and dental remains, there have been a large number of postcranial elements collected and attributed to the various species of sloth lemurs (Jungers et al., 1997; Hamrick et al., 2000). This has allowed for thorough and reliable reconstructions of positional behavior (Jungers et al., 1997; Hamrick et al.,

2000; Shapiro et al., 2005; Granatosky et al., 2014b) . *Mesopropithecus, Babakotia*, and *Palaeopropithecus* have all been interpreted as antipronograde primates with varying degrees of suspensory locomotion. This interpretation has led many to believe that these genera filled a similar ecological role to living sloths, and they have argued that some parts of the anatomy, such femoral neck and head, knee joint, elbow, and back are similar to and convergent on a sloth-like anatomy (Jungers et al., 1997; Hamrick et al., 2000; Godfrey and Jungers, 2003; Shapiro et al., 2005; Granatosky et al., 2014b).

Among the South American platyrrhines, the atelines are most often observed using suspensory positional behaviors, although suspensory locomotion is present in many other platyrrhine species (Table 1). The atelines use both arm-swinging and below branch quadrupedal locomotion, and accordingly have evolved a number of anatomical features that are commonly considered adaptive for proficient suspensory locomotion (Stern et al., 1980a; Jenkins, 1981; Jungers et al., 1997; Johnson and Shapiro, 1998; Turnquist et al., 1999; Rosenberger et al., 2008). Arm-swinging in the atelines has evolved independently from other arm-swinging primates, and although the mechanics of arm-swinging in the atelines are similar in many ways, there are also substantial differences (Turnquist, 1975; Turnquist et al., 1999; Schmitt et al., 2005, 2009; Tripp et al., 2015). Perhaps most obvious is the aid of a prehensile tail that makes contact with the support throughout an arm-swinging cycle, and is thought by most to support a substantial portion of body weight (Lemelin, 1995; Bergeson, 1996; Laska, 1998; Meldrum, 1998; Schmitt et al., 2005; Organ, 2008).

Traditional interpretations of the cercopithecids have suggested that suspensory locomotion was extremely rare or even absent, but recent work (Byron and Covert, 2004; Workman and Covert, 2005; Wright et al., 2008; Su and Jablonski, 2009; Granatosky, 2015) has demonstrated that suspensory locomotion is present in at least some Old World monkeys. First described by Byron and Covert (2004), and later corroborated by Workman and Covert (2005) and Wright et al. (2008), is the unexpected ability of the red-shanked douc langur (*Pygathrix nemaeus*) to commonly [46%; (Byron and Covert, 2004)] engage in arm-swinging locomotion. This observation is surprising, because anatomically *P. nemaeus* closely resembles other phylogenetically related Asian colobines [but see Su and Jablonski (2009) and Bailey and Pampush (2015a)], and shows few of the anatomical similarities with other arm-swinging primates. Until recently no detailed mechanical analysis was available to understand the proficiency of suspensory locomotion in this species. Granatosky (2015) demonstrated the mechanics of the arm-swinging in red-shanked douc langur are remarkably similar to what has been reported for arm-swinging mechanics in other species (i.e., *Ateles* and *Hylobates*)

For many, the hominoids are the group of primates most associated with suspensory locomotion, but in reality, beyond the juvenile stage, suspensory locomotion in *Pan troglodytes* and *Gorilla* is incredibly rare (Doran, 1992, 1993, 1996, 1997; Hunt, 1992; Doran and Hunt, 1996; Congdon, 2012). This led Stern and Oxnard (1973) and Larson (1998) to refer to these species as suspensory primarily during postural behaviors, but not locomotion. Suspensory locomotion is more common in *Pan paniscus*, and according to Doran (1992) this is evidence of behavioral paedomorphism retained in this

species. The hylobatids and *Pongo* on the other hand are highly suspensory throughout life, and each has become a specialist for arm-swinging and below branch quadrupedal locomotion, respectively. The gibbons are well-known for their acrobatic abilities below branches, and based on the finding that suspensory locomotion compromises upwards of 84.4% of the locomotor repertoire of some gibbon species (Srikosamatara, 1984), it is not surprising that their skeleton has been drastically reorganized to reflect numerous adaptations for suspensory locomotion (Andrews and Groves, 1976; Michilsens et al., 2009, 2010; Cheyne, 2011). The gibbons are solely arboreal, and almost never descend to the ground. The relatively large-bodied siamang (*Symphalangus syndactylus*) tends to travel primarily by continuous contact arm-swinging (Fleagle, 1974), while the smaller species are much more apt at ricochetal movements in which they launch themselves (with sometimes a substantial aerial phase) from tree to tree (Bertram et al., 1999; Usherwood, 2003; Bertram, 2004; Cheyne, 2011).

In comparison to the gibbons, the movement of *Pongo* is slow and deliberate, and has been referred to as "antipronograde" locomotion (Stern, 1975). Suspensory locomotion makes up a large portion of the orangutan overall diverse movement repertoire. This has resulted in extreme modifications of postcranial skeleton, including incredibly long forelimbs, highly curved phalanges, and a highly mobile hip joint (Jungers et al., 1997; Larson, 1998; Hammond, 2014). Although *Pongo* is capable of arm-swinging, this is usually done over short distances and is never ricochetal (Fleagle, 2013). Instead, it uses a clambering form of suspensory locomotion usually referred to as quadrumanus suspension (Thorpe and Crompton, 2006; Thorpe et al., 2007a, b, 2009;

Manduell et al., 2011) . While formal definitions of quadrumanus suspension have been difficult to ascertain from the literature, this movement has been likened to the quadrupedal suspensory walking of lorises (Walker, 1974).

1.2.5 Scandentia

The locomotor behaviors of the scandentians, like so many other mammalian species, are woefully understudied and most of our behavioral inferences are based on anatomical interpretations and anecdotal reports [but see Emmons, (2000)] rather than rigorous surveys. All scandentians demonstrate postcranial morphology associated with arboreal locomotion, although most species are habitually terrestrial (Emmons, 2000; Sargis, 2001a, 2004). This has led to serious inquiry concerning the ancestral condition of Scandentia and whether arboreality or terrestriality represents the primitive locomotor mode. Sargis (2004) has examined this question in detail, and because *Ptilocercus lowii*, the most morphologically primitive treeshrew species (Sargis, 2007), is strictly arboreal, and all species retain morphological adaptations for arboreality it seems almost a certainty that the living species all derive form an arboreal ancestor (Emmons, 2000; Sargis, 2004, 2007). Because arboreal anatomy is present in all extant scandentians, it is possible that all living treeshrews may be capable of suspensory locomotion. Data from Sargis (2001b) supports this notion as both *Tupaia minor* (a highly arboreal species of treeshrew) and *Tupaia tana* (a primarily terrestrial treeshrew) were reported to use suspensory locomotion (5.0% and 0.2% respectively).

1.2.6 Chiroptera

All chiropterans utilize suspensory positional behaviors. This is thought to be a consequence of reorganizing the postcranial skeleton for specialized powered flight (Lawrence, 1969; Howell and Pylka, 1977). In general, the forearm bones of bats are long and curved compared to similarly-sized terrestrial mammals. The radius is large relative to the ulna (with which it is often fused), and the digits are elongated to provide a supporting frame for the membranous wing (known as a patagium). The hindlimb skeleton is also extensively modified. The fibula is reduced or absent, the femur and tibia are long and slim relative to those of similarly sized terrestrial mammals, and these bones are rotated laterally from the typical mammalian pattern. As a result, the femur extends laterally or caudally, and the flexor surface of the knee faces ventrally (Riskin et al., 2005). This combination of specializations is presumed to result in the poor upright walking ability seen in bats (Lawrence, 1969; Howell and Pylka, 1977; but see Riskin and Hermanson, 2005; Riskin et al., 2005, 2006).

While many of the features associated with upright movement have been lost in the chiropterans, numerous features associated with increasing the efficiency of suspensory positional behaviors are present throughout the postcranial skeleton. This includes large hooked distal phalanges, elongated intermediate phalanges (Boyer and Bloch, 2008) and digital locking tendons in the foot (Schutt, 1993; Simmons and Quinn, 1994), powerful forelimb flexor musculature (Fujiwara et al., 2011), and anatomically rigid lumbar vertebrae (Granatosky et al., 2014b). While suspensory postures are ubiquitous across chiropterans, the proportion of suspensory locomotion used by

chiropterans in their locomotor repetoire is poorly known. Vandoros and Dumont (2004) recorded the incidence of suspensory locomotion in 11 bat species and determined that the relative amounts of suspensory movement appear to be phylogenetically influenced. In general, the phyllostomids (leaf-nosed bats) rarely used suspensory locomotion, but the pteropids (megachiropteran fruit bats) used suspensory locomotion quite regularly. This pattern appears to be reflected in vertebral morphology of chiropterans (Granatosky et al., 2014b).

1.2.7 Carnivora

Carnivorans demonstrate a great deal of locomotor diversity within the order, including swimming, cursoriality, arboreality, fossoriality, and many combinations in-between (Van Valkenburgh, 1987; Taylor, 1989). Due to these locomotor specializations, suspensory locomotion is rare, and appears to only be present in the procyonids (raccoons, coatis, kinkajous, olingos, olinguitos, ringtails and cacomistles; McClearn, 1992; Organ, 2008; Fujiwara et al., 2011). It is possible that suspensory locomotion is also present in the highly arboreal viverrids (civets, genets, and binturongs), but detailed locomotor accounts are severely lacking. Much of the quantitative analysis of procyonid locomotion is based on laboratory-controlled experimental gait analysis (Lemelin and Cartmill, 2010) and qualitative data (McClearn, 1992). According to McClearn (1990, 1992), *Procyon* (raccoon) and *Nasua* (coati) are careful, although not particularly graceful, climbers, and their elongated limbs and digitigrade postures make them better suited for terrestrial cursorial locomotion rather than arboreal movement. During climbing, Kaufmann (1962) and McClearn (1992) notes that *Nasua* and *Procyon*

occasionally progress on the underside of an arboreal substrate. In contrast, *Potos flavus* (kinkajou) are highly arboreal and commonly use suspensory locomotion when moving among terminal branches (McClearn, 1992; Organ, 2008).

1.2.8 Rodentia

The great taxonomic diversity of the rodents has resulted in a range of locomotor adaptations including some highly arboreal species. Until recently however, locomotor profiles on these species have been absent. While data are still limited, we begin to understand the role of suspensory locomotion within the normal behavioral repertoires of certain species. Among the sciurids (squirrels), the most arboreal of the rodents, suspensory locomotion has not been observed (Youlatos, 1999; Stafford et al., 2003; Essner, 2007; Youlatos et al., 2007; Youlatos and Samaras, 2010). Suspensory locomotion was however observed in the murids [Micromys minutus; 2.4% of locomotor repertoire; (Urbani and Youlatos, 2013)] and the glirids [Graphiurus murinus; 8.2% of locomotor repertoire; (Youlatos et al., 2015)]. It is also likely that *Coendou* (prehensile-tailed porcupine) also uses some degree of suspensory locomotion, but these behaviors have not been documented.

1.3 Postcranial morphology associated with suspensory locomotion

Across the wide range of suspensory mammals, certain anatomical patterns have arisen convergently that are thought to allow for more proficient below branch locomotion. It is important to note that, although many anatomical modifications are present within the postcranial skeleton of suspensory mammals, these features are not

required to adopt suspensory locomotion. As stated above, the ability to adopt suspensory locomotion does not require any particular anatomical necessity beyond the ability to flex the digits of the hand and/or foot into a functional hook. This is problematic for paleontologists because without clear diagnostic anatomical features linked specific behaviors, it is impossible to accurately reconstruct the locomotor repertoire of a fossil organism. Below are the general anatomical trends that have been observed in suspensory mammals. This outline is by no means exhaustive, but instead is meant to focus on functional features that potentially inform biomechanical behaviors.

1.3.1 Manual and pedal phalangeal morphology

During both arm-swinging and inverted quadrupedal locomotion, the hand and foot (during below branch quadrupedal locomotion only), can be described as being positioned like a hook to wrap above and around the support (Swartz et al., 1989; Jungers et al., 1997; Richmond, 2007; Fleagle, 2013). The proximal phalanx is usually positioned above the support, while intermediate and distal phalanges make contact on the side and near the bottom of the support, respectively (Richmond, 2007). In most cases the metacarpals have no contact with the support, and the pollex is thought to be of little importance during suspensory movement (Fleagle, 2013; but see McClure et al., 2012). The relative degree of phalangeal curvature of the proximal phalanx is thought to be an accurate predictor of the importance and proportion of arboreality and suspensory positional behaviors (Stern and Susman, 1983; Stern et al., 1995; Jungers et al., 1997; Richmond, 2007; Congdon, 2012). The hook style grip observed during suspensory locomotion serves as an important mechanism for mitigating bending strain while below

branches. Basically, as a digit is loaded during suspensory postures, joint reaction forces load the articular ends of the phalanx in compression and dorsally, while digital flexor musculature pulls the midshaft towards the palm (Richmond, 2007). The presence of highly curved digits substantially mitigates the strains experienced during suspensory locomotion, and these strains can be further mitigated by behavioral changes to hand position (Stern et al., 1995; Jungers et al., 1997; Richmond, 2007; Congdon, 2012). Among living primates, phalangeal curvature appears to be greatest in highly suspensory species, such as gibbons, orangutans, and spider monkeys (Jungers et al., 1997; Congdon, 2012).

Unlike primates, highly suspensory non-primate mammalian species, such as sloths, bats, and colugos, have relatively straight proximal phalanges (Beard, 1990; Hamrick et al., 1999; Boyer and Bloch, 2008). These animals instead support the body with long and highly curved claws of the distal phalanx (Boyer and Bloch, 2008). Perhaps most interesting is the presence of a digital locking tendon that has arisen convergently in the dermopterans and chiropterans. The functional unit consists of two components, a tuberculated fibrocartilage patch on the proximal plantar surface of the combined tendons of the flexor digitorum longus and plantaris muscles, and an adjacent plicated portion of the synovial layer of the flexor tendon sheath. The tendon lock is engaged when the flexor tendon is pulled proximally, as occurs when the digit is flexed (Schutt, 1993; Simmons and Quinn, 1994). Once the tendon tubercles engage with the plicae, the tendon remains locked in place as long as the claw remains under tension (i.e., as long as the body weight of the animal is suspended from the flexed claw).

1.3.2 Forelimb morphology

Perhaps no anatomical feature has been associated with suspensory locomotion more than the elongation of the forelimbs. The role of the long forelimb has been a matter of considerable inquiry, and a number of biomechanical solutions have been proposed to explain why this feature has evolved (Avis, 1962; Preuschoft and Demes, 1984; Swartz, 1989; Bertram et al., 1999; Chang et al., 2000; Bertram, 2004; Michilsens et al., 2011). Longer forelimbs have commonly been cited as mechanism to reduce the cost of locomotion during arm-swinging. This is because as the amplitude of the swing increases (i.e., effective limb length) so does the distance traversed between subsequent handholds. This results in fewer interactions with the substrate in a set locomotor bout. Although the pendular movement observed in some species is thought to be highly efficient, every time a limb makes contact with the support a certain amount of energy is lost, and additional muscular energy must contributed to continue forward movement (Parsons and Taylor, 1977; Stern et al., 1980b; Jungers and Stern, 1981; Swartz, 1989; Michilsens et al., 2011, 2012). By decreasing the number of handholds within a locomotor bout an animal is thought to be able to increase the overall efficiency of locomotion (Temerin and Cant, 1983).

This explanation for the elongation of the forelimbs is not without criticism (Swartz, 1989; Bertram et al., 1999; Bertram, 2004). First, there is no reason to assume that the same biomechanical principles described above would not apply to upright locomotion (Swartz et al., 1989). Next, the assumption that arm-swinging is governed by simple pendular mechanics is overly simplistic. Arm-swinging should be considered as a

combination of forelimb length, pendular motion, and collisional mechanics (Bertram et al., 1999; Bertram and Chang, 2001; Bertram, 2004; Michilsens et al., 2011, 2012). This viewpoint makes no assumptions about limb length and overall energetic efficiency (Usherwood, 2003; Bertram, 2004). With these mechanistic criticisms in mind, alternative explanations for limb elongation may be worth considering. As proposed by Swartz et al. (1989), the altered loading environment during below branch motion released the forelimb from the physical constraints of compressive loading, and as a consequence the limb was able to become longer, perhaps for other purposes such as reaching for unevenly spaced supports.

There are many other features within the forelimb that are also thought to be driven by the mechanical challenges associated with suspensory locomotion. The scapula of suspensory animals has been highly modified to deal with below branch locomotion. The glenoid fossa in most suspensory animals is cranially positioned, shallow and small. This arrangement is highly mobile, but is severely lacking in stability (Erikson, 1963; Roberts, 1974; Ankel-Simons, 2000; Grass, 2014; Bailey and Pampush, 2015a). The acromion and coracoid processes also tends to be expanded. This is thought to provide a strong anchor point for muscles of the shoulder, especially the deltoid (Miller, 1935; Roberts, 1974; Taylor, 1997; Ankel-Simons, 2000; Nyakatura and Fischer, 2010a). In most cases, the acromion and coracoid processes are joined by a strong coracoacromial ligmament, but the expansion of these processes is so great in *Choloepus* (the two-toed sloth) that the two are fused into one bony arch (Nyakatura and Fischer, 2010a). The scapula of highly suspensory primates tends to be mediolateral compressed with a

craniocaudally oriented scapular spine (Larson, 1995). This reorientation of the scapular spine impacts the line of action of the infrapinatus muscle, which is an important muscle for maintaining stability during suspensory locomotion (Larson and Stern, 1986). Additionally, subscapularis is a large muscle in most suspensory taxa that is important for arm overhead reaching and movement (Larson and Stern, 1986). This muscles size can be so large that it may have a lateral expansion of the subscapular fossa beyond the ventral bar (Larson, 1995).

The clavicle connects the scapula to the sternum, provides leverage and attachment for various muscles of the shoulder, and permits a full range of motion at the glenohumeral joint (Voisin, 2006; Kagaya et al., 2010; Gebo, 2014; Squyres and DeLeon, 2015). All species that use suspensory locomotion have a clavicle (LeGros Clark, 1926; Walton and Walton, 1970; Diogo, 2009; Nyakatura and Fischer, 2010a; Lambert et al., 2014; Squyres and DeLeon, 2015). In general, the clavicle of suspensory animals tends to be twisted cranially on its lateral end, is longer than in non-suspensory animals, and generally has a great deal of curvature (Kagaya et al., 2010; Squyres and DeLeon, 2015). The strong ventral curvature of the medial clavicle is thought to prevent the bone from cutting across the thoracic outlet during arm-swinging, particularly when the arm of interest is in the craniodorsal-most position. In this position the clavicle is primarily aligned along a dorso-ventral axis and its ventral curvature prevents it from impinging on soft structures of the root of the neck (Jenkins et al., 1978; Squyres and DeLeon, 2015).

The humerus of suspensory animals is highly modified to promote mobility at the glenohumeral and elbow joint. For some species mobility is so high that the shoulder can

rotate in a full circle (circumduction) around the glenohumeral joint (Ashton and Oxnard, 1964; Oxnard, 1967; Jenkins et al., 1978; Ankel-Simons, 2000). This ability is important for overhead reaching during arm-swinging, and the large amount of shoulder excursion during below branch quadrupedal locomotion (Jenkins et al., 1978; Nyakatura et al., 2010; Tripp et al., 2015). In most suspensory taxa, the humeral head is a large ball-like structure that extends well above the tubercles. This, in addition to smaller greater and lesser tubercles, allows for a great range of motion without the tubercles impinging on movement at the glenohumeral joint (Rose, 1983; Ankel-Simons, 2000; MacLatchy et al., 2000; Rosenberger et al., 2008; Gebo, 2014).

In suspensory species, the humerus tends to be straight (Swartz, 1990; Yamanaka et al., 2005; Nyakatura and Fischer, 2010a) with moderate levels of medial torsion (although this varies among species) (Gebo et al., 1988; Larson, 1988, 1996; Gebo, 2014). Medial torsion allows the humeral head to contact the scapula, which now faces laterally as it lies along a barrel-shaped thorax, and positions the distal humerus (elbow joint) forward (Gebo et al., 1988; Larson, 1988, 1996; Gebo, 2014). The straight shape of the humerus is thought to be a way to mitigate high-shear loading that occurs during arm-swinging (Swartz, 1990; Yamanaka et al., 2005). Under shearing stress, diaphyseal cortical bone is much weaker relative to other stress environments and curvature only accentuates this weakness (Crowninshield and Pope, 1974; Swartz, 1990; Fung, 1993, 2013). By straightening out the humerus, arm-swinging animals are able to better resist exceptionally high shearing stresses (Swartz et al., 1989). The ulna and radius do not

experience as much shear, and therefore may not under the same selective pressure (Swartz et al., 1989).

The distal aspect of the humerus also reflects modifications for suspensory locomotion. The capitulum is ball-like, and promotes greater mobility of the radius during pronation and supination (Rose, 1983, 1988; Gebo, 2014; Johnston, 2014). The trochlea tends to be beveled, which allows the ulna to be held firmly onto the humerus during full extension of the forearm (Rose, 1988; Gebo, 2014). The medial epicondyle is also quite large in comparison to the lateral epicondyle. This reflects the need for a large attachment site for the strong flexor musculature that originates from this structure (Miller, 1935; Gebo, 2014). The same features are also observed in arboreal species in general, but not to the same degree (Rose, 1983, 1988; Harrison, 1989; Gebo, 2014).

The ulna of suspensory mammals is highly modified compared to other arboreal animals (Michilsens et al., 2010; Fleagle, 2013; Rein et al., 2015). The ulna is elongated (Rein et al., 2015), and has relatively short olecranon process, which is the site of attachment for powerful extensor musculature (i.e., the triceps brachii). The shortening of this feature is thought to enhance the speed of elbow extension during the swing phase of suspensory behaviors (Turnquist, 1975; Rein et al., 2015). This feature is also thought to allow a greater degree of arm extension, which can result in a greater effective limb length (Su and Jablonski, 2009).

Similar to the ulna, the radius is elongated compared to non-suspensory species. This, as mentioned above, results in an overall lengthening of the arm. In contrast to the ulna, the radius is quite robust, and demonstrates significant curvature (Tuttle, 1972;

Turnquist, 1975; Preuschoft and Demes, 1985; Swartz, 1990; Michilsens et al., 2009). The reason for this significant curvature is not well known, but it is believed to provide a large attachment site for the supinator muscle (Swartz, 1990). Supination is thought to be incredibly important during arm-swinging as substantial rotation of the body occurs underneath the support for certain species (Jenkins, 1981).

In association with the rotation of the body underneath the support, there also appear to have been significant anatomical modifications to both the proximal and distal radius. Increased mobility corresponds to a highly circular radial head and more symmetrical distal articular surface for the articulation with the radial notch of the ulna (Napier and Davis, 1959; Morbeck, 1972; Rose, 1988; Ankel-Simons, 2000). The radiocarpal joint is also considerably expanded to allow high mobility between the bones of the wrist and the distal radius (Hamrick, 1996; Hamrick et al., 2000).

Patterns of wrist morphology in suspensory species are thought to promote mobility and overall range of motion (Lewis, 1971, 1985a; b; Cartmill and Milton, 1977; Mendel, 1979; Jenkins, 1981; Kivell et al., 2013). Many species that commonly adopt suspensory postures: (1) lack an ulna-pisiform and ulnotriquetral articulation; (2) have a slender styloid process of the ulna ending in a smaller articular surface; and (3) have an increased expansion of radiocarpal joint surfaces. Additionally, certain arm-swinging primates possess a rotary mid-carpal region where the scaphoid is capable of rotating around the medial ulnar side of the capitate (Jenkins, 1981). Like primates, sloths also have wrist morphology that promotes anatomical mobility (Miller, 1935; Mendel, 1979). The sloth wrist is considerably modified from the primitive mammalian pattern in order

to allow a great deal wrist flexion (average 100º), extension (average 81º), and ulnar deviation (average 99º) (Mendel, 1979). As mentioned above, extreme ulnar deviation appears to be a trait consistent with species that practice suspensory positional behaviors; the sloth is no exception (Cartmill and Milton, 1977).

A deep carpal tunnel also typifies vertical clinging and suspensory mammals (Miller, 1935; Mendel, 1979; Hamrick, 1996; Hamrick et al., 2000). This allows for the passage of powerful digital flexor tendons. In many species, ulnar deepening of the carpal tunnel is accomplished by an elongated hamate hamulus, which serves as the attachment site of the transverse carpal ligament. Sloths have an elongate, palmarly directed scaphoid tubercle that deepens the radial border of the carpal tunnel (Mendel, 1979; Hamrick, 1996; Hamrick et al., 2000). The sloth carpal bones are proximo-distally short, but deeply concavo-convex ventro-dorsally. The volar surfaces of these deep concave bones form the floor of the carpal tunnel (Mendel, 1979). Together, these traits are thought to reflect adaptations for high joint mobility and the passage of powerful flexor tendons that allow species to move fluidly and rapidly below branches (Lewis, 1971; Cartmill and Milton, 1977; Mendel, 1979; Jenkins, 1981; Hamrick, 1996; Hamrick et al., 2000).

1.3.3 Hindlimb morphology

Compared to the forelimb, the hindlimb has been largely ignored in discussions of suspensory locomotion. This is most likely due to the fact that most morphological studies of suspensory locomotion have been conducted on arm-swinging primate rather than species that use below branch quadrupedal locomotion. Like the shoulder, the hip joint of suspensory species has been modified to promote a greater deal of mobility,

especially in respects to abduction and external rotation (Hammond, 2014). The mobility of the hip joint appears primarily due to modifications of the proximal femur, which includes a longer femoral neck and greater trochanter that lies inferior to the femoral head (Simons et al., 1992; Godfrey and Jungers, 2003; Gebo, 2014). Both of these features allow a greater potential space for movement to occur without adjacent bony structures abutting against one another. The femoral shaft of suspensory animals tends to be straight, and mediolaterally flattened with thicker cortical bone on the mediolateral aspects (Gebo, 1989, 2014). The flattening and increased cortical bone deposition on the mediolateral aspects is thought to strengthen the bone due to habitual mediolateral forces experienced during below branch movement (Gebo, 1989, 2014). As with the humerus, the straight femoral shaft is thought to be a mechanism to mitigate high-shear loading that occurs during suspensory movement (Swartz, 1990; Yamanaka et al., 2005). The distal femur is broad with a wide patellar facet. This morphology is thought to allow a maximum range of flexion and extension, which is important for locomotion that utilizes a high variety of leg positions when grasping odd-angled supports with the foot (Gebo, 1989, 2014).

The morphology of the tibia and fibula of suspensory animals are rarely discussed beyond general shape and size. The most detailed analysis is provided by Mendel (1981) in his discussion of the foot of *Choloepus*. In most suspensory animals, the tibia and fibula are more similar in size to one another (Ankel-Simons, 2000; Gebo, 2014) compared to cursorial animals, that show fibular reduction. In the sloth, the tibia is a stout bone that bows medially and anteriorly. Like the distal femur, the articular surface on the

proximal tibia is flat and broad, which allows a large amount of knee flexion and extension. The proximal tibia is roughly triangular in cross section, but becomes progressively more anteroposteriorly flattened from mid-shaft to the distal articulating surface. The medial malleolus is separated from the inferior articular surface of the tibia by 3-5 mm, and has a deeply notched posterior aspect, which serves to guide the tendon of tibialis posterior (Mendel, 1981).

Based on the description of Mendel (1981), the sloth fibula is large (relatively close in size to the tibia), especially in its distal half. It bows slightly laterally, and forms a tight fibrous connection with the proximal tibia via dense capsular ligaments. The distal tibio-fibular joint is covered anteriorly and posteriorly by ligaments that are continuous with the interosseous membrane. The fibula is tightly bound to the tibia, but some antero-posterior sliding is possible (~1 mm; Mendel, 1981).

As with the wrist, the ankle of suspensory animals promotes a high level of mobility, especially for suspensory quadrupeds (e.g., sloths and lorises). The lorisid talocrural joint, like that of other primates, comprises the articulation of the talus with the distal extremities of the lower leg bones, whereby the talus is securely locked beneath the tibia and fibula during inversion and eversion (Gebo, 1989, 2014). The hinge like mechanism of the joint permits plantar/dorsiflexion across a range of about 100° of motion (Grand, 1967). The ligaments of the joint assist in retaining the single plane of motion in this joint (Grand, 1967; Read, 2001). Like the lorisine talocural joint, there is remarkable mobility in sloths as well (Mendel, 1981). Based on the cadaveric descriptions of Mendel (1981), the sloth talus is a narrow bone with a hemispherical

trochlea. The articular surface for the tibia is convex and tapered slightly posteriorly. There is no articulating surface for the medial malleolus. From a neutral position the ankle can be flexed approximately 90° and dorsiflexed (extended) 50-60°. Further motion of these joints is limited when the calcaneus abuts against the posterior aspect of the tibia and fibula (flexion), and when the neck of the talus strikes the anterior tibia (dorsiflexion). Medial and lateral collateral ligaments limit ankle inversion and eversion (Mendel, 1981).

The subtalar joint consists of two articular facets, jointly contributing to a single axis of movement (Read, 2001). As the talus is tightly bound, allowing restricted mediolateral excursion, the calcaneus, navicular and distal foot move relative to the talus, at the subtalar joint, to contribute to the range of mobility (Grand, 1967; Gebo, 1989; Read, 2001). These movements take place at the posterior and anterior talocalcaneal articulations, and at the transverse tarsal joint. The primary direction of motion at these points is inversion/eversion. The navicular articulates mediolaterally with the anterior surface of the flattened talar head, facilitating inversion/eversion across a range of approximately 60-70° (Grand, 1967; Read, 2001). Additional inversion and flexion also occurs at the metatarsals and digits. This inverted posture of the foot, accompanied by plantarflexion at the talocrural joint, is documented as the natural position of the tarsus and digits relative to the ankle (Grand, 1967; Read, 2001).

As described by Mendel (1981), the sloth transverse tarsal joint (talonavicular and calcaneocuboid joints) is the primary site of inversion and eversion of the foot. Eversion is extremely limited (5-10°), but overall inversion is quite high (90°). Distal tarsal joints

and the metatarsophalangeal joints permit an additional 10-15° of inversion. The transverse tarsal joints also allows another 20-40° of overall flexion.

1.3.4 Axial morphology

The ribs of many suspensory mammals are heavily bent near their articulation with the thoracic vertebrae, and the transverse process on which the ribs articulate are angled more dorsally (Erikson, 1963; Ankel-Simons, 2000; Rosenberger et al., 2008). Together this results in a broader more barrel-shaped rib cage. This is thought to aid in the repositioning of the scapula more dorsally, which allows for better overhead reaching and more abducted positioning of the forelimb (Erikson, 1963; Ward, 1993; Ankel-Simons, 2000; Rosenberger et al., 2008). The ribs of suspensory mammals also tend to be cranio-caudally expanded compared to those of pronograde species. It has been suggested that cranio-caudal expansion of the ribs limits back flexion by passively reducing intercostal spaces between adjacent ribs (Jenkins, 1970; Sargis, 2001a; Granatosky et al., 2014a). In certain taxa like *Cyclopes* (the silky anteater), this expansion is so radical that adjacent ribs have grooves that might serve to limit axial rotation as well (Jenkins, 1970).

In sloths, the ribs also serve an important attachment site for the abdominal organs (i.e., liver and glandular stomach). These extra attachments are thought to have evolved to prevent the abdominal organs from impinging on the diaphragm, therefore allowing greater overall lung volume (Cliffe et al., 2014). It is unclear whether this anatomical arrangement is present in other highly suspensory species.

Animals that use suspensory locomotion are all characterized by cranio-caudally elongated and dorsoventrally short spinous processes, dorsally oriented transverse

processes, and dorsoventrally and mediolaterally elongated vertebral bodies (Sargis, 2001a; Shapiro et al., 2005; Granatosky et al., 2014a, b). These features are proposed to provide either (1) bony stops that limit movement between adjacent vertebrae, or (2) more effective levers that aid in maintaining erect or semi-erect postures by resisting ventral flexion of the trunk (Shapiro, 1995, 2007; Shapiro and Simons, 2002; Shapiro et al., 2005; Granatosky et al., 2014a, b). Cranio-caudally elongated and dorsoventrally short spinous processes are presumed to passively limit axial extension by providing a bony stop between adjacent vertebrae (Sargis, 2001a; Shapiro and Simons, 2002; Granatosky et al., 2014a, b). The dorsal orientation of the transverse processes has been inferred to align the insertion points of the erector spinae closer to the midline resulting in more effective levers that aid in maintaining erect or semi-erect postures by resisting ventral flexion of the trunk (Johnson and Shapiro, 1998; Sargis, 2001a; Shapiro and Simons, 2002; Granatosky et al., 2014a, b).

Vertebral body shape within suspensory mammals is dorsoventrally high and mediolaterally wide compared to that of pronograde, vertical clinging, and gliding mammals. These features have been interpreted as another form of passive resistance limiting flexion within the spine. Mediolaterally wide and dorsoventrally elongated vertebral bodies would abut against one another when gravity is acting to flex the spine, as in inverted postures (Shapiro, 1995, 2007; Johnson and Shapiro, 1998; Sargis, 2001a; Shapiro and Simons, 2002; Granatosky et al., 2014a, b). Again these features may be especially important for inverted quadrupeds, passively reducing the total flexion in the

spine and reducing overall energy expenditure by reducing muscular effort (Cartmill and Milton, 1977).

1.4 The evolutionary origins of suspensory locomotion

From the information above, it is clear that suspensory locomotion has evolved independently in numerous mammalian clades, and that the acquisition of suspensory locomotion is sometimes accompanied with substantial anatomical reorganization. What remains less clear, and often confusing, is how suspensory locomotion first arose in each of these clades. Usually the origin of suspensory locomotion is discussed as a single event, but more fruitful investigation may arise by considering the evolution of below branch quadrupedal locomotion and the evolution of arm-swinging as two distinct entities. This is an important distinction, because the transition to below branch quadrupedal locomotion is thought to require very little anatomical and neuromuscular reorganization, and as a result has evolved numerous times among varying mammalian clades (Demes et al., 1990; Nyakatura, 2011). In contrast, arm-swinging is a highly specialized form of suspensory locomotion that requires significant anatomical specializations, especially in the forelimb, and has only evolved in certain primate clades. The restriction of arm-swinging to the order Primates is incredibly important and interesting, because it suggests that there is something inherently unique to Primates that has allowed them to adopt this highly specialized form of suspensory locomotion.

It is safe to assume that below-branch quadrupedal locomotion represents the simplest way for an upright arboreal animal to adopt suspensory positional behaviors. Nyakatura (2011) suggested that the transition from above to below branch quadrupedal

locomotion is so simple (at least in ancestral sloths) that animals utilize conserved neural control of locomotion. Other studies agree with this interpretation, and some argue based on very limited data and species that animals walking quadrupedally below a support are simply inverting normal patterns observed during upright walking (Turnquist, 1975; Parsons and Taylor, 1977; Jouffroy and Petter, 1990; Jouffroy and Stern, 1990; Nyakatura et al., 2010). For example, Parsons and Taylor (1977) observed a slow loris as it walked above and below a motor-driven rope and found no significant differences in timing or energy consumption between the two modes of locomotion. Jouffroy and Petter (1990) and Jouffroy and Stern (1990) corroborated these results, demonstrating that step length, duty factor, limb excursion, muscle activation, and overall body contour line were mirrored between above and below branch quadrupedalism in lorises. It should be noted that the anatomical and locomotor adaptations of lorisids are highly derived, and are not typical for primates (Grand, 1967; Cartmill and Milton, 1977; Jouffroy and Stern, 1990; Read, 2001; Schmitt and Lemelin, 2004; Shapiro, 2007; Granatosky et al., 2014a, b).

There are two non-exclusive theories as to why animals may adopt below branch quadrupedal locomotion. From an ecological perspective, one theory posits that below branch movements are associated with increased food acquisition, and as a means for relatively large-bodied arboreal mammals to move along thin, compliant supports often associated with the terminal ends of branches (Grand, 1972). These branches provide important foraging locations, as they are often the site of young leaves, fruit, blooming flowers, and insect prey (Sussman, 1991; Cartmill, 1992; Schmitt and Lemelin, 2002). Access to these branches, however, is difficult for animals whose repertoire includes only

above branch locomotion (Grand, 1972; Cartmill, 1985; Cartmill et al., 2002; Lammers and Gauntner, 2008). Using suspensory positional behavior allows animals to more efficiently exploit these terminal branch resources, opening or expanding an animals feeding niche (Grand, 1972; Cheyne, 2011).

A second theory considers a biomechanical model that predicts the ratio of body size to support varies inversely with the ability to remain balanced above the support. As the body size to support size ratio increases, above branch quadrupedal locomotion becomes perilous (Napier, 1967; Cartmill, 1985; Lammers and Gauntner, 2008). Thus, as body size increases an animal's ability to safely and efficiently move above relatively small arboreal supports rapidly declines. One solution to this balance problem may be for arboreal animals to move their COM below branch, thereby adopting suspensory behaviors (Napier, 1967; Cartmill, 1985; Figure 2).

As will be discussed in section 1.5, there are many strategies besides suspensory locomotion that animals use to prevent falling off of thin supports (Figure 2). Many of the other solutions involve adjustments to intrinsic gait parameters to better maintain balance and improve security while moving on top of thin supports (Kimura et al., 1979; Larson et al., 2000; Cartmill et al., 2002). Interestingly, few studies have explored whether these gait characteristics that have evolved for above branch quadrupedal locomotion are retained when moving below branches. It may be possible that the adaptive benefits of these features are nullified when moving below branches. Moreover, the gait mechanics of below branch quadrupedal locomotion may represent a "mechanical release" from the highly modified gait characteristics observed during primate quadrupedal locomotion.

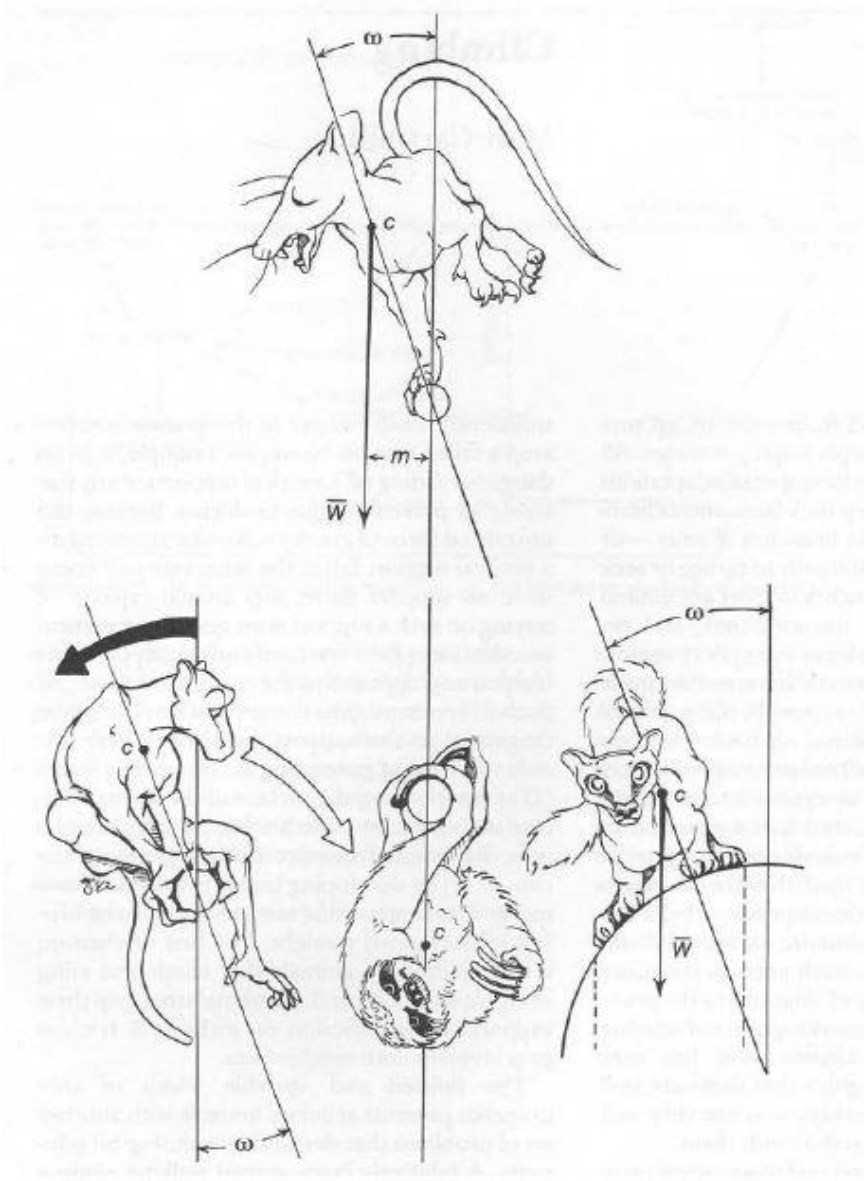

Figure 2: The various solutions to prevent toppling off a thin arboreal support. An animal standing on a relatively small horizontal cylinder (top) can easily roll or pitch into a position where its center of mass (c) no longer lies above its narrow base of support, whereupon gravity produces a rotatory moment of magnitude (*W*m) that topples the animal from the support. This can be resisted in several ways: by using grasping extremities (bottom left) to generate a torque (white arrow) equal and opposite to *W*m (black arrow), by hanging underneath the support (bottom center); by reducing height of c above the support (bottom right), or producing a relative increase in the size of the support polygon (dashed lines). Figure from Cartmill (1985).

As mentioned above, adopting below branch quadrupedal locomotion does not seem to require significant anatomical or mechanical modifications all that different from above-branch quadrupedal locomotion. This is not the case for arm-swinging as the transition from an above-branch arboreal quadruped to a primate capable of bimanual locomotion appears to require significant anatomical and neural reorganization. Specifically, the greatest change that must occur is a functional reorganization of the forelimb to become the primary propulsive and load-bearing limb. Currently, some studies have addressed this transition (Fleagle et al., 1981; Gebo, 1996; Meldrum, 1998), with one study formalizing it (Cartmill and Milton, 1977).

First reported by Cartmill and Milton (1977), and later supported by Larson (1998) and Read (2001), is the finding that some arm-swinging primates bear considerable anatomical similarities in the wrist (especially hominoids) – and other aspects of the postcranial anatomy (Larson 1998) – with slow, deliberate moving arboreal quadrupeds (e.g., lorisids). The convergence between these two very different primate groups implies a shared mechanical convergence that Cartmill and Milton (1977) assumed may indicate a connection to the evolution of arm-swinging. This idea was later refined by Mendel (1979) to suggest that it may not be deliberate arboreal quadrupeds that gave rise to arm-swinging primates, but instead animals that commonly use below branch quadrupedal locomotion and bridging (i.e., lorises and sloths). As proposed by these authors (Cartmill and Milton, 1977; Mendel, 1979; Larson, 1998), a possible scenario to explain the acquisition of arm-swinging is that as relatively large-bodied, anatomically unspecialized arboreal primates began to adopt a greater proportion of

below branch quadrupedal locomotion the mechanical challenges associated with suspensory locomotion would have driven certain anatomical features (e.g., changes in the wrist, elbow, and shoulder, and increased finger and forelimb length) to be selectively favored. These features would in turn be beneficial for the eventual acquisition and arm-swinging. Eventually, arm-swinging would have replaced below branch quadrupedal locomotion as the primary mode of suspensory locomotion observed in primates.

This scenario is to some degree supported by the finding of a partial skeleton of the extinct dryopithecine *Hispanopithecus laietanus*, which is characterized by a unique combination of anatomical features suggesting both pronograde arboreal locomotion and suspensory behaviors. Most notable are highly curved phalanges (Almécija et al., 2007) and an elbow complex suitable for enabling considerable pronation and supination (Alba et al., 2012). These features, commonly associated with suspensory locomotion, are paired with olecranon morphology usually consistent with above branch quadrupedal locomotion. This mosaic of features led Almécija et al. (2007) and Alba et al. (2012) to suggest that *H. laietanus* likely moved in a fashion similar to that of the orangutan, which commonly adopts below branch quadrupedal locomotion (Thorpe and Crompton, 2006). This finding potentially indicates that an animal capable adopting both above and below branch quadrupedal locomotion may have represented an intermediate stage between the transition from a generalized arboreal quadruped to a specialized suspensory primate (Cartmill and Milton, 1977; Mendel, 1979; Read, 2001; Almécija et al., 2007; Alba et al., 2012).

The most serious criticism of this theory comes from the obvious fact that there are many animals that use below branch quadrupedal locomotion in their normal locomotor repertoire, but there are only a few primate species that are capable of arm-swinging. Granatosky et al. (2016) addressed this issue by exploring limb loading patterns in two species of anatomically generalized primates (*Lemur catta* and *Varecia variegata*) during above and below branch quadrupedal locomotion, and determined that these species alter the functional role of the forelimb to become the primary propulsive and load-bearing limb during below branch quadrupedal locomotion. A similar pattern was observed by Stern et al. (1980a) that observed serratus anterior function changed during below branch quadrupedal locomotion to more closely match what was observed during arm-swinging than above branch quadrupedal locomotion. Granatosky et al. (2016) proposed that the ability of primates to alter limb loading patterns may reflect high levels of mechanical flexibility (Wainwright et al., 2008; Iriarte-Diaz et al., 2012) that may not be present in non-primate mammals.

The capacity for animals to change intrinsic aspects of locomotion (e.g., limb loading patterns and limb kinematics) fluidly and efficiently is key to animal locomotor success in different settings. This ability seems especially important in a complex arboreal milieu occupied by many mammalian species (Blanchard and Crompton, 2011; Fleagle, 2013). The idea that primates have a well-developed capacity for adjusting aspects of forelimb positioning and/or gait to effectively adjust to particular environmental circumstances is not new (Vilensky and Larson, 1989; Lemelin and Schmitt, 1998; Schmitt, 1999; Nyakatura et al., 2008), and this mechanical flexibility

(Wainwright et al., 2008; Iriarte-Diaz et al., 2012) has been seen as reflecting underlying neuromuscular mechanisms that may have allowed for the great amount of locomotor diversity within the primate order (Vilensky and Larson, 1989; Schmitt, 2010).

For most non-primate mammals, locomotion is thought to be controlled by central pattern generators, which are neural networks that produce rhythmic outputs without significant cortical feedback (MacKay-Lyons, 2002; Drew et al., 2004; Ijspeert, 2008) and produce the basic action of stepping without higher commands from the cortex (Mori, 1987; Mori et al., 1996; Golubitsky et al., 1999; MacKay-Lyons, 2002; Drew et al., 2004). Evidence for such circuits in higher order primates, including humans, is tenuous, and studies suggest that supraspinal inputs, and likely cortical inputs, have a more important role in the generation of primate locomotion (Mori, 1987; Vilensky and Larson, 1989; Mori et al., 1996; Schmitt, 2010).

Demonstrating evidence of cortical control during locomotion has been difficult, but recent neuromuscular studies suggest that humans, and some non-human primates, may have evolved a flexible coupling of thoracolumbar and cervical centers that allows them to use the upper limbs for manipulative and skilled movements, or for locomotor tasks (Dietz, 2002, 2003). This flexible coupling of the forelimbs and hindlimbs has received considerable attention in studies of primate locomotion (Wood Jones, 1916; Kimura et al., 1979; Schmitt and Lemelin, 2002; Schmitt, 2010; Patel et al., 2015), and has been proposed by some to be the underlying reason for many important locomotor transitions within the evolutionary history of primates (Wood Jones, 1916; Sylvester, 2006; Schmitt, 2010; Granatosky et al., 2016). It was Wood Jones (1916) that first

identified the importance of flexible coupling between the forelimbs and hindlimbs as a possible mechanism underlying the evolution of arm-swinging and bipedalism. From this early work, many other have demonstrated clear examples of functional decoupling between the forelimbs and hindlimbs in primates (Kimura et al., 1979; Reynolds, 1985a; Larney and Larson, 2004; Franz et al., 2005; Patel et al., 2015), and it is likely that this unusual neuromuscular pattern evolved early in basal primates (Patel et al., 2015). Arm-swinging is a clear example of functional decoupling of the forelimbs and hindlimbs in which the forelimbs become the sole weight-bearing limb and propulsive limb while the hindlimbs are released from their weight-bearing function. Based on the data collected from Granatosky et al. (2016), it is evident that the same pattern of functional decoupling is occurring during below branch quadrupedal locomotion in primates. As proposed by Granatosky et al. (2016), the functional shift of the forelimb as the primary propulsive and weight-bearing limb may reflect the best possible biomechanical solution for primates to effectively move below branches. If this assertion is correct, then this may explain the level of convergence that is observed in arm-swinging primates both across and within certain clades (Lewis, 1971; Cartmill and Milton, 1977; Rose, 1983; Larson, 1998; Read, 2001; Almécija et al., 2007; Alba et al., 2012, 2015).

1.5 Mechanical strategies during suspensory locomotion

As evident above, theories concerning the evolution of suspensory locomotion are incomplete, and leave open two important and testable questions: (1) is below branch quadrupedal locomotion simply a neuromuscular mirror of above branch quadrupedal locomotion; and (2) is there some connection between below branch quadrupedal

locomotion and arm-swinging? While anatomical studies can help identify species that use suspensory locomotion, they provide generally little information concerning the questions above. Through biomechanical analyses, we can better understand how animals adjust to the mechanical stresses associated with below branch locomotion and ascertain the varying solutions animals have evolved to move in this manner. The following section reviews what is currently known about the mechanics of suspensory locomotion, and outlines how each form of below branch movement (i.e., below branch quadrupedal locomotion and arm-swinging) relates to each other. Additionally, patterns of above-branch quadrupedal locomotion will be discussed in order to understand the transitions that must have occurred during the evolution of suspensory locomotion. This section will be broken down into four parts that specifically discuss COM movements, kinetics, kinematics, and overall footfall patterns and timing.

1.5.1 Center-of-mass movements

As mentioned earlier, the COM movements of suspensory locomotion have often been compared to a simple pendulum, especially in respects to arm-swinging (Avis, 1962; Fleagle, 1974; Preuschoft and Demes, 1984, 1985; Swartz, 1989). A simple pendulum is an idealized system in which a dimensionless point mass is suspended from a massless cord. At rest, the pendulum will be aligned with the gravitational vector, but once in motion, it will swing back and forth in periodic, oscillatory motion. Pendular motion results in out-of-phase fluctuation of the body's kinetic and potential energy, creating the opportunity of energy exchange (Bertram et al., 1999; Bertram and Chang, 2001; Michilsens et al., 2011), and therefore, highly efficient locomotion.

While the comparison between arm-swinging locomotion and a simple pendulum has served as an incredibly valuable heuristic tool, this comparison should be made with caution when making detailed mechanical analyses. The first problem with purely pendular motion during arm-swinging is that, based on the animal's limb length and mass, there is only a narrow range of speeds and distances between supports the animal can use to maximize energetic efficiency (Preuschoft and Demes, 1984; Swartz, 1989; Bertram et al., 1999; Michilsens et al., 2011). While there is evidence that some animals do confine themselves to these speeds and support distances (Preuschoft and Demes, 1984), it seems improbable that in a complex arboreal environment animals would be able to maintain a constant direction and speed for any extended period of time.

Another aspect of pendular motion that must be considered is collisional losses of energy. A collisional loss can be described as a type of mechanical energy loss due to abrupt changes in the direction of motion (e.g., when grasping a new support) (Bertram et al., 1999; Bertram, 2004; Michilsens et al., 2011). In a simple pendulum, no energy is lost during subsequent supports because collisional losses are eliminated by the motion coming to rest (i.e., velocity = 0) at the end of each arc of motion. As discussed above, in order for an arm-swinging animal to benefit from the energy saving advantages of simple pendular motion that animal must restrict its movement considerably to a particular speed and stride distance. Any deviation from that restricted range would result in low energy recovery due to collisional losses. Obviously, arm-swinging animals are not restricted in this regard, and to prevent collisional losses arm-swinging animals use a number of kinematic mechanisms to modify COM movements to maximize overall energy recovery.

The type of mechanism used to prevent collisional losses is dependent upon the type of arm-swinging behavior. At slower speeds, animals use gaits that are characterized by dual-limbed support phase with duty factors of each limb $\geq$ 0.5, meaning at least one limb is always in contact with the support (Bertram et al., 1999; Turnquist et al., 1999). Arm-swinging gaits with continuous contact closely resemble simple pendular motion, where the animal's COM moves along a sequence of circular arcs. Collisional losses can be avoided during continuous-contact arm-swinging by taking hold of the support at the same time that the position of the COM is at its highest point in the arc. At higher speeds, animals tend to use ricochetal gaits that are characterized by an aerial (non contact) phase between support phases of each step (Bertram et al., 1999; Michilsens et al., 2011). Center-of-mass movements during ricochetal arm-swinging closely match a sine wave, where the trough coincides with the lowest position of the COM during support phase [i.e., usually at mid-support (50% of support phase)], and the crest represents the highest point of the COM during a no-contact flight phase. Collisional losses can be reduced by assuring the trajectory of the COM at the end of the flight phase is coincident with the swing arc around the next handhold (Bertram et al., 1999; Bertram, 2004; Michilsens et al., 2011).

Both collisional loss and pendular mechanics play a role in determining locomotor behavior, as they do in upright walking (Lee et al., 2013), and are not mutual exclusive. A complete model considers them both and how they complement or conflict with each other. It is important to note that arm-swinging animals are not inherently simple pendulums, but instead alter many intrinsic aspects of their gait in order to

replicate pendular movement. This leads to a very important point and a common misconception that is rampant throughout the literature. As discussed above, the movement of a simple pendulum allows for high levels of energy exchange, and theoretically, more efficient locomotion. This begs the question as to whether or not arm-swinging animals are particularly good (as measured by energetic efficiency) at modifying their gait to move like simple pendulums. The answer to this appears to be simultaneously yes and no. While arm-swinging animals appear to be very good at replicating the energy exchange observed during pendular motion [energy recovery 40-80% (Michilsens et al., 2011)], the cost do to so appears quite high (Parsons and Taylor, 1977). Parsons and Taylor (1977) measured the cost of locomotion during arm-swinging and show that arm-swinging (at least in *Ateles*) was energetically more expensive when compared to walking. This finding suggests that arm-swinging may have evolved due other selective advantages such as reducing overall travel distance (Parsons and Taylor, 1977; Temerin and Cant, 1983), the ability to occupy a unique and unoccupied niche, escape from slower predators, and reach for fruits at the end of fine branches.

While considerable attention has been given to COM dynamics in arm-swinging animals, only one study has explored this topic during below branch quadrupedal locomotion. Nyakatura and Andrada (2012) proposed that while arm-swinging can be modeled as a simple pendulum, below branch quadrupedal locomotion could best be seen as simple connected pendulum. They tested this assumption by comparing the kinematic movements of a two-toed sloth to that of a freely swinging connected pendulum. Analysis of swing frequency and the vertical oscillation of the approximated COM demonstrate

that these parameters do not match values predicted for a simple connected pendulum. Nyakatura and Andrada (2012) proposed that sloths actively slow themselves down throughout the stride, and subsequently, use shoulder retraction and elbow flexion to propel themselves forward prior to the swing phase. The reason for this active perturbation of pendular motion has been argued as promoting deliberate movements necessary for a slow moving animal unable to react quickly if a branch were to break. It is unclear whether this pattern is present in all animals that move quadrupedally below branches, or if sloths are unusual in this regard.

While suspensory locomotion (both quadrupedal and bimanual) is usually modelled as some form of a simple pendulum, above-branch quadrupedal locomotion is commonly referred to as an inverted pendulum, which is characterized by a cyclic exchange between gravitational potential energy and kinetic energy (Cavagna et al., 1977; Griffin et al., 2004). Energy recovery via this exchange is never 100% perfect, as the transition from one leg to the next inevitably results in energy loss (Griffin et al., 2004; O'Neill and Schmitt, 2012). Accordingly, the maximum values of mechanical energy recovery tend to be lower for quadrupeds (30–65%) than for bipeds (70–80%), suggesting that the inverted pendulum mechanism for exchange of center of mass energy may be less effective in quadrupedal animals (Cavagna et al., 1977; Griffin et al., 2004; O'Neill and Schmitt, 2012).

As discussed above with respect to arm-swinging, there are many ways in which animals walking above-branch can modify overall COM movements (Schmitt, 1998; Bishop et al., 2008; O'Neill and Schmitt, 2012), and reduce collisional losses (Ruina et

al., 2005). During upright locomotion, the most commonly discussed mechanism to modify COM movements is through increased flexion at the elbows and knees (Schmitt, 1994, 1995, 1998; O'Neill and Schmitt, 2012). This pattern results in generally lower oscillations of the COM, and therefore lower collisional losses and overall smoother gaits (Bishop et al., 2008). This pattern tends to be especially important for stealthy walking and arboreal animals. With respect to arboreal animals walking on compliant branches, lower COM oscillations result in lower substrate oscillations (Schmitt, 1994; Schmitt and Hanna, 2004). Reduced substrate oscillations make arboreal locomotion safer by reducing the risk of breaking or falling off arboreal supports. Obviously, animals walking below branches are under similar environmental pressures, but it is unclear whether similar mechanisms are used during below branch quadrupedal locomotion.

It is clear that overall, the patterns of COM movements are largely conserved between upright and inverted locomotion, with the only variable that substantially changes is the reliance of a simple or inverted pendulum. This switch in orientation is accompanied with significant downstream effects on the results of kinetic and kinematic patterns. Currently, few studies have addressed these effects, and minimal information is available on whether animals adopt differing mechanical strategies when switching from above to below branch quadrupedal locomotion, or simply modify the existing gait patterns.

1.5.2 Kinetics

In finer-scaled analyses of movement, measured ground reaction forces during locomotion can be broken down into mediolateral, horizontal, and vertical components

(Eberhart and Inman, 1951; Kimura et al., 1979; Budsberg et al., 1987; Figure 3). The vertical force component is usually of highest magnitude and has been used in numerous studies to understand how animals load their limbs (Kimura et al., 1979; Reynolds, 1985a; b; Schmitt, 1995; Schmitt and Lemelin, 2002). The horizontal force component allows us to explore how animals accelerate and decelerate by examining at the distribution of braking and propulsive forces within a stride (Eberhart and Inman, 1951; Kimura et al., 1979; Demes et al., 1994). Throughout a stride, mediolateral forces are generally low and measure the side-to-side movement of the COM and/or muscular forces applied by the animal to maintain stability (Schmitt, 2003a; Carlson et al., 2005; Franz et al., 2005). Force analysis provides one type of direct test of the relationship between anatomical shape and mechanical function. Unfortunately, collecting this sort of data is difficult, especially for suspensory species, and limited information is available for many species and locomotor modes.

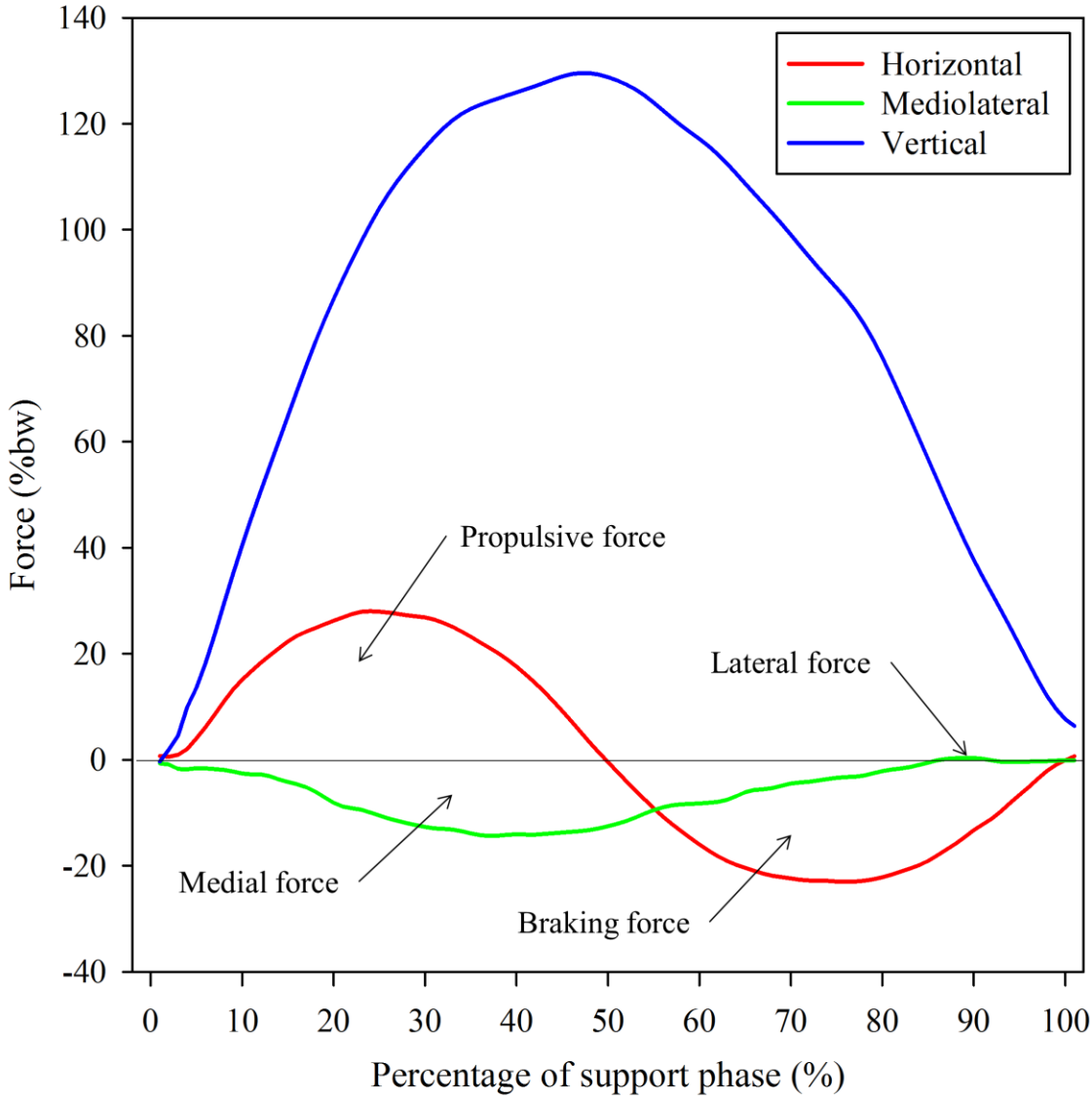

Figure 3: Schematic diagram of force traces observed during suspensory locomotion. Force traces are presented as a proportion of support phase (the portion of the stride in which the limb is in contact with the support).

Numerous studies have concentrated on limb loading patterns of above branch quadrupedal locomotion (Kimura et al., 1977, 1979; Reynolds, 1985a; Ishida et al., 1990; Demes et al., 1994; Schmitt, 1994, 1995, 1998, 1999; Schmitt and Lemelin, 2002; Schmitt and Hanna, 2004; Franz et al., 2005), and to describe all these studies in detail will be a momentous task, so information presented below will only address generalizations for above-branch quadrupedal locomotion and pertinent information for future comparisons to suspensory locomotion. For all forms of upright walking (i.e., bipedal or quadrupedal), horizontal forces appear to be consistent. As the limb makes contact with the substrate it first applies a braking force that acts to decelerate the body's COM followed by a propulsive force that subsequently accelerates the COM (Demes et al., 1994). In bipeds, the relative contributions of braking and propulsive forces tend to be equal for each step, and the braking to propulsive transition (B/P) generally occurs at mid-stance (the point at which the ankle is underneath the hip) (Kimura et al., 1977; Inman et al., 1981). In contrast, during quadrupedal locomotion there is a functional differentiation of the braking and propulsive roles of the limbs, in which the forelimb serves a net braking function and the hindlimb has a net propulsive role (Ishida et al., 1990; Demes et al., 1994; Franz et al., 2005).

While this finding of differential braking and propulsive roles of the forelimbs and hindlimbs has been reported in numerous studies, no explanation has been put forward to explain the mechanism that drives this pattern. Based on characteristics of bipedal walking, it can reasonably be assumed that the B/P generally occurs at mid-stance

for quadrupeds as well, and variation in the limb's general braking/propulsive role is due to differing degrees of limb protraction (i.e., relatively greater limb protraction results in a longer period of the stride in which the limb can brake) and retraction (i.e., relatively greater limb retraction results in a longer period of the stride in which the limb can propel). Unfortunately, limited evidence is available to address this notion. Data collected by Schmitt (1994, 1995) on five Old World monkeys and one New World monkey reveal that the B/P does not occur at mid-stance, but later during the forelimb support phase (about 22% after mid-stance on average). If this finding is consistent across other quadrupeds, then it is obvious that the B/P is independent of mid-stance and some other mechanism must be driving the differing braking and propulsive roles of the forelimb and hindlimb.

Vertical forces are usually the highest magnitude forces observed during locomotion and have revealed important patterns on how animals distribute loads across the limbs. Most quadrupedal primates experience higher peak vertical forces (Vpk) on the hindlimbs relative to the forelimbs, resulting in a relatively lower forelimb to hindlimb Vpk force ratio, while most other quadrupedal mammals are characterized by relatively higher forelimb to hindlimb Vpk force ratios (Figure 4) (Kimura et al., 1977, 1979; Reynolds, 1985a; b; Demes et al., 1994; Schmitt and Lemelin, 2002; Shine et al., 2015). This difference in weight distribution on the forelimbs versus the hindlimbs between most primates and most non-primate mammals may represent a basal adaptation to arboreal locomotion and foraging (Demes et al., 1994; Schmitt and Lemelin, 2002; Lemelin and Schmitt, 2004; Franz et al., 2005; Wallace and Demes, 2008; Raichlen et al.,

2009). Successful arboreal locomotion and foraging would have required early primates to exploit food sources placed off the path of locomotion and make rapid directional changes along branches, both of which require a highly responsive forelimb. In those cases, a highly mobile forelimb bearing a smaller portion of the animal's body weight would provide a distinct advantage, as it would allow the animal to test supports prior to committing a majority of body weight. Additionally, the disparity in limb loading is thought to free the forelimb from its locomotor function permitting the forelimb to evolve as a highly manipulative organ (Wood Jones, 1916; Schmitt and Lemelin, 2002). The increased disparity of the functional roles between the forelimb and hindlimb on arboreal supports further supports this connection (Schmitt and Hanna, 2004; Wallace and Demes, 2008).

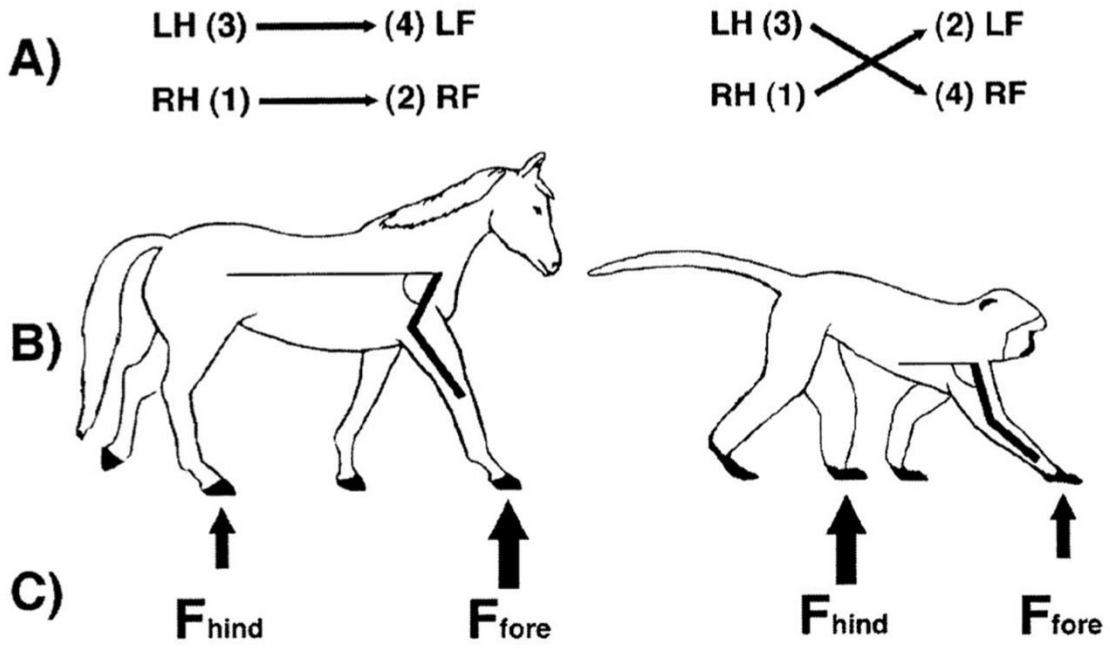

Figure 4: Three locomotor characteristics that distinguish primates from other non-primate mammals. Primates (right) use (A) diagonal-sequence walking gaits (i.e., footfall of right hindfoot is followed by that of left forefoot). In comparison, most non-primate mammals (left) use lateral-sequence walking gaits (i.e., footfall of right hindfoot is followed by that of right forefoot). Primates also tend to have (B) protracted humeral positions at forelimb touchdown (i.e., humeral angles greater than 90° relative to horizontal body axis), in comparison to most non-primate mammals that have more retracted humeral positions at forelimb touchdown (i.e., humeral angle less than 90° relative to horizontal body axis). Finally, when landing on a substrate, (C) forelimbs of primates experience lower peak vertical substrate reaction forces than do hindlimbs. The reverse is true for most other non-primate mammals. Figure from Schmitt and Lemelin (2002).

As mentioned above, the standard limb loading pattern observed in primates is thought to be an important mechanism to free the forelimbs from their normal weight-bearing role in locomotion (Wood Jones, 1916; Reynolds, 1985a; Schmitt and Lemelin, 2002). The mechanism for how this is accomplished is still a matter of inquiry. There remains productive discussion as to whether this altered limb loading pattern in primates is an active process (i.e., active shift of a cranially positioned COM caudally toward the hindlimbs; Reynolds, 1985a; b, 1987; Schmitt, 1999) or a passive one (i.e., by-product of other aspects of normal primate locomotor patterns; Raichlen et al., 2009). As a group, primates are characterized by relatively greater limb excursion during above branch quadrupedal locomotion (Larson et al., 2000) that tends to place relatively protracted hindlimbs underneath the COM for longer periods of time than relatively retracted forelimbs (Raichlen et al., 2009). It has been argued that this pattern is thought to result in relatively greater hindlimb Vpk forces simply because the hindlimb's position in relation to the body's COM, though its importance was disputed by Larson and Demes (2011).

In respect to the hypothesis that primates actively shift (have higher forces) weight to the hindlimbs, two biomechanical models have been proposed to explain how primates maintain relatively higher Vpk forces on their hindlimbs. The first model, proposed by (Reynolds, 1985a; b) and supported by Larson and Stern (2009), suggests that primates actively shift weight caudally on their relatively protracted hindlimbs using powerful muscular retractors of the hindlimb. The second model, proposed by Schmitt, (1994, 1999) and tested by Larney and Larson (2004), argues that primates change

vertical stiffness of their limbs by increasing limb yield, contact time, and angular excursion. These models are not mutually exclusive and both provide important mechanisms by which locomotor forces on the limbs can be moderated (Schmitt and Hanna, 2004; Young, 2012).

Compared to horizontal and vertical forces, data on mediolateral forces are more limited. This is because these forces are generally low magnitude and highly variable between individuals (Schmitt, 2003a; Carlson et al., 2005). Mediolateral forces are important for interpreting how animals deal with balance (Schmidt and Fischer, 2010). During terrestrial locomotion animals tend apply a laterally directed force to the substrate that can be quite high for species with lumbering gaits (i.e., gaits with high degree of side-to-side movement; Shine et al., 2015). This switches during arboreal locomotion, with animals appling medially directed forces onto the substrate in order to maintain balance (Schmitt, 2003a; Carlson et al., 2005; Schmidt and Fischer, 2010).

Compared to what has been collected during upright locomotion, kinetic studies of arm-swinging primates have been rare. Chang et al. (2000) collected multiaxial force data during continuous-contact arm-swinging from a freely moving gibbon (*Hylobates lar*) on a instrumented runway. From these data, Chang et al. (2000) determined that (1) vertical forces displayed a single peak pattern with maximum vertical force (Vpk) reaching approximately 1.8% of body weight; (2) as the limb makes contact with the support it applies a propulsive force to the substrate during the first half of support phase, followed by a braking force throughout the remainder of support phase; and (3) mediolateral forces were low and inconsistent (suggesting little movement other than the

parasagittal plane). These findings reported by Chang et al. (2000) are consistent with data collected from other hylobatids during arm-swinging (Bertram et al., 1999; Michilsens et al., 2012).

The patterns described above are largely replicate the movements of a simple pendulum, and it is possible, as suggested by Chang et al. (2000), that all arm-swinging primates may solve the mechanical challenges of suspensory locomotion through similar kinematic and kinetic strategies. Not enough information was available to test this assumption until Granatosky (2015) collected kinetic and kinematic data during arm-swinging in the red-shanked douc langur (*Pygathrix nemaeus*) to test whether patterns of movement in this species were similar to other arm-swinging primates (i.e., *Ateles* and *Hylobates*). The force traces collected from *P. nemaeus* closely match those of *Hylobates* described by Chang et al. (2000), and are characterized by single vertical peak occurring approximately at mid-support, a propulsive force occurring within the first half of support phase, and a braking force occurring during the latter portion of support. Mediolateral forces were higher than expected for a simple pendulum, which should be close to, or fluctuate around, zero. This finding supports earlier findings by Byron and Covert (2004) that demonstrate that *P. nemaeus* uses some side-to-side movement during arm-swinging. A similar pattern has also been reported during arm-swinging in *Lagothrix* based on video analysis (Schmitt et al., 2005).

As with arm-swinging, limited information is available on the limb loading patterns of below branch quadrupedal locomotion. Ishida et al. (1990) collected multiaxial force data from freely moving slow lorises (*Nycticebus coucang*) on an upright

and inverted instrumented runway. From these data, Ishida et al. (1990) determined that (1) Vpk magnitude and distribution between forelimbs and hindlimbs did not change between above and below branch quadrupedal locomotion; (2) during above branch quadrupedal locomotion, animals exerted relatively greater peak propulsive forces in the hindlimbs than the forelimbs, and this pattern was reversed during below branch quadrupedal locomotion; (3) during above branch quadrupedal locomotion, animals exerted relatively lower peak braking forces in the hindlimbs than the forelimbs, and this pattern was reversed during below branch quadrupedal locomotion; (4) during above branch quadrupedal locomotion, the limb (forelimb or hindlimb) first applied a braking force to the substrate during the first portion of support phase, followed by a propulsive force throughout the remainder of support phase, and this pattern was reversed during below branch quadrupedal locomotion; (5) during above branch quadrupedal locomotion animals generated a net braking force [i.e., braking impulse > propulsive impulse = net negative horizontal impulse (HI)] in the forelimbs and a net propulsive force (i.e., net positive HI) in the hindlimbs, and this pattern was reversed during below branch quadrupedal locomotion; and (6) mediolateral forces were low in both the forelimbs and hindlimbs and animals tended to apply a medially oriented force to the substrate. Together, these findings indicate that movements during below branch quadrupedal locomotion might be effectively modeled as simple pendulum system [but see Nyakatura and Andrada (2012)], in which the forelimbs act as the primary propulsive limb, and the hindlimbs serve a minor braking role acting to decelerate the body's forward moving COM.

While Ishida et al. (1990) laid the groundwork for interpretation of the kinetics of below branch quadrupedal locomotion, their use of the slow loris may constrain the broad applicability of these data to understanding the mechanical behavior of more generalized primates. As a group, the lorisids have a highly derived postcranial anatomy specialized for slow and cautious quadrupedalism (Cartmill and Milton, 1977; Schmitt and Lemelin, 2004). Additionally, lorises exhibit a number of unusual gait patterns including the variable use of diagonal- and lateral-sequence gaits (Ishida et al., 1990; Schmitt and Lemelin, 2004). More pertinent to this study, lorises have a higher Vpk forces on their forelimb compared to the hindlimb during above-branch quadrupedal walking (Ishida et al., 1990; Schmitt and Lemelin, 2004). This pattern is common to non-primate mammals, but not found in most other primates, which have the reverse pattern (Kimura et al., 1979; Reynolds, 1985a; Demes et al., 1994; Schmitt and Lemelin, 2002; Franz et al., 2005). This unusual Vpk force ratio observed in most primates is thought to be a mechanism to reduce high substrate reaction forces on highly mobile and weak shoulder joints (Reynolds, 1985a). The combination of derived anatomy and specialized gait characteristics potentially makes the lorises a poor model for understanding the mechanisms by which generalized primates manage to switch effectively from above to below branch quadrupedal locomotion.

To explore whether the patterns reported by Ishida et al. (1990) are present in more generalized primates, Granatosky et al. (2016) examined limb loading behavior of two quadrupedal primates, *Varecia variegata* [a committed arboreal quadruped that commonly adopts suspensory positional behaviors (Gebo, 1987; Meldrum et al., 1997)]

and *Lemur catta* [the most terrestrial of all the lemurs that moves mostly quadrupedally or by leaping, and that rarely adopts suspensory positional behaviors (Gebo, 1987)] during above and below branch quadrupedal walking. During below branch quadrupedal locomotion, data was consistent with that of Ishida et al. (1990), but also deviated from the pattern they reported for lorises in key ways. In lemurs, braking peak forces were always relatively greater on the forelimbs and did not vary between above and below branch quadrupedal locomotion. Second, and more importantly, while animals did exert greater Vpk forces on the hindlimbs compared to the forelimbs during above branch quadrupedal locomotion, both *V. variegata* and *L. catta* completely reversed this pattern during below branch quadrupedal locomotion. It is likely that the lack of notable differences in Vpk forces distribution patterns between above and below branch quadrupedal locomotion observed by Ishida et al. (1990) for *N. coucang* is a result of the unusual locomotor mechanics of lorises compared to other primates. Granatosky et al (2016) argued that lorisids did not shift the primary weight-bearing roles of the limbs during below branch quadrupedal locomotion because these animals already demonstrate relatively higher Vpk forces on the forelimbs during above branch quadrupedal locomotion (Schmitt and Lemelin, 2004).

The findings from this study provide insight into how primates may accommodate limb loading patterns to adjust mechanically to a new biomechanical environment. The primary kinetic changes that occur when *V. variegata* and *L. catta* switch from above to below branch quadrupedal locomotion can be summarized as follow: (1) the forelimb becomes the primary propulsive element, while the hindlimb serves a braking role; and

(2) the forelimb serves as the primary weight-bearing limb, while the hindlimb reduces its weight-bearing function. These patterns were similar for both species and did not appear to be affected by the relative frequency each species utilized suspensory locomotor behaviors during their normal locomotor repertoires. Granatosky et al. (2016) provided important evidence for how anatomically generalized animals adopt below branch quadrupedal locomotion, but this dataset consisted of only two species and it remains unclear whether the patterns observed in this study are true for all mammals that use below branch quadrupedal locomotion.

1.5.3 Kinematics

Understanding the transition from upright to below branch locomotion requires not only insight about how the limbs are loaded, but also information as to how the limbs move. Kinematic analyses provide direct evidence for how animals adjust to locomotor demands, and, as suggested by (Vilensky, 1987), represents the best observable measure of neural intent. Currently, little information is available on the transition from above to below branch locomotion, and experimental studies focused on the kinematics of below branch quadrupedal locomotion have been limited to select taxa and small sample sizes (Turnquist, 1975; Jouffroy and Petter, 1990; Nyakatura et al., 2010; Fujiwara et al., 2011). While these studies appear to agree on certain aspects, there is still considerable disagreement on whether below branch quadrupedal locomotion is kinematically unique, demonstrates greater similarities to arm-swinging, or is simply a mirrored version of above branch locomotion.

The kinematics of upright quadrupedal locomotion has been studied in a variety of species (Schmitt, 1994, 1995, 1999; Larson et al., 2000, 2001; Larney and Larson, 2004; Schmidt, 2005; Schmidt and Fischer, 2010), and will only be summarized here. Patterns of limb movements are generally consistent across quadrupeds with some notable exceptions for highly arboreal species. At touchdown the level of humeral and femoral protraction varies substantially between species with primates and some arboreal mammals showing relatively high levels of protraction(Figure 4), while most non-primate mammals have relatively retracted arms and thighs (Larson et al., 2000, 2001; Schmitt and Lemelin, 2002, 2004). The same pattern is present during lift-off, in which primates and other arboreal mammals display significant humeral and femoral retraction, while most non-primate mammals show lower levels of retraction in both the forelimb and the hindlimb. This pattern of exaggerated protraction and retraction results in overall higher levels of shoulder and hip excursion (Larson et al., 2001). Greater limb excursion has been interpreted as adaptive for highly arboreal species because it results in longer strides, covering further distance. This tends to reduce stride frequency, which in turn decreases contact frequency with the substrate and its oscillation (Larson et al., 2000, 2001; Schmitt, 2011).

As with the shoulder and hip, patterns of elbow and knee movement tend to vary depending on the amount of arboreality present within a species locomotor repertoire. Generally, for terrestrial species elbow and knee angles tend to be extended throughout the stride (Schmitt, 1994; Larson et al., 2000; Schmidt and Fischer, 2010). This is thought to result in longer stride distances and greater energy recovery because the COM vaulting

over long stiff limbs better replicates inverted pendular motion (Schmitt, 2011; O'Neill and Schmitt, 2012). In arboreal species, elbow and knee movements are characterized by significant flexion occurring approximately at mid-support (Schmitt, 1994, 1995, 1998; Schmidt and Fischer, 2010). In the forelimb, this flexion is commonly referred to as "elbow yield", and in some cases, has been argued to reduce peak vertical forces on highly mobile and relatively weaker forelimb joints. Additionally, this flexion has the effect of lowering an animal's COM closer to the support, which is thought to be an important mechanism for maintaining balance above thin arboreal supports. There is also evidence suggesting that when elbow and knee flexion are timed appropriately throughout the stride, it reduces COM oscillations and collisional losses (Schmitt, 2011).

Patterns of wrist and ankle movements are poorly known for upright quadrupedal species. In primates, wrist and ankle position throughout a stride is prone to substantial intra-individual variation (Lemelin and Schmitt, 1998). Levels of variation are poorly known for non-primate mammals, but certain studies suggest this may be lower (Schmidt and Fischer, 2010). Much of the variation in wrist and ankle movements is dependent on whether the animal is: (1) moving on arboreal supports or on the ground; and (2) how the animal grasps the support. Unfortunately, this information is rarely recorded in kinematic analyses of wrist and ankle movements. The position at which the animal grasps the support determines what a two-dimensional wrist and ankle angle is actually measuring. For animals walking on the ground or grasp a branch (between the second and third digit, or along the axis of the third digit), wrist and ankle angle provides a measure of joint flexion and extension. For these animals, the joint tends to be in a slightly extended or

neutral position at touchdown, and then is further extended throughout the remainder of support phase. Near the end of support phase (just prior to lift-off), the wrist and ankle begins to flex quickly, and may even be in a flexed position as the limb leaves the substrate. In grasps during which the support is between the first and second digit, the wrist angle gives us a sense of radial and ulnar deviation in a stride. For arboreal animals that grasp the support in this manner, the wrist tends to be ulnarly deviated at touchdown and is subsequently radially deviated throughout the remainder of the stride. Ulnar deviation may occur again at the end of support phase. In a similar vein, when animals grasp the support between the first and second digit on the foot the movements of the ankle can be best described as being cranially and caudally oriented. As the foot makes contact with the support, the ankle is cranially oriented. As support phase continues the ankle sweeps caudally until it reaches a more neutral, or even caudally oriented, position prior to lift-off.

Kinematic patterns of below branch quadrupedal locomotion are poorly known, and most of the information available is based on the movement of sloths (Nyakatura et al., 2010) and a small number of other mammalian taxa (Turnquist, 1975; Fujiwara et al., 2011). Nyakatura et al. (2010) observed that the overall kinematic patterns of below branch quadrupedal locomotion in the sloth were remarkably similar to those observed in other upright quadrupedal mammals. This was especially evident in the forelimb, in which the kinematics of arm, elbow, and forearm were similar to those of pronograde mammals and arboreal primates. Despite kinematic differences observed in the distal limbs elements, which were attributed to the sloths specialized hand and foot anatomy,

Nyakatura et al. (2010) argued for a pattern of conserved gait kinematics between above branch and below branch quadrupedalism.

One significant difference in the overall kinematics of upright and below branch quadrupedal locomotion that deserves special attention relates to the patterns of elbow and knee flexion. During upright quadrupedal locomotion, this flexion is a passive process, but during below branch movement this requires an active input of energy to hoist the body closer to the support. Currently, it is unclear why mammals that move quadrupedally below branches all demonstrate this substantial level of flexion. According to Nyakatura (2011), this pattern (at least in sloths) simply represents conserved neural control over locomotion between above and below branch locomotion. In contrast, Fujiwara et al. (2011) suggests that the amount of flexion is positioned to maximize the mechanical advantage of powerful flexor musculature. Experimental studies directly comparing the kinematics of upright and below branch quadrupedal locomotion are missing, making the underlying mechanisms for limb flexion during below branch quadrupedal locomotion difficult to ascertain.

While kinematic patterns of quadrupedal locomotion are considered generally similar regardless of orientation, the orthograde trunk posture during arm-swinging drastically alters the movements in the limbs. Currently, kinematic analyses of arm-swinging have been limited to a few species, but in general movements appear to be fairly consistent across taxa. While overall kinematic patterns during arm-swinging appear to be generally the same for all species, patterns of muscle recruitment are highly variable between species (at least between *Ateles* and *Hylobates*) (Stern et al., 1980a; b;

Jungers and Stern, 1981) . This finding suggests that there are many ways to converge upon the same kinematic pattern. At touchdown, the shoulder tends to be protracted beyond the neutral position and is subsequently retracted throughout the remainder of the stride (Turnquist, 1975; Turnquist et al., 1999; Wright et al., 2008; Michilsens et al., 2010). The levels of protraction and retraction observed in arm-swinging species are approximately equidistant from the neutral position, demonstrating substantial angular excursion throughout support phase (Jenkins et al., 1978; Turnquist et al., 1999; Su and Jablonski, 2009; Michilsens et al., 2011, 2012; Granatosky, 2015). Patterns of elbow movements are also fairly similar across different species of arm-swinging primates. In general, the elbow joint is slightly flexed at the beginning of the support phase, and then begins to extend. This extension continues until approximately mid-support, at which time the forelimb is almost fully extended. Near the end of support phase the limb experiences varying levels of flexion at the elbow (Turnquist, 1975; Turnquist et al., 1999; Michilsens et al., 2010). This pattern of elbow movement likely represents the animal adjusting COM position to maximize pendular motion, while simultaneously limiting collisional losses of energy (Bertram et al., 1999; Usherwood, 2003; Bertram, 2004; Ruina et al., 2005).

The movements of the wrist during arm-swinging are less clear, and appear to be highly variable between species. During arm-swinging in the red-shanked douc langur (*Pygathrix nemaeus*), animals grab the support with pronated handholds and show substantial forward and backward movement at the radiocarpal joint. This means that as *P. nemaeus* grabs onto the support the wrist is first ulnarly deviated, and subsequently

radially deviated throughout the remainder of the stride. In contrast, during arm-swinging in *Ateles* and *Hylobates*, animals are thought to grab the support with supinated hand positions and show little radial and ulnar deviation (Turnquist, 1975). The wrist joint does experience substantial rotary movements due to the rotation of the body below the support (Jenkins, 1981), and this is thought to be a largely passive movement that results from the forward momentum of the body. Unfortunately, detailed experimental studies of wrist movements during arm-swinging are few, and it remains difficult to interpret "normal' wrist kinematics during arm-swinging.

1.5.4 Footfall patterns and timing

Spatiotemporal gait variables provide an easily measured means of assessing interlimb coordination and timing of particular events within a stride that affects overall stability, security, and quality of a particular locomotor sequence. Analyses of spatiotemporal gait variables have been rare for suspensory locomotion, and what we do know is based off of small sample sizes and select species (e.g., sloths, lorises, *Ateles*, and *Hylobates*). In contrast, numerous studies have reported and analyzed spatiotemporal gait variables during upright quadrupedal gaits, and, consequently, most of our interpretations are based on the movements of upright quadrupeds. It is unclear as to whether suspensory species use similar patterns, and whether the adaptive scenarios currently proposed for upright quadrupedal gaits even apply in an inverted context.

A number of assumptions about neuromuscular control of locomotion and balance are derived from patterns of interlimb coordination (Vilensky, 1987; Vilensky and Larson, 1989; Vilensky et al., 1992, 1994). All symmetrical walking gaits in mammals

can be broken down into two categories based on the sequence in which the limbs make contact with the substrate. A lateral-sequence gait is one in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., the feet touch down in the order of right hindlimb, right forelimb, left hindlimb, left forelimb). A diagonal-sequence gait is one in which each hindlimb footfall is followed by a contralateral forelimb footfall (i.e., the feet touch down in the order of right hindlimb, left forelimb, left hindlimb, right forelimb). The footfall sequences described above have been of incredible interest to researchers because the presence of these gait patterns is divided along fairly firm phylogenetic and/or functional boundaries (Muybridge, 1887; Magne de la Croix, 1936; Hildebrand, 1967; Tomita, 1967; Rollinson and Martin, 1981; Vilensky and Larson, 1989; Meldrum, 1991; Cartmill et al., 2002, 2007; Shapiro and Raichlen, 2005, 2007; Lemelin and Cartmill, 2010). Generally, primates and other highly arboreal mammals tend to use diagonal-sequence footfall patterns, especially when walking on arboreal supports. In contrast, most non-primate mammals almost exclusively use lateral-sequence footfall patterns (Figure 4). While there has been considerable debate concerning the functional reasons for this division (see below), perhaps most interesting is the argument that primates are able to adopt diagonal-sequence footfall patterns because of a unique arrangement of the neuromuscular system. As described above, it is thought that cortical inputs have a more important role in the generation of primate locomotion compared to non-primate mammals. This more direct cortical network is thought to allow greater flexibility in interlimb coordination, and as a result primates may be better equipped to adjust to the locomotor demands of their environment with greater proficiency than non-

primate mammals (Vilensky, 1987; Vilensky and Larson, 1989; Vilensky et al., 1994; Schmitt, 2010).

The functional interpretations of lateral- and diagonal-sequence footfall patterns remain an issue of considerable debate (Vilensky and Larson, 1989; Cartmill et al., 2002, 2007; Shapiro and Raichlen, 2005, 2007; Lemelin and Cartmill, 2010), and to more fully understand the current theories we must add two further modifiers to our concept of interlimb coordination. Commonly, during normal walking gaits the forelimbs and hindlimbs are traveling together as a slightly asynchronous couplet. When the ipsilateral forelimbs and hindlimbs are traveling together, this is referred to as a lateral couplet; when the contralateral forelimbs and hindlimbs are traveling together, this is referred to as a diagonal couplet. Very rarely do the limbs move together in perfect synchrony. When these gait patterns receive their own unique names of a trot (contralateral synchrony) and a pace (ipsilateral synchrony).

While descriptions of these gait patterns have been known for some time (Muybridge, 1887; Magne de la Croix, 1936; Hildebrand, 1967), the adaptive benefit of each of these gaits remains an area of active inquiry. Lateral-sequence, lateral-couplet (LSLC) footfall patterns tend to be present in long-legged terrestrial mammals,and are thought to be the best mechanism to prevent interlimb interference. However, this footfall pattern is thought to be inherently unstable because a majority (~66%) of the stride is spent as a unilateral bipod (i.e., only two ipsilateral limbs in contact with the support), which tends to roll the body side-to-side throughout the stride. This instability is thought to be negligible for long-legged animals, but can be devastating for short-limbed broad-

chested quadrupeds. For these species, lateral-sequence, diagonal-couplet (LSDC) footfall patterns tend to be more common. This footfall sequence is inherently more stable than LSLC gaits due to the generally low proportion of the stride spent as a unilateral bipod (~22%), and the relatively high proportion of the stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support). In general, foot positions arranged as diagonal bipods and large tripods are thought to be highly stable because a quadruped with a nearly centered COM is more nearly balanced over a line passing through diagonally opposite feet than over one passing through the two feet on one side (Cartmill et al., 2002).

In contrast to the patterns described above, primates and other highly arboreal mammals tend to use diagonal-sequence, diagonal-couplet (DSDC) footfall patterns when moving along relatively thin arboreal supports (Muybridge, 1887; Hildebrand, 1967; Cartmill et al., 2002). This gait pattern maximizes the proportion of the stride in which the limbs are arranged as a widely splayed diagonal bipod, and ensures that one of the grasping hindfeet is placed in a protracted position (and thus lies roughly underneath the animal's COM) on a tested support at the moment when the contralateral forefoot strikes down on an untested support during arboreal locomotion (Cartmill et al., 2002, 2007; Lemelin and Cartmill, 2010). The legitimacy of this adaptive scenario for DSDC gaits has received considerable debate (see Shapiro and Raichlen, 2005, 2007). However, the presence of DSDC gaits in other highly arboreal mammals (McClearn, 1992; Schmitt and Lemelin, 2002; Lemelin et al., 2003; Lemelin and Cartmill, 2010; Karantanis et al., 2015)

and the tendency for animals to increase DSDC footfall patterns as they move from terrestrial to arboreal supports (Wallace and Demes, 2008; Shapiro and Young, 2010) appears to largely refute any doubt about the association between DSDC gaits and arboreality.

With respect to suspensory locomotion, it is obvious that quadrupedal interlimb coordination does not apply during arm-swinging, but still has important implications for below branch quadrupedal locomotion. Currently, relatively few studies have reported patterns of limb placement and timing during below branch quadrupedal locomotion (Jouffroy and Petter, 1990; Nyakatura et al., 2010), but, at least for *Nycticebus*, it appears that animals are utilizing similar gait patterns both above and below branches. This finding supports Nyakatura's (2011) assertion that that transition from above to below branch quadrupedal locomotion requires few mechanical adjustments, and animals are utilizing conserved neural control of locomotion. If this is the case, then we should expect that primates will use DSDC gaits both above and below branches.

In opposition to Nyakatura's (2011) hypothesis, there are functional reasons why a DSDC gait may not be advantageous during below branch movement. As mentioned above, the argument for DSDC gaits above supports is that they: (1) lower the chance of rolling off the support; and (2) ensure that a grasping hindfoot is placed in a protracted position on a tested support at the moment when the contralateral forefoot strikes down on an untested support. The problem with the applicability of these scenarios below branches is twofold. First, animals moving below branches do not have worry about rolling off the support (Napier, 1967; Cartmill, 1985). Instead, they may want to

minimize the risk of interlimb interference or maximize the proportion of the stride in which the limbs are arranged as tripods. If either of these scenarios is true, then LSDC or LSLC gaits may be more appropriate during below branch quadrupedal locomotion. Secondly, a protracted hindlimb on a tested support only works if an animal is able to subsequently retract itself if the untested support proves unstable. While this works for animals that support a majority of their body weight on their hindlimbs (i.e., primates walking above branches), it is unlikely that this limb placement would be of any use for animals that support a majority of their body weight on their forelimbs (i.e., primates moving quadrupedally below branches) (Granatosky et al., 2016). Without additional data, it is difficult to test the validity of these hypotheses.

Thus far, discussion in this subsection has largely centered on rhythmicity and interlimb coordination. However, it is important to note that other spatiotemporal gait variables (e.g., stride length, stride frequency, and swing time) can have profound effects on the overall quality and security of the stride. For example, increased contact time and decreased swing phase results in a lower potential for a whole-body aerial phase. The added security is believed to be important for moving on thin arboreal supports, and it is likely that the same pattern, or even an exaggerated version, occurs during below branch quadrupedal locomotion. That being said, it is interesting to note that often times an aerial phase is present during arm-swinging (Turnquist et al., 1999; Chang et al., 2000; Usherwood, 2003; Michilsens et al., 2010, 2012).

Another important set of spatiotemporal gait variables that have implications for overall cost and security of the stride is the relationship between stride duration, stride

frequency, and stride length. In most cases, quadrupedal gaits are typified by long and smooth locomotor cycles with low stride frequency. Lower stride frequency results in more energetically efficient strides (O'Neill and Schmitt, 2012) and lower COM oscillations (Schmitt, 2011). As discussed earlier, lower COM oscillations result in lower substrate oscillations, which is important for maintaining balance on compliant supports. It is unclear what patterns of stride duration, stride frequency, and stride length are used during below branch quadrupedal locomotion, but it is likely that the same rules related to security and energetic efficiency that occur during above branch quadrupedal locomotion also apply during below branch movement. Data collected from arm-swinging in *Ateles* and *Hylobates* support this notion as these animals are characterized by long fluid strides. This is not always the case though, as arm-swinging in *Lagothrix* is characterized by high stride frequency and short stride distance (Turnquist et al., 1999; Guillot, 2011).

1.6 Specific goals

From the information provided above, it is clear that although we know quite a lot about the anatomical features and certain aspects of the mechanics associated with suspensory locomotion, epistemological deficits to our overall understanding of the mechanical and evolutionary origins of suspensory locomotion remain, and how the varying forms of suspensory locomotion (i.e., below branch quadrupedal locomotion and arm-swinging) relate to each other. Some of the more fundamental questions that need clarification include whether above and below branch quadrupedal locomotion represent neuromuscular mirrors of each other, or whether the mechanics of below branch

quadrupedal locomotion represent a “mechanical release” from the highly modified gait characteristics observed during primate quadrupedal locomotion. Also, it remains unknown whether the nature of the flexible coupling between the forelimb and hindlimb observed in primates during above and below branch quadrupedal locomotion is a uniquely primate feature and could this have promoted the evolution of arm-swinging. To fill these gaps, this study takes an experimental approach to compare the mechanics of above branch quadrupedal locomotion, below branch quadrupedal locomotion, and arm-swinging in a broad phylogenetic sample of primate and non-primate mammals. Specifically, this study addresses three **Research Objectives**: (1) an intraspecific comparison of the mechanics of above and below branch quadrupedal locomotion to determine whether primates are using similar mechanical strategies during above and below branch quadrupedal locomotion; (2) an interspecific comparison of the mechanics of below branch quadrupedal locomotion to determine if the patterns of below branch quadrupedal locomotion are similar between primate and non-primate mammals; and (3) an interspecific comparison of the mechanics of below branch quadrupedal locomotion and arm-swinging to determine whether there are mechanical similarities between these two forms of suspensory locomotion in primates. Data from this study will provide insight into an essential, but understudied, evolutionary transition within our own clade, and, more broadly, aid in our understanding of how animals deal with the mechanical demands of switching from one form of locomotion to another.

1.7 Hypotheses and predictions

Based on previous data, observations, and models, the following hypotheses have been developed to focus investigation. The data collected in this study are designed to test the validity of these specific hypotheses, and ultimately, to evaluate the scenarios of primate locomotor evolution. Predictions, based on the information outlined in the introduction, are provided for each hypothesis and are specifically designed to be mutually exclusive to allow for better discriminatory power of the results.

Research Objective 1: ***An intraspecific comparison of the mechanics of above and below branch quadrupedal locomotion***

Hypothesis 1a: With the exception of the timing of the braking and propulsive forces, which must switch for simple mechanical reasons, gait mechanics will be similar during above and below branch quadrupedal locomotion in primates due to neuromuscular patterns of movement that are conserved regardless of body orientation relative to the substrate.

(P1) Limb loading patterns will be generally similar during above and below branch quadrupedal locomotion in primates, with the exception that the propulsive and braking portions of the horizontal force component will switch due to the change in pendular mechanics. Specific results to support this prediction include: (1) relatively higher Vpk forces on the hindlimbs compared to the forelimbs; (2) relatively low medially oriented (the animal applies a medial forces to the substrate) mediolateral forces; and (3) the forelimb will serve a net braking role, while the hindlimb will be net propulsive.

(P2) Kinematic patterns of limb movements will be similar during above and below branch quadrupedal locomotion in primates. Specific results in support of this prediction include: (1) relatively high levels of humeral and femoral protraction at touchdown and similar levels of joint excursion throughout the support phase; (2) flexed elbow and knee positions throughout support phase and similar levels of joint excursion; and (3) similar movements of the wrist and ankle throughout the stride and similar levels of joint excursion.

(P3) Spatiotemporal gait patterns will be similar during above and below branch quadrupedal locomotion in primates. Specific results to support this prediction include: (1) similar stride duration and distance; (2) similar forelimb and hindlimb duty factors and relative swing phase; and (3) DSDC gaits will be the most common pattern of interlimb coordination.

Hypothesis 1b: Gait mechanics will differ between above and below branch quadrupedal locomotion in primates due to the change from inverted to conventional pendular mechanics, the shift from compressive to tensile forces acting on the body, and the mechanical release from the challenges associated with balancing and moving on top of thin compliant branches.

(P1) Limb loading patterns will differ between above and below branch quadrupedal locomotion in primates. Specific results to support this prediction include: (1) a switch in Vpk forces between the forelimbs and hindlimbs during below branch quadrupedal locomotion; (2) relatively higher medially oriented (the animal applies a medial forces to the substrate) mediolateral forces during

below branch quadrupedal locomotion; and (3) the forelimb will serve a net propulsive role, while the hindlimb will be net braking during below branch quadrupedal locomotion.

(P2) Kinematic patterns of limb movements will differ during above and below branch quadrupedal locomotion in primates. Specific results to support this prediction include: (1) lower levels of humeral and femoral protraction at touchdown and relatively higher levels of joint excursion throughout support phase during below branch quadrupedal locomotion; (2) increased levels elbow and knee flexion throughout support phase and relatively higher levels of joint excursion during below branch quadrupedal locomotion; and (3) a tendency to keep wrist and ankle movements close to the neutral position throughout support phase, and reduced levels of wrist and ankle excursion during below branch quadrupedal locomotion.

(P3) Spatiotemporal gait patterns will differ between above and below branch quadrupedal locomotion in primates. Specific results to support this prediction include: (1) reduced stride duration and distance during below branch quadrupedal locomotion; (2) relatively longer forelimb and hindlimb duty factors and relatively shorter swing phase during below branch quadrupedal locomotion; and (3) DSDC gaits will be reduced, and animals may favor LSDC gaits.

Research Objective 2: ***An interspecific comparison of the mechanics of below branch quadrupedal locomotion***

Hypothesis 2a: Gait mechanics will differ during below branch quadrupedal locomotion between primates and non-primate mammals due the unusal neuroumuscular pattern that evolved early in primates and is absent in non-primate mammals. It is also possible that the greater number of anatomical features associated with suspensory locomotion observed in the non-primate mammals will result in differences in limb

the potential that primates will maintain the set unusual gait characteristics

(P1) Limb loading patterns will differ during below branch quadrupedal locomotion in primate and non-primate mammals. Specific results to support this prediction include: (1) relatively higher Vpk forces on the hindlimbs compared to the forelimbs in primates; (2) relatively lower medially oriented (the animal applies a medial forces to the substrate) mediolateral forces in primates; and (3) differing braking and propulsive functions of the forelimb and hindlimbs between primate and non-primate mammals.

(P2) Kinematic patterns of limb movement will differ during below branch quadrupedal locomotion in primate and non-primate mammals. Specific results to support this prediction include: (1) primates will show relatively high levels of humeral and femoral protraction at touchdown and relatively higher ranges of joint excursion throughout support phase compared to non-primate mammals; (2) non-primate mammals will show greater levels of elbow and knee extension throughout support phase; and (3) non-primate mammals will keep wrist and

ankle movements close to the neutral position throughout support phase and show reduced ranges of wrist and ankle excursion during below branch quadrupedal locomotion.

(P3) Spatiotemporal gait patterns will differ during below branch quadrupedal locomotion in primate and non-primate mammals. Specific results to support this prediction include: (1) reduced stride duration and distance in non-primate mammals; (2) relatively longer forelimb and hindlimb duty factors and relatively shorter swing phase in non-primate mammals; and (3) DSDC gaits will be the most common pattern of interlimb coordination in primates, while other types of interlimb coordination may be more common in non-primate mammals.

Hypothesis 2b: Gait mechanics will be similar during below branch quadrupedal locomotion in both primate and non-primate mammals because all animals share the same biomechanical challenges associated with the change from inverted to standard pendular mechanics, the shift from compressive to tensile forces acting on the body, and the mechanical release from the challenges associated with balancing and moving on top of thin compliant branches.

(P1) Limb loading patterns will be similar during branch quadrupedal locomotion in primate and non-primate mammals. Specific results to support this prediction include: (1) no differences in Vpk forces between the forelimbs and hindlimbs during in any of the species; (2) high medially oriented (the animal applies a medial forces to the substrate) mediolateral forces in all the species; and (3) the

forelimb will serve a net propulsive role, while the hindlimb is net braking in all species

(P2) Kinematic patterns of limb movement will be similar during branch quadrupedal locomotion in primate and non-primate mammals. Specific results to support this prediction include: (1) retracted humeral and femoral positions at touchdown and similar joint excursions in all species; (2) similar levels of elbow and knee flexion throughout support phase, and similar joint excursions in all species; and (3) a tendency to keep wrist and ankle movements close to the neutral position throughout support phase, and low levels of wrist and ankle excursion in all species.

(P3) Spatiotemporal gait patterns will be similar during below branch quadrupedal locomotion in primate and non-primate mammals. Specific results to support this prediction include: (1) similar stride duration and distance in all species; (2) relatively longer forelimb and hindlimb duty factors and relatively shorter swing phase in all species; and (3) all species will display similar patterns of interlimb coordination.

Research Objective 3: ***An interspecific comparison of the mechanics of below branch quadrupedal locomotion and arm-swinging***

Hypothesis 3a: Forelimb gait mechanics during below branch quadrupedal locomotion in primates will be more similar to what is observed during below branch quadrupedal locomotion in non-primate mammals than to what is observed during arm-swinging

than to due to shared biomechanical pattern of using all four limbs to support and propel the body.

(P1) During below branch quadrupedal locomotion, forelimb kinetic patterns in primates and non-primate mammals will be more similar to each other than what is observed in primates during arm-swinging. Specific results to support this prediction include: (1) Vpk forces during below branch quadrupedal locomotion will be relatively similar in all species and significantly lower than what is observed during arm-swinging; and (2) the braking/propulsive role of the forelimb will differ than what is observed during arm-swinging.

(P2) During below branch quadrupedal locomotion, kinematic patterns of the forelimb in primates and non-primate mammals will be more similar to each other than what is observed in primates during arm-swinging. Specific results to support this prediction include: (1) lower levels of shoulder excursion during below branch quadrupedal locomotion compared to arm-swinging; and (2) greater levels of elbow flexion during below branch quadrupedal locomotion compared to arm-swinging.

(P3) During below branch quadrupedal locomotion, spatiotemporal gait patterns in primates and non-primate mammals will be more similar to each other than what is observed in primates during arm-swinging. Specific results to support this prediction include: (1) differing levels of stride duration and distance during below branch quadrupedal locomotion compared to arm-swinging; and (2)

differing levels of forelimb duty factor and relative swing phase during below branch quadrupedal locomotion compared to arm-swinging.

Hypothesis 3b: Forelimb gait mechanics during below branch quadrupedal locomotion in primates will be more similar to what is observed during arm-swinging than to what is observed during below branch quadrupedal locomotion in non-primate mammals due to shared anatomical features among primates, and the tendency for greater forelimb and hindlimb neuromuscular disparity observed in primates compared to other mammals.

(P1) During below branch quadrupedal locomotion, forelimb kinetic patterns in primates and non-primate mammals will be distinct from each other, and primates will show greater similarity to what is observed during arm-swinging. Specific results to support this prediction include: (1) primates will show relatively higher Vpk forces in the forelimbs compared to non-primate mammals; and (2) the forelimb will be the primary propulsive limb, while the braking and propulsive roles of the limbs will be more equal in non-primate mammals.

(P2) During below branch quadrupedal locomotion, kinematic patterns of forelimb movement in primates and non-primate mammals will be distinct from each other, and primates will show greater similarity to what is observed during arm-swinging. Specific results to support this prediction include: (1) levels of shoulder excursion will be relatively higher in primates compared to non-primate mammals; and (2) non-primates will show relatively greater levels of

elbow flexion during below branch quadrupedal locomotion compared to what is observed in primates.

(P3) During below branch quadrupedal locomotion, spatiotemporal gait variables in primates and non-primate mammals will be distinct from each other, and primates will show greater similarity to what is observed during arm-swinging. Specific results to support this prediction include: (1) non-primate mammals will show differing levels of stride duration and distance during below branch quadrupedal locomotion compared to what is observed during below branch quadrupedal locomotion in primates and during arm-swinging; and (2) non-primate mammals will demonstrate differing levels of forelimb duty factor and relative swing phase during below branch quadrupedal locomotion compared to what is observed during below branch quadrupedal locomotion in primates and during arm-swinging.

2. Materials and Methods

2.1 Subjects

Locomotor data was collected from animals housed at the Duke Lemur Center (Durham, NC), Greensboro Science Center (Greensboro, NC), North Carolina Zoological Park (Asheboro, NC), Central Florida Zoo and Botanical Gardens (Sanford, FL), Lubee Bat Conservancy (Gainesville, FL), Monkey Jungle Dumont Conservancy (Miami, FL), Gumbalimba Park (West Bay, Honduras), and the Endangered Primate Rescue Center (Cuc Phuong National Park, within the Nho Quan District of Ninh Binh Province). All animal use was approved by the Duke Lemur Center (DLC Research Project #MO-10-11-3) and Duke's Institutional Animal Care and Use Committee (IACUC protocol # A270-11-10 and A245-14-10). All animals were adults and were clear of any pathologies or gait abnormalities (Table 2).

Table 2. Animal subjects used in the study

Species	Subject	Sex	Body mass (kg)	Date of birth (mm/dd/yyyy)
Varecia variegata	Individual 1	Male	3.3	05/24/2010
	Individual 2	Female	3.76	04/17/2005
	Individual 3	Female	3.7	05/31/2001
Lemur catta	Individual 1	Male	2.58	05/03/2010
	Individual 2	Female	2.1	05/16/2011
	Individual 3	Female	2.34	04/09/2012
Propithecus coquereli	Individual 1	Male	4.12	02/03/2010
	Individual 2	Female	4.38	02/22/1998
	Individual 3	Female	5.09	02/04/2009
Daubentonia madagascariensis	Individual 1	Male	2.86	06/05/1994
	Individual 2	Female	2.95	01/06/1996
	Individual 3	Female	3.02	04/15/1996
Cebus capucinus	Individual 1	Male	n/a	n/a
	Individual 2	Female	n/a	n/a
Choloepus didactylus	Individual 1	Female	7.25	11/9/2000
	Individual 2	Female	6.85	5/8/2003
Pteropus vampyrus	Individual 1	Male	1.23	06/07/2001
	Individual 2	Male	1.28	06/24/1999
	Individual 3	Male	0.98	03/30/2013
	Individual 4	Male	1.41	07/12/2012
Desmodus rotundus	Individual 1	Male	0.028	n/a
	Individual 2	Male	0.030	n/a
	Individual 3	Male	0.029	n/a
	Individual 4	Female	0.027	n/a
	Individual 5	Female	0.030	n/a
Pygathrix nemaeus	Individual 1	Male	9.23	n/a
	Individual 2	Female	8.16	n/a
Ateles fusciceps	Individual 1	Male	n/a	n/a
	Individual 2	Female	n/a	n/a
Hylobates moloch	Individual 1	Male	7.2	n/a
	Individual 2	Male	6.8	n/a

[n/a]Data not avaliable

Following the work of Losos and Miles (1994) and Larson and Losos (1996), species were chosen based on a convergence approach. By comparing how distantly related animals solve the same mechanical problems, it is easier to separate phylogenetic constraints from behavioral or mechanical adaptations. The study sample consisted of seven primate species and three non-primate species. Even though there are reported differences in locomotor ecology and performance between the sexes in many animals (Cullum, 1998; Bokkers and Koene, 2002; Bonnet et al., 2005), few sex-based differences in kinematics have been reported for primates (Cant, 1987a; Doran, 1993; Remis, 1999; Prates and Bicca-Marques, 2008). As many of the known differences between the sexes are attributed to body size (Cant, 1987a; Doran, 1993), this study attempted to collected data for both male and female subjects for each species for a more representative species mean. In most species this was possible, but for *Pteropus vampyrus* (4 male subjects), *Choloepus didactylus* (2 female subjects), and *Hylobates moloch* (2 male subjects), this proved unfeasible. It is unlikely that any unforeseen consequences will arise from this sampling bias because sexual dimorphism is generally low in these species. A brief description of the behavioral and morphological characteristics of each species follows.

2.1.1 Species profiles

Varecia variegata

Varecia variegata, the ruffed lemur, is a large-bodied (3.1-4.1 kg; Smith and Jungers, 1997) arboreal lemurid endemic to Madagascar (Pereira et al., 1988; Meldrum et al., 1997; Fleagle, 2013). *Varecia variegata* is commonly separated into two subspecies

based on external pelage [*Varecia variegata variegata* (the black-and-white ruffed lemur) and *Varecia variegata rubra* (the red ruffed lemur)], but both subspecies are similar in body mass and locomotor behavior (Gebo, 1987; Fleagle, 2013), and therefore were analyzed as a single study species. Locomotor behavior exhibited by *V. variegata* centers on arboreal quadrupedalism on medium and thin arboreal supports (Oxnard et al., 1990; Dagosto, 1995; Dagosto and Yamashita, 1998; Goodenberger et al., 2015). *Varecia variegata* is also considered the most suspensory of all the Malagasy strepsirrhines and is commonly observed hanging from the hindlimbs or walking quadrupedally below branches (Meldrum et al., 1997). Its anatomy is fairly generalized with slightly longer hindlimbs than forelimbs (intermembral index = 72), and displays few anatomical features commonly associated with suspensory locomotion (Stern et al., 1995; Fleagle, 2013; Congdon, 2014; Granatosky et al., 2014b).

Lemur catta

Lemur catta, the ring-tailed lemur, is a medium-bodied (average body mass 2.2 kg; Smith and Jungers, 1997) largely terrestrial lemurid endemic to Madagascar (Dagosto, 1995; Fleagle, 2013; LaFleur and Sauther, 2015). The locomotor behavior exhibited by *L. catta* centers on terrestrial quadrupedalism, but arboreal movements are also common especially on large or medium sized supports (Gebo, 1987; Oxnard et al., 1990; Goodenberger et al., 2015). *Lemur catta* rarely adopts suspensory behaviors (4%) during its normal locomotor repertoire (Gebo, 1987). Its anatomy is fairly generalized with slightly shorter forelimbs than hindlimbs (intermembral index = 70), and shows few

features commonly associated with suspensory locomotion (Fleagle, 2013; Congdon, 2014).

Propithecus coquereli

Propithecus coquereli, the Coquerel's sifaka, is a large-bodied (average body mass 3.7 kg; Smith and Jungers, 1997) largely arboreal indriid endemic to Madagascar. *Propithecus coquereli* is best known for its anatomical features associated with vertical-clinging and leaping (intermembral index ~ 64) (Fleagle, 2013). This anatomical pattern is thought to make quadrupedal locomotion ungainly and inefficient (Wunderlich et al., 2011, 2014), but despite this, upright quadrupedal locomotion has been witnessed in *P. coquereli*, albeit rarely (6%) (Gebo, 1987). Suspensory locomotor behaviors are more common, and *P. coquereli* is known to walk quadrupedally below branches (5%) and adopt arm-swinging behavior (10%) (Gebo, 1987). Suspensory positional behaviors are so common in this species that Oxnard (1967) classified *Propithecus* in the "hanger" category along with the lorisids. It should be noted that *P. coquereli*, as well as the other extant indriids, share a close phylogenetic relationship to the extinct sloth lemurs. This close relationship suggests that suspensory behaviors may have been quite common in the last common ancestor of these species (Gebo and Dagosto, 1988; Godfrey and Jungers, 2003).

Daubentonia madagascariensis

Daubentonia madagascariensis, the aye-aye, is a medium-bodied (average body mass 2.5 kg; Smith and Jungers, 1997) largely arboreal lemurid endemic to Madagascar. *Daubentonia madagascariensis* is best known for its unusual cranial and manual features

that have evolved for extractive foraging (Ancrenaz et al., 1994; Soligo, 2005; Fleagle, 2013). Generally, the locomotion of *D. madagascariensis* is centered on arboreal quadrupedalism and leaping, but suspensory locomotion is present (Ancrenaz et al., 1994; Curtis and Feistner, 1994). Besides the hand, postcranial anatomy is fairly generalized with slightly shorter forelimbs than hindlimbs (intermembral index = 71), and shows few features commonly associated with suspensory locomotion (Fleagle, 2013). It is unclear how the specialized hand anatomy observed in this species will effect patterns of suspensory locomotion (Soligo, 2005).

Cebus capucinus

Cebus capucinus, the white-headed capuchin, is a medium-bodied (average body mass 3.9 kg; Smith and Jungers, 1997) primate native to Central America. The locomotion of this species is most often classified as an arboreal quadruped, but high locomotor diversity is observed in this species (Gebo, 1992; Bergeson, 1996, 1998; Bezanson, 2009). Below branch quadrupedal locomotion is common in this species, especially in young animals (Hunt et al., 1996; Bergeson, 1998). Its anatomy is fairly generalized with slightly shorter forelimbs than hindlimbs (intermembral index = 81), and besides the prehensile (or partially-prehensile) tail, shows few anatomical features typically associated with suspensory locomotion.

Hylobates moloch

Hylobates moloch, the Silvery gibbon, is a relatively large-bodied (average body mass 6.3 kg; Smith and Jungers, 1997) hominoid endemic to the island of Java (Indonesia). The locomotor behavior exhibited by *H. moloch* centers on arm-swinging on

relatively thin arboreal substrates. Like all the gibbons, suspensory locomotion is very common and makes up a majority of the locomotor repertoire. Its anatomy is highly specialized (intermembral index = 127; Fleagle, 2013) for arm-swinging behaviors.

Pygathrix nemaeus

Pygathrix nemaeus, the red-shanked douc langur, is a large-bodied (8.1–10.9 kg; Smith and Jungers, 1997) highly arboreal colobine native to Southeast Asia. While primarily considered as an arboreal quadruped, *P. nemaeus* commonly engages in arm-swinging locomotion (46%; Byron and Covert, 2004). This observation is surprising given *P. nemaeus* close anatomical resemblance with other closely-related Asian colobines [but see Su and Jablonski (2009) and Bailey and Pampush (2015a)]. It shows few of the anatomical similarities with other arm-swinging primates (intermembral index = 94; Fleagle, 2013).

Ateles fusciceps

Ateles fusciceps, the black-headed spider monkey, is a large-bodied (8.8 kg; Smith and Jungers, 1997) highly arboreal New World monkey found in Central and South America. *Ateles fusciceps* commonly uses arboreal quadrupedal locomotion, but is also well-known for its use of suspensory positional behaviors, and especially tail-assisted arm-swinging (Bergeson, 1996; Rosenberger et al., 2008; Schmitt et al., 2009; Guillot, 2011). Interestingly, tail-assisted support is observed every other hand-hold (Turnquist et al., 1999), and it is only these strides that were used for subsequent analysis. Anatomy is highly specialized (intermembral index = 103; Fleagle, 2013) for arm-swinging behaviors (Rosenberger et al., 2008).

Choloepus didactylus

Choloepus didactylus, Linnaeus's two-toed sloth, is a medium-bodied (4-8 kg) highly arboreal xenarthran native to South America (Mendel, 1981; Gaudin, 2004; Grass, 2014). The locomotor repertoire of *C. didactylus* is centered on below quadrupedal locomotion on thin arboreal supports (Mendel, 1979, 1981). The anatomy of this species is so highly modified for suspensory locomotion in the form of below branch quadrupedal locomotion that other forms of locomotion are ungainly and clumsy (Mendel, 1979, 1981; Billet et al., 2012; Granatosky et al., 2014b; Grass, 2014). There is also evidence suggesting that the anatomy of this species is so highly modified for small supports that any support wider in diameter than 7.62 cm makes wrapping the claw on top of the support almost impossible (Mendel, 1979, 1981; Nyakatura et al., 2010).

Pteropus vampyrus

Pteropus vampyrus, the large flying fox, is the largest species (0.65–1.1 kg) of bat (Fujiwara et al., 2011). It is native to Southeast Asia, and locomotes primarily by flight (Vandoros and Dumont, 2004). The anatomy of *P. vampyrus* reflects the adaptations to flight, and consequently is incapable of proficient upright locomotion (Lawrence, 1969; Riskin and Hermanson, 2005; Riskin et al., 2005, 2006). When moving on supports, the locomotion of *P. vampyrus* centers on below branch quadrupedal locomotion (Fujiwara et al., 2011). The mechanics of below branch quadrupedal locomotion in *P. vampyrus* is poorly known and it remains unclear as to whether this species, with its highly modified anatomy, adopts the same mechanics as other species that move quadrupedally below branches.

Desmodus rotundus

Desmodus rotundus, the common vampire bat, is a small-bodied (0.025-0.040 kg) bat native to North and Central America (Nowak, 1999). While the anatomy of this species is primarily modified for flight (Riskin et al., 2005), *D. rotundus* has independently re-evolved terrestrial locomotion in order to aid in its sanguivorous feeding habits (Riskin and Hermanson, 2005; Riskin et al., 2005, 2006). While arboreal locomotion is rare, suspensory locomotion is still quite common in cave and roosting sites (Nowak, 1999). It remains unclear whether the gait patterns observed during terrestrial locomotion will remain the same during suspensory locomotion, or whether this species adopts an entirely different mechanical strategy.

2.2 Data Collection

In order to address the research objectives outlined in section 1.6, kinematic, kinetic, and spatiotemporal gait variables were collected as animals moved across a runway aligned parallel to the direction of movement. The construction of the runway varied depending on the specific research objective and study species. To address **Research Objective 1**, animals (*V. variegata, L. catta, P. coquereli,* and *D. madagascariensis*) were trained to walk above and below an instrumented (details on runway instrumentation below) runway measuring approximately 3.66 m in length and 3.1 cm in diameter. The construction of the runway followed and expanded on procedures used in other studies to collected data on limb loading patterns during above (Kimura et al., 1979; Reynolds, 1985a; Demes et al., 1994; Schmitt, 1994, 1995, 2003b; Schmitt and Lemelin, 2002, 2004; Lemelin and Schmitt, 2004; Schmitt and Hanna, 2004;

Granatosky et al., 2016) and below branch locomotion (Ishida et al., 1990; Chang et al., 2000; Michilsens et al., 2011, 2012; Granatosky, 2015; Granatosky et al., 2016). To address **Research Objectives 2 and 3**, the same runway was used to collect locomotor data during below branch quadrupedal walking in *P. vampyrus* and *C. didactylus*, and data during arm-swinging in *H. moloch* and *P. nemaeus*. The runway used to collect locomotor data during arm-swinging in *A. fusciceps* was the same dimensions as described above, but contained no instrumented section (Turnquist et al., 1999; Schmitt et al., 2005). Locomotor data from *C. capucinus* was collected opportunistically from wild animals. Analysis of strides from this species was restricted to supports approximating 1.25 cm in diameter. In most trials, animals were encouraged to move back and forth on the runway through food rewards. Locomotor data on below branch quadrupedal locomotion in *D. rotundus* was collected in a custom-made plexiglass enclosure (0.48 m x 0.15 m x 0.11 m) with an instrumented ceiling following the runway design outlined in Riskin and Hermanson (2005) and Riskin et al. (2006). The use of this enclosure was required to prevent *D. rotundus* from flying away during trials. Animals were encouraged to walk back and forth on the ceiling by lightly blowing on them through a straw (Riskin and Hermanson, 2005). The material makeup of the ceiling consisted of a wire mesh, in which animals were able to grasp with their claws.

For all trials, animals were filmed from a lateral view. Most animals (*C. capucinus, V. variegata, L. catta, P. coquereli, D. madagascariensis, P. nemaeus, P. vampyrus, C. didactylus, H. moloch,* and *D. rotundus*) were videotaped using a GoPro camera (Hero 3+ Black Edition; GoPro, San Mateo, CA) modified with a Back-Bone

Ribcage (Ribcage v1.0; Back-Bone, Ottawa, ON), which allows the GoPro cameras to be outfitted with interchangeable lenses and eliminates image distortion inherent to the camera (Figure 5). For these animals videos were recorded at 120 fields/second. Video-recordings of *A. fusciceps* were made available from previous studies (Turnquist et al., 1999; Schmitt et al., 2005), and were recorded at 60 fields/second.

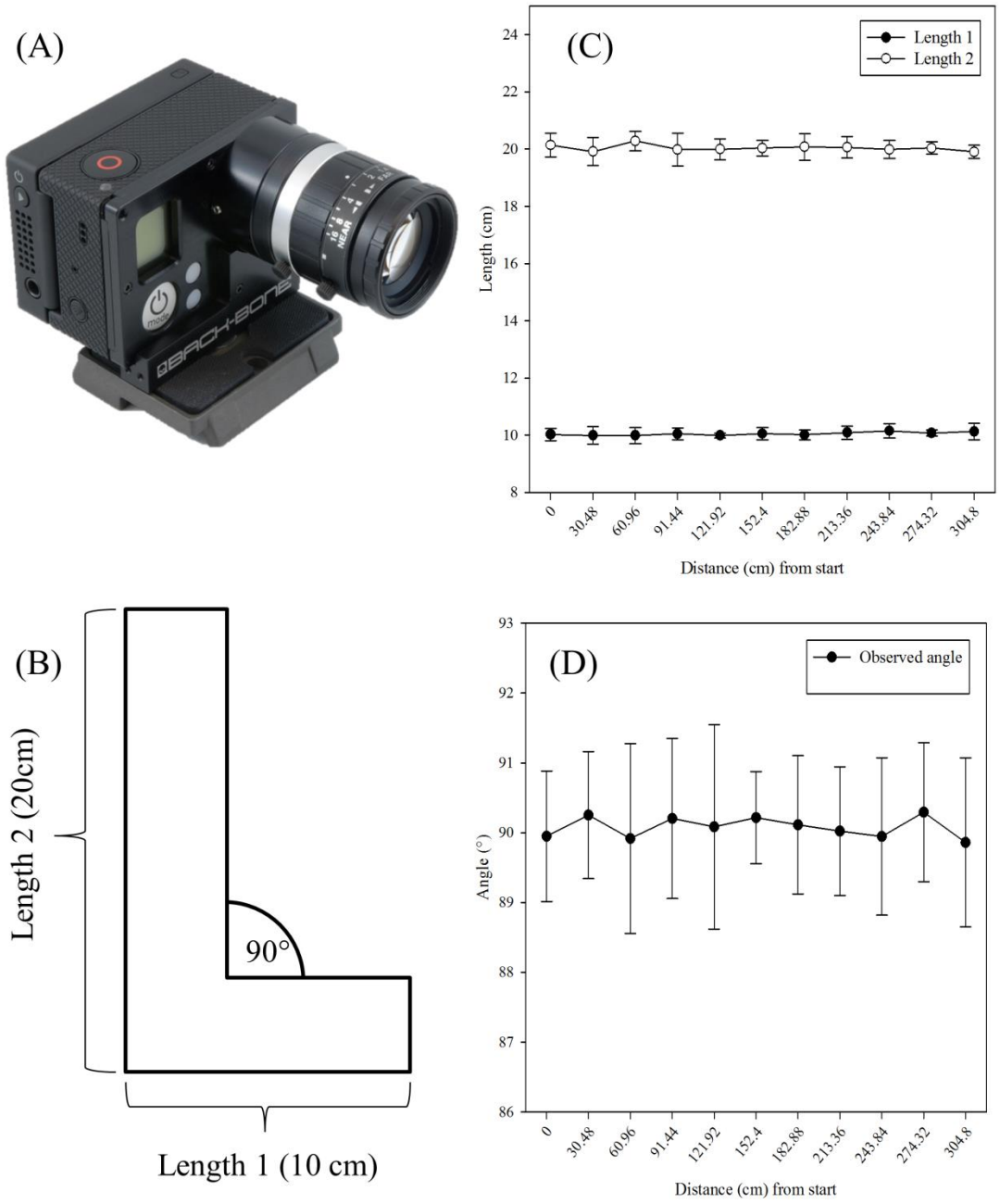

Figure 5: Description and results of camera verification. All trials were filmed from lateral view using a (A) GoPro camera (Hero 3+ Black Edition; GoPro, San Mateo, CA) modified with a Back-Bone Ribcage (Ribcage v1.0; Back-Bone, Ottawa, ON), which allows the GoPro cameras to be outfitted with interchangeable lenses and eliminates image distortion inherent to the camera. In order to validate that no

camera distortion was present during filming, we constructed a 3.048 m runway with intervals marked every 30.48 cm. The camera was placed 3.048 m from the runway. We then had a participant (MCG) walk an object (B) with markers attached at specific points representing a known angle and lengths. This was repeated 10 times. These points were digitized using ImageJ (Schneider et al., 2012; http://rsbweb.nih.gov/ij/download.html) at each interval along the runway for each of the 10 passes across the runway. The result of this validation indicates only minor fluctuations in (C) length and (D) angular measurements. These fluctuations are most likely a result of digitization error rather than distortion from the camera.

Following Hildebrand (1967) and Cartmill et al. (2002), for above and below branch quadrupedal locomotion, only symmetrical (i.e., opposing limb's touchdown occurred at between 40% and 60% of the cycle duration) walking steps (i.e., limb duty factor over 50%) in which the animal was traveling in a straight path and not accelerating or decelerating (i.e., steady-state locomotion) were selected for analysis. For arm-swinging, only steady-state strides approximating continuous-contact (i.e., aerial phase below $1/20^{th}$ of a second) were selected for analysis. It was the case that many of the strides analyzed in this study from *Ateles fusciceps* and *Pygathrix nemaeus* showed a brief aerial phase before touching down with the next limb. This behavior is distinct from ricochetal brachiation because ricochetal brachiation has very specific kinematic and COM movements not observed in any of the study species (Bertram et al., 1999; Bertram and Chang, 2001; Usherwood, 2003; Michilsens et al., 2011, 2012). Steady-state locomotion was determined by selecting a point on the subject (usually the nose) and calculating the instantaneous velocity between of this point between subsequent video frames throughout the entire stride, and then using regression analysis to determine whether velocity changed throughout the stride. Only strides in which no change in velocity was detected were used for subsequent analyses.

As many gait variables are influenced by variance in speed, a single velocity value was collected for every stride to aid in later covariance analyses. Furthermore, variation in limb length can result in drastically different velocity values that may artificially exaggerate difference in gait parameters based on differences in body size alone. To rectify this and normalize speed, Alexander and Jayes (1983) and Alexander

(1984, 1991) proposed the use of the Froude number, which is a dimensionless number that allows for speed comparisons between subjects of different body size. This approach attempts to control for size and speed simultaneously by taking into account the limb length of the subject and controlling for its influence. Alexander and Jayes (1983) proposed that gaits with equivalent Froude numbers should be dynamically similar to each other. The equation for Froude number is as follows:

$$F = \frac{v^2}{l*g}$$

In this equation v = velocity, l = forelimb length (m), and g = gravitational acceleration. This velocity value was calculated by digitizing a point on the subject's head and determining the time necessary to cross a known distance marked on the runway, and forelimb length was measured as the distance between the glenohumeral joint and the radiocarpal joint. The square root of Froude number results in normalized speed. A normalized speed was calculated for every stride in order to more properly compare certain gait variables across individuals of differing body sizes.

2.2.1 Kinetics

To address **Research Objectives 1 and 2** (see section 1.6 and 1.7) forelimb and hindlimb single-limb forces were collected while animals walked above (*V. variegata, L. catta, P. coquereli,* and *D. madagascariensis*) and below (*V. variegata, L. catta, P. coquereli, D. madagascariensis, P. vampyrus, C. didactylus,* and *D. rotundus*) the instrumented runways described above. No kinetic data was collected from *C. capucinus*. The instrumented portion of the runways consisted of two Kistler force plates (model

9317B; Dimensions- 0.030 m x 0.025 m x 0.025 m, Mass- 85g, Measuring range- Fx and Fy ± 1kN, Fz ±2kN, Sensitivity- Fx and Fy -26pC/N, Fz -11pC/N, Frequency Fx and Fy 5kHz, fnz 21kHz) that have been used in previous studies (Bishop et al., 2008). For *D. rotundus*, the force plates were secured to piece of stiff wire mesh (0.025 m x 0.15 m). For all other species, a small section of dowel was secured on one end of each force plate measuring the same diameter as the rest of the runway and large enough to accommodate an entire hand or foot (~ 0.10 m). These instrumented sections were mounted in the middle of the runway flush with, but separated by a small gap from, the rest of the runway. Force plate output was sampled at 12,000 Hz, and imported, summed, and processed using BioWare™ v.5.1 software, and then filtered (Butterworth, 30 Hz) and analyzed using MATLAB. Prior to all trials, animals were weighed, and forces for each day of trials were normalized to the body weight recorded for that day.

To address **Research Objectives 3**, forelimb single-limb forces were collected from animals (*H. moloch* and *P. nemaeus*) during arm-swinging on the instrumented runway described above. No kinetic data was collected from *A. fusciceps*. The instrumented portion of the runway consisted of an AMTI multi-axis force plate (MC3A-100) attached to a section of dowel (0.45 m) measuring the same diameter as the rest of the runway. This instrumented section was mounted in the middle of the runway flush with, but separated by a small gap from, the rest of the runway. Force plate output was sampled at 1,200 Hz, and imported, summed, and processed using AMTI-NetForce software, and then filtered (Butterworth, 30 Hz) and analyzed using MATLAB. Prior to

all trials, animals were weighed, and forces for each day of trials were normalized to the body weight recorded for that day.

The methods outlined above are all built upon the works of many others that have used force plates to analyze the movements and limb loading patterns in animals. Kimura et al. (1979) and Reynolds (1985a) were among the first to explore the limb loading patterns of primates and set the standard for which kinetic studies of primates should be compared. Their work was expanded by Ishida et al. (1990), Demes et al. (1994), and Schmitt (1995) to include the addition of simulated arboreal supports that more accurately replicate the conditions of an arboreal environment in which primates are most commonly observed. Relatively rapidly, more and more information has been collected across primates to gain a better understanding of the taxonomic [lemurids (Carlson et al., 2005; Franz et al., 2005), New World monkeys (Wallace and Demes, 2008; Larson and Demes, 2011; Young, 2012), Old World monkeys and hominoids (Reynolds, 1985a; Demes et al., 1994; Schmitt, 1995, 1998; Chang et al., 2000)] and locomotor [suspensory locomotion (Ishida et al., 1990; Michilsens et al., 2011, 2012), quadrupedal locomotion (Demes et al., 1994,; Schmitt, 1995; Schmitt and Hanna, 2004), leaping (Demes et al., 1995; Byrnes et al., 2008), and climbing (Hirasaki et al., 2000)] variations in limb loading observed within primates. Studies mentioned above represent only a small sample of the work achieved by many researchers that has explored limb loading patterns in primates. It is upon the work of these researchers, and many others, that the research described in this study is based.

All force data were corrected to indicate the applied force by the animal and was standardized for the direction of travel, differing body mass, orientation, and whether the limb that touched the instrumented portion of the force plate was left or right. This resulted in comparable force curves that all displayed vertical force as positive value on the vertical axis, braking force as a negative value on the horizontal axis, propulsive force as a positive value on the horizontal axis, medially oriented force (i.e., the animal applied a medially directed force) as negative value on the mediolateral axis, and laterally oriented force (i.e., the animal applied a laterally directed force) as a positive value on the mediolateral axis. In order to make comparisons between subjects of differing body masses all forces traces originally measured in Newtons (N) were converted into a proportion of the animal's body weight (%bw).

From these data, only steps with single-limb contacts on the plate or those steps in which the forelimb and hindlimb forces were clearly differentiated were analyzed. In total, 11 variables were calculated for each step: (1) peak vertical (Vpk) force; (2) first occurring horizontal peak (FHpk) force; (3) second occurring horizontal peak (SHpk) force; (4) first occurring horizontal impulse (FHI); (5) second occurring horizontal impulse (SHI); (6) net horizontal impulse (HI); (7) peak medial (Mpk) force; (8) peak lateral (Lpk) force; (9) medial impulse (MI); (10) lateral impulse (LI); and (11) net mediolateral impulse (MLI). Additionally, the timing at which Vpk, FHpk, SHpk, Mpk, Lpk, and the B/P transition (braking to propulsive transition during above branch quadrupedal locomotion and propulsive to braking transition during below branch quadrupedal locomotion) occurred was also recorded within each stride. The peak forces

are simply measured as the highest magnitude point measured on a particular portion of a tri-axial force curve. The impulse measurements represent the area under a particular portion of the force-time curve. The HI is measured as the area under the force-time curve in the horizontal component of the substrate reaction force. The HI provides a means for differentiating the overall braking or propulsive role of the limb during particular locomotor behaviors (Demes et al., 1994). The overall HI for each limb was calculated by subtracting the FHI from the SHI. Positive values indicate a net propulsive limb, while negative values indicate a net braking limb (Kimura et al., 1979; Ishida et al., 1990; Demes et al., 1994). Values approximating zero represent single limb contact forces were braking and propulsive impulses are approximately equal. The MLI is measured as the area under the force-time curve in the mediolateral component of the substrate reaction force. The MLI provides a means for differentiating if the limb is applying an overall medially or laterally directed force (Schmitt, 2003a; Carlson et al., 2005). The overall MLI for each limb was calculated by subtracting the MI from the LI. Positive values indicate that throughout the step the limb is applying a net laterally oriented force, while negative values indicate that throughout the step the limb is applying a net medially oriented force (Budsberg et al., 1987; Schmitt, 2003a; Carlson et al., 2005). In order to make comparisons between subjects of differing body masses, Vpk, FHpk, SHpk, Mpk, and Lpk forces are given in multiples of body weight (%bw), and FHI, SHI, HI, MI, LI, and MLI are given in body weight seconds (%bws).

2.2.2 Kinematics

To address **Research Objectives 1 and 2** patterns of limb movement were collected from the forelimbs and hindlimbs while animals walked quadrupedally above (*C. capucinus, V. variegata, L. catta, P. coquereli,* and *D. madagascariensis*) and below (*C. capucinus, V. variegata, L. catta, P. coquereli, D. madagascariensis, P. vampyrus,* and *C. didactylus*) the instrumented runways described above. From video recordings, the position of the shoulder, elbow, wrist, hip, knee, ankle, and forelimb and hindlimb point-of-contact were collected over the course of support phase (i.e., when the limb is in contact with the substrate). The resulting x-y coordinate data was used to track angular movements in the shoulder, elbow, wrist, hip, knee, and ankle. In addition to overall characterization of movement, joint excursion (maximum change in joint angle throughout the stride) was collected for each joint throughout the stride. All limb angles were digitized using DLT Dataviewer (Hedrick, 2008) in MATLAB. No kinematic measures of limb movement were collected from *D. rotundus* due to the highly modified hand morphology and diminutive size. To address **Research Objectives 3,** similar measures were collected during arm-swinging in *H. moloch, A. fusciceps,* and *P. nemaeus,* but were restricted to the forelimb (i.e., shoulder, elbow, and wrist).

All angular movements were measured in degrees (°). To make joint movements comparable between strides, different individuals, and different species, all joint data were scaled as a percentage of support phase. Following Larson et al. (2000) shoulder and hip angles were measured relative to the vertical axis of the shoulder or hip joint [i.e., when the arm passed directly above or below (depending on orientation) the shoulder or

hip joint this was considered the neutral position (0°)]. Angles greater than 0° represent shoulder or hip protraction, while angles less than 0° represent shoulder or hip retraction. Elbow and knee angles always reflect flexion, where 180° represents maximum elbow or knee extension.

Wrist and ankle measures required additional processing depending upon the way the animal grasped the support. As mentioned above, the position at which the animal grasps the support with its foot or hand determines what a two-dimensional wrist and ankle angle is actually measuring. For animals walking on the ground and during grasps in which the support is between the second and third digit, or along the axis of the third digit, wrist and ankle angle provides a measure of joint flexion and extension. In grasps during which the support is between the first and second digit, or the hand is functioning as a hook (i.e., no involvement of first digit or first digit is aligned with other digits), the wrist angle gives us a sense of radial and ulnar deviation in a stride, and ankle angle can be best described as being cranially and caudally oriented. Additionally, during arm-swinging, animals are known to grasp the support with either a pronated or supinated hand position. While these hand postures still provide a measure of radial and ulnar deviation, the order and magnitude of radial and ulnar deviation likely changes drastically. In pronated hand positions the wrist is first ulnarly deviated, and then subsequently radially deviated throughout the remainder of support phase. In supinated hand positions the wrist is first radially deviated, and then subsequently ulnarly deviated throughout the remainder of support phase.

To make the proper adjustments for measures of wrist and ankle movements, the position in which the animal grasped the support was recorded for every step. In the wrist, these positions were broken down into three categories for comparison: (1) flexion/extension grasps (animals grasp the support between second and third digit, or along axis of third digit); (2) supinated hook grasps (animals grasp the support between the first and second digit or as a hook with a supinated hand); and (3) pronated hook grasps (animal grasp support between first and second digit or as a hook with a pronated hand). For all grasp types, wrist angles were measured based on the position of the wrist relative to the point-of-contact with the support and the elbow. Neutral position (180°) was defined as the point in which the wrist was in line with the point-of-contact and the elbow. During flexion/extension grasps angles less than 180° indicate wrist flexion, while angles greater than 180° indicate wrist extension. During supinated and pronated hook grasps, wrist angles greater than 180° represent radial deviation, while angles less than 180° represent ulnar deviation.

In the ankle, these positions were broken down into two categories for comparison: (1) flexion/extension grasps (animals grasp the support between second and third digit, or along axis of third digit); and (2) hook grasps (animals grasp the support between the first and second digit or as a hook). For all grasp types, ankle angles were measured based on the position of the ankle relative to the point-of-contact with the support and the knee. Neutral position (180°) was defined as the point in which the ankle was in line with the point-of-contact and the knee. During flexion/extension grasps angles less than 180° indicate ankle flexion, while angles greater than 180° indicate ankle

extension. During hook grasps, ankle angles greater than 180° represent cranial deviation, while angles less than 180° represent caudal deviation.

2.2.3 Spatiotemporal gait variables

To address **Research Objectives 1 and 2,** spatiotemporal gait parameters and footfall sequences were collected while animals walked quadrupedally above (*C. capucinus, V. variegata, L. catta, P. coquereli,* and *D. madagascariensis*) and below (*C. capucinus, V. variegata, L. catta, P. coquereli, D. madagascariensis, P. vampyrus, D. rotundus,* and *C. didactylus*) the instrumented runway described above. From the video-recordings, cycle duration, stride length, forelimb and hindlimb duty factor and relative swing proportion, and the proportion of the stride at which mid-stance occurs were determined by reviewing the video sequences frame-by-frame using VirtualDub. Following Hildebrand (1967), Turnquist et al. (1999), Cartmill et al. (2002) and Schmitt (2011) cycle duration is defined as the time between two touchdowns by the same extremity. Stride length is defined as the distance between two successive points of contact by the same extremity; the reference point is the right hindlimb. Duty factor is the fraction of the cycle duration that a particular limb is in contact with the substrate, and relative swing proportion is the fraction of the cycle duration that a particular limb is not in contact with the substrate. The proportion of the stride at which mid-stance occurs was recorded as the fraction of cycle at which the wrist passes below the shoulder joint. This is an important metric because it provides a measure of the proportion of the stride that the limb (forelimb or hindlimb) is spent in protraction or retraction. To address **Research**

Objectives 3, similar measures were collected during arm-swinging in *H. moloch*, *A. fusciceps*, and *P. nemaeus*, but were restricted to the forelimb.

Interlimb coordination was also collected while animals walked quadrupedally above (*C. capucinus, V. variegata, L. catta, P. coquereli,* and *D. madagascariensis*) and below (*C. capucinus, V. variegata, L. catta, P. coquereli, D. madagascariensis, P. vampyrus, D. rotundus,* and *C. didactylus*) the runway. These footfall sequences were broken down into two categories based on the sequence in which the limbs make contact with the substrate. A lateral-sequence gait is one in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., the feet touch down in the order of right hindlimb, right forelimb, left hindlimb, left forelimb). A diagonal-sequence gait is one in which each hindlimb footfall is followed by a contralateral forelimb footfall (i.e., the feet touch down in the order of right hindlimb, left forelimb, left hindlimb, right forelimb). These gait sequences were further subdivided to describe the synchrony of paired limbs. When the ipsilateral forelimbs and hindlimbs are traveling together this is referred to as a lateral couplet, and when the contralateral forelimbs and hindlimbs are traveling together this is referred to as a diagonal couplet. Very rarely do the limbs move together in perfect synchrony, and these gait patterns receive their own unique names of a trot (contralateral synchrony) and a pace (ipsilateral synchrony). Interlimb coordination was analyzed using the gait formula introduced by Hildebrand (1967). Diagonality (D) is the percentage of the stride interval a forelimb lags behind the touchdown of the ipsilateral hindlimb. Diagonality facilitates the quantitative discrimination of diagonal sequences (DS; $D > 0.5$), lateral sequences (LS; $D < 0.5$), trots ($D = 0.5$), paces ($D = 0.0$), diagonal couplets

(DC; 0.25 < D < 0.75), and lateral couplets (LC; 0 < D < 0.25 and 0.75 < D < 1.0). No such measures of interlimb coordination were collected during arm-swinging.

2.3 Data analysis

To address the research objectives of this study, statistical analyses were broken down into three primary comparisons based on the three research objectives described in section 1.6: (1) an intraspecific comparison of the mechanics of above and below branch quadrupedal locomotion in *C. capucinus, V. variegata, L. catta, P. coquereli,* and *D. madagascariensis*; (2) an interspecific comparison between the mechanics of below branch quadrupedal locomotion in *C. capucinus, V. variegata, L. catta, P. coquereli, D. madagascariensis, P. vampyrus, D. rotundus,* and *C. didactylus*; and (3) an interspecific comparison between the mechanics of below branch quadrupedal locomotion in *C. capucinus, V. variegata, L. catta, P. coquereli, D. madagascariensis, P. vampyrus, D. rotundus,* and *C. didactylus* and arm-swinging in *H. moloch, A. fusciceps,* and *P. nemaeus*. While all data was processed using custom written codes in MATLAB, all statistical tests were conducted using JMP Pro v. 11 (SAS Institute Inc., Cary, NC). Prior to all statistical comparisons, Shapiro–Wilk and Levene's tests were used to determine normality and equal variance within the data (Sokal and Rohlf, 2012). In the case of multiple statistical comparisons, all P-values were Bonferroni adjusted to account for increased type I error that occurs do to multiple statistical comparisons.

2.3.1 An intraspecific comparison of the mechanics of above and below branch quadrupedal locomotion

To determine whether primates use differing mechanical strategies between above and below branch quadrupedal locomotion, this portion of the study compared kinetic, kinematic, and spatiotemporal gait variables of above and below branch walking in five species of primate (*C. capucinus, V. variegata, L. catta, P. coquereli,* and *D. madagascariensis*). Prior to any statistical comparisons, body weight normalized Vpk, FHpk, SHpk, Mpk, Lpk forces, and FHIs, SHIs HIs, MIs, LIs, and MLIs collected during above and below branch walking were compared with the corresponding normalized speed number using a regression analysis to determine if the variables of interest were influenced by variation in speed or body size within the sample. As mentioned above, the magnitude of substrate reaction forces are thought to be influenced by speed (Demes et al., 1994) and body size (Alexander and Jayes, 1983). If a relationship was observed, kinetic data was compared using a non-parametric ANCOVA with normalized speed as the covariate to compare across limbs and orientation (Olejnik and Algina, 1984; Vickers, 2005). For those variables that showed no association with a normalized number, a Kruskal-Wallis test, a non-parametric ANOVA, was used to determine whether there were statistically significant differences across limbs and orientation. Each species was analyzed separately, and only qualitative comparisons were made between species in order to confirm broad kinetic patterns.

As another means of assessing the similarity between limb loading patterns during above and below branch quadrupedal locomotion, the timing of at which Vpk, FHpk,

SHpk, Mpk, Lpk, and B/P occurred within each support phase was compared between orientations for each limb separately (i.e., the timing of these events for forelimb and hindlimb loading were not compared to each other in either orientation). A Mann–Whitney *U*-test was used to determine whether the timing of limb loading patterns for each limb varied significantly between above and below branch quadrupedal locomotion.

As outlined in section 1.5.2, little information is available on what determines whether a quadruped's limb is net braking or net propulsive, and it remains unclear why the patterns of braking and propulsive limbs switch between above and below branch quadrupedal locomotion. Current thought indicates that this variation in the limb's general braking/propulsive role is due to differing levels of protraction and retraction (Kimura et al., 1977; Reynolds, 1985b). To address this assumption, two separate statistical analyses were conducted to determine whether the: (1) B/P generally occurs at mid-stance; and (2) proportion of protraction to retraction within a step determines whether the limb is braking or propulsive. To determine if the B/P generally occurs at mid-stance, an ANOVA was conducted to analyze the likelihood of these two events occurring at a similar time. To assess the hypothesis that the proportion of protraction to retraction within a step determines whether the limb is braking or propulsive, a regression analysis was conducted between the protraction to retraction ratio and HI. Additionally, normalized speed was included as a secondary independent variable within the regression analysis as HI has been shown to be affected by speed and body size (Demes et al., 1994). Data for each limb and orientation were analyzed separately.

From the scaled data on joint movements, shoulder, elbow, hip, and knee angles were compared statistically at specific intervals of support phase (i.e., touchdown, mid-support, and lift-off). Each species was analyzed separately, and only qualitative comparisons were made between species in order to confirm broad kinematic patterns. As all comparisons were intraspecific, a Mann–Whitney *U*-test was used to determine whether joint movements were significantly different between above and below branch quadrupedal locomotion for each species.

As mentioned previously, movements of the wrist and ankle are difficult to quantify, and vary greatly depending on the type of grasp. Prior to analyzing movements of the wrist and ankle, all grasps were classified into one of the three grasp categories for the wrist (i.e., flexion/extension grasps, supinated hook grasps, and pronated hook grasps) and two grasp types for the ankle (i.e., flexion/extension grasps, and hook grasps). Once grasp type was determined, wrist and ankle movements were compared between orientations following the same methods as the other limb elements described above. Only similar grasp categories were statistically compared to each other (i.e., flexion/extension grasps were not compared to supinated or pronated hook grasps, but supinated hook grasps, and pronated hook grasps were statistically compared to each other).

With regard to spatiotemporal gait variables, prior to any statistical comparisons, stride duration, stride length, forelimb and hindlimb duty factor and relative swing proportion collected during above and below branch walking were compared with the corresponding normalized speed using a regression analysis to determine if the variables

of interest were influenced by variation in speed or body size within the sample. If a relationship was observed, spatiotemporal data was compared using an ANCOVA with normalized speed as the covariate to compare across limbs and orientation (Olejnik and Algina, 1984; Vickers, 2005). For those variables that showed no association with normalized speed, a Kruskal-Wallis test, a non-parametric ANOVA, was used to determine whether there are statistically significant differences between the differing orientations. Each species was analyzed separately, and only qualitative comparisons were made between species in order to confirm broad spatiotemporal patterns.

Interlimb coordination was presented and analyzed in two different ways. In order to perform statistical comparisons, diagonality values were analyzed between above and below branch quadrupedal locomotion for each species was using a Mann–Whitney *U*-test. To graphically display patterns of interlimb coordination, diagonality was correlated with hindlimb duty factor following Hildebrand (1967) and Cartmill et al. (2002). The use of the Hildebrand gait plot allows interlimb coordination data collected from above and below branch quadrupedal locomotion in *V. variegata, L. catta, P. coquereli,* and *D. madagascariensis* to be placed in a comparative context, and better allows functional interpretations for observed limb patterns.

2.3.2 An interspecific comparison of the mechanics of below branch quadrupedal locomotion

To determine whether primates and non-primates use differing mechanical strategies between below branch quadrupedal locomotion, this portion of the study compared kinetic, kinematic, and spatiotemporal gait variables of below branch walking

in five species of primate (*C. capucinus, V. variegata, L. catta, P. coquereli,* and *D. madagascariensis*), and three species of non-primate (*P. vampyrus, D. rotundus,* and *C. didactylus*) mammals. Prior to any statistical comparisons, kinetic variable including body weight normalized Vpk, FHpk, SHpk, Mpk, Lpk forces, and FHIs, SHIIs HIs, MIs, LIs, and MLIs collected during below branch walking were compared with the corresponding normalized speed using a regression analysis to determine if the variables of interest were influenced by variation in speed or body size within the sample. If a relationship was observed, kinetic data was compared using a non-parametric ANCOVA with normalized speed as the covariate to compare across limbs and species (Olejnik and Algina, 1984; Vickers, 2005). For those variables that showed no association with normalized speed, a Kruskal-Wallis test was used to determine whether there were statistically significant differences across limbs and species.

From the scaled data on joint movements, shoulder, elbow, hip, and knee angles were compared statistically at specific intervals of the support phase (i.e., touchdown, mid-support, and lift-off). Joint movements of each species were compared to other species using a Kruskal-Wallis test to determine whether kinematics vary significantly between below branch quadrupedal locomotion in different species.

As mentioned previously, movements of the wrist and ankle are difficult to quantify, and vary greatly depending on the type of grasp. Prior to analyzing movements of the wrist and ankle, all grasps were classified into one of the grasp categories. Once grasp type was determined, wrist and ankle movements were compared between species

following the same methods as the other limb elements described above. Only similar grasp categories were statistically compared to each other.

Prior to any statistical comparisons, spatiotemporal gait variables including stride duration, stride frequency, stride length, forelimb and hindlimb duty factors, and relative swing proportion collected during below branch walking were compared with the corresponding normalized speed using a regression analysis to determine if the variables of interest were influenced by variation in speed or body size within the sample. If a relationship was observed, spatiotemporal gait data were compared using a non-parametric ANCOVA with normalized speed as the covariate to compare across limbs and species (Olejnik and Algina, 1984; Vickers, 2005). For those variables that showed no association with normalized speed, a Kruskal-Wallis test was used to determine whether there are statistically significant differences across limbs and species.

Interlimb coordination was presented and analyzed in two different ways. In order to perform statistical comparisons, diagonality values were analyzed between species during below branch quadrupedal locomotion using a Kruskal-Wallis test. To graphically display patterns of interlimb coordination, diagonality was correlated with hindlimb duty factor following Hildebrand (1967) and Cartmill et al. (2002). The use of the Hildebrand gait plot allows interlimb coordination data collected during below branch quadrupedal locomotion to be presented in a comparative context and functional interpretations of the observed limb patterns to be drawn.

2.3.3 An interspecific comparison of the mechanics of below branch quadrupedal locomotion and arm-swinging

To determine whether the mechanics of below branch quadrupedal locomotion and arm-swinging are similar, this portion of the study compared kinetic, kinematic, and spatiotemporal gait variables of below branch walking in five species of primate (*C. capucinus*, *V. variegata*, *L. catta*, *P. coquereli*, and *D. madagascariensis*), and three species of non-primate (*P. vampyrus*, *D. rotundus*, and *C. didactylus*) mammals and arm-swinging in three species of primate (*H. moloch*, *A. fusciceps*, and *P. nemaeus*). In order to make biologically meaningful comparisons between below branch quadrupedal locomotion and arm-swinging, the entire data collection focused only on the forelimbs. Prior to any statistical comparisons, kinetic variables including body weight normalized Vpk, FHpk, SHpk, Mpk, Lpk forces, and FHIs, SHIs HIs, MIs, LIs, and MLIs collected during below branch walking and arm-swinging were compared with the corresponding normalized speed using a regression analysis to determine if the variables of interest were influenced by variation in speed or body size within the sample. If a relationship was observed, kinetic data was compared using a non-parametric ANCOVA with normalized speed as the covariate to compare across limbs and species (Olejnik and Algina, 1984; Vickers, 2005). For those variables that showed no association with normalized speed, a Kruskal-Wallis test was used to determine whether there were statistically significant differences across species.

As another means of assessing the similarity between forelimb loading patterns during below branch quadrupedal locomotion and arm-swinging, the timing of at which

Vpk, FHpk, SHpk, Mpk, Lpk, and B/P occurred within support phase was compared for each species. An ANOVA was used to determine whether the timing of forelimb loading patterns varied significantly between below branch quadrupedal locomotion and arm-swinging in different species.

From the scaled data on joint movements, shoulder and elbow were compared statistically at specific intervals of support phase (i.e., touchdown, mid-support, and lift-off). Joint movements of each species were compared to other species using a Kruskal-Wallis test to determine whether kinematics vary significantly between below branch quadrupedal locomotion and arm-swinging in different species.

As mentioned previously, movements of the wrist is difficult to quantify and varies greatly depending on the type of grasp. Prior to analyzing movements of the wrist, all grasps were classified into one of the three grasp categories. Once grasp type was determined, wrist movements were compared between species following the same methods as the other limb elements described above. Only similar grasp categories were statistically compared to each other.

In regards to spatiotemporal gait variables, prior to any statistical comparisons, stride duration, stride frequency, stride length, forelimb duty factor and relative swing proportion collected during below branch walking and arm-swinging were compared with the corresponding normalized speed using a regression analysis to determine if the variables of interest were influenced by variation in speed or body size within the sample. If a relationship was observed, spatiotemporal gait data was compared using a non-parametric ANCOVA with normalized speed as the covariate to compare across species

and locomotor mode (Olejnik and Algina, 1984; Vickers, 2005). For those variables that showed no association with normalized speed, a Kruskal-Wallis test was used to determine whether there are statistically significant differences across limbs and species.

3. Results

This research involved comparisons of several categories of data: kinetic data, kinematic data, and spatiotemporal gait data. In addition, there are both intra- and interspecific comparisons. Intraspecific comparisons are first addressed in order to determine whether there are kinetic, kinematic, and spatiotemporal gait differences between above and below branch quadrupedal locomotion. These comparisons are followed by interspecific analyses to determine whether there are kinetic, kinematic, and spatiotemporal gait differences between different mammalian species that commonly use below branch quadrupedal locomotion, and whether the mechanics of below branch quadrupedal locomotion are similar to what is observed in arm-swinging.

3.1 An intraspecific comparison of the mechanics of above and below branch quadrupedal locomotion

3.1.1 Kinetics

In total, 544 single limb forces were collected and analyzed in primates during above and below branch quadrupedal locomotion. Table 3 and 4 summarizes the number of steps collected per limb for each orientation, intraspecific statistical comparisons, and data for the FHpk, SHpk, FHI, SHI, HI, Mpk, Lpk, MI, LI, MLI, and Zpk, and the timing associated with FHpk, SHpk, B/P, Mpk, Lpk, and Zpk. All data displayed a non-normal distribution and unequal variances, therefore non-parametric statistics were used for all comparisons. A significant ($P \leq 0.001$) positive association was observed between Vpk and normalized speed. No significant relationship between normalized speed and the other kinetic variables collected were observed.

Table 3: Limb loading data (mean ± standard deviation) and significance tests for above and below quadrupedal locomotion in four species of primate.

Species	Orientation	Limb	N	FHpk (%bw)	SHpk (%bw)	FHI (%bws)	SHI (%bws)	HI (%bws)	Mpk (%bw)	Lpk (%bw)	MI (%bws)	LI (%bws)	MLI (%bws)	Vpk (%bw)
Daubentonia madagascariensis	Above	Forelimb	46	-13.39 ± 6.75	4.45 ± 3.69	-3.08 ± 1.66	0.28 ± 0.41	-2.79 ± 1.65	-5.15 ± 2.25	1.70 ± 1.33	-0.97 ± 0.62	0.11 ± 0.11	-0.86 ± 0.64	53.48 ± 9.11
		Hindlimb	28	-12.12 ± 5.95 *	15.25 ± 6.12 *	-0.26 ± 0.38 *	4.24 ± 2.29 *	3.98 ± 2.42 *	-5.11 ± 2.08 ns	1.95 ± 1.68 Ns	-1.42 ± 0.83 *	0.12 ± 0.13 ns	-1.30 ± 0.88 *	73.54 ± 8.19 *
	Below	Forelimb	26	23.34 ± 7.45	-13.64 ± 6.42	6.63 ± 3.94	-2.31 ± 1.69	4.32 ± 4.80	-7.29 ± 3.99	3.13 ± 2.56	-1.99 ± 1.35	0.32 ± 0.25	-1.67 ± 1.36	66.96 ± 8.33
		Hindlimb	22	4.93 ± 3.60 *	-12.85 ± 2.83 ns	0.55 ± 0.69 *	-3.54 ± 2.49 *	-2.98 ± 2.55 *	-5.59 ± 2.95 ns	2.66 ± 1.17 Ns	-1.30 ± 0.74 *	0.34 ± 0.26 ns	-0.97 ± 0.79 *	49.04 ± 10.14 *
Lemur catta	Above	Forelimb	28	-11.62 ± 4.30	3.73 ± 1.16	-3.36 ± 1.09	0.44 ± 0.21	-2.92 ± 1.05	-2.07 ± 0.90	0.90 ± 0.64	-0.54 ± 0.32	0.09 ± 0.10	-0.45 ± 0.37	44.28 ± 5.10
		Hindlimb	25	-7.43 ± 2.37 *	11.28 ± 2.95 *	-0.69 ± 0.29 *	3.27 ± 1.15 *	2.58 ± 1.29 *	-3.12 ± 1.04 *	1.59 ± 0.90 *	-0.82 ± 0.42 *	0.14 ± 0.16 ns	-0.69 ± 0.49 *	78.63 ± 9.86 *
	Below	Forelimb	52	23.14 ± 7.09	-14.79 ± 6.90	3.90 ± 1.70	-1.81 ± 1.07	2.09 ± 2.23	-11.84 ± 5.35	5.14 ± 2.99	-2.11 ± 1.06	0.52 ± 0.47	-1.59 ± 1.15	70.12 ± 9.32
		Hindlimb	41	7.82 ± 4.66 *	-15.24 ± 7.24 ns	0.63 ± 0.68 *	-2.98 ± 1.82 *	-2.36 ± 1.75 *	-7.50 ± 3.48 *	3.51 ± 1.73 *	-1.34 ± 0.87 *	0.29 ± 0.24 *	-1.05 ± 0.85 *	43.79 ± 10.84 *
Propithecus coquereli	Above	Forelimb	16	-14.94 ± 7.89	0.91 ± 0.70	-3.05 ± 1.93	0.02 ± 0.09	-3.03 ± 1.87	-4.96 ± 2.53	1.64 ± 1.12	-0.89 ± 0.67	0.14 ± 0.14	-0.75 ± 0.72	52.99 ± 14.39
		Hindlimb	15	-1.96 ± 1.52 *	14.43 ± 6.48 *	-0.06 ± 0.10 *	3.46 ± 1.59 *	3.40 ± 1.60 *	-5.51 ± 2.87 ns	2.81 ± 1.68 *	-1.13 ± 0.81 ns	0.20 ± 0.18 ns	-0.93 ± 0.88 ns	83.81 ± 15.11 *
	Below	Forelimb	59	22.21 ± 5.59	-13.56 ± 6.86	4.59 ± 1.47	-1.88 ± 1.13	2.71 ± 1.92	-9.15 ± 3.71	3.29 ± 2.54	-2.14 ± 1.31	0.35 ± 0.35	-1.80 ± 1.47	79.90 ± 10.71
		Hindlimb	51	5.80 ± 2.29 *	-11.63 ± 4.07 ns	0.59 ± 0.40 *	-3.33 ± 1.96 *	-2.74 ± 2.00 *	-6.55 ± 2.80 *	1.76 ± 1.18 *	-1.62 ± 0.82 *	0.21 ± 0.26 *	-1.41 ± 0.94 *	34.98 ± 7.80 *
Varecia variegata	Above	Forelimb	40	-18.04 ± 4.77	4.85 ± 2.13	-3.29 ± 0.89	0.29 ± 0.30	-3.00 ± 0.96	-4.69 ± 2.21	2.20 ± 1.32	-0.78 ± 0.61	0.13 ± 0.11	-0.65 ± 0.65	56.37 ± 7.34
		Hindlimb	31	-7.84 ± 3.15	10.61 ± 3.27	-0.70 ± 0.70	2.86 ± 1.14	2.16 ± 1.59	-6.74 ± 2.69	3.69 ± 1.84	-1.25 ± 0.66	0.24 ± 0.24	-1.00 ± 0.77	77.04 ± 8.83

			*	*	*	*	*	*	*	*	*	*	*
Below	Forelimb	38	25.54 ± 7.70	-10.85 ± 4.27	5.12 ± 1.65	-1.39 ± 0.74	2.99 ± 1.67	-7.85 ± 3.30	3.99 ± 2.61	-1.81 ± 0.96	0.44 ± 0.35	-1.36 ± 1.08	82.54 ± 14.95
	Hindlimb	33	7.44 ± 4.17	-11.91 ± 5.11	0.79 ± 0.61	-2.42 ± 1.34	-1.73 ± 1.36	-6.76 ± 2.80	2.37 ± 1.50	-1.75 ± 0.89	0.15 ± 0.21	-1.60 ± 0.98	61.64 ± 12.92
			*	ns	*	*	*	ns	*	ns	*	ns	*

[*] Significant difference observed ($P \leq 0.05$)
[ns] No significant difference observed ($P > 0.05$)
[FHpk] First horizontal peak force
[SHpk] Second horizontal peak force
[FHI] First horizontal impulse
[SHI] Second horizontal impulse
[Mpk] Medial peak
[Lpk] Lateral peak
[MI] Medial impulse
[LI] Lateral impulse
[MLI] Mediolateral impulse
[Vpk] Vertical peak

Table 4. The timing of limb loading events throughout support phase (mean ± standard deviation) and significance tests observed during above and below branch quadrupedal locomotion in four species of primate.

Species	Orientation	Limb	N	FHpk	SHpk	B/P	Mid-stance†	Mpk	Lpk	Vpk
Daubentonia madagascariensis	Above	Forelimb	46	0.36 ± 0.17	0.83 ± 0.13	0.74 ± 0.12	0.52 ± 0.09	0.46 ± 0.23	0.68 ± 0.37	0.57 ± 0.16
		Hindlimb	28	0.14 ± 0.11	0.53 ± 0.21	0.19 ± 0.09	0.38 ± 0.08	0.50 ± 0.25	0.27 ± 0.32	0.28 ± 0.05
				*	*	*	*	ns	*	*
	Below	Forelimb	26	0.21 ± 0.10	0.78 ± 0.15	0.60 ± 0.11	0.43 ± 0.14	0.52 ± 0.26	0.64 ± 0.34	0.60 ± 0.11
		Hindlimb	22	0.11 ± 0.11	0.60 ± 0.13	0.21 ± 0.13	0.28 ± 0.11	0.38 ± 0.22	0.43 ± 0.33	0.33 ± 0.11
				*	*	*	*	ns	ns	*
Comparison between forelimbs				*	*	*	*	ns	ns	ns
Comparison between hindlimbs				ns	ns	ns	*	ns	ns	ns
Lemur catta	Above	Forelimb	28	0.26 ± 0.06	0.84 ± 0.07	0.69 ± 0.06	0.45 ± 0.05	0.30 ± 0.28	0.44 ± 0.40	0.57 ± 0.10
		Hindlimb	25	0.15 ± 0.04	0.68 ± 0.13	0.29 ± 0.05	0.36 ± 0.05	0.42 ± 0.31	0.18 ± 0.20	0.31 ± 0.09
				*	*	*	*	ns	*	*
	Below	Forelimb	52	0.21 ± 0.07	0.76 ± 0.08	0.56 ± 0.10	0.45 ± 0.09	0.47 ± 0.20	0.53 ± 0.38	0.55 ± 0.11
		Hindlimb	41	0.09 ± 0.07	0.65 ± 0.12	0.19 ± 0.08	0.25 ± 0.08	0.39 ± 0.23	0.35 ± 0.35	0.33 ± 0.12
				*	*	*	*	ns	ns	*
Comparison between forelimbs				ns	*	*	Ns	*	ns	ns
Comparison between hindlimbs				ns	ns	ns	Ns	ns	ns	ns
Propithecus coquereli	Above	Forelimb	16	0.20 ± 0.20	0.63 ± 0.32	0.78 ± 0.19	0.56 ± 0.09	0.43 ± 0.19	0.54 ± 0.40	0.45 ± 0.10
		Hindlimb	15	0.05 ± 0.07	0.56 ± 0.18	0.07 ± 0.08	0.44 ± 0.12	0.36 ± 0.21	0.21 ± 0.27	0.42 ± 0.07
				*	*	*	*	ns	ns	ns
	Below	Forelimb	59	0.25 ± 0.07	0.77 ± 0.05	0.58 ± 0.09	0.43 ± 0.13	0.48 ± 0.20	0.41 ± 0.39	0.53 ± 0.12
		Hindlimb	51	0.09 ± 0.05	0.68 ± 0.12	0.25 ± 0.12	0.19 ± 0.10	0.30 ± 0.17	0.36 ± 0.37	0.28 ± 0.09
				*	ns	*	*	ns	ns	*
Comparison between forelimbs				*	ns	ns	Ns	ns	ns	ns
Comparison between hindlimbs				ns	ns	ns	Ns	ns	ns	ns
Varecia variegata	Above	Forelimb	40	0.31 ± 0.08	0.75 ± 0.08	0.66 ± 0.08	0.47 ± 0.06	0.27 ± 0.22	0.31 ± 0.32	0.52 ± 0.07
		Hindlimb	31	0.14 ± 0.05	0.66 ± 0.10	0.26 ± 0.08	0.39 ± 0.05	0.21 ± 0.22	0.23 ± 0.21	0.28 ± 0.06
				*	*	*	*	ns	ns	*
	Below	Forelimb	38	0.19 ± 0.08	0.74 ± 0.08	0.58 ± 0.08	0.40 ± 0.06	0.45 ± 0.20	0.38 ± 0.35	0.54 ± 0.10
		Hindlimb	33	0.13 ± 0.07	0.56 ± 0.16	0.31 ± 0.11	0.48 ± 0.06	0.33 ± 0.15	0.17 ± 0.30	0.34 ± 0.11
				*	*	*	*	*	ns	*
Comparison between forelimbs				*	ns	ns	Ns	*	ns	ns
Comparison between hindlimbs				ns	ns	ns	Ns	ns	ns	ns

[*] Significant difference observed ($P \leq 0.05$)
[ns] No significant difference observed ($P > 0.05$)
[FHpk] First horizontal peak force

[SHpk] Second horizontal peak force
[B/P] Braking to propulsive transition during above branch quadrupedal locomotion and/or propulsive to braking transition during below branch quadrupedal locomotion
[†]Mid-stance collected from kinematic analysis and therefore the number of strides analyzed matches what was collected in the kinematic analysis
[Mpk] Medial peak
[Lpk] Lateral peak
[Vpk] Vertical peak

All primate species displayed significantly different ($P \leq 0.001$) Vpk forces between the forelimb and hindlimb during both above and below branch quadrupedal locomotion. For all primate species, forelimb Vpk forces were significantly ($P \leq 0.001$) lower than hindlimb Vpk forces during above branch quadrupedal locomotion. The opposite limb loading pattern was observed during below branch quadrupedal locomotion in which forelimb Vpk forces were significantly ($P \leq 0.001$) greater than hindlimb Vpk forces (Figures 6-8). All vertical force traces (both forelimb and hindlimb) were represented by a single peak. In the forelimb, this peak occurred approximately at 54% of support phase, and in the hindlimb this peak occurred approximately at 32% of support phase. In all species, except *P. coquereli*, the timing of Vpk varied significantly between forelimb and hindlimb. No significant differences were observed between the timing of these peaks between above and below branch quadrupedal locomotion.

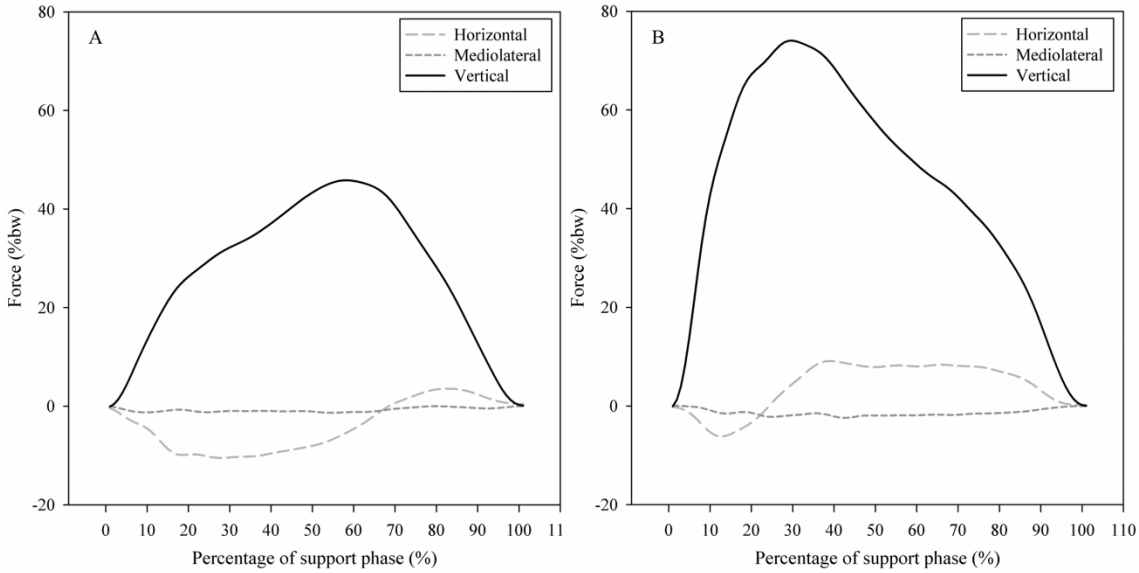

Figure 6: Representative force traces for *Lemur catta* during above branch quadrupedal locomotion. All data are presented as a percentage of body weight (%bw). Data presented for the forelimb (A) and hindlimb (B).

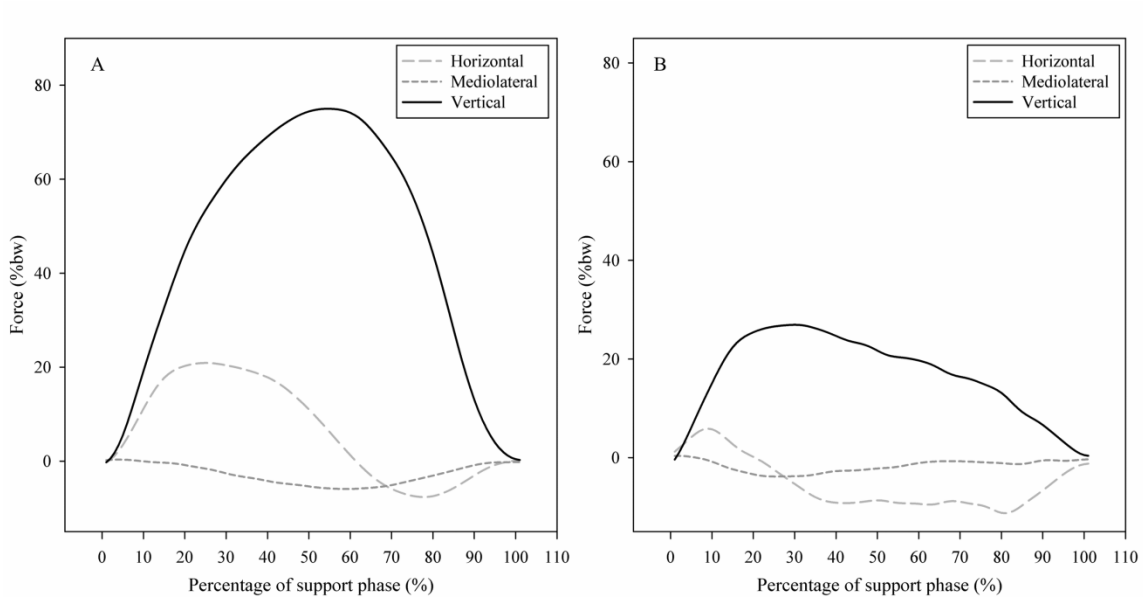

Figure 7: Representative force traces for *Propithecus coquereli* during below branch quadrupedal locomotion. All data are presented as a percentage of body weight (%bw). Data presented for the forelimb (A) and hindlimb (B).

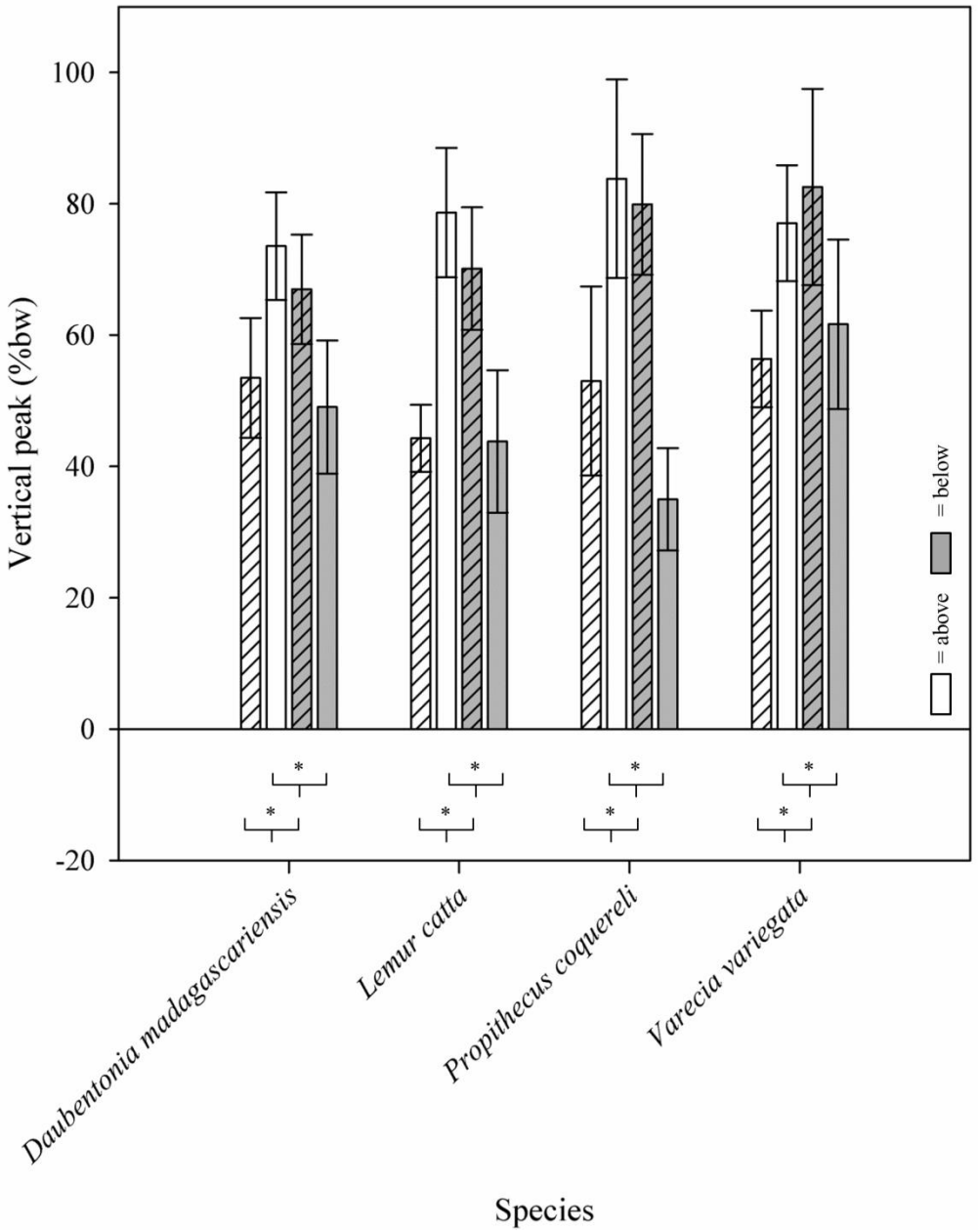

Figure 8: Mean and standard deviation values of peak vertical forces in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at P < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

During above branch quadrupedal locomotion, a consistent limb loading pattern was observed, in which as the limb (forelimb or hindlimb) touched down, it first applied a braking force to the substrate followed by a propulsive force prior to lift-off. This pattern was the norm for quadrupedal locomotion as it acts to decelerate and accelerate the COM during a stride (Demes et al., 1994; Kimura et al., 1979). In contrast, during below branch quadrupedal locomotion as the limb (forelimb or hindlimb) touched down, it first applied a propulsive force to the substrate followed by a braking force prior to lift-off. This pattern was consistent for all species (Figures 9 and 10). In all species and for both orientations, the first occurring horizontal peak occurred within the first 40% of support phase. This first occurring horizontal peak always occurred later in the forelimb compared to the hindlimb. In all species and for both orientations, the second occurring horizontal peak occurred within the latter 50% of support phase. This second occurring horizontal peak always occurred later in the forelimb compared to the hindlimb. In all species and for both orientations, the B/P transition always occurred during the latter 50% of support phase in the forelimb, and within the first 35% of support phase in the hindlimb.

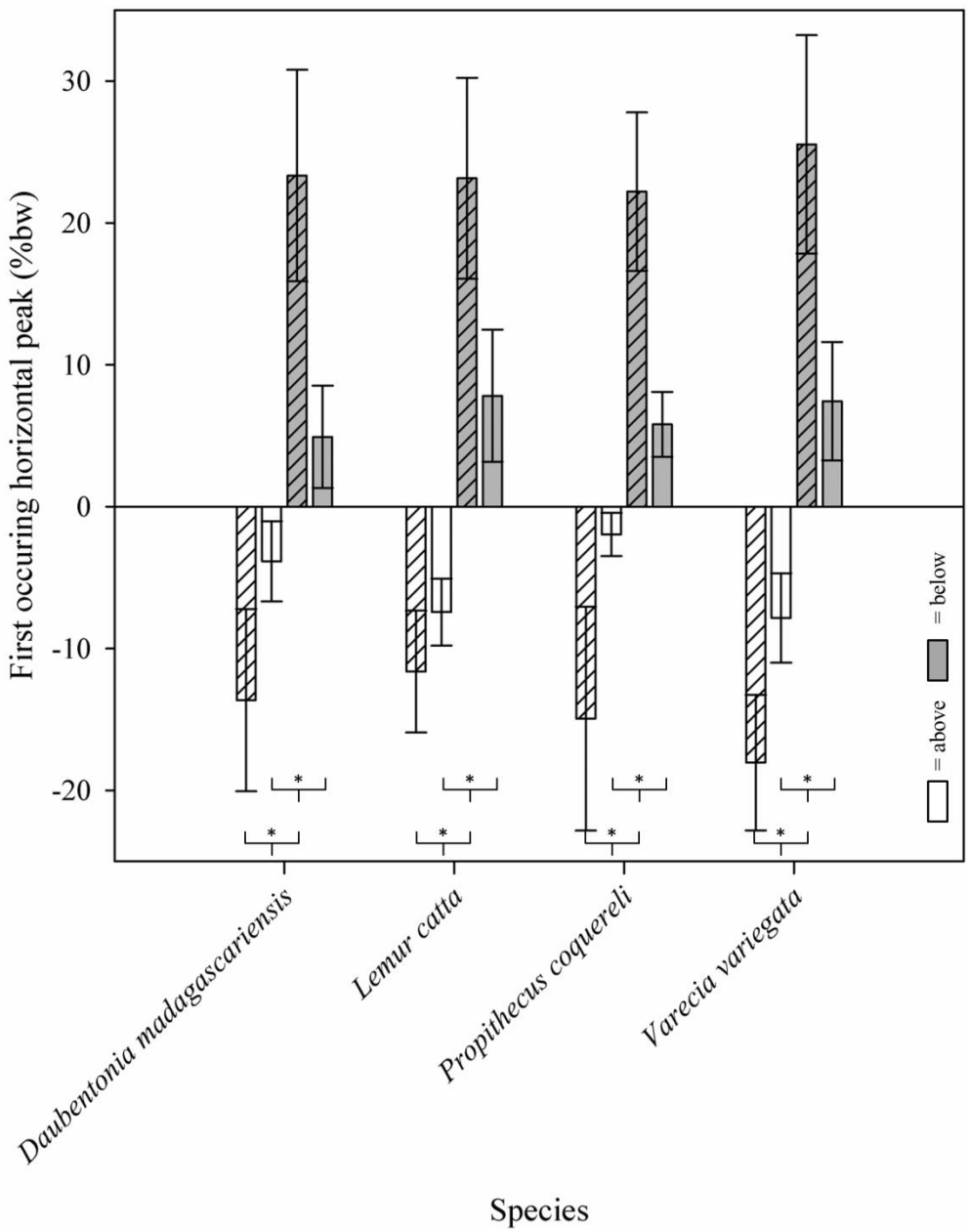

Figure 9: Mean and standard deviation values of the first occurring horizontal peak force in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at P < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

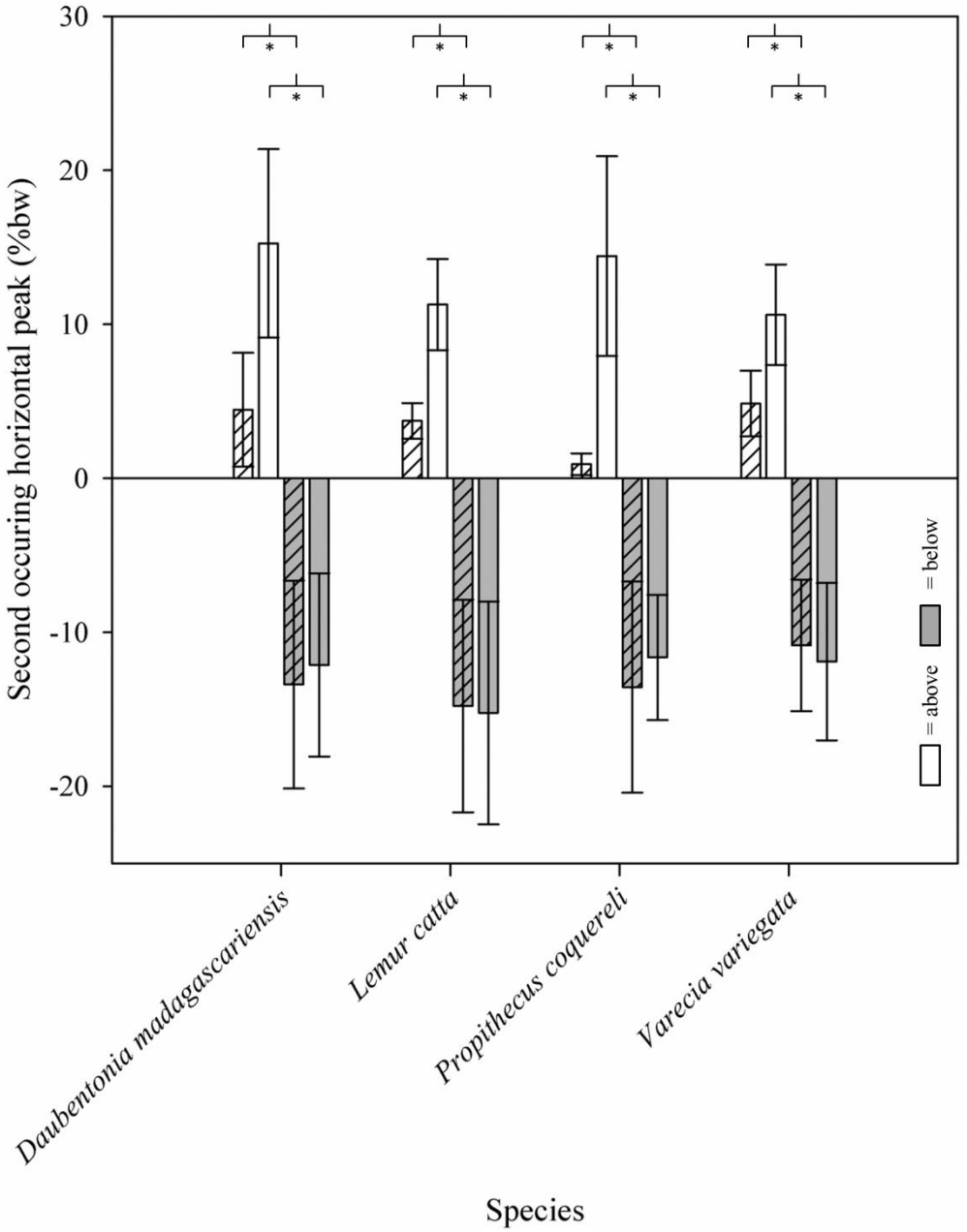

Figure 10: Mean and standard deviation values of the second occurring horizontal peak force in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at P < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

During above branch quadrupedal walking, all species displayed a negative net HI in the forelimbs and positive net HI in the hindlimbs, meaning that the forelimbs were net braking whereas the hindlimbs were net propulsive, a pattern consistent with previous studies (Kimura et al., 1979; Demes et al., 1994; Franz et al., 2005; Granatosky et al., 2016). This pattern was reversed during below branch quadrupedal locomotion, in which the sample animals displayed a positive net HI in the forelimbs and negative net HI in the hindlimbs (Figure 11).

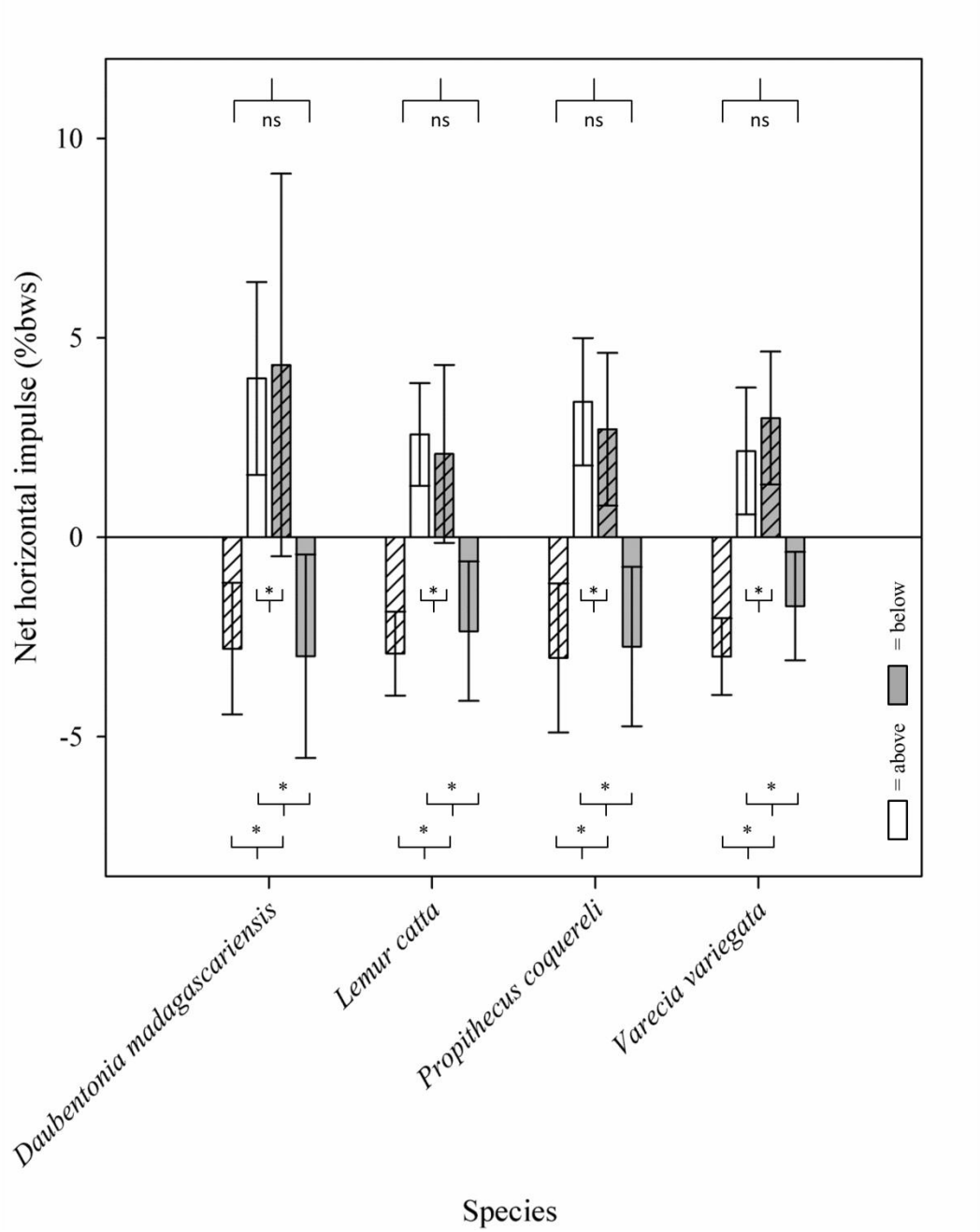

Figure 11: Mean and standard deviation values of the net horizontal impulse in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at P < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

An analysis of the first occurring horizontal impulse (Figure 12) and the second occurring horizontal impulse (Figure 13) separately for each limb showed that during above branch quadrupedal walking, the first occurring horizontal impulse was associated with a braking force, and is significantly greater in the forelimb when compared to the hindlimb. The opposite pattern was observed during below branch quadrupedal locomotion. The second occurring horizontal impulse was associated with a propulsive impulse during above branch quadrupedal locomotion, and the hindlimb exerts a significantly greater propulsive impulse than the forelimb. The opposite pattern was observed during below branch quadrupedal locomotion.

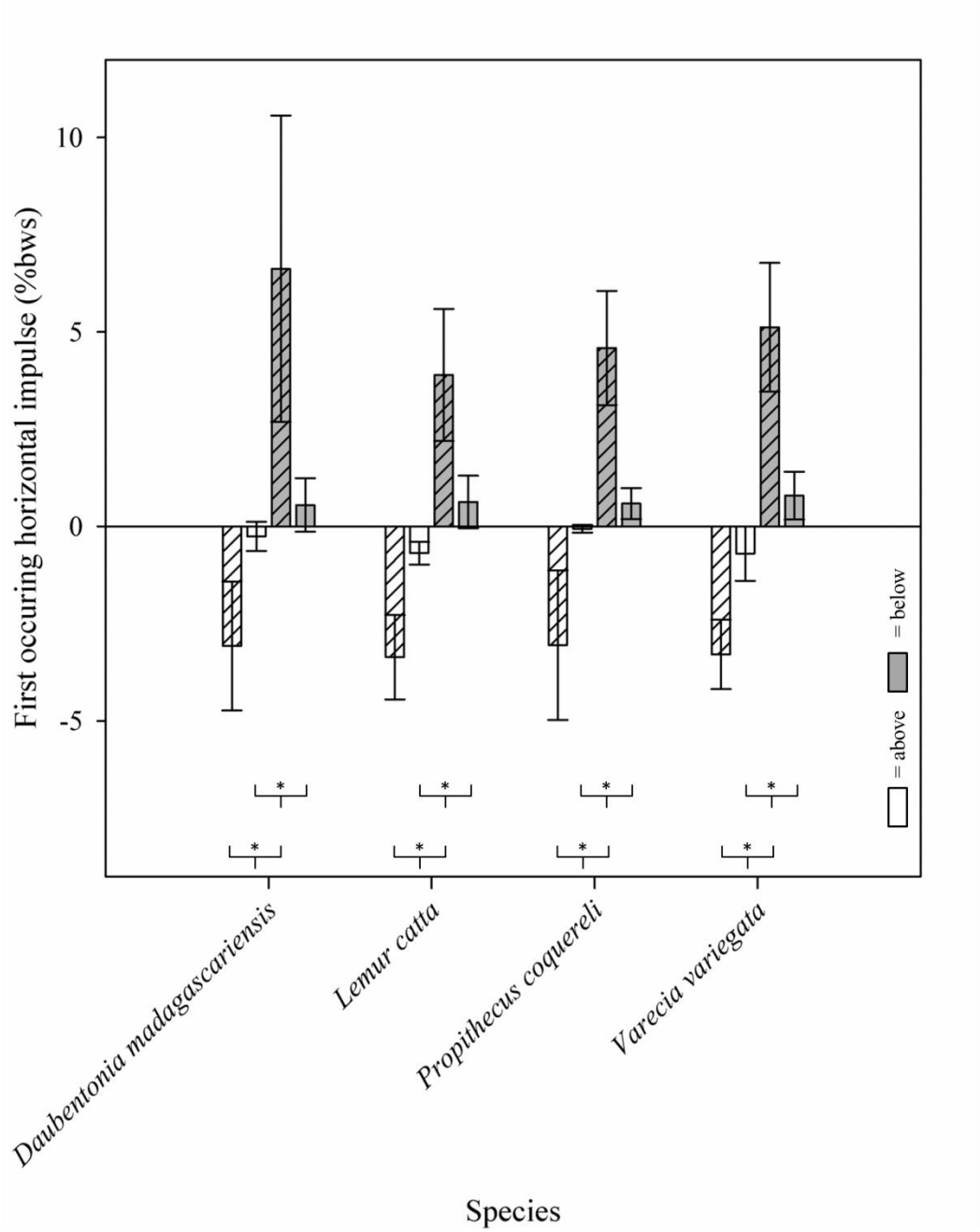

Figure 12: Mean and standard deviation values of the first horizontal impulse in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at *P* < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

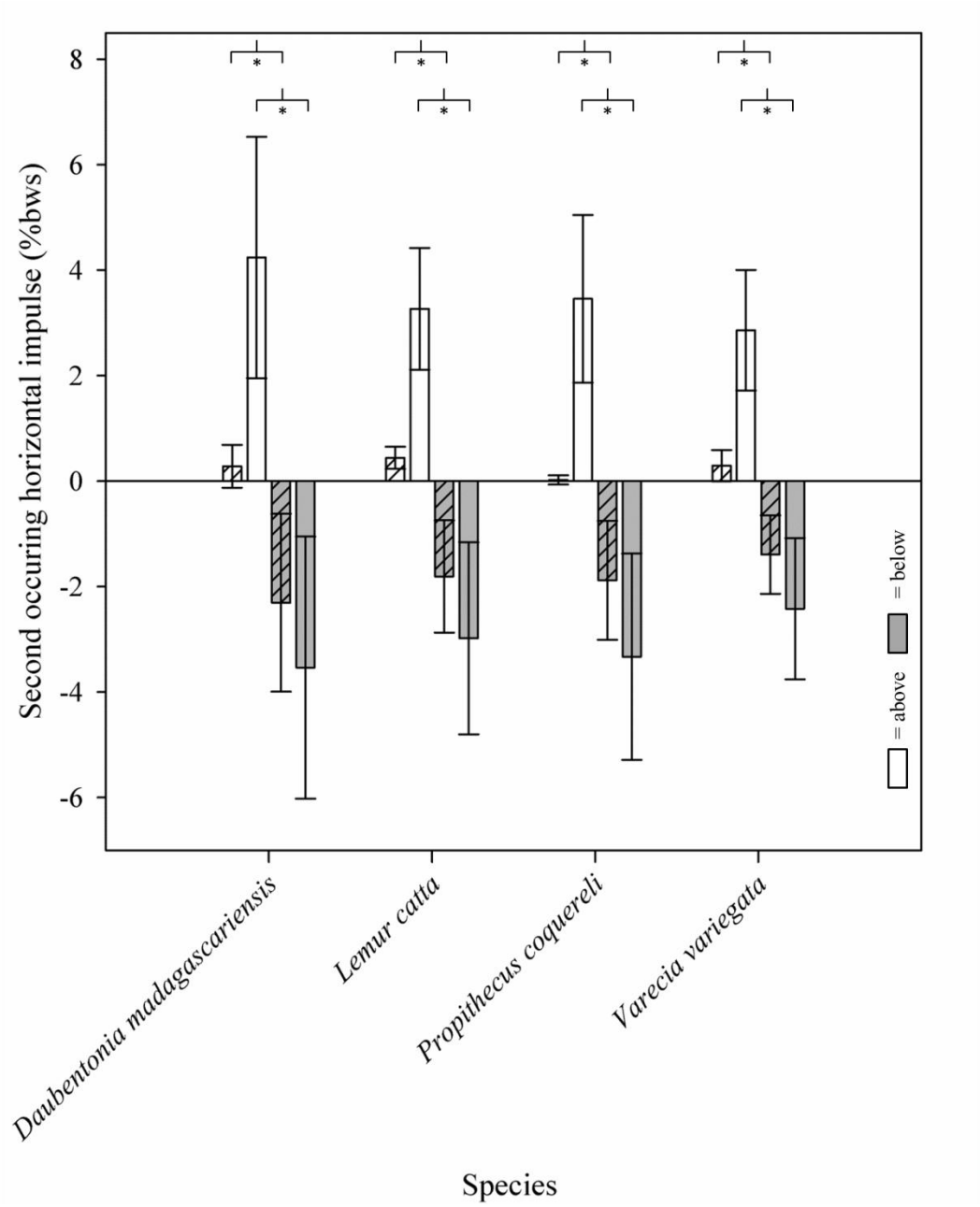

Figure 13: Mean and standard deviation values of the second horizontal impulse in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at *P* < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

Across all species and both orientations mediolateral forces were highly variable, and were dominated by medially directed forces. This means that the animal is applying a medial force to the substrate during support phase. These forces were generally low in comparison to vertical and horizontal forces. In general, Mpk, Lpk, MI, LI, MLI were greater during below branch quadrupedal locomotion compared to above branch quadrupedal locomotion. Although some significant differences were identified in the timing associated with the Lpk and Mpk between above and below branch quadrupedal locomotion, the patterns were inconsistent across species (Figures 14-18).

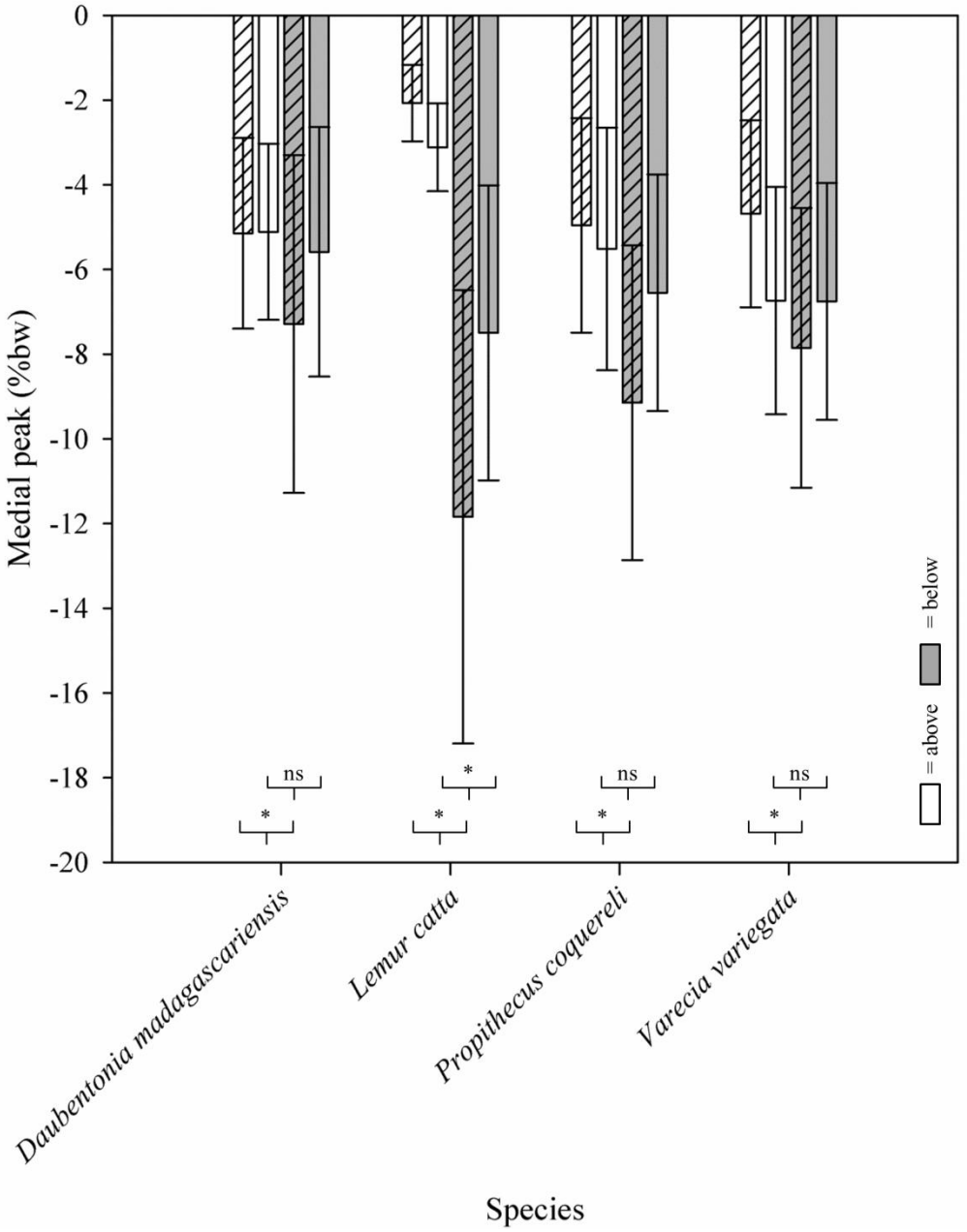

Figure 14: Mean and standard deviation values of the medial peak in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at $P < 0.05$. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

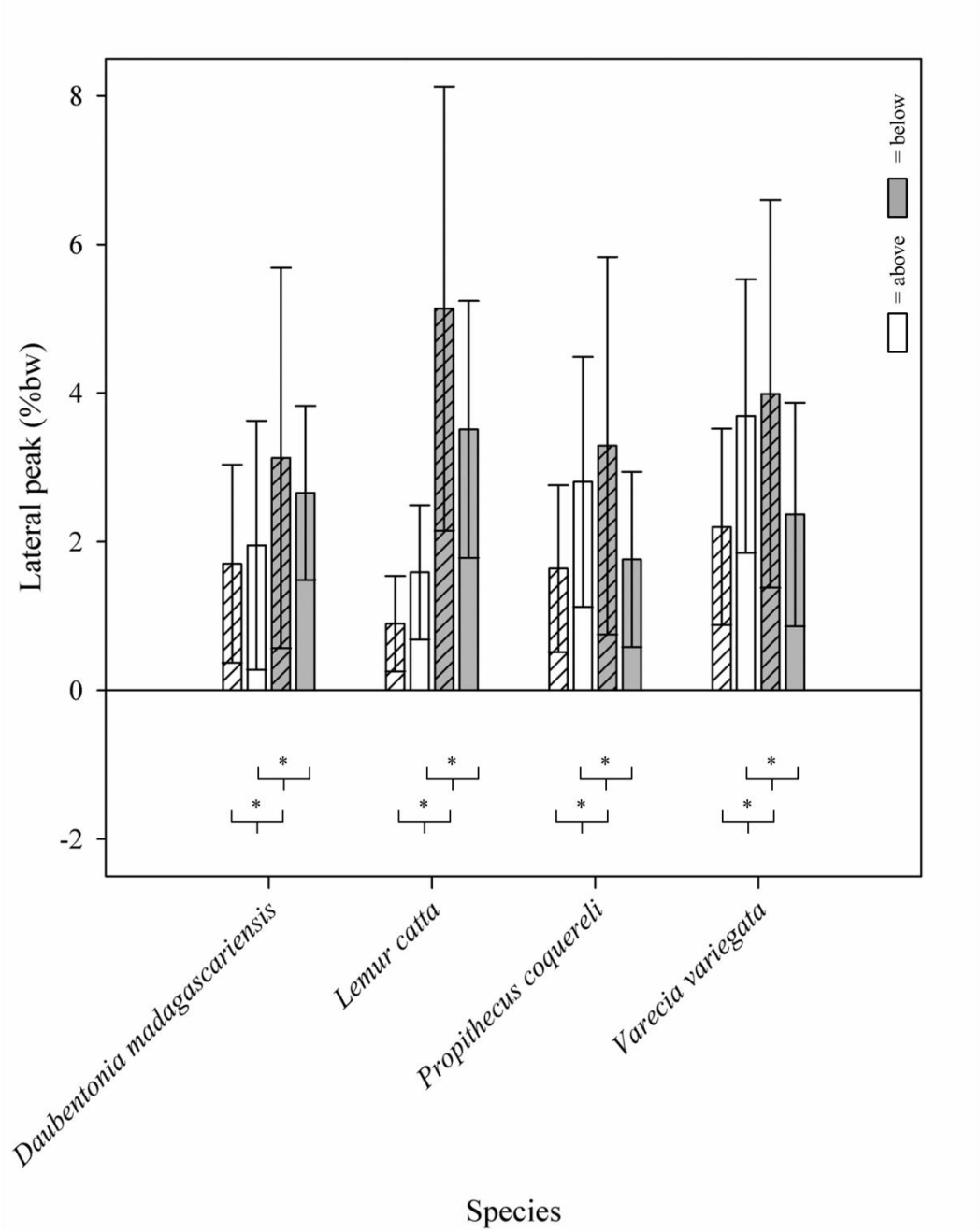

Figure 15: Mean and standard deviation values of the lateral peak in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at *P* < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

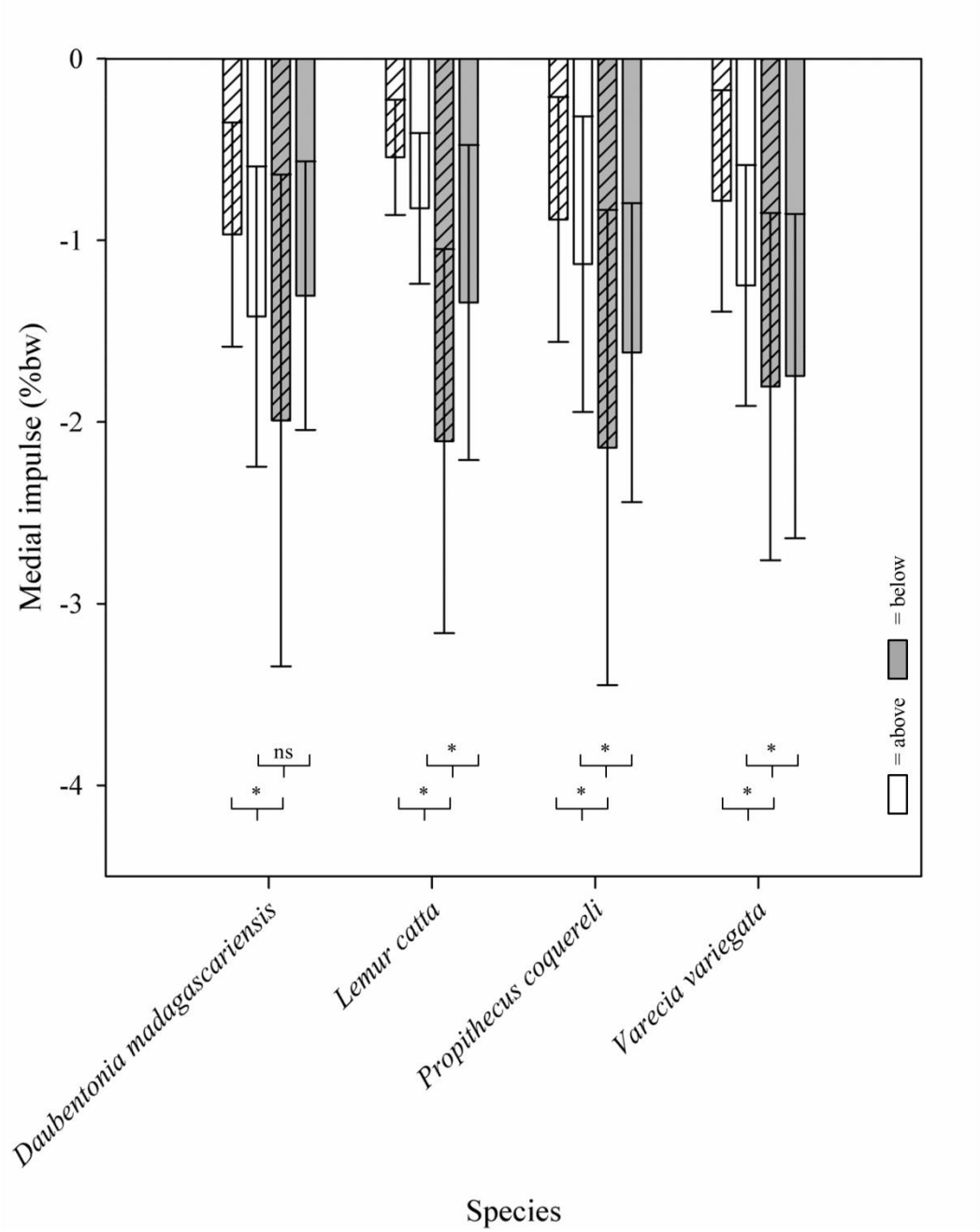

Figure 16: Mean and standard deviation values of the medial impulse in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at P < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

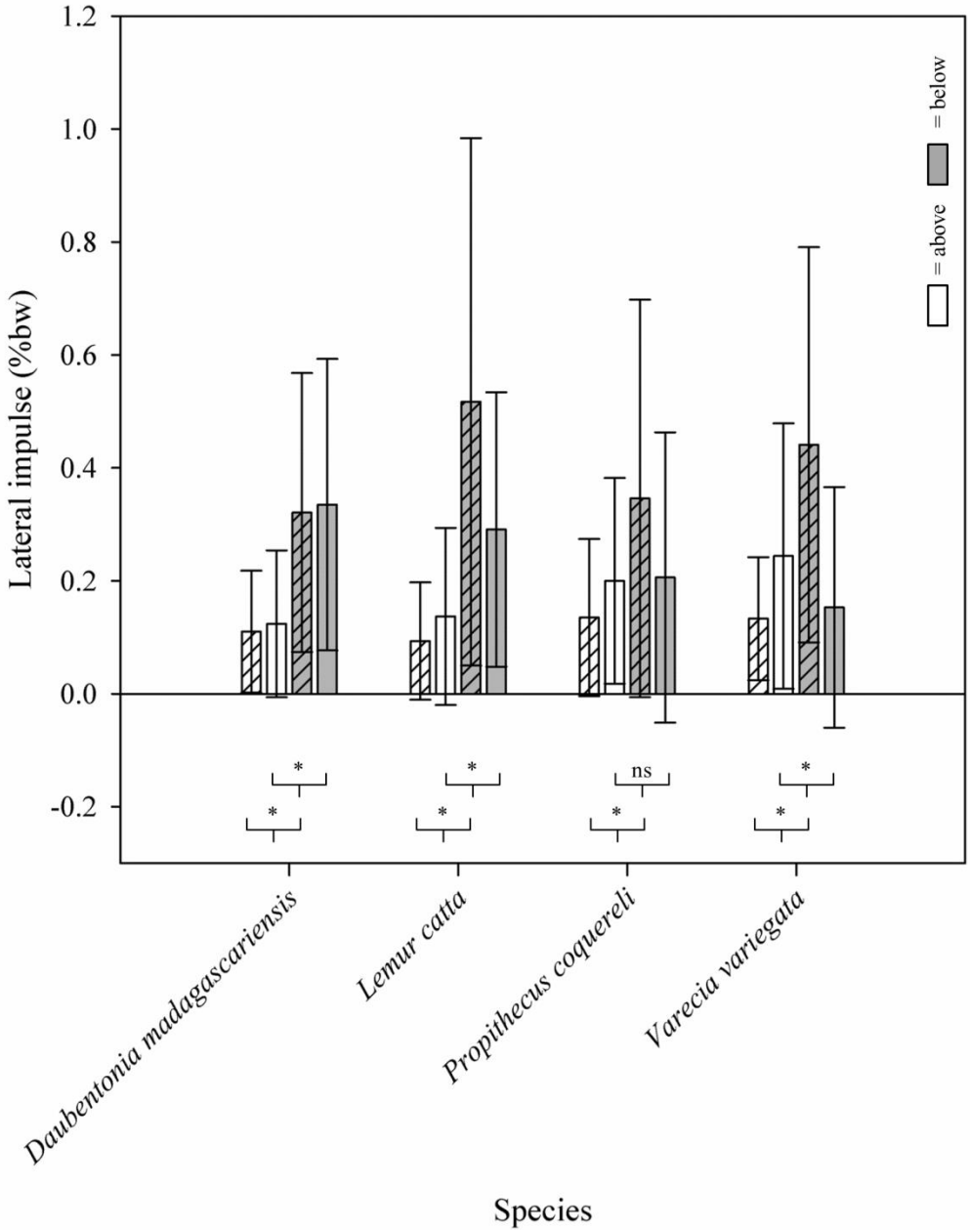

Figure 17: Mean and standard deviation values of the lateral impulse in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at *P* < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

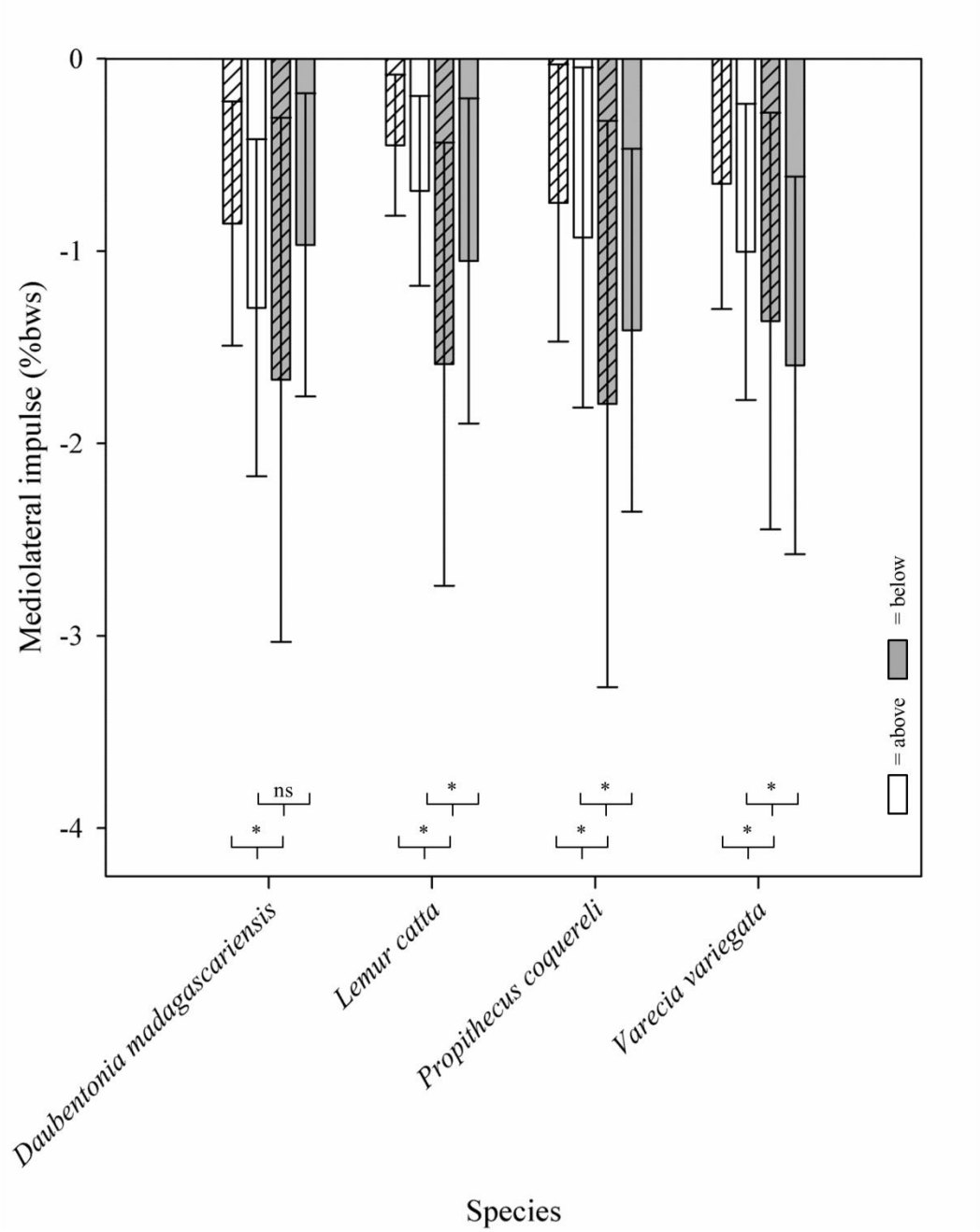

Figure 18: Mean and standard deviation values of the mediolateral impulse in the forelimbs and hindlimbs in four species of primates. All data presented as a percentage of body weight (%bw). Statistical comparisons are presented as brackets. The presence of an asterisk (*) represents significance at *P* < 0.05. The presence of an "ns" represents that no significant difference was observed. Hashed data bars indicate forces collected from the forelimbs, while solid data bars indicate forces collected from the hindlimbs.

As discussed in section 1.5.2, and confirmed in this study, patterns of HI changed significantly during above and below branch quadrupedal locomotion. During above branch quadrupedal locomotion the forelimb served a net braking role, while the hindlimb was net propulsive. The functional roles of the limbs were opposite during below branch quadrupedal locomotion (Figure 9). To understand the mechanism underlying this switch, this study tested the assumption that levels of protraction and retraction determine whether a limb serves a braking or propulsive role; as is the case during bipedal walking (Kimura et al., 1977; Inman et al., 1981) and outlined by Reynolds (1985b). With respect to the hypothesis that the B/P occurs at mid-stance, significant differences ($P < 0.001$) were observed between these two events in all species, both limbs, and both orientations. In all species and for both orientations, the B/P transition always occurred after mid-stance in the forelimb, and before mid-stance in the hindlimb (Table 4). With regard to the hypothesis that the proportion of protraction to retraction within a step determines whether the limb is braking or propulsive, no significant association was observed between these two variables in any of the species, limbs, or orientations (Figures 19 and 20).

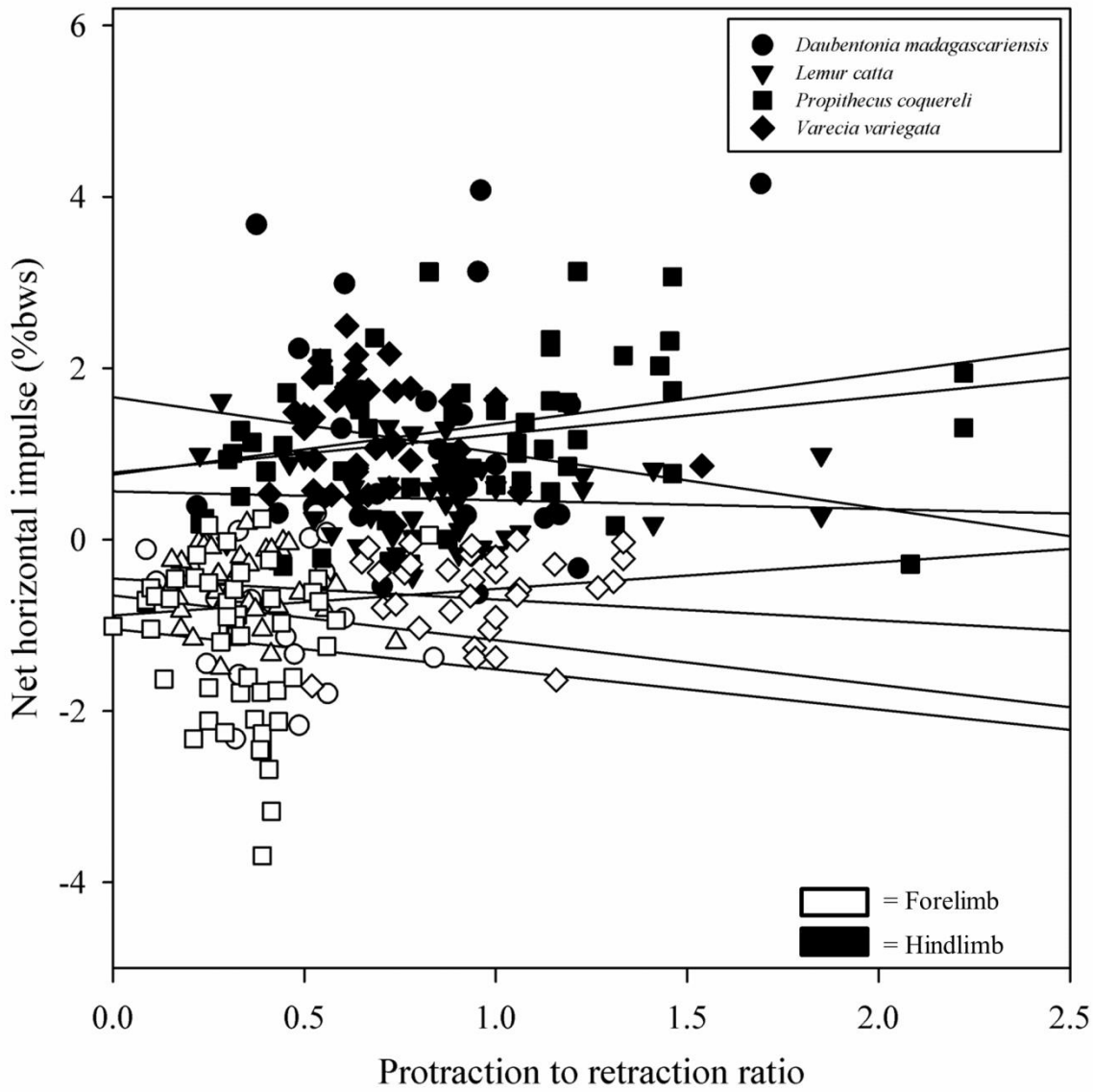

Figure 19: The relationship between protraction to retraction ratio and net horizontal impulse during above branch quadrupedal locomotion in four primate species. Protraction to retraction ratio was calculated as the proportion of the stride a limb was spent in protraction divided by the proportion of the stride spent in retraction. Smaller numbers represent greater retraction while larger numbers represent greater protraction. All data for net horizontal impulse presented as a percentage of body weight (%bw).

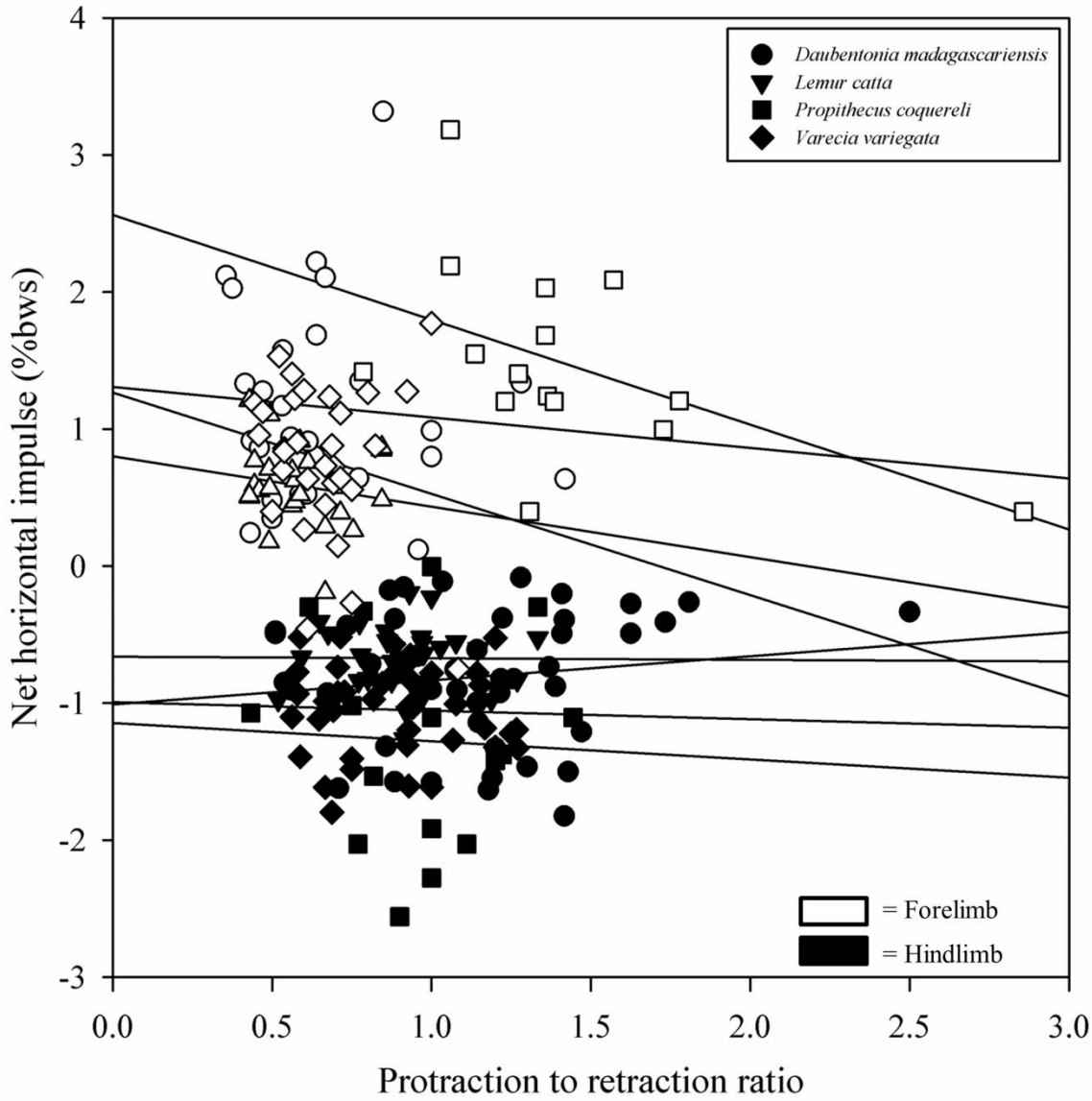

Figure 20: The relationship between protraction to retraction ratio and net horizontal impulse during below branch quadrupedal locomotion in four primate species. Protraction to retraction ratio was calculated as the proportion of the stride a limb was spent in protraction divided by the proportion of the stride spent in retraction. Smaller numbers represent greater retraction while larger numbers represent greater protraction. All data for net horizontal impulse presented as a percentage of body weight (%bw).

3.1.2 Kinematics

In total, 255 strides were used for kinematic analysis. Table 5 summarizes the number of strides collected per limb for each orientation, intraspecific statistical comparisons, and data for touchdown angle, mid-support angle, end of support phase angle, and joint excursion. Overall, kinematic movements of the all measured joints, and the overall excursion observed at those joints, tended to vary significantly from each other during above and below branch locomotion in the sample primate species, although there were exceptions.

Table 5: Mean and standard deviation values for kinematic gait variables collected during above and below branch quadrupedal locomotion in five species of primates.

Species	Joint	Orientation	N	Touchdown angle (°)	Mid-support angle (°)	End of support phase angle (°)	Joint excursion (°)
Cebus capucinus	Shoulder	Above	9	24.49 ± 8.91	-23.80 ± 4.00	-45.22 ± 5.32	71.32 ± 12.35
		Below	6	-3.27 ± 5.92	-56.75 ± 12.33	-70.38 ± 5.35	80.39 ± 4.25
				*	*	*	ns
	Elbow	Above	9	133.22 ± 2.95	114.83 ± 3.99	137.89 ± 7.04	29.88 ± 5.66
		Below	6	128.54 ± 9.70	104.67 ± 10.23	132.84 ± 7.43	41.51 ± 7.78
				ns	Ns	ns	*
	Wrist	Above	9	177.67 ± 5.33	200.58 ± 5.19	198.39 ± 10.92	43.16 ± 9.67
		Below	6	171.97 ± 7.26	185.59 ± 5.11	178.33 ± 7.03	29.89 ± 5.61
				ns	*	*	*
	Hip	Above	9	41.65 ± 1.67	25.30 ± 6.56	-8.06 ± 3.83	50.71 ± 2.71
		Below	6	54.07 ± 4.83	31.25 ± 3.46	-12.41 ± 3.98	67.69 ± 4.31
				ns	Ns	ns	*
	Knee	Above	9	136.64 ± 8.40	109.12 ± 5.36	116.27 ± 5.74	32.92 ± 6.67
		Below	6	107.91 ± 8.84	90.12 ± 6.17	121.51 ± 4.23	35.00 ± 10.33
				*	*	*	ns
	Ankle	Above	9	228.82 ± 6.43	263.71 ± 4.59	252.18 ± 5.57	38.31 ± 8.24
		Below	6	236.67 ± 5.75	254.86 ± 6.57	240.21 ± 11.43	27.59 ± 5.91
				*	*	ns	*
Daubentonia madagascariensis	Shoulder	Above	30	18.75 ± 11.48	-39.23 ± 4.74	-64.42 ± 5.83	83.26 ± 15.70
		Below	30	4.35 ± 10.23	-48.37 ± 10.25	-80.04 ± 9.42	85.57 ± 11.17
				*	*	*	ns
	Elbow	Above	30	137.29 ± 12.44	101.75 ± 5.05	126.68 ± 5.77	38.60 ± 8.59
		Below	30	121.86 ± 17.90	102.06 ± 13.94	119.76 ± 10.37	32.25 ± 13.54
				*	Ns	*	ns
	Wrist	Above	30	190.92 ± 4.40	208.28 ± 10.61	218.80 ± 10.38	54.45 ± 9.90
		Below	30	175.11 ± 13.17	192.43 ± 11.08	206.07 ± 11.53	36.23 ± 11.30
				n/a	n/a	n/a	n/a
	Hip	Above	30	50.12 ± 4.86	19.83 ± 8.50	-23.48 ± 7.34	74.35 ± 6.25
		Below	30	60.04 ± 8.84	27.92 ± 11.17	-28.68 ± 7.78	90.04 ± 11.10
				*	*	*	*

	Knee	Above	30	123.51 ± 8.18	120.36 ± 8.49	142.39 ± 8.63	34.66 ± 8.15
		Below	30	90.88 ± 11.19	92.43 ± 10.68	137.33 ± 9.26	55.34 ± 10.96
				*	*	*	*
	Ankle	Above	30	239.07 ± 8.39	263.24 ± 4.63	244.02 ± 9.31	33.22 ± 8.42
		Below	30	237.42 ± 9.38	241.93 ± 5.15	238.00 ± 7.06	15.90 ± 6.31
				ns	*	*	*
Lemur catta	Shoulder	Above	30	22.94 ± 9.40	-14.06 ± 10.56	-44.93 ± 7.83	67.91 ± 6.08
		Below	30	1.36 ± 15.99	-48.41 ± 15.73	-77.98 ± 5.54	80.59 ± 18.32
				*	*	*	*
	Elbow	Above	30	158.46 ± 8.29	144.55 ± 8.26	158.15 ± 8.38	19.94 ± 4.38
		Below	30	122.89 ± 16.39	112.82 ± 12.81	126.12 ± 8.27	27.45 ± 15.20
				*	*	*	*
	Wrist	Above	30	195.65 ± 8.44	219.96 ± 11.05	241.27 ± 9.31	49.96 ± 8.73
		Below	30	172.35 ± 11.08	192.72 ± 7.62	190.63 ± 6.57	30.61 ± 11.35
				n/a	n/a	n/a	n/a
	Hip	Above	30	56.82 ± 5.32	32.89 ± 6.27	-8.39 ± 5.83	65.40 ± 8.07
		Below	30	51.49 ± 7.13	25.59 ± 8.55	-6.32 ± 12.43	58.07 ± 9.71
				*	*	ns	*
	Knee	Above	30	121.45 ± 6.72	105.29 ± 5.54	124.65 ± 6.81	25.19 ± 6.10
		Below	30	83.84 ± 9.96	87.64 ± 12.41	117.96 ± 18.42	40.53 ± 16.19
				*	*	ns	*
	Ankle	Above	30	230.27 ± 10.14	253.36 ± 7.33	243.57 ± 4.57	28.43 ± 9.87
		Below	30	261.82 ± 7.85	263.38 ± 6.82	239.85 ± 10.90	27.96 ± 7.70
				*	*	ns	Ns
Propithecus coquereli	Shoulder	Above	30	18.99 ± 6.68	-15.72 ± 7.69	-39.36 ± 8.64	58.37 ± 9.66
		Below	30	-18.57 ± 13.16	-65.91 ± 10.87	-85.34 ± 5.65	68.96 ± 11.86
				*	*	*	*
	Elbow	Above	30	155.02 ± 7.89	132.86 ± 12.63	141.99 ± 10.99	25.97 ± 11.47
		Below	30	95.84 ± 15.03	90.35 ± 11.10	107.00 ± 11.87	23.24 ± 10.26
				*	*	*	Ns
	Wrist	Above	30	173.78 ± 6.06	185.73 ± 7.00	205.58 ± 6.93	37.66 ± 6.86
		Below	30	160.79 ± 7.11	184.57 ± 6.22	194.35 ± 7.17	37.57 ± 8.17
				*	Ns	*	Ns
	Hip	Above	30	70.82 ± 8.75	45.26 ± 7.04	9.08 ± 7.19	62.18 ± 8.31
		Below	3	48.45 ± 6.52	16.76 ± 8.05	-15.30 ±	64.32 ±

			0			11.97	15.36
				*	*	*	ns
	Knee	Above	30	98.58 ±5.88	90.18 ± 9.45	105.46 ± 9.33	22.76 ± 6.75
		Below	30	68.82 ± 5.99	79.10 ± 8.36	115.78 ± 15.41	51.87 ± 17.77
				*	*	*	*
	Ankle	Above	30	244.29 ± 10.79	268.49 ± 12.22	260.53 ± 12.33	30.21 ± 6.93
		Below	30	272.60 ± 6.59	271.54 ± 7.61	238.39 ± 11.86	41.50 ±14.55
				*	Ns	*	*
Varecia variegata	Shoulder	Above	30	19.56 ± 12.25	-24.04 ± 5.45	-46.72 ± 9.11	68.93 ± 16.72
		Below	30	4.82 ± 18.29	-53.78 ± 14.08	-67.78 ± 10.11	87.00 ± 15.62
				*	*	*	*
	Elbow	Above	30	147.04 ± 9.62	128.93 ± 8.15	153.85 ± 15.78	39.07 ± 10.56
		Below	30	127.94 ± 18.97	104.26 ± 12.59	134.15 ± 11.72	48.84 ± 14.13
				*	*	*	*
	Wrist	Above	30	177.84 ± 12.87	200.15 ± 8.20	198.77 ± 17.39	51.91 ± 15.07
		Below	30	169.45 ± 12.68	183.73 ± 12.39	176.85 ± 9.01	36.88 ± 14.04
				*	*	*	*
	Hip	Above	30	43.09 ± 5.28	25.99 ± 7.88	-7.44 ± 6.61	51.81 ± 5.76
		Below	30	57.92 ± 6.48	34.78 ± 7.11	-8.22 ± 5.74	67.95 ± 8.04
				*	*	ns	*
	Knee	Above	30	139.95 ± 10.49	110.97 ± 9.35	119.22 ± 10.97	33.26 ± 8.98
		Below	30	109.47 ± 13.65	94.48 ± 13.36	124.08 ± 8.00	35.38 ± 11.92
				*	*	ns	ns
	Ankle	Above	30	229.01 ± 10.28	262.33 ± 6.43	249.50 ± 8.35	36.95 ± 9.09
		Below	30	228.74 ± 20.26	245.85 ± 19.03	233.37 ± 17.65	30.01 ± 10.48
				ns	*	*	*

[*] Significant difference observed ($P \leq 0.05$)
[ns] No significant difference observed ($P > 0.05$)

At the shoulder joint, all species showed relatively high degrees of humeral protraction at touchdown during above branch quadrupedal locomotion. Throughout the remainder of support phase the humerus was subsequently retracted past the neutral position. This movement resulted in a relatively high amount of joint excursion at the shoulder. In comparison, humeral protraction at touchdown was quite low during below branch quadrupedal locomotion, but the overall level of retraction was significantly greater by the end of support phase (Figure 21). In all species, levels of joint excursion tended to be greater during below branch quadrupedal locomotion, but significant differences were only observed in three of the sample species (Figure 22).

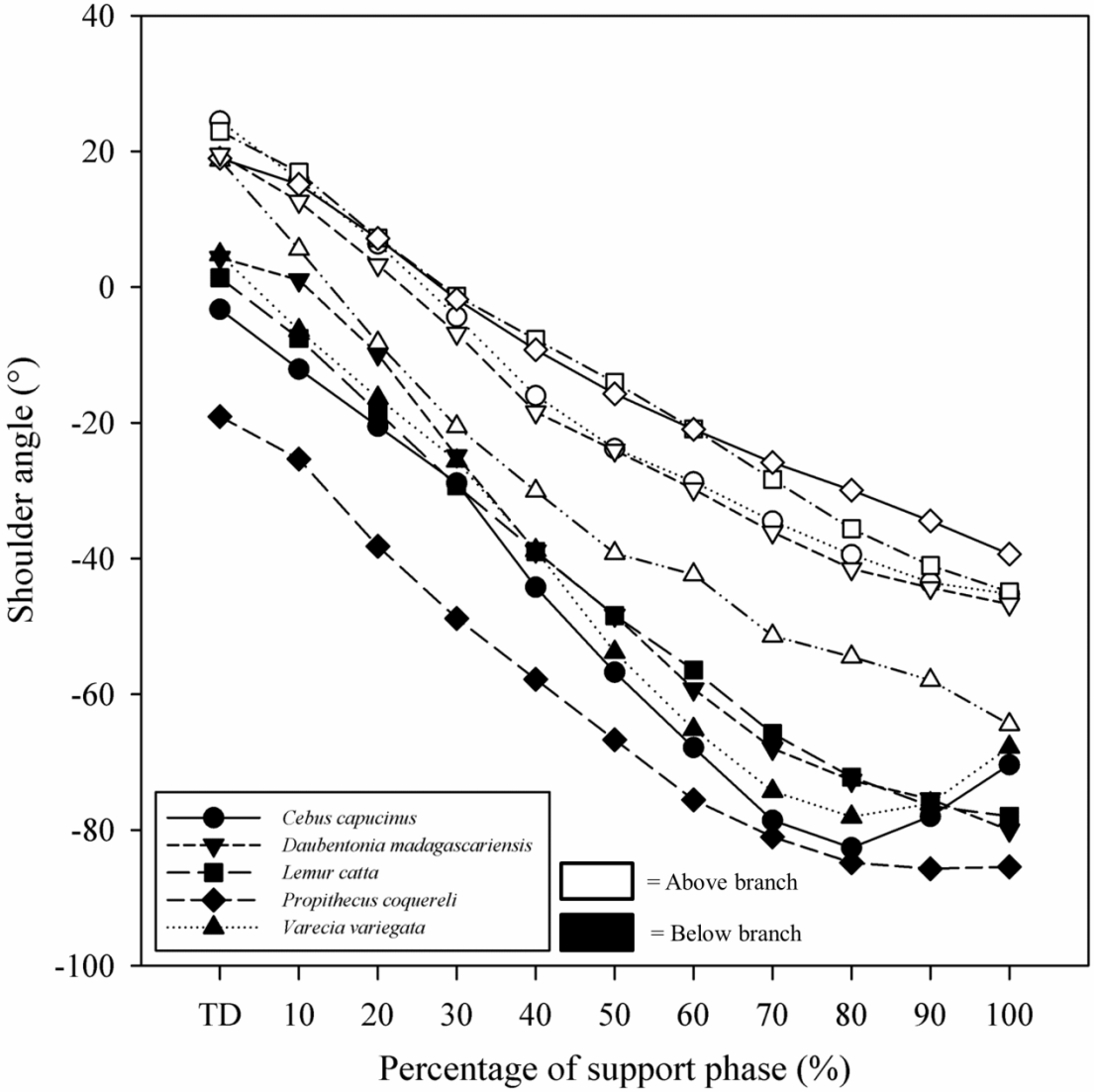

Figure 21: Patterns of mean shoulder movement (°) observed during above and below branch quadrupedal locomotion in five species of primates.

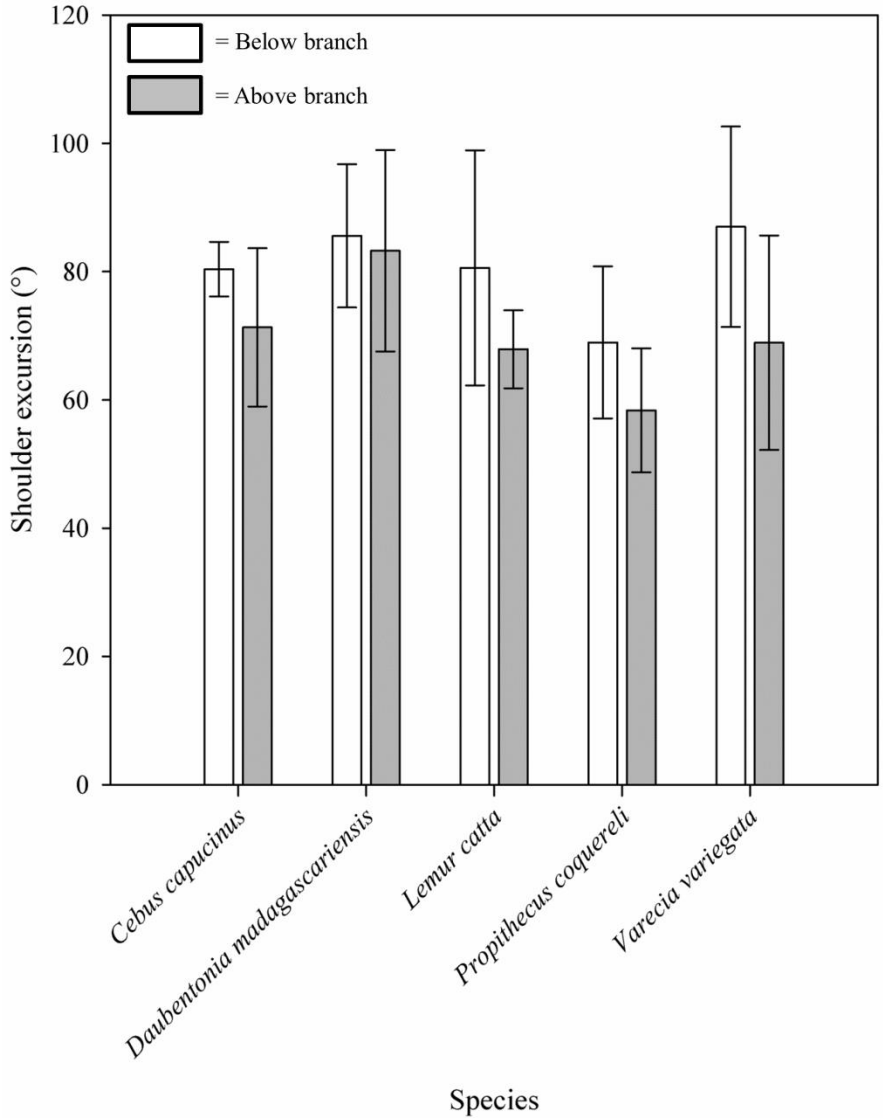

Figure 22: Mean and standard deviation values of shoulder excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates.

Patterns of elbow movement also tended to vary significantly during above and below branch quadrupedal locomotion in the sample primate species. In general, during above branch quadrupedal locomotion the elbow began support phase in a relatively extended (the level of extension was quite variable between primate species) position, and subsequently yielded until approximately mid-support. After mid-support, the elbow then began to re-extend until the end support phase. *Cebus capucinus* and *V. variegata* both maintained greater levels of elbow flexion throughout support phase compared to other species (Figure 23).

During below branch quadrupedal locomotion the elbow demonstrated an overall similar pattern of movement compared to what is observed during above branch quadrupedal locomotion with the exception that the elbow remains in a relatively more flexed position throughout support phase. For *C. capucinus*, *V. variegata,* and *L. catta*, elbow excursion was significantly greater during below branch quadrupedal locomotion compared to above branch quadrupedal locomotion. In contrast, *Daubentonia madagascariensis* and *Propithecus coquereli* both demonstrated greater joint excursion during above branch quadrupedal locomotion, although the difference was only significant for *D. madagascariensis* (Figure 24).

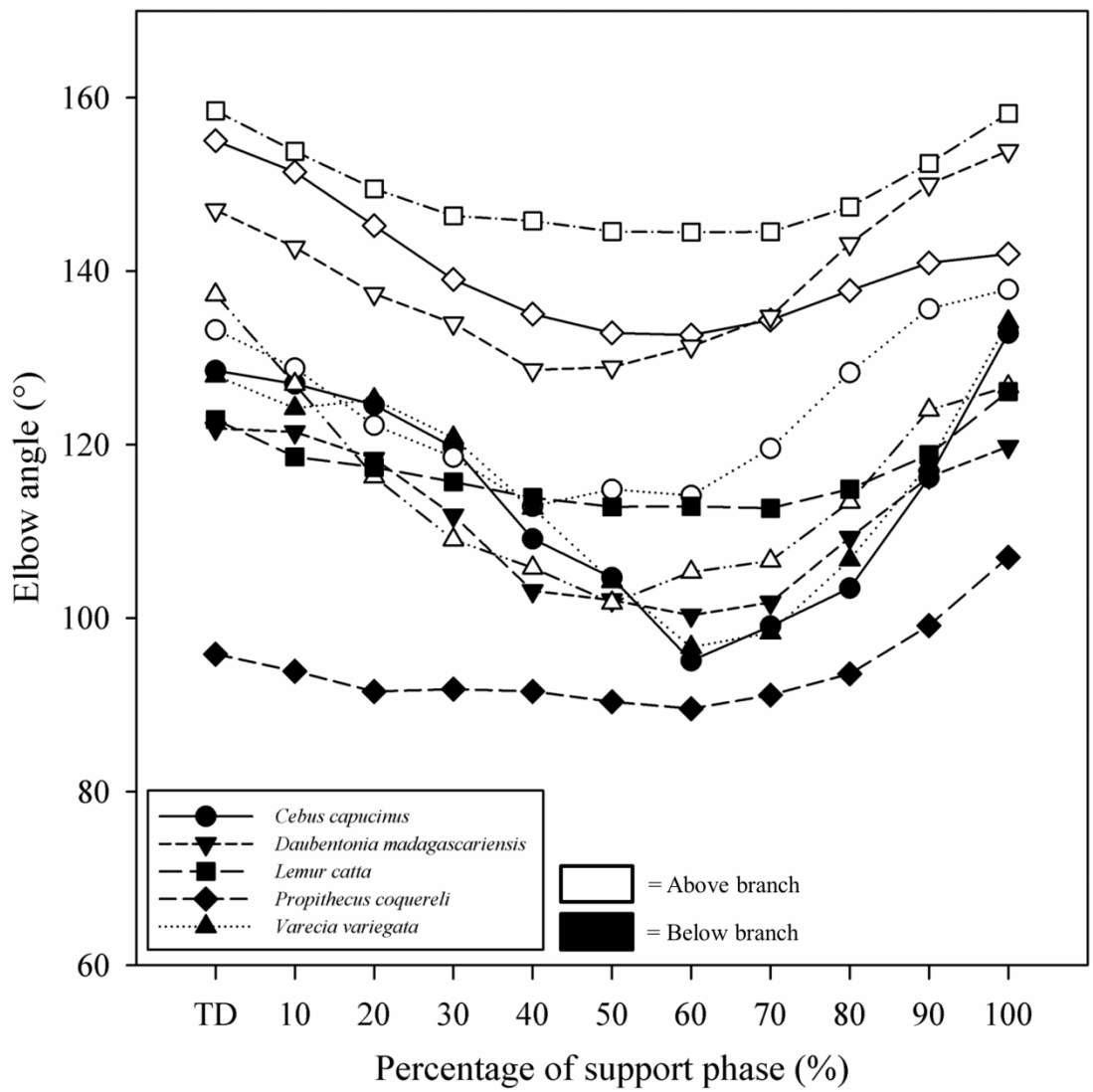

Figure 23: Patterns of mean elbow movement (°) observed during above and below branch quadrupedal locomotion in five species of primates.

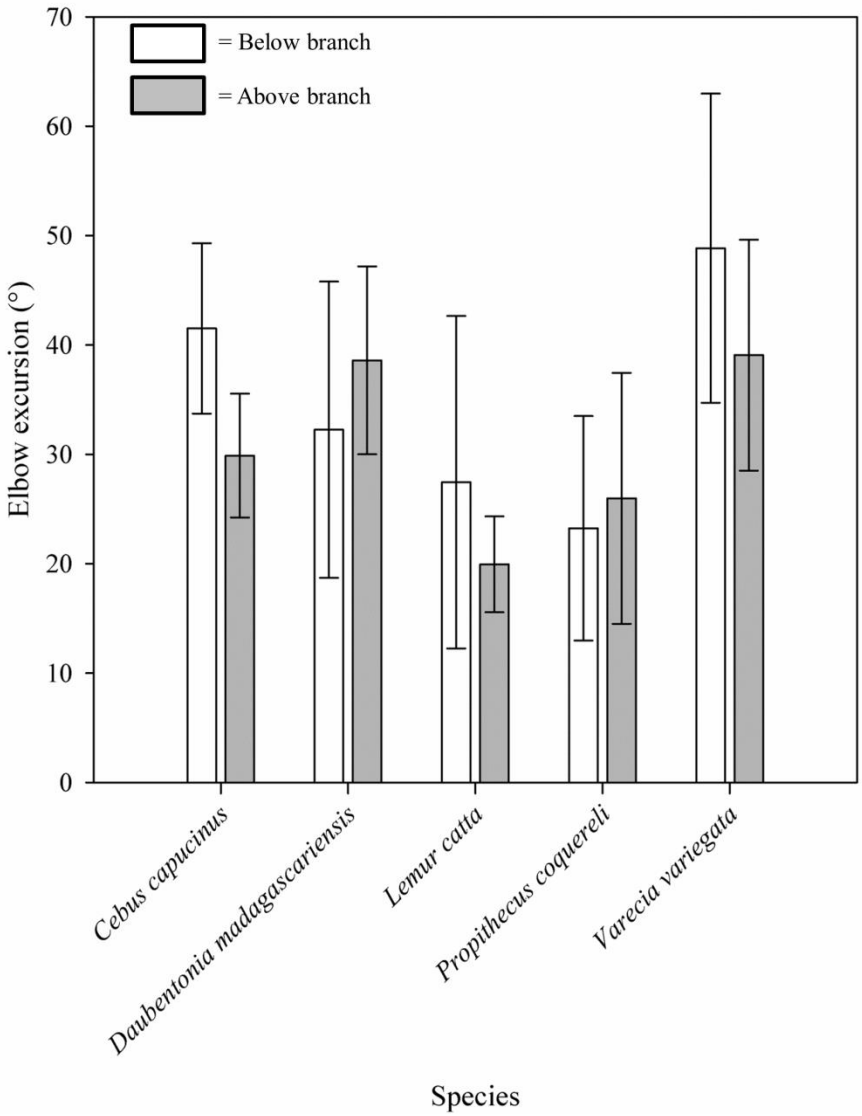

Figure 24: Mean and standard deviation values of elbow excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates.

Movements of the wrist were highly variable within strides and between orientations (Table 5), but the overall patterns of movement were largely similar within grasp types. During above branch quadrupedal locomotion, two distinct grasp types were observed. *Lemur catta* and *D. madagascariensis* used flexion/extension grasps, while other species used supinated hook grasps. During flexion/extension grasps the wrist is in a slightly extended position at touchdown. Throughout the remainder of the support phase the wrist was hyper-extended until just prior to lift-off, which at that point the wrist acted to push-off the support, and therefore approached a slightly more neutral position (Figure 25). During supinated hook grasps, movements of the wrist are largely confined to ulnar and radial deviation. For animals that use this grasp type, the wrist was ulnarly deviated at touchdown, and then subsequently radially deviated throughout the remainder of support phase. Just prior to lift-off, the wrist ulnarly deviated once again and enters a slightly more neutral position.

During below branch quadrupedal locomotion all species used supinated hook grasps. The overall pattern of wrist movement was largely similar to what was observed during supinated hook grasps during above branch quadrupedal locomotion, with exception of relatively greater levels of ulnar deviation early in support phase and lower levels of radial deviation late in support phase (Figure 26). For all species, with the exception of *P. coquereli*, levels of wrist excursion were greater during above branch quadrupedal locomotion compared to below branch quadrupedal locomotion (Figure 27).

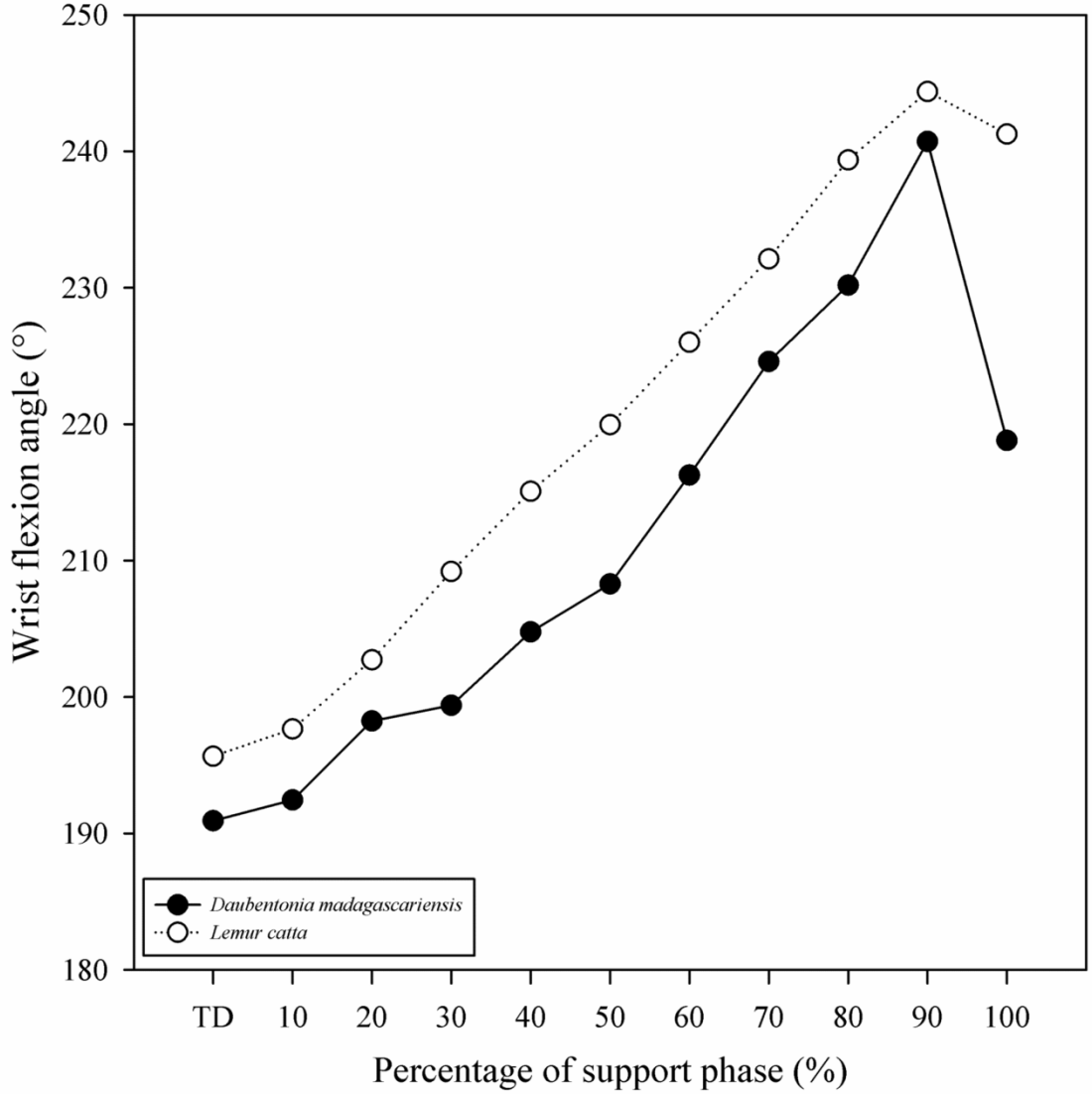

Figure 25: Patterns of mean wrist movement (°) observed in two species of primate that use flexion/extension grasps during above branch quadrupedal locomotion.

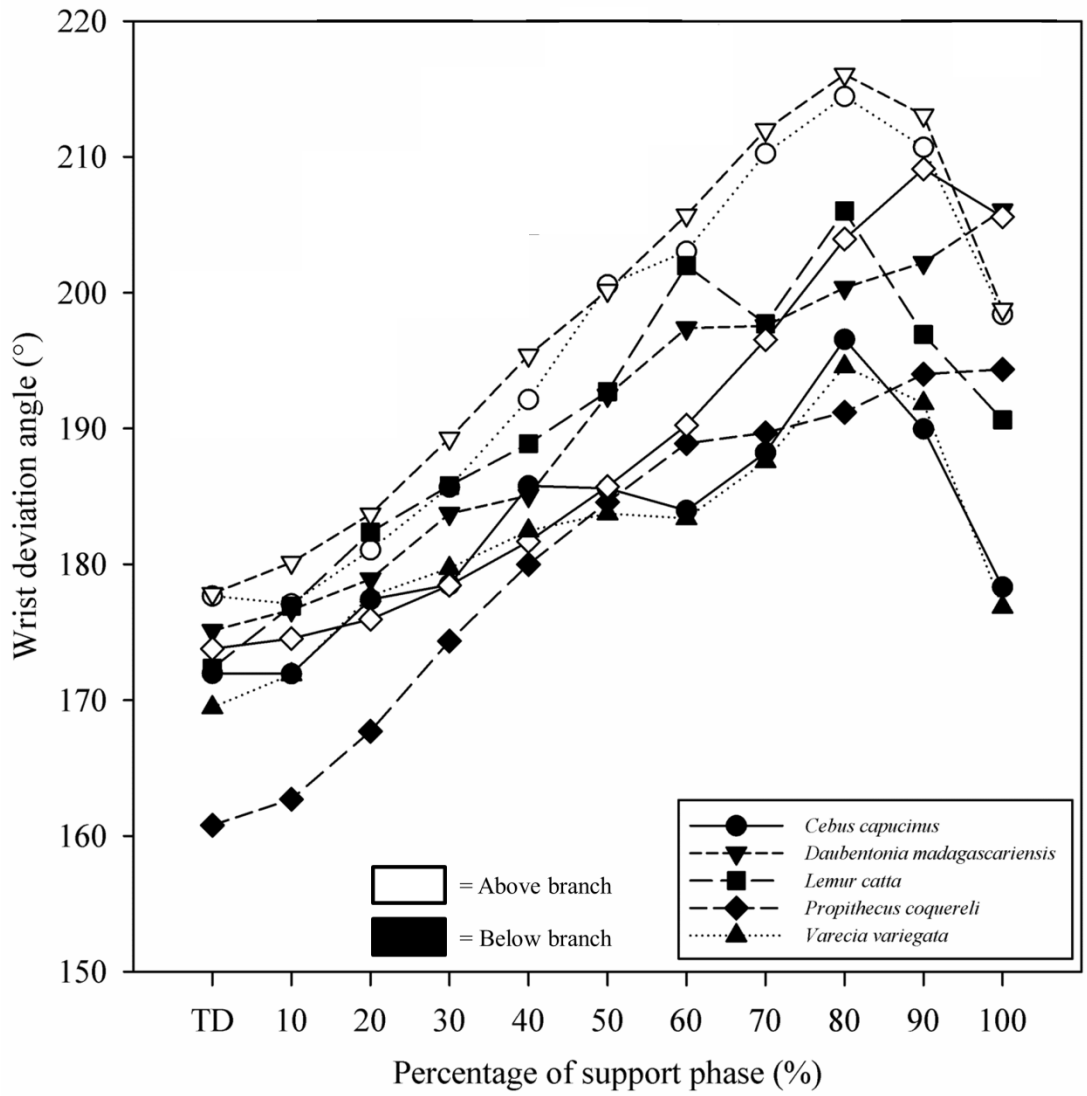

Figure 26: Patterns of mean wrist movement (°) observed in five species of primate that use supinated hook grasps during above and below branch quadrupedal locomotion.

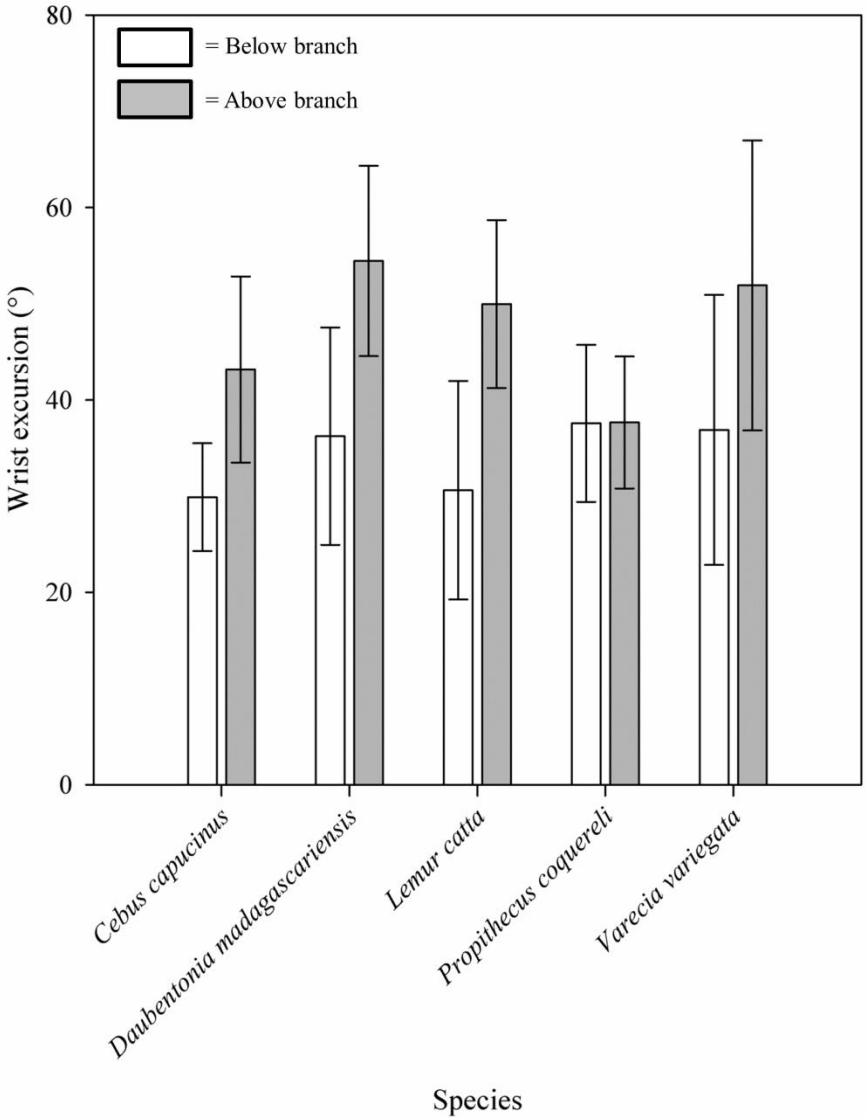

Figure 27: Mean and standard deviation values of wrist excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates.

The overall movement of the hip was largely similar during above and below branch quadrupedal locomotion. At touchdown, the femur was placed in a protracted position and then was subsequently retracted throughout the remainder of support phase. Femoral angle did not enter into a truly retracted position until relatively late in support phase. *Propithecus coquereli* showed the greatest levels of femoral protraction at touchdown, and femoral position rarely entered a truly retracted in most strides. This is likely due to the highly specialized hindlimb anatomy observed in this species.

A comparison of femoral protraction and retraction angles between above and below branch quadrupedal locomotion revealed relatively inconsistent patterns at touchdown, but for all species (with the exception of *L. catta*) femoral retraction was greater during below branch quadrupedal locomotion (Figure 28). This greater level of femoral retraction near the end of support phase tended to result (with the exception of *L. catta*) in greater limb excursion at the hip joint when animals moved below branches (Figure 29).

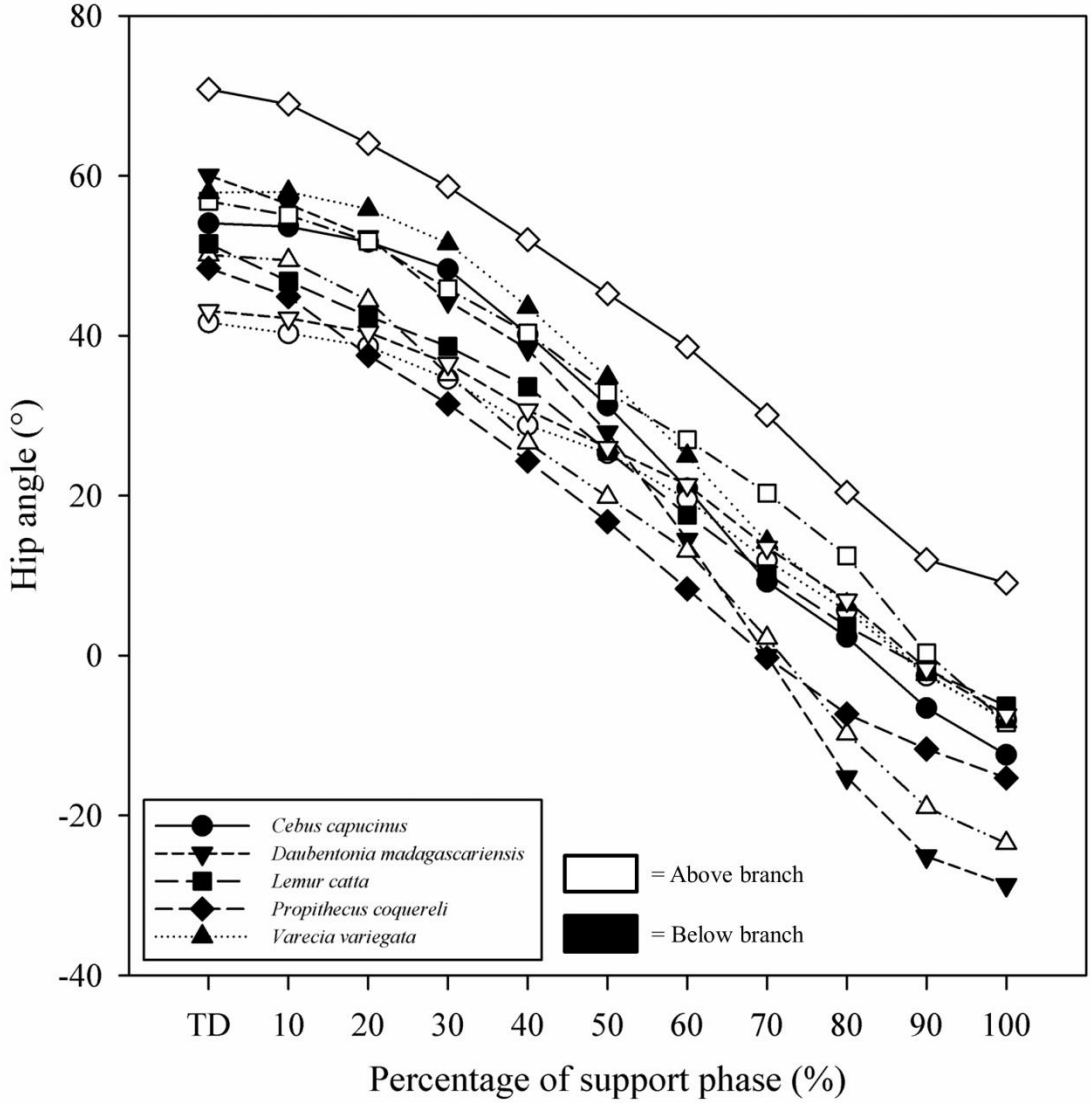

Figure 28: Patterns of mean hip movement (°) observed during above and below branch quadrupedal locomotion in five species of primates.

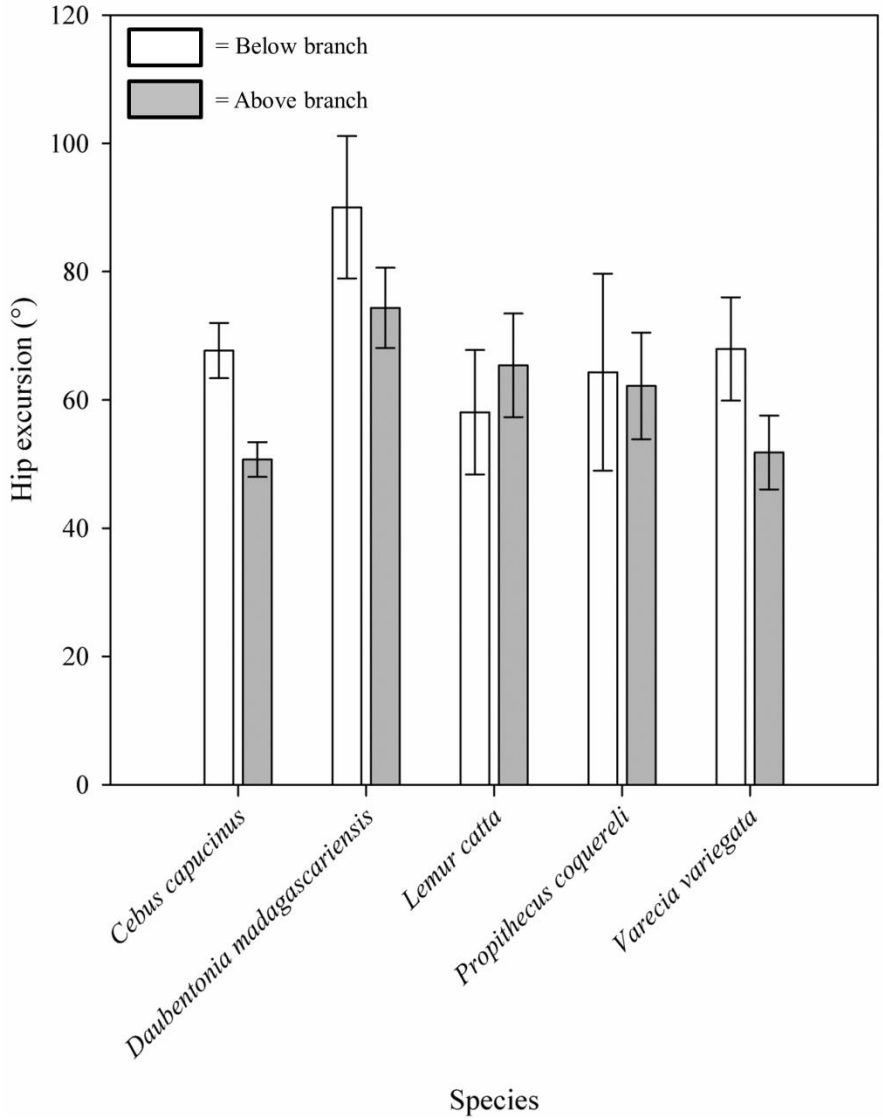

Figure 29: Mean and standard deviation values of hip excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates.

Kinematic patterns of knee movement were highly variable between above and below branch quadrupedal locomotion in all species. During above branch quadrupedal locomotion the knee tends to be relatively extended at touchdown (but see *P. coquereli*), and then flexed until approximately mid-support. After mid-support, the knee is re-extended throughout the remainder of support phase. A similar pattern of movement is observed during below branch quadrupedal locomotion, but as with the elbow, the knee maintains a greater level of flexion compared to above branch quadrupedal locomotion (Figure 30). Overall joint excursion at the knee is greater for all species during below branch quadrupedal locomotion, although significant differences in joint excursion are not observed between above and below branch quadrupedal locomotion in *C. capucinus* and *V. variegata* (Figure 31).

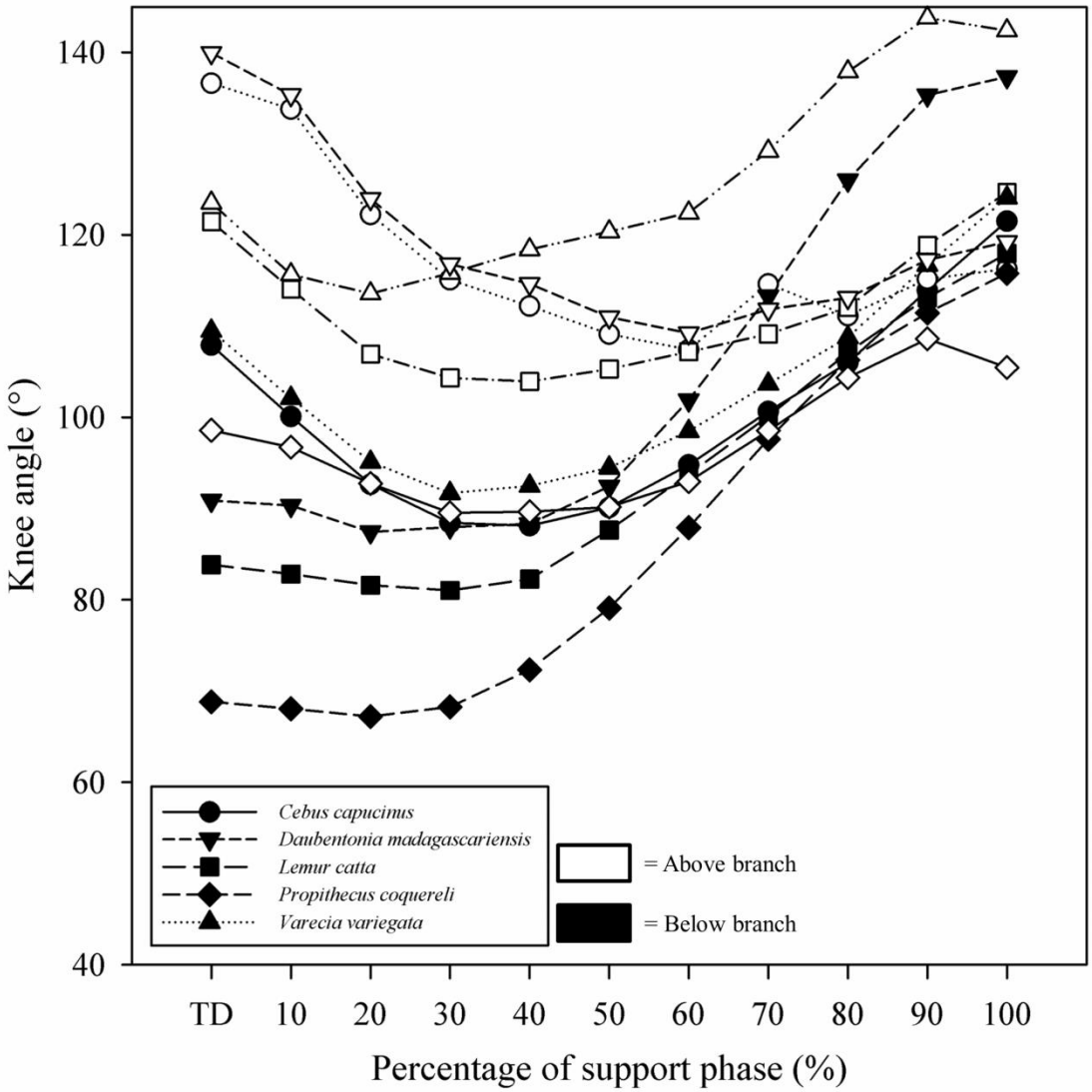

Figure 30: Patterns of mean knee movement (°) observed during above and below branch quadrupedal locomotion in five species of primates.

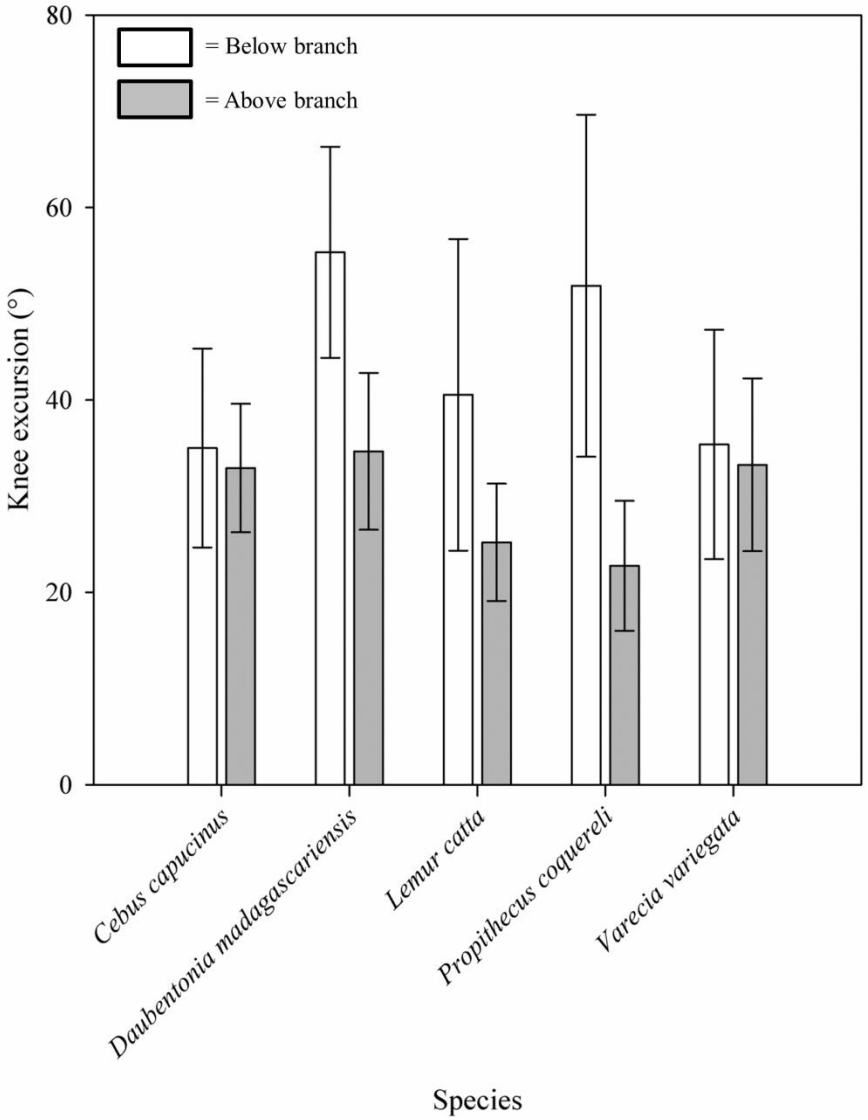

Figure 31: Mean and standard deviation values of knee excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates.

With respect to the ankle, during both above and below branch quadrupedal locomotion all species used hook grasp. This, as outlined in section 2.2.2, resulted in primarily cranially directed and caudally directed ankle movements. During above branch quadrupedal locomotion all species demonstrated a cranially oriented ankle position at touchdown. The ankle was then further cranially oriented until close to the end of the support phase, and at this point the ankle deviated to more neutral position. During below branch quadrupedal locomotion, ankle movements showed no characteristic pattern between all species, and instead two general patterns were observed. In *C. capucinus*, *V. variegata*, and *D. madagascariensis*, the movement of the ankle was largely similar to what was observed during above branch quadrupedal locomotion, with the exception that the ankle did not achieve the same level of cranial deviation. In *L. catta* and *P. coquereli* the ankle was placed in a highly cranially oriented position at touchdown, and throughout the remainder of support phase the ankle was deviated into a more neutral position. All species walking below branches demonstrated a similar craniocaudal ankle angle near the end of support phase (Figure 32). Patterns of ankle excursion were highly variable during above and below branch quadrupedal locomotion. In *C. capucinus*, *V. variegata*, and *D. madagascariensis* ankle excursion was relatively greater during below branch quadrupedal locomotion. In contrast, ankle excursion was relatively greater during above branch quadrupedal locomotion in *P. coquereli*. No differences in ankle excursion were observed in *L. catta* (Figure 33).

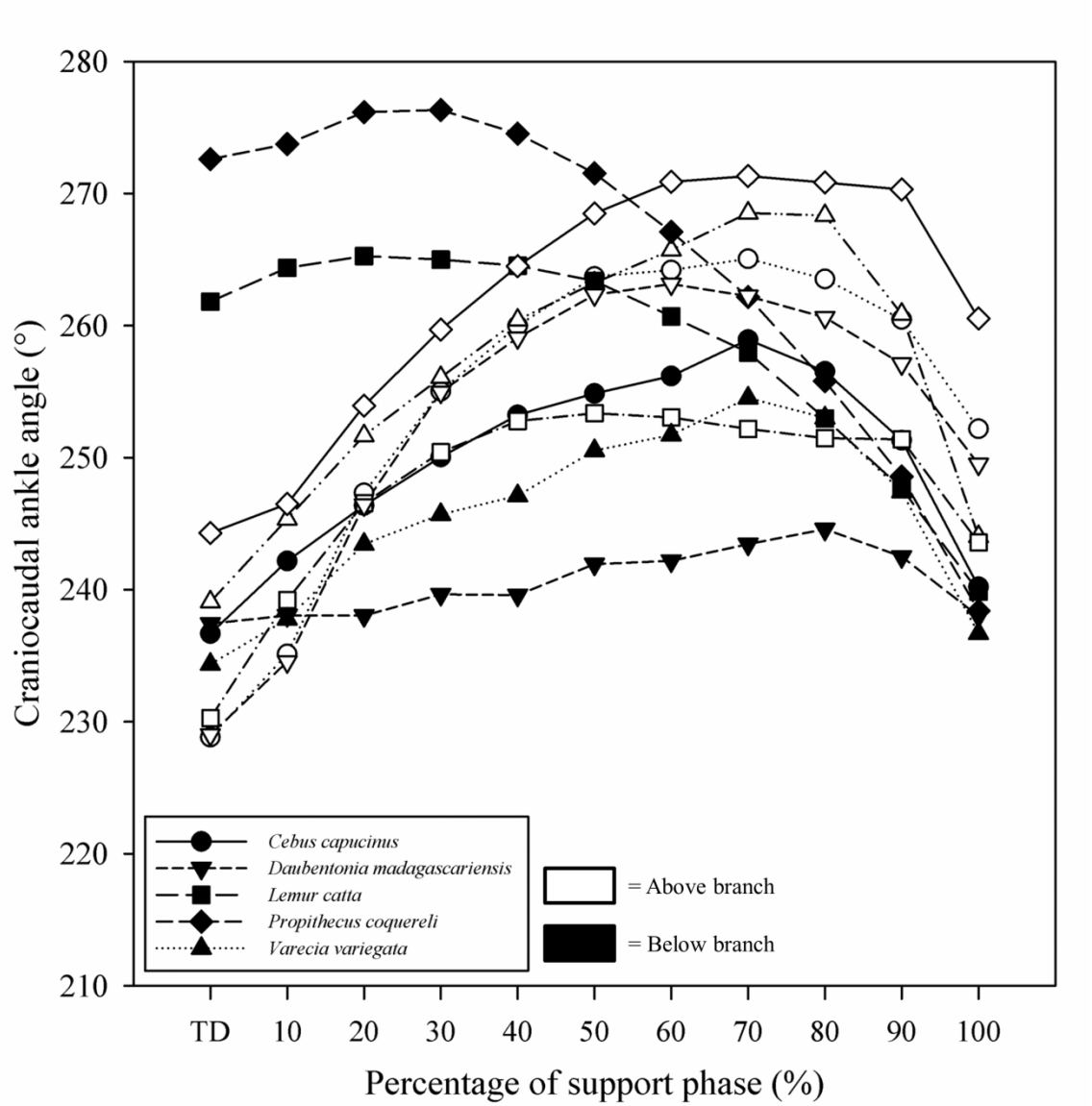

Figure 32: Patterns of mean ankle movement (°) observed during above and below branch quadrupedal locomotion in five species of primates.

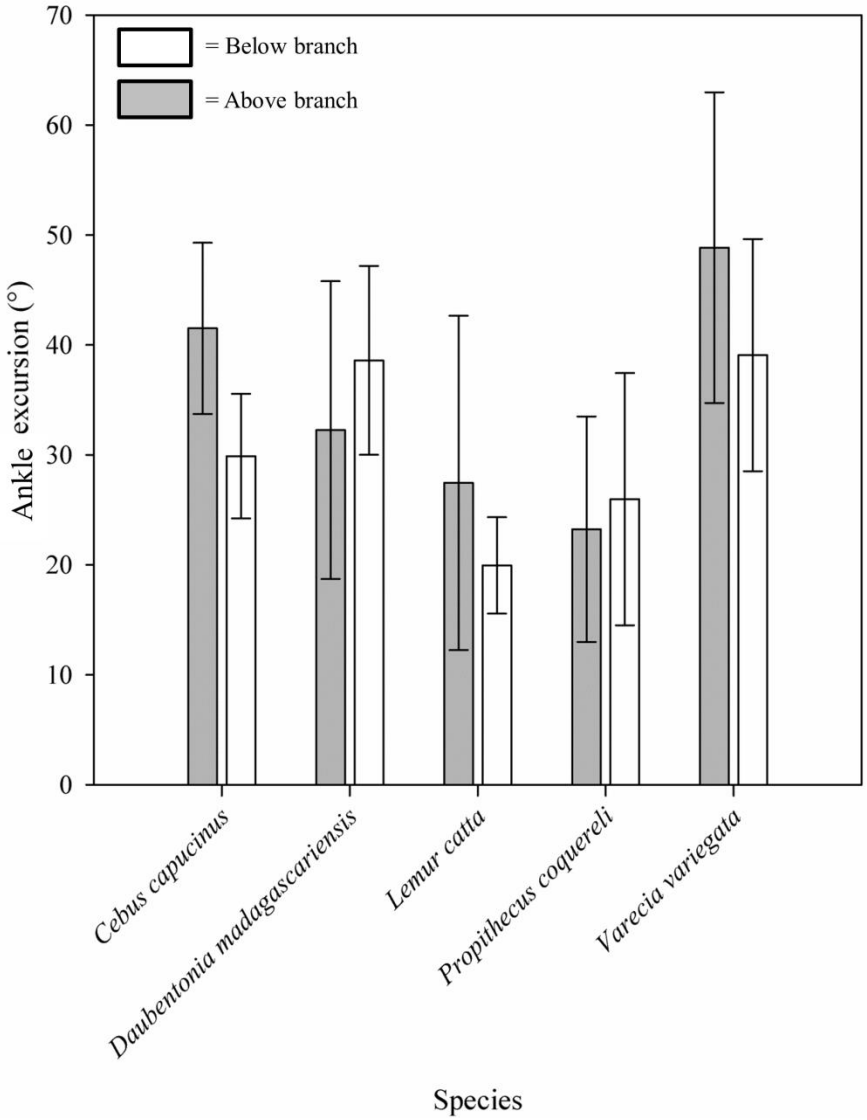

Figure 33: Mean and standard deviation values of ankle excursion (°) observed during above and below branch quadrupedal locomotion in five species of primates.

3.1.3 Spatiotemporal gait variables

In total, 541 strides were used for spatiotemporal gait analysis. Table 6 summarizes the number of steps collected per limb for each orientation, demonstrates intraspecific statistical comparisons, and data for diagonality, stride duration, stride length, and forelimb and hindlimb duty factor and relative swing proportion. All data displayed a non-normal distribution and unequal variances, therefore non-parametric statistics were used for all comparisons. A significant ($P \leq 0.001$) positive association was observed between stride duration and stride length. No significant relationship between normalized speed and the other spatiotemporal gait variables collected were observed.

Table 6: Mean and standard deviation values for spatiotemporal gait variables collected during above and below branch quadrupedal locomotion in five species of primates

Species	Orientation	N	Velocity (m/s)	Diagonality	Relative forelimb swing	Relative hindlimb swing	Forelimb duty factor	Hindlimb duty factor	Stride distance (m)	Stride duration (sec)
Cebus capucinus	Above	9	0.80 ± 0.15	0.65 ± 0.04	0.47 ± 0.07	0.45 ± 0.05	0.54 ± 0.07	0.55 ± 0.05	0.65 ± 0.05	0.97 ± 0.07
	Below	6	0.59 ± 0.07	0.54 ± 0.07	0.43 ± 0.07	0.43 ± 0.05	0.57 ± 0.07	0.57 ± 0.05	0.57 ± 0.05	0.83 ± 0.13
			*	*	ns	ns	Ns	ns	*	*
Daubentonia madagascariensis	Above	60	0.66 ± 0.20	0.65 ± 0.11	0.51 ± 0.07	0.44 ± 0.03	0.49 ± 0.07	0.56 ± 0.03	0.58 ± 0.10	0.92 ± 0.21
	Below	49	0.47 ± 0.15	0.56 ± 0.07	0.45 ± 0.11	0.40 ± 0.08	0.56 ± 0.14	0.60 ± 0.08	0.53 ± 0.10	1.29 ± 0.43
			*	*	*	ns	*	*	*	*
Lemur catta	Above	90	0.56 ± 0.13	0.64 ± 0.08	0.42 ± 0.07	0.36 ± 0.04	0.59 ± 0.09	0.64 ± 0.04	0.53 ± 0.07	0.97 ± 0.15
	Below	76	0.54 ± 0.18	0.49 ± 0.08	0.36 ± 0.10	0.32 ± 0.05	0.65 ± 0.11	0.68 ± 0.05	0.39 ± 0.11	0.75 ± 0.12
			ns	*	*	*	*	*	*	*
Propithecus coquereli	Above	56	0.67 ± 0.18	0.64 ± 0.08	0.52 ± 0.06	0.37 ± 0.04	0.49 ± 0.09	0.63 ± 0.04	0.51 ± 0.09	0.80 ± 0.13
	Below	84	0.51 ± 0.08	0.41 ± 0.12	0.44 ± 0.12	0.36 ± 0.06	0.56 ± 0.14	0.64 ± 0.06	0.52 ± 0.09	1.05 ± 0.23
			*	*	*	ns	*	ns	*	*
Varecia variegata	Above	60	0.75 ± 0.13	0.65 ± 0.03	0.47 ± 0.06	0.43 ± 0.05	0.58 ± 0.08	0.59 ± 0.05	0.64 ± 0.06	0.87 ± 0.11
	Below	52	0.60 ± 0.08	0.53 ± 0.05	0.42 ± 0.02	0.41 ± 0.05	0.59 ± 0.09	0.57 ± 0.05	0.57 ± 0.07	0.97 ± 0.10
			*	*	*	ns	Ns	ns	*	*

[*] Significant difference observed ($P \leq 0.05$)
[ns] No significant difference observed ($P > 0.05$)

With regard to stride duration and distance, significant differences were observed between above and below branch quadrupedal locomotion in all species. Stride duration demonstrated a negative association with normalized speed, and although significant differences were observed for all species no appreciable patterns were detected as a whole. For *C. capucinus* and *L. catta* stride duration was significantly shorter during below branch quadrupedal locomotion. In contrast, stride duration increased during below branch quadrupedal locomotion in *P. coquereli*, *V. variegata*, and *D. madagascariensis* (Figure 34). Stride distance was positively correlated with normalized speed, and for most species (with the exception of *P. coquereli*) stride distance was significantly shorter during below branch quadrupedal locomotion when compared to above branch quadrupedal locomotion (Figure 35).

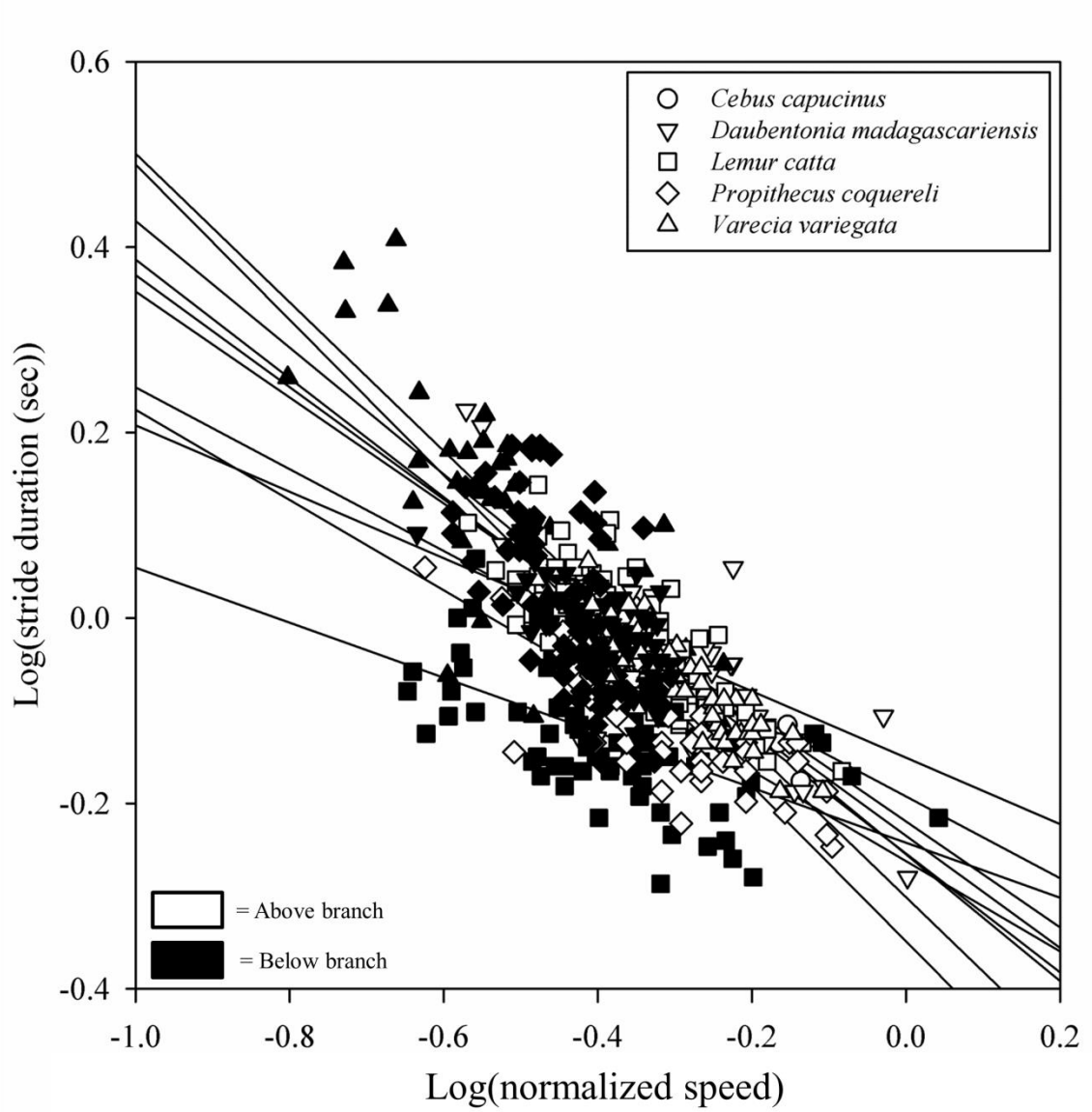

Figure 34: The relationship between log-transformed normalized speed and stride duration (sec) during above and below branch quadrupedal locomotion in five species of primates.

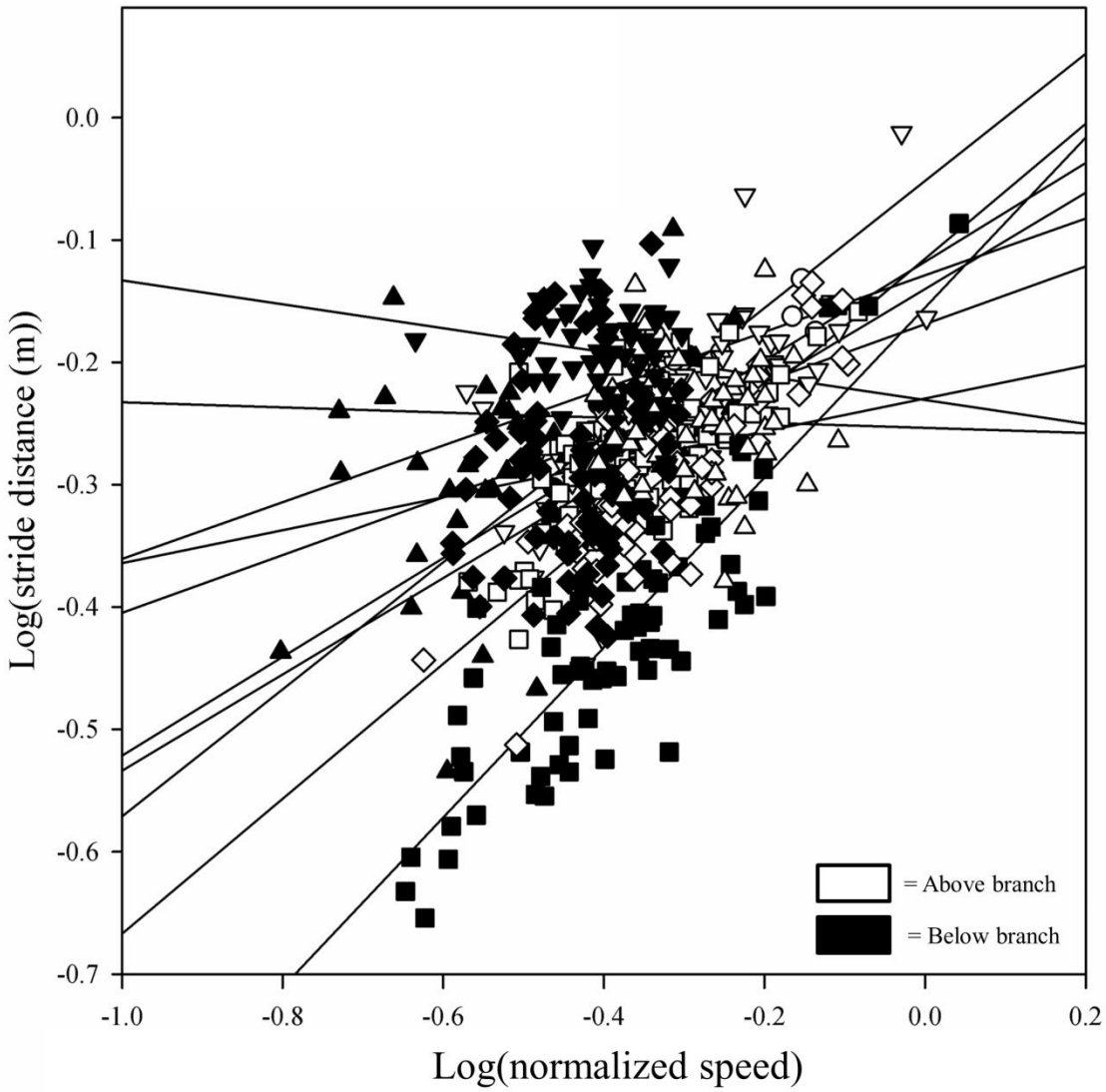

Figure 35: The relationship between log-transformed normalized speed and stride distance (sec) during above and below branch quadrupedal locomotion in five species of primates.

Patterns of relative forelimb and hindlimb support and swing phase largely showed the same pattern across all species, although some exceptions were present. In general, during below branch quadrupedal locomotion relative forelimb and hindlimb support phase increased while relative swing phase decreased (but see *P. coquereli* and *V. variegata*). This finding indicates that for most species, there is a tendency to increase the period the limbs are in contact with the support when adopting below branch quadrupedal locomotion (Figure 36-39).

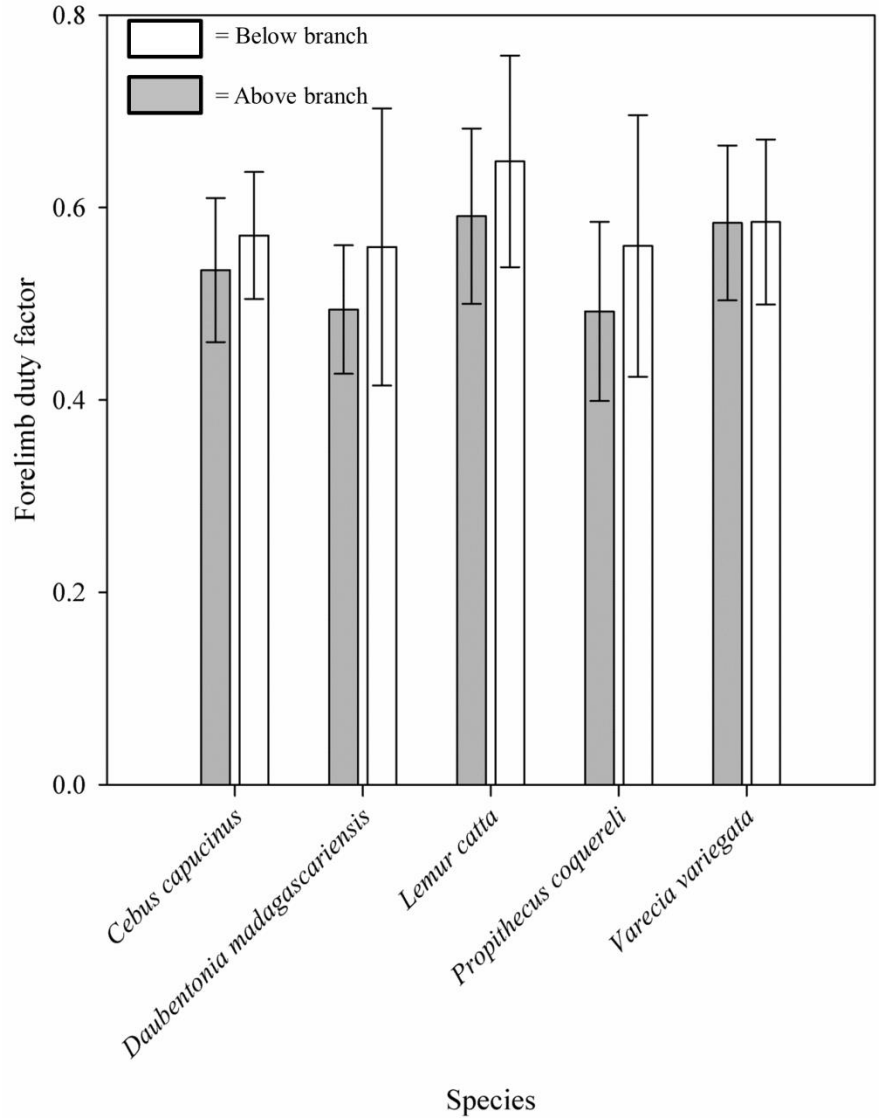

Figure 36: Forelimb duty factor (mean and standard deviation) during above and below branch quadrupedal locomotion in five species of primates.

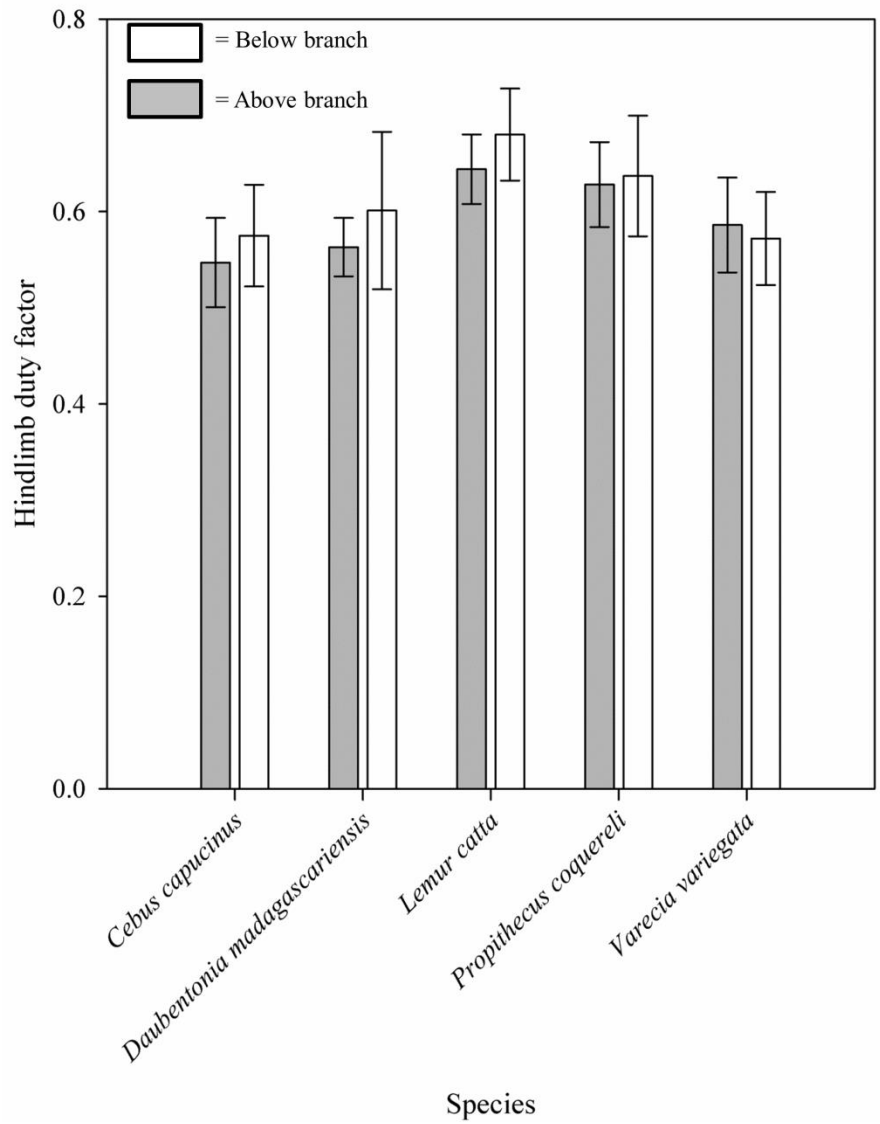

Figure 37: Hindlimb duty factor (mean and standard deviation) during above and below branch quadrupedal locomotion in five species of primates.

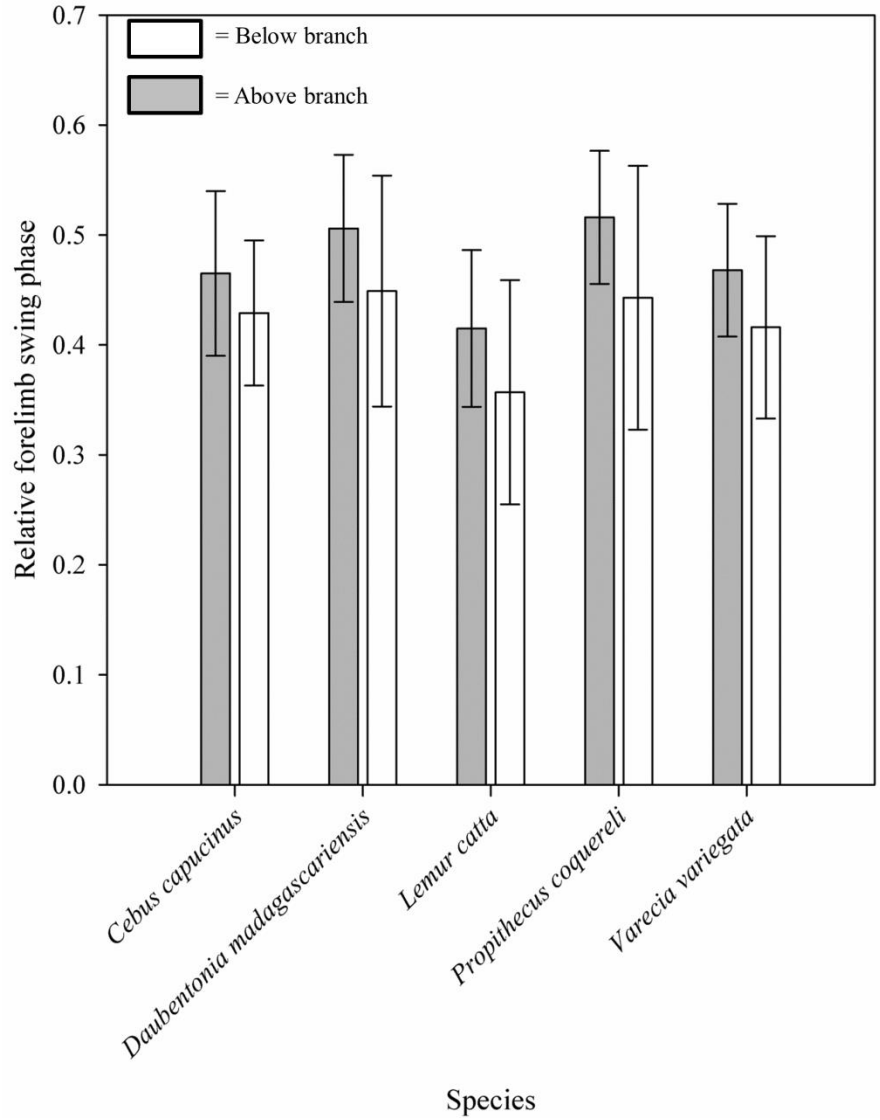

Figure 38: Relative forelimb swing phase (mean and standard deviation) during above and below branch quadrupedal locomotion in five species of primates.

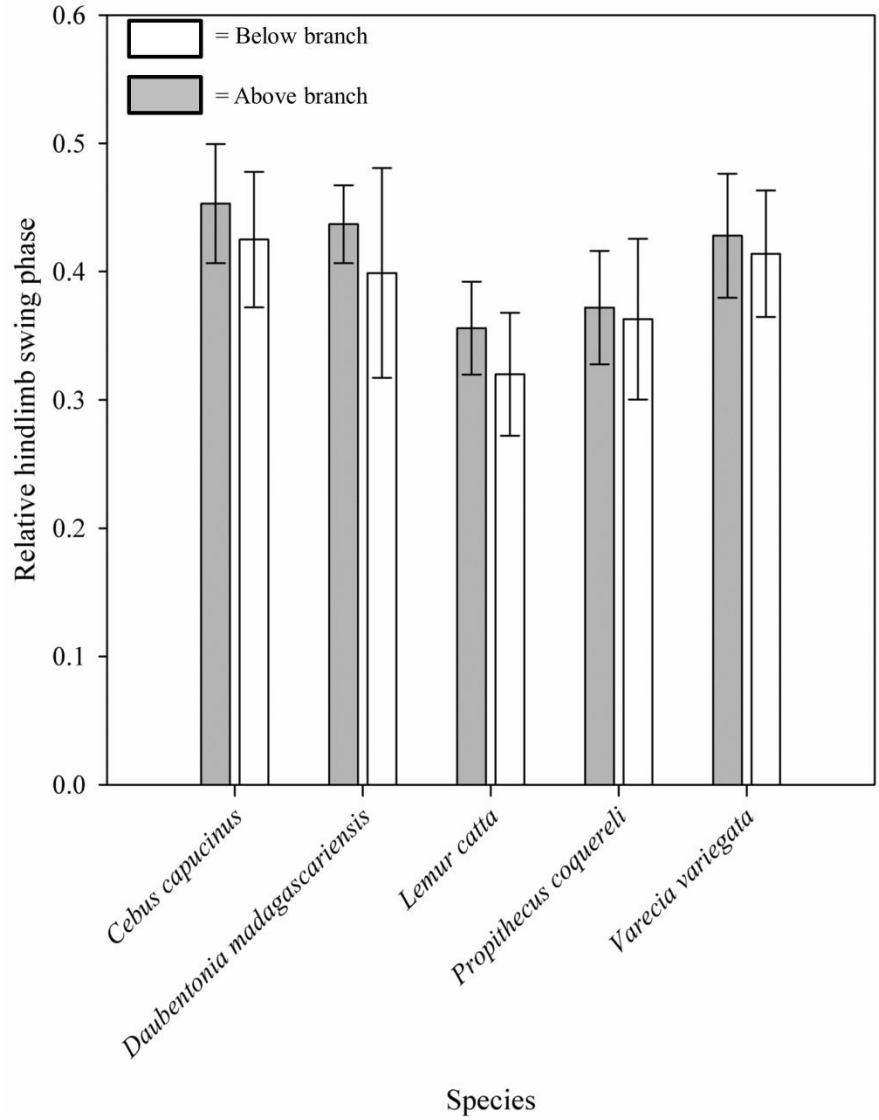

Figure 39: Relative hindlimb swing phase (mean and standard deviation) during above and below branch quadrupedal locomotion in five species of primates.

Interlimb coordination was drastically different between above and below branch quadrupedal locomotion in all species. During above branch quadrupedal locomotion all species primarily used DSDC gaits following the predicated relationship between diagonality and hindlimb duty factor described by Cartmill et al. (2002) as “Rule 1: The Primate Line”, which reflects timings that minimize unilateral bipedality and allows animals to place a hindfoot on a substrate tested by its forelimb. Several strides were lateral-sequence, lateral-couplets (LSLC), lateral-sequence, diagonal-couplets (LSDC) gaits, and right on the border of DSDC gaits. When moving below branches interlimb coordination was much more variable, and although DSDC gaits were still the most common gait pattern observed there was a marked increase in the amount of LSDC and LSLC gaits. This resulted in an overall decrease in diagonality during below branch quadrupedal locomotion (Figure 40).

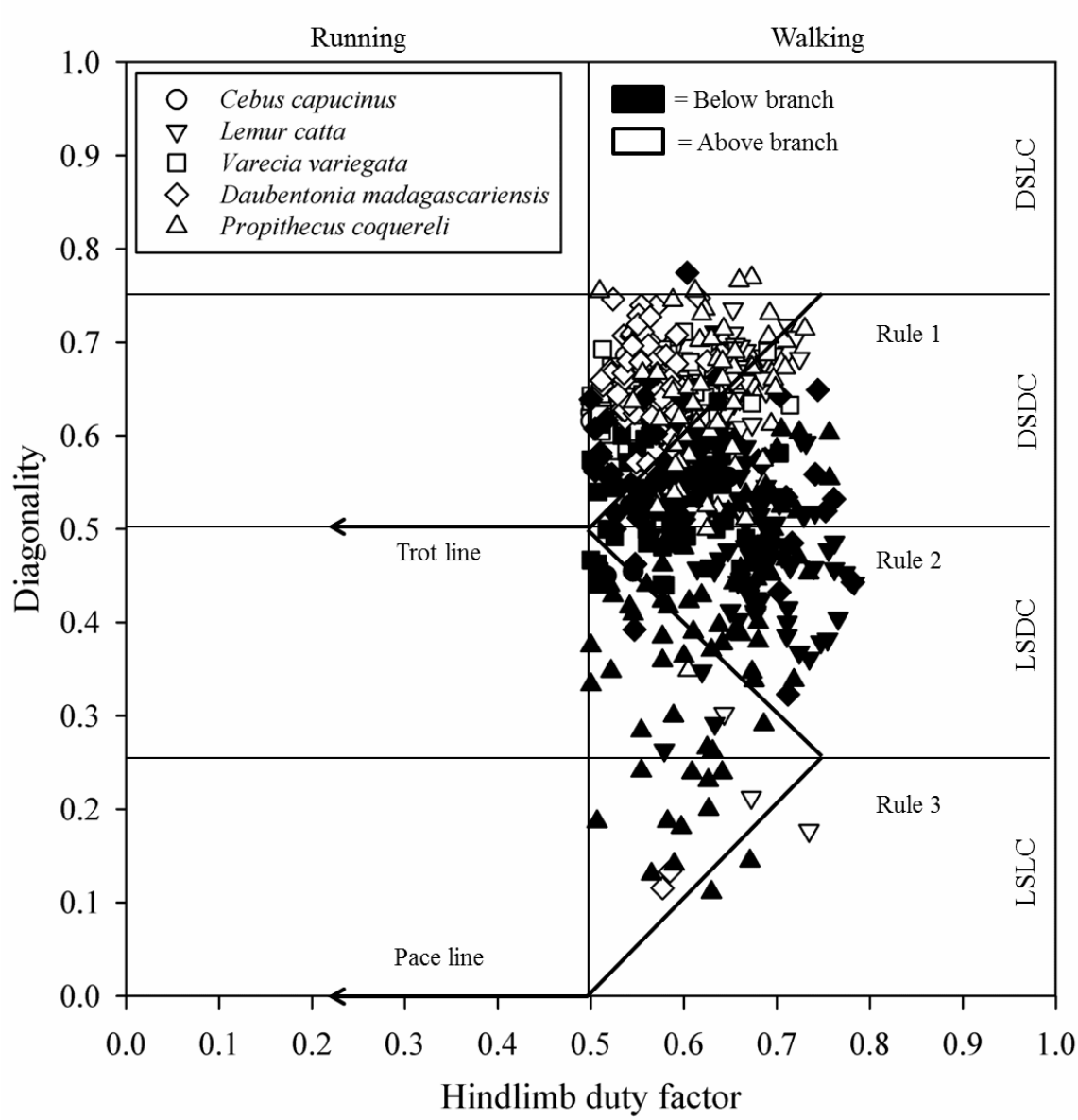

Figure 40: A modified "Hildebrand" plot (following the approach of Cartmill et al. 2002) displaying diagonality for multiple strides of each of the study species over hindlimb duty factor during above and below branch quadrupedal locomotion.

3.2 An interspecific comparison of the mechanics of below branch quadrupedal locomotion

3.2.1 Kinetics

In total, 452 single limb forces were collected and analyzed during below branch quadrupedal locomotion in four species of primate and three species of non-primate mammal. Table 7 and 8 summarizes the number of steps collected per limb for each species, intraspecific statistical comparisons, data for FHpk, SHpk, FHI, SHI, HI, Mpk, Lpk, MI, LI, MLI, and Zpk, and the timing associated with FHpk, SHpk, B/P, Mpk, Lpk, and Zpk. All data displayed a non-normal distribution and unequal variances, therefore non-parametric statistics were used for all comparisons. A significant ($P \leq 0.001$) positive association was observed between Vpk and normalized speed. No significant relationship between normalized speed and the other kinetic variables collected were observed.

Table 7: Limb loading data (mean ± standard deviation) and significance tests for below branch quadrupedal locomotion in primate and non-primate mammals.

Species	Limb	N	FHpk (%bw)	SHpk (%bw)	FHI (%bws)	SHI (%bws)	HI (%bws)	Mpk (%bw)	Lpk (%bw)	MI (%bws)	LI (%bws)	MLI (%bws)	Vpk (%bw)
Daubentonia madagascariensis	Forelimb	26	23.34 ± 7.45	-13.64 ± 6.42	6.63 ± 3.94	-2.31 ± 1.69	4.32 ± 4.80	-7.29 ± 3.99	3.13 ± 2.56	-1.99 ± 1.35	0.32 ± 0.25	-1.67 ± 1.36	66.96 ± 8.33
	Hindlimb	22	4.93 ± 3.60	-3.85 ± 2.83	0.55 ± 0.69	-3.54 ± 2.49	-2.98 ± 2.55	-5.59 ± 2.95	2.66 ± 1.17	-1.30 ± 0.74	0.34 ± 0.26	-0.97 ± 0.79	49.04 ± 10.14
			*	ns	*	*	*	ns	ns	*	ns	*	*
Lemur catta	Forelimb	52	23.14 ± 7.09	-14.79 ± 6.90	3.90 ± 1.70	-1.81 ± 1.07	2.09 ± 2.23	-11.84 ± 5.35	5.14 ± 2.99	-2.11 ± 1.06	0.52 ± 0.47	-1.59 ± 1.15	70.12 ± 9.32
	Hindlimb	41	7.82 ± 4.66	-15.24 ± 7.24	0.63 ± 0.68	-2.98 ± 1.82	-2.36 ± 1.75	-7.50 ± 3.48	3.51 ± 1.73	-1.34 ± 0.87	0.29 ± 0.24	-1.05 ± 0.85	43.79 ± 10.84
			*	ns	*	*	*	*	*	*	*	*	*
Propithecus coquereli	Forelimb	59	22.21 ± 5.59	-13.56 ± 6.86	4.59 ± 1.47	-1.88 ± 1.13	2.71 ± 1.92	-9.15 ± 3.71	3.29 ± 2.54	-2.14 ± 1.31	0.35 ± 0.35	-1.80 ± 1.47	79.90 ± 10.71
	Hindlimb	51	5.80 ± 2.29	-11.63 ± 4.07	0.59 ± 0.40	-3.33 ± 1.96	-2.74 ± 2.00	-6.55 ± 2.80	1.76 ± 1.18	-1.62 ± 0.82	0.21 ± 0.26	-1.41 ± 0.94	34.98 ± 7.80
			*	ns	*	*	*	*	*	*	*	*	*
Varecia variegata	Forelimb	38	25.54 ± 7.70	-10.85 ± 4.27	5.12 ± 1.65	-1.39 ± 0.74	2.99 ± 1.67	-7.85 ± 3.30	3.99 ± 2.61	-1.81 ± 0.96	0.44 ± 0.35	-1.36 ± 1.08	82.54 ± 14.95
	Hindlimb	33	7.44 ± 4.17	-11.91 ± 5.11	0.79 ± 0.61	-2.42 ± 1.34	-1.73 ± 1.36	-6.76 ± 2.80	2.37 ± 1.50	-1.75 ± 0.89	0.15 ± 0.21	-1.60 ± 0.98	61.64 ± 12.92
			*	ns	*	*	*	ns	*	ns	*	ns	*
Choloepus didactylus	Forelimb	25	10.24 ± 4.88	-2.49 ± 2.20	25.41 ± 19.35	-2.02 ± 2.90	20.20 ± 16.26	-10.33 ± 6.58	1.00 ± 0.70	-18.09 ± 9.16	0.25 ± 0.35	-17.84 ± 9.29	61.64 ± 15.74
	Hindlimb	18	4.61 ± 3.80	-7.73 ± 5.35	5.05 ± 6.41	-18.27 ± 18.90	-16.67 ± 18.56	-8.40 ± 4.61	1.41 ± 1.07	-14.62 ± 7.91	0.82 ± 1.57	-13.80 ± 8.46	59.75 ± 15.41
			*	*	*	*	*	ns	ns	ns	ns	ns	ns
Pteropus vampyrus	Forelimb	16	9.83 ± 6.54	-6.99 ± 6.14	6.84 ± 8.09	-3.05 ± 5.29	3.79 ± 9.54	-6.06 ± 2.38	5.27 ± 3.66	-2.84 ± 1.74	1.47 ± 1.47	-1.37 ± 1.28	42.28 ± 12.40
	Hindlimb	25	9.47 ± 6.88	-13.74 ± 7.13	4.11 ± 5.32	-8.22 ± 8.33	-4.23 ± 8.09	-7.81 ± 2.75	4.13 ± 2.33	-4.29 ± 3.71	1.08 ± 0.94	-3.21 ± 3.69	65.62 ± 20.13
			ns	*	*	*	*	*	ns	ns	ns	ns	*
Desmodus rotundus	Forelimb	21	13.45 ± 6.05	-5.20 ± 2.85	3.66 ± 2.29	-0.87 ± 1.30	3.27 ± 2.63	-9.58 ± 10.80	1.82 ± 1.64	-1.77 ± 0.98	0.71 ± 1.10	-1.06 ± 1.26	59.74 ± 20.70
	Hindlimb	25	7.28 ± 4.63	-11.25 ± 6.29	2.33 ± 3.54	-5.25 ± 5.12	-3.51 ± 4.05	-8.72 ± 8.56	2.24 ± 1.59	-2.55 ± 2.45	0.60 ± 0.55	-1.95 ± 2.27	51.91 ± 20.78

	*	*	*	*	*	ns	ns	ns	ns	ns	ns

[*] Significant difference observed ($P \leq 0.05$)
[ns] No significant difference observed ($P > 0.05$)
[FHpk] First horizontal peak force
[SHpk] Second horizontal peak force
[FHI] First horizontal impulse
[SHI] Second horizontal impulse
[Mpk] Medial peak
[Lpk] Lateral peak
[MI] Medial impulse
[LI] Lateral impulse
[MLI] Mediolateral impulse
[Vpk] Vertical peak

Table 8: The timing of limb loading events throughout support phase (mean ± standard deviation) and significance tests observed during below branch quadrupedal locomotion in primate and non-primate mammals.

Species	Limb	N	FHpk	SHpk	B/P	Mpk	Lpk	Vpk
Daubentonia madagascariensis	Forelimb	26	0.21 ± 0.10	0.78 ± 0.15	0.60 ± 0.11	0.52 ± 0.26	0.64 ± 0.34	0.60 ± 0.11
	Hindlimb	22	0.11 ± 0.11	0.60 ± 0.13	0.21 ± 0.13	0.38 ± 0.22	0.43 ± 0.33	0.33 ± 0.11
			*	*	*	Ns	ns	*
Lemur catta	Forelimb	52	0.21 ± 0.07	0.76 ± 0.08	0.56 ± 0.10	0.47 ± 0.20	0.53 ± 0.38	0.55 ± 0.11
	Hindlimb	41	0.09 ± 0.07	0.65 ± 0.12	0.19 ± 0.08	0.39 ± 0.23	0.35 ± 0.35	0.33 ± 0.12
			*	*	*	Ns	ns	*
Propithecus coquereli	Forelimb	59	0.25 ± 0.07	0.77 ± 0.05	0.58 ± 0.09	0.48 ± 0.20	0.41 ± 0.39	0.53 ± 0.12
	Hindlimb	51	0.09 ± 0.05	0.68 ± 0.12	0.25 ± 0.12	0.30 ± 0.17	0.36 ± 0.37	0.28 ± 0.09
			*	ns	*	Ns	ns	*
Varecia variegata	Forelimb	38	0.19 ± 0.08	0.74 ± 0.08	0.58 ± 0.08	0.45 ± 0.20	0.38 ± 0.35	0.54 ± 0.10
	Hindlimb	33	0.13 ± 0.07	0.56 ± 0.16	0.31 ± 0.11	0.33 ± 0.15	0.17 ± 0.30	0.34 ± 0.11
			*	*	*	*	ns	*
Choloepus didactylus	Forelimb	25	0.42 ± 0.15	0.89 ± 0.12	0.77 ± 0.18	0.56 ± 0.17	0.69 ± 0.44	0.56 ± 0.11
	Hindlimb	18	0.20 ± 0.17	0.61 ± 0.24	0.30 ± 0.24	0.44 ± 0.17	0.49 ± 0.47	0.42 ± 0.15
			*	*	*	*	ns	*
Pteropus vampyrus	Forelimb	16	0.27 ± 0.21	0.72 ± 0.24	0.65 ± 0.26	0.45 ± 0.29	0.46 ± 0.28	0.49± 0.20
	Hindlimb	25	0.20 ± 0.17	0.61 ± 0.20	0.30 ± 0.23	0.44 ± 0.25	0.35± 0.32	0.38± 0.14
			ns	ns	*	Ns	ns	ns
Desmodus rotundus	Forelimb	21	0.32 ± 0.18	0.80 ± 0.11	0.66 ± 0.19	0.57 ± 0.26	0.46 ± 0.43	0.50 ± 0.21
	Hindlimb	25	0.20 ± 0.16	0.67 ± 0.20	0.30 ± 0.23	0.43 ± 0.25	0.44 ± 0.41	0.39 ± 0.17
			*	*	*	Ns	ns	ns

[*] Significant difference observed ($P \leq 0.05$)
[ns] No significant difference observed ($P > 0.05$)
[FHpk] First horizontal peak force
[SHpk] Second horizontal peak force
[B/P] Braking to propulsive transition during above branch quadrupedal locomotion and/or propulsive to braking transition during below branch quadrupedal locomotion
[Mpk] Medial peak
[Lpk] Lateral peak
[Vpk] Vertical peak

In large part, limb loading patterns were fairly similar for all species during below branch quadrupedal locomotion, and most of the differences appear to be due to the extremely slow and careful movement of *C. didactylus*. One major difference observed was the distribution of Vpk force in the the forelimbs and hindlimbs between primates and non-primate mammals (Figures 41 and 42). All primate species displayed significantly different ($P \leq 0.001$) Vpk forces between the forelimb and hindlimb during below branch quadrupedal locomotion. For all primate species, forelimb Vpk forces were significantly ($P \leq 0.001$) greater than hindlimb Vpk forces during below branch quadrupedal locomotion. In *P. vampyrus*, forelimb Vpk forces were significantly ($P \leq 0.001$) lower than hindlimb Vpk forces during below branch quadrupedal locomotion. No significant differences were observed between forelimb and hindlimb Vpk forces in *C. didactylus* or *D. rotundus* (Figures 43 and 44). All vertical force traces (both forelimb and hindlimb) were represented by a single peak. In the forelimb, this peak occurred approximately at 54% of support phase, and in the hindlimb this peak occurred approximately at 35% of support phase. In all species, except *P. vampyrus* and *D. rotundus*, the timing of Vpk varied significantly between forelimb and hindlimb. No significant difference was observed between the timing of the Vpk in the forelimb between species, but the hindlimb Vpk did occur significantly earlier in *P. coquereli* compared to the three non-primate species (Figure 45).

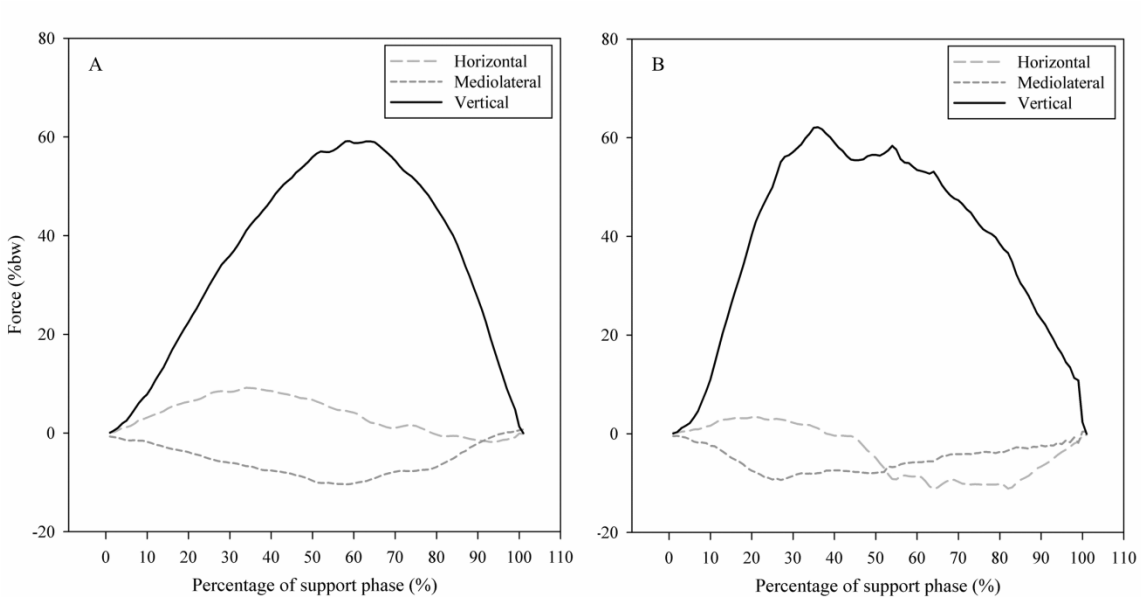

Figure 41: Representative force traces for *Choloepus didactylus* during below branch quadrupedal locomotion. All data are presented as a percentage of the animal's body weight (%bw). Data presented for the forelimb (A) and hindlimb (B).

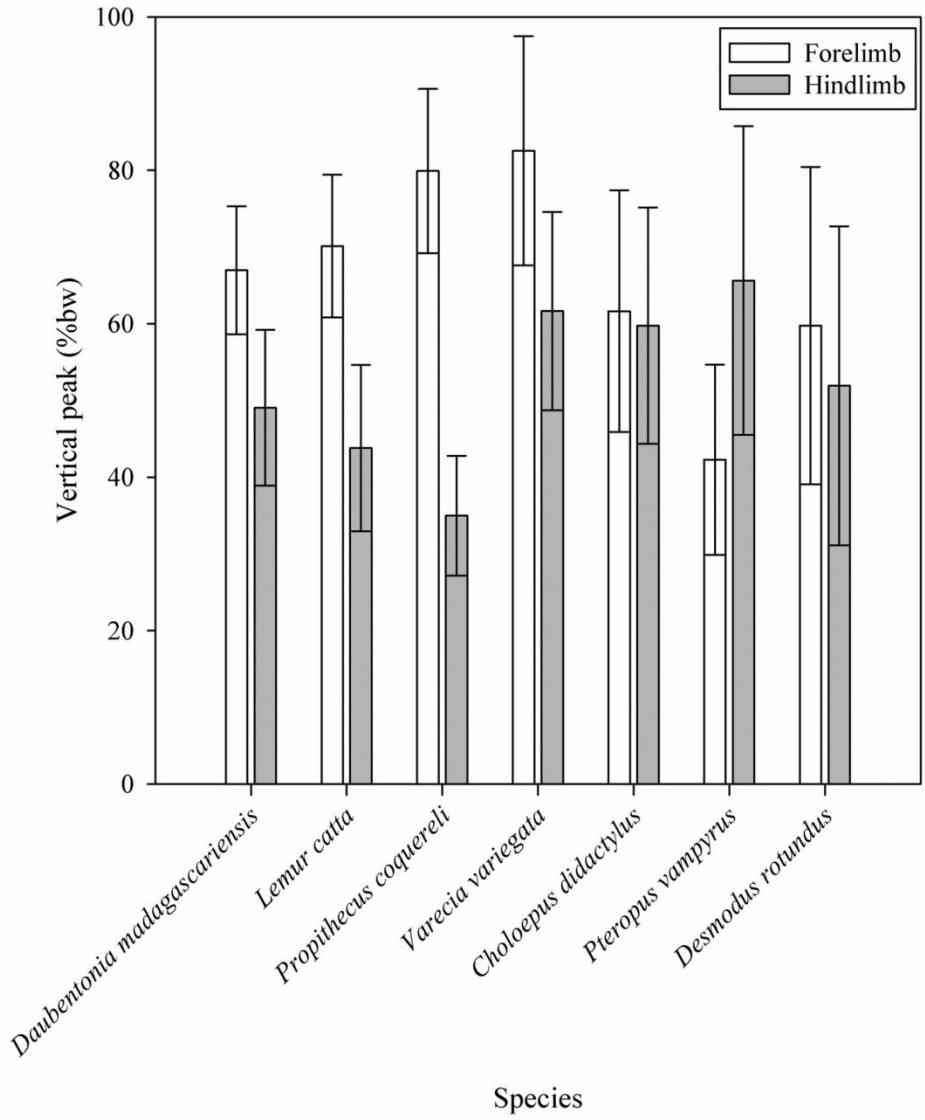

Figure 42: Mean and standard deviation values of peak vertical forces in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

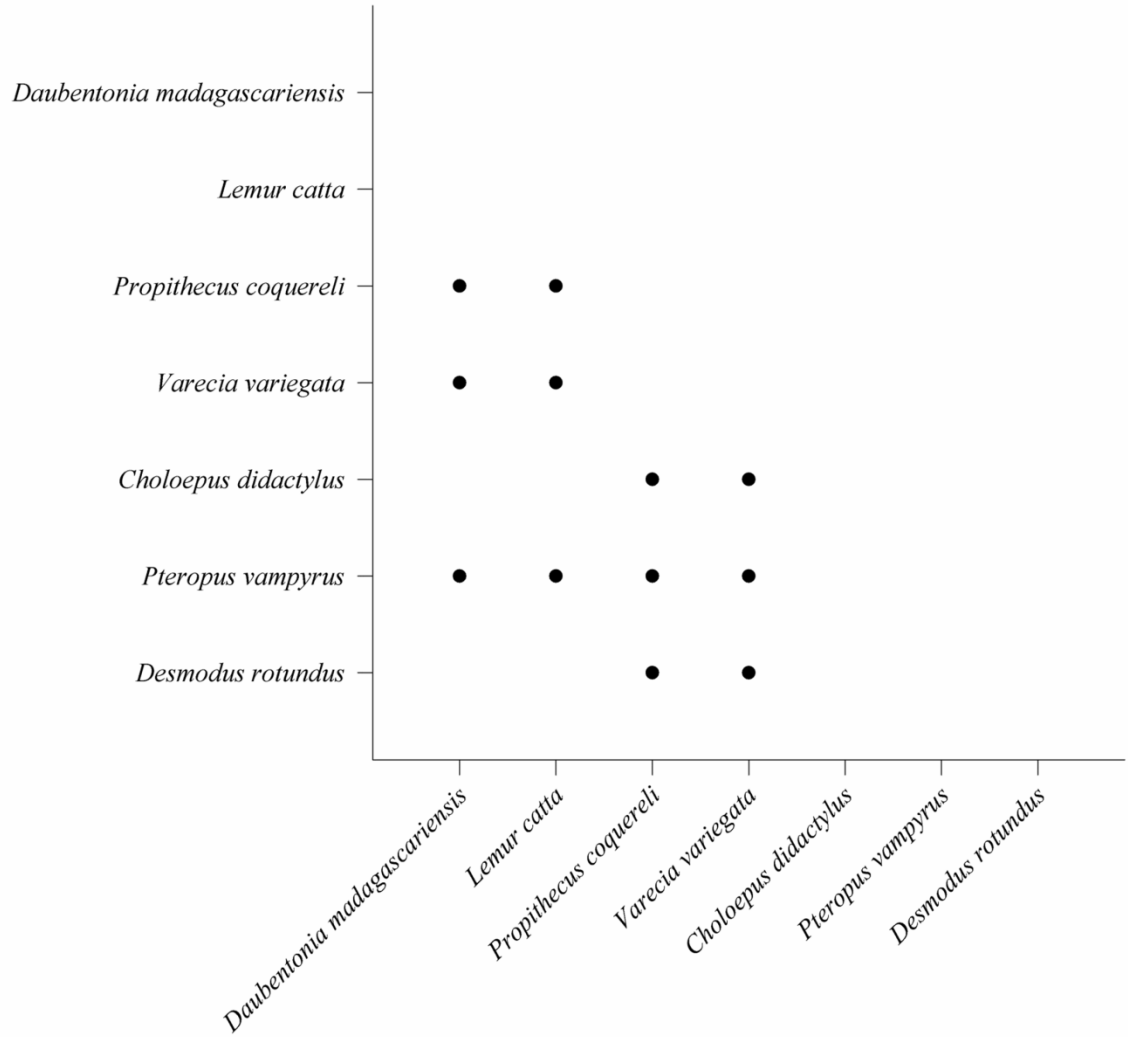

Figure 43: Multiple statistical comparisons between peak vertical forces in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

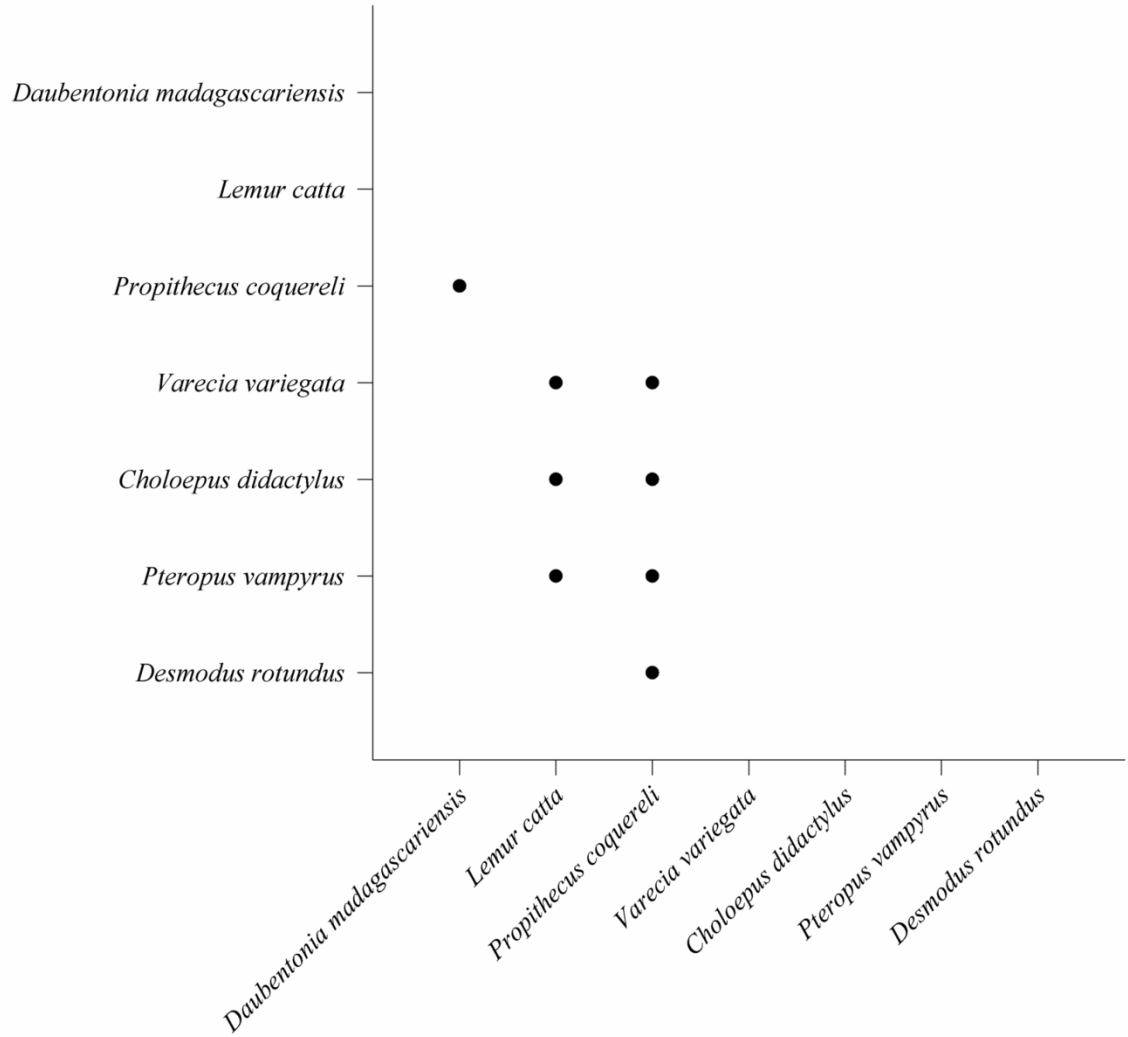

Figure 44: Multiple statistical comparisons between peak vertical forces in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

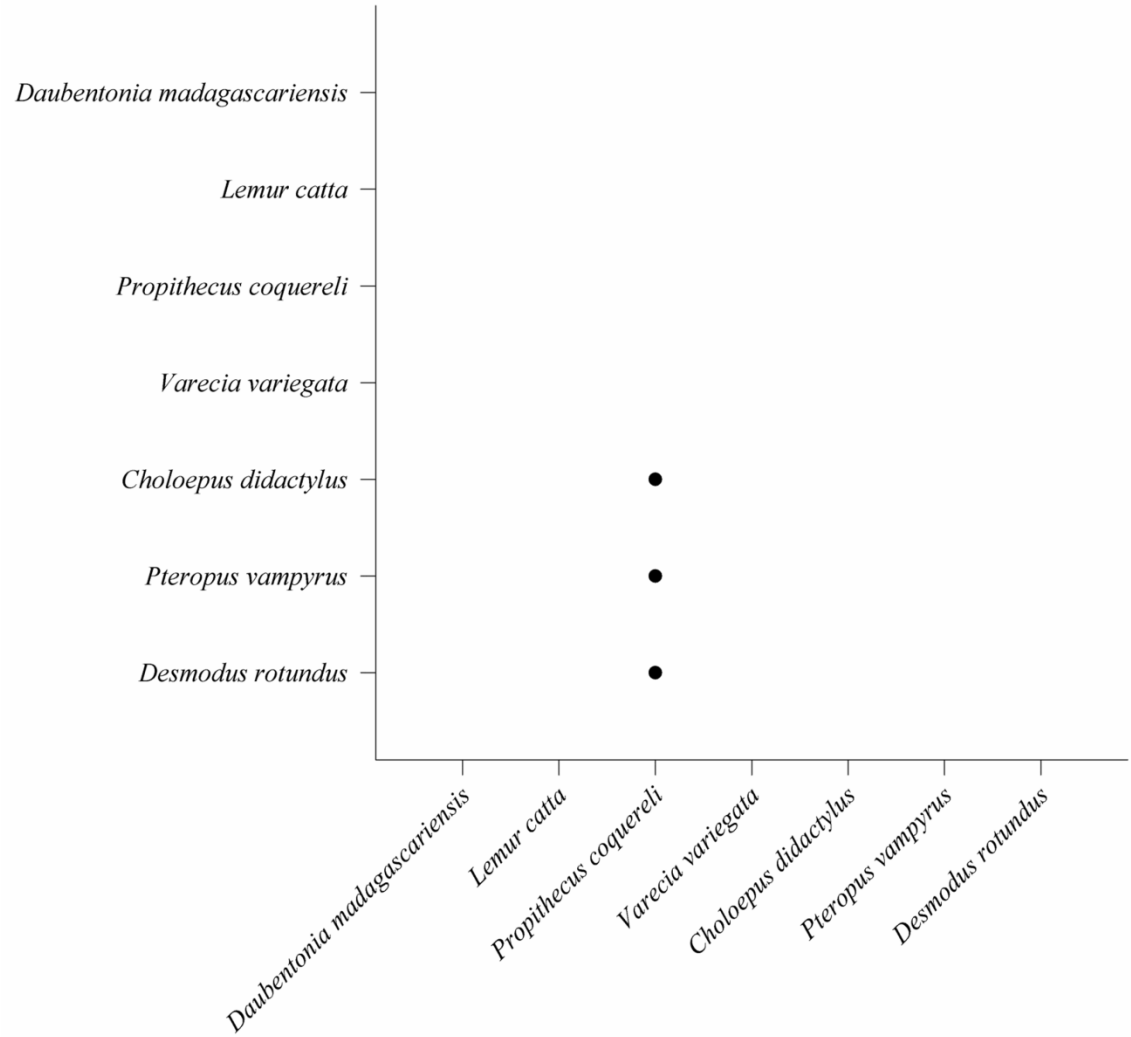

Figure 45: Multiple statistical comparisons between the timing of the peak vertical force in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

During below branch quadrupedal locomotion, a consistent limb loading pattern was observed for all species, in which as the limb (forelimb or hindlimb) touches down, it first applies a propulsive force (Figure 46) to the substrate followed by a braking force prior to lift-off (Figure 47). In all primates, the magnitude of the first occurring horizontal peak in the forelimb was significantly greater than what was observed in non-primate mammals (Figure 48). No significant difference in the magnitude of the first occurring horizontal peak in the hindlimb was observed between any of the species. With regard to the second occurring horizontal peak, the magnitude of this force was relatively greater in the hindlimbs of non-primate mammals, but no such difference was observed in primates. Interspecific comparisons revealed that in all primates, the magnitude of the second occurring horizontal peak in the forelimb was significantly greater than what was observed in non-primate mammals (Figure 49). In the hindlimb, the only significant difference observed in the magnitude of the second occurring horizontal peak was between *C. didactylus* and *L. catta* (Figure 50). In all species, the first occurring horizontal peak occurred within the first 45% of support phase. This first occurring horizontal peak always occurred later in the forelimb compared to the hindlimb. The timing of the first occurring horizontal peak was somewhat later in the forelimb of *C. didactylus* and *D. rotundus*, and quite early in the hindlimb of *V. variegata* compared to most of the other species. This resulted in some significant differences between the timing of this event in each limb amongst the sample species (Figures 51 and 52). In all species, the second occurring horizontal peak occurred within the latter 60% of support phase. This second occurring horizontal peak always occurred later in the forelimb

compared to the hindlimb. The late occurrence of this second occurring horizontal peak in the forelimb of *C. didactylus* was significantly different from most of the primates and *P. vampyrus* (Figure 53). No significant differences in the occurrence of the SHpk in the hindlimb were observed between species. In all species, the B/P transition always occurred during the latter 55% of support phase in the forelimb, and within the first 35% of support phase in the hindlimb. The occurrence of the B/P tended to occur later in both the forelimb and hindlimb of non-primate species. This resulted in significant differences between the timing of the B/P in the forelimb between *C. didactylus* and all the primates, and between *L. catta* and all the non-primate mammals (Figure 54). The only significant difference observed in timing of the B/P in the hindlimb was between *L. catta* and *V. variegata* (Figure 55).

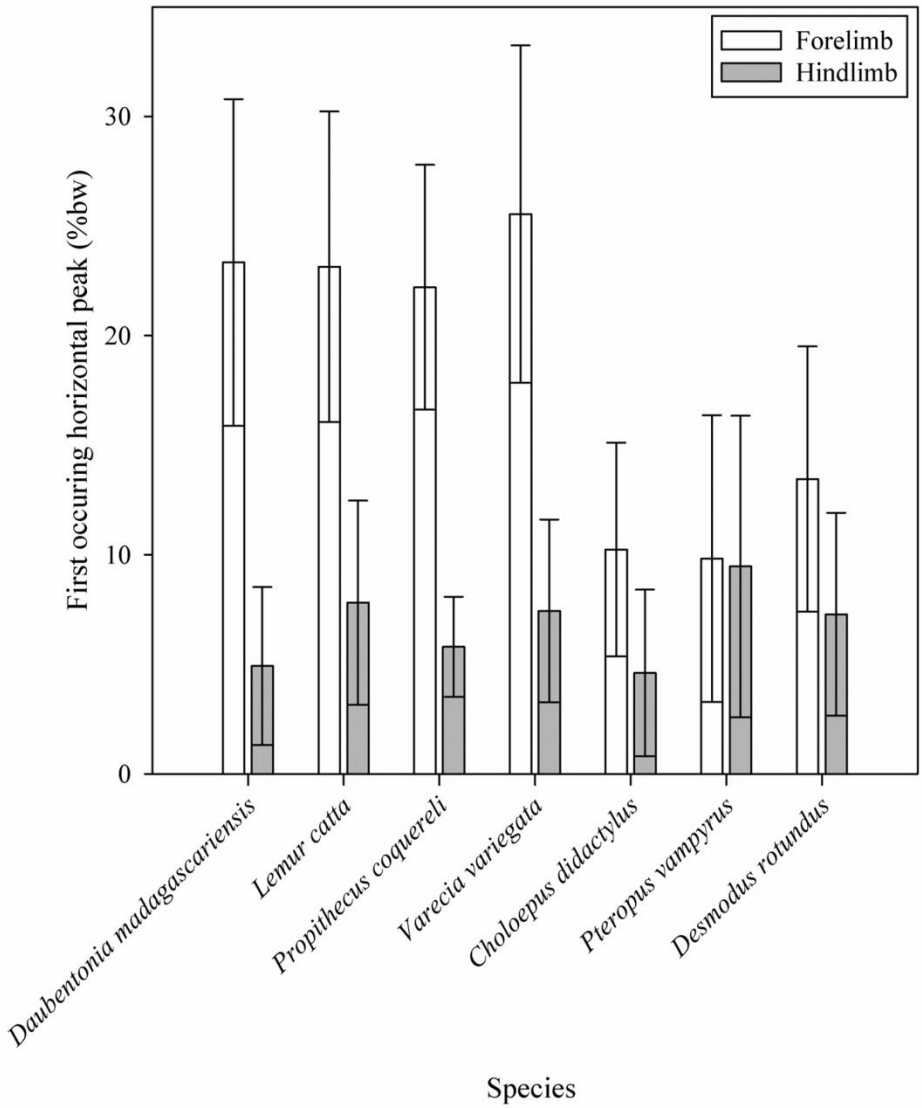

Figure 46: Mean and standard deviation values of first occurring horizontal peak in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

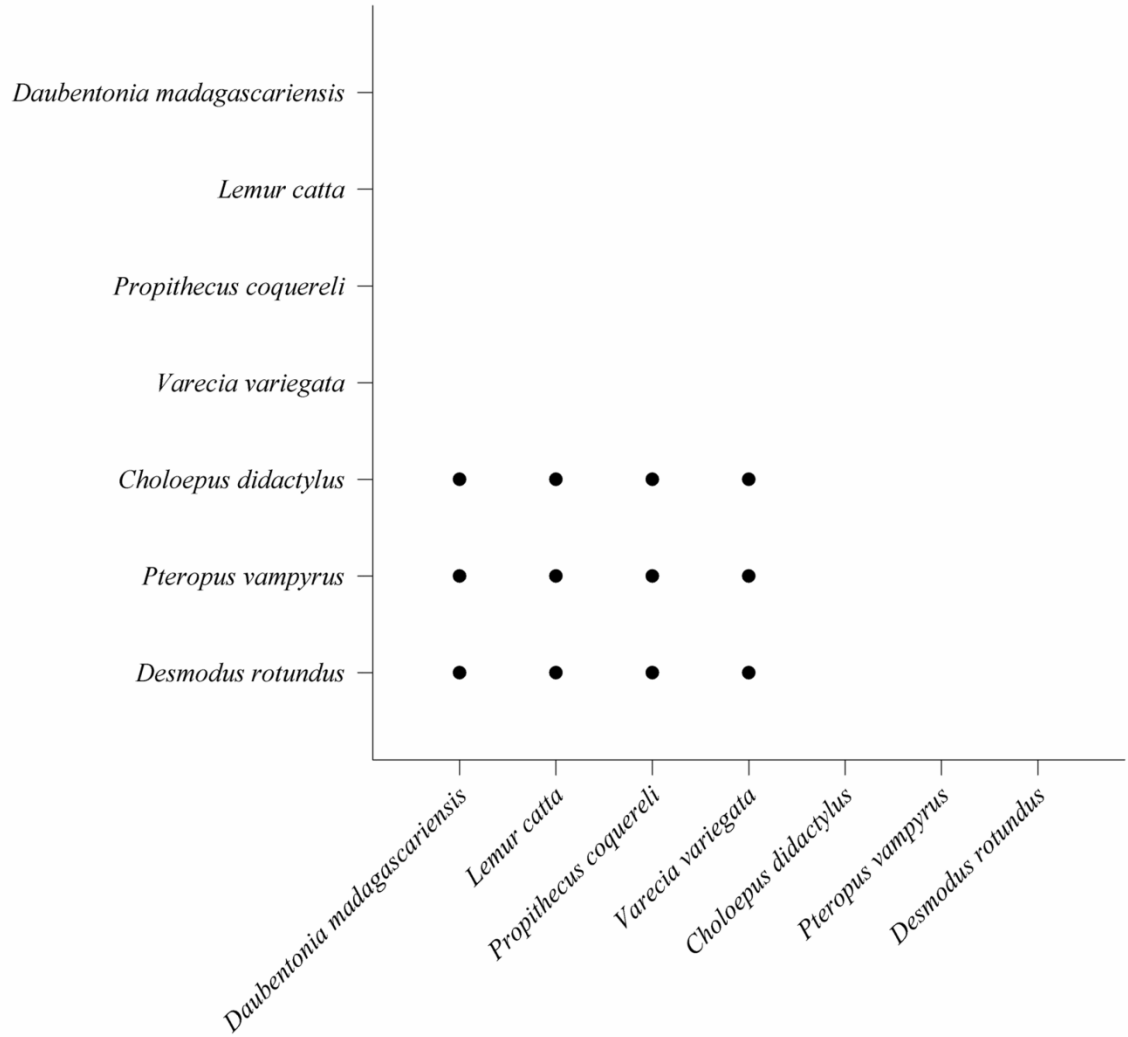

Figure 47: Multiple statistical comparisons between the first occurring horizontal peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

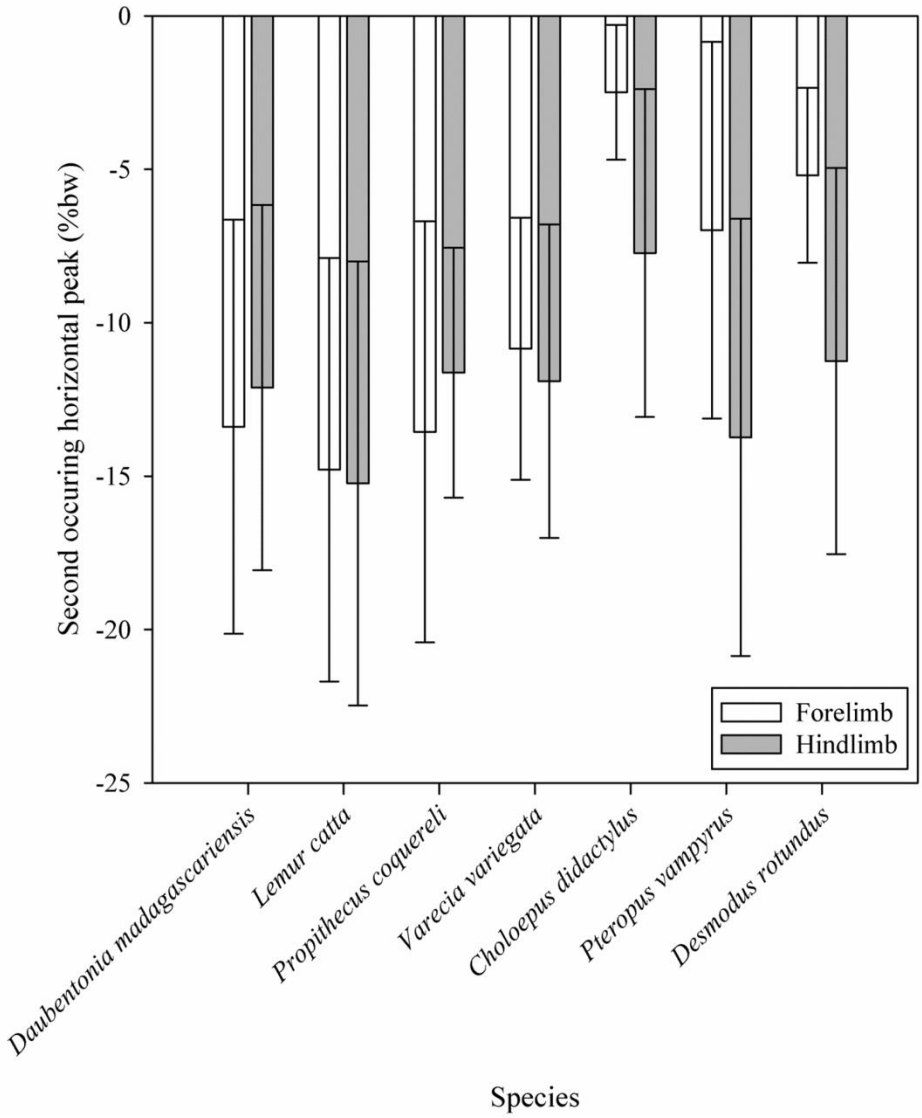

Figure 48: Mean and standard deviation values of second occurring horizontal peak in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

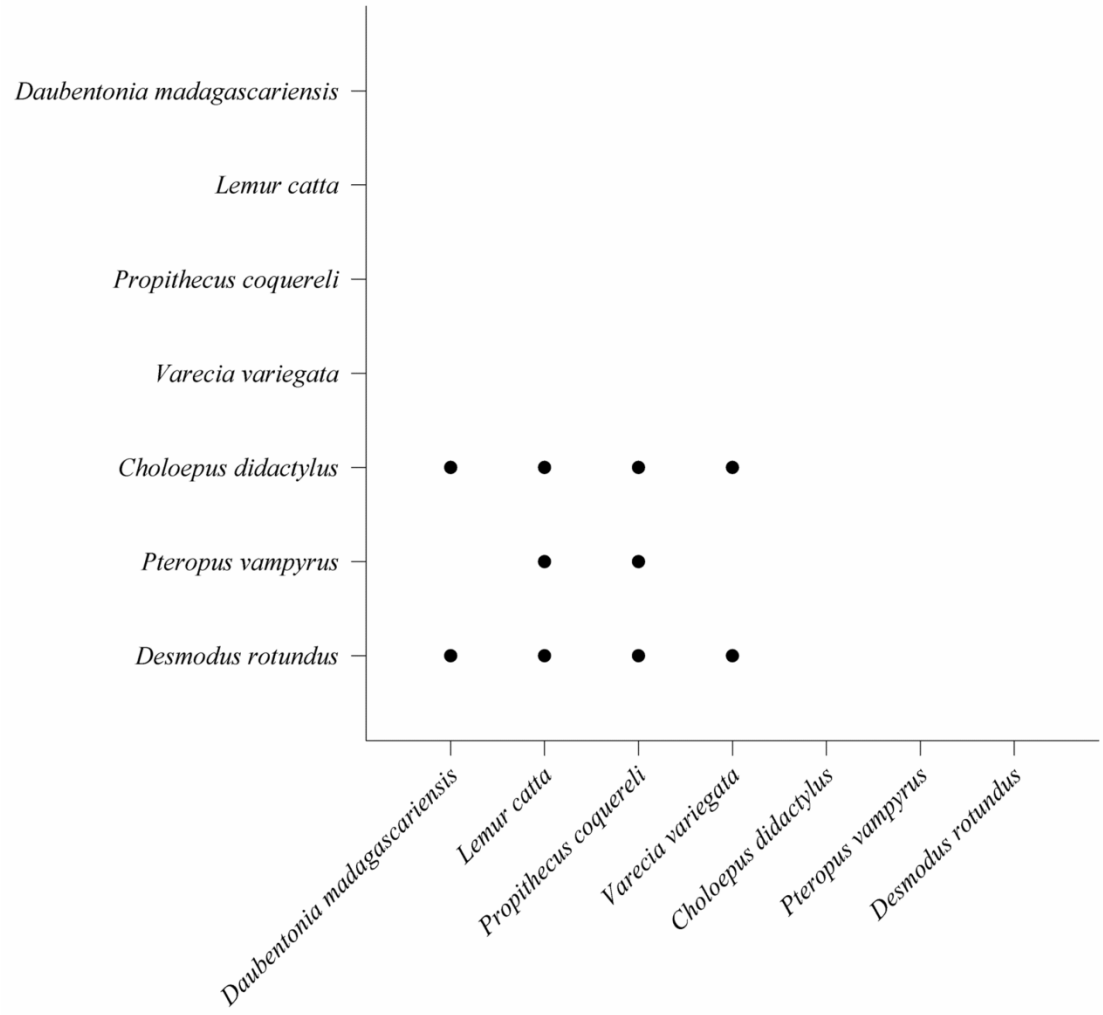

Figure 49: Multiple statistical comparisons between the second occurring horizontal peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

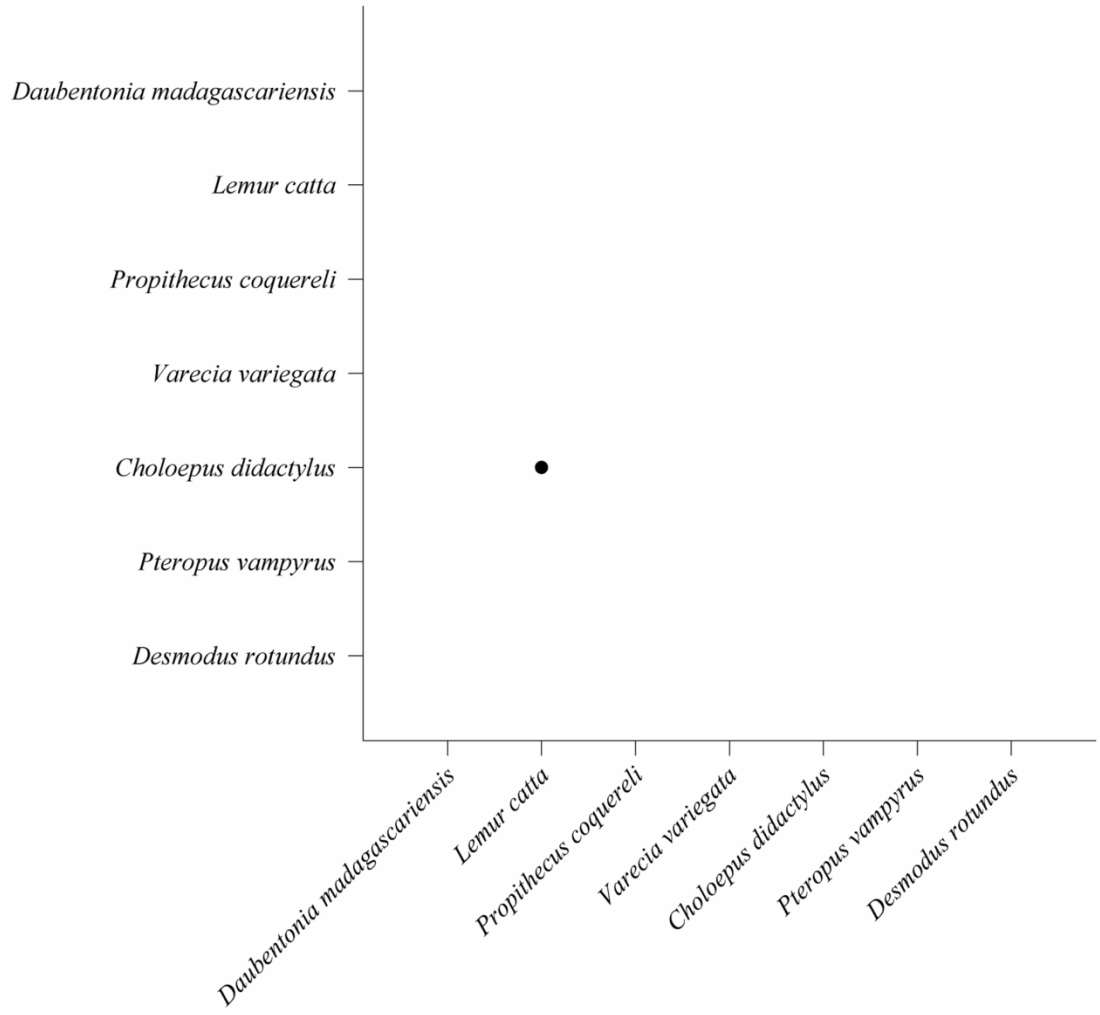

Figure 50: Multiple statistical comparisons between the second occurring horizontal peak in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

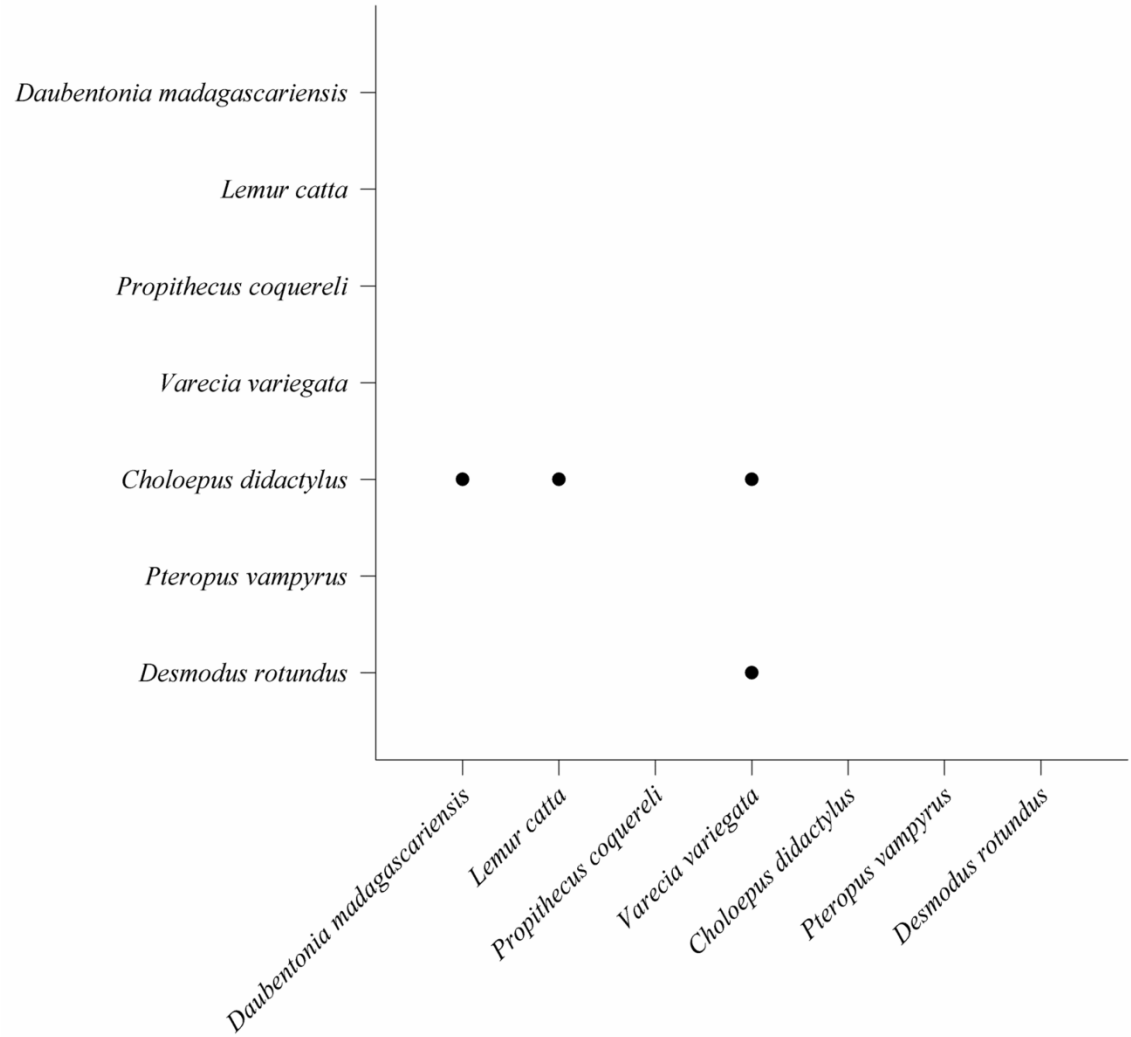

Figure 51: Multiple statistical comparisons between the timing of first occurring horizontal peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

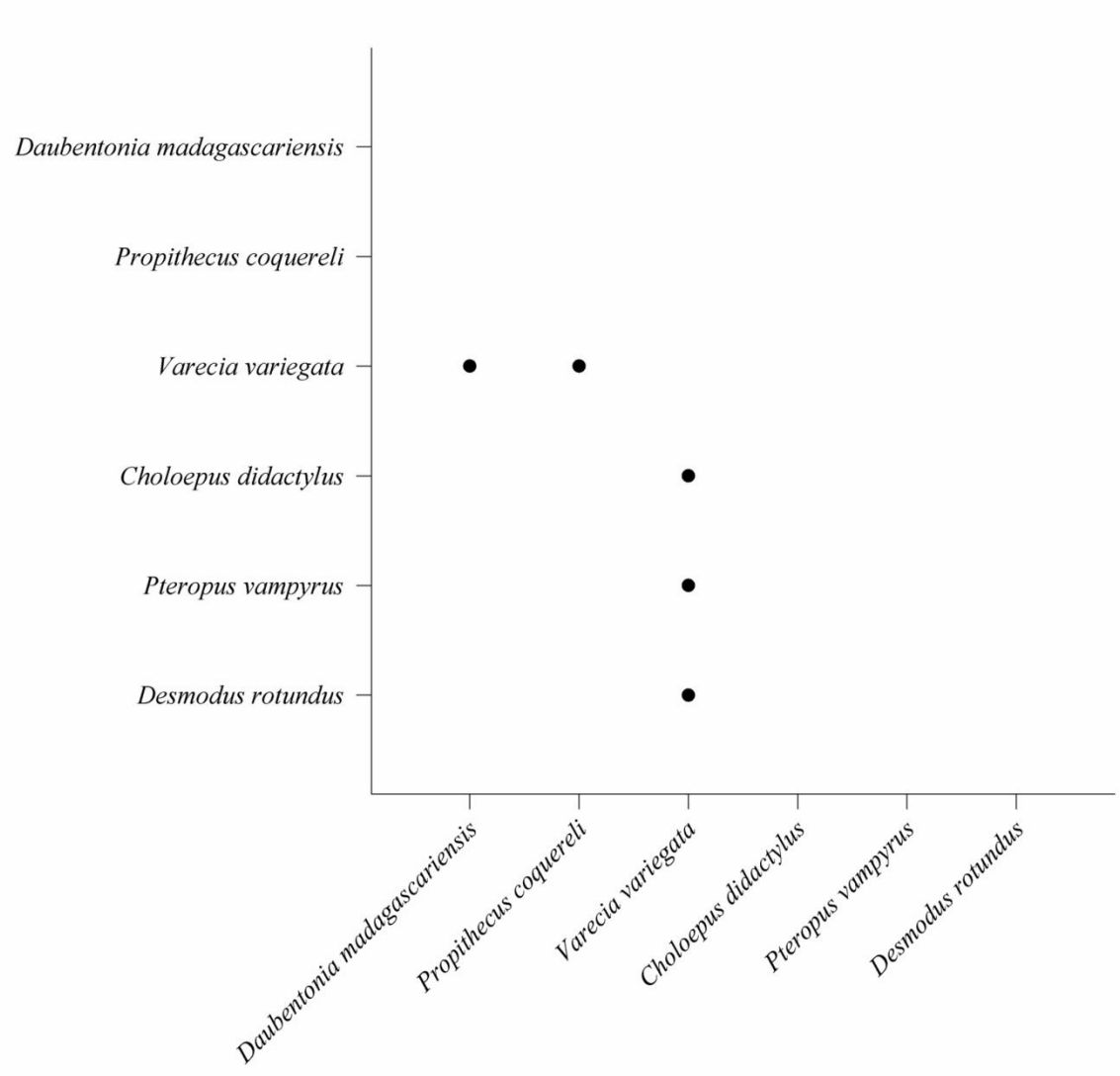

Figure 52: Multiple statistical comparisons between the timing of first occurring horizontal peak in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

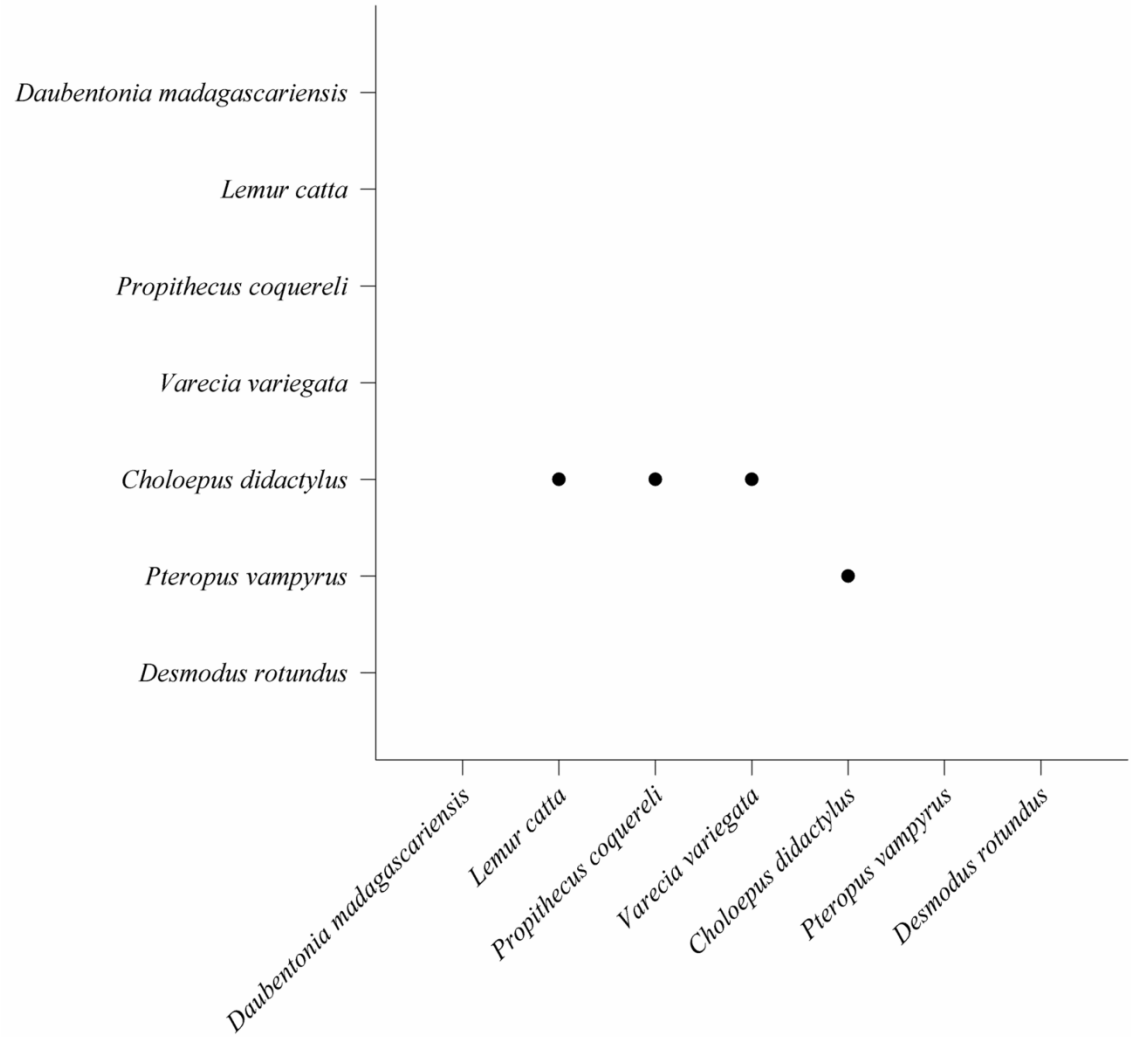

Figure 53: Multiple statistical comparisons between the timing of second occurring horizontal peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

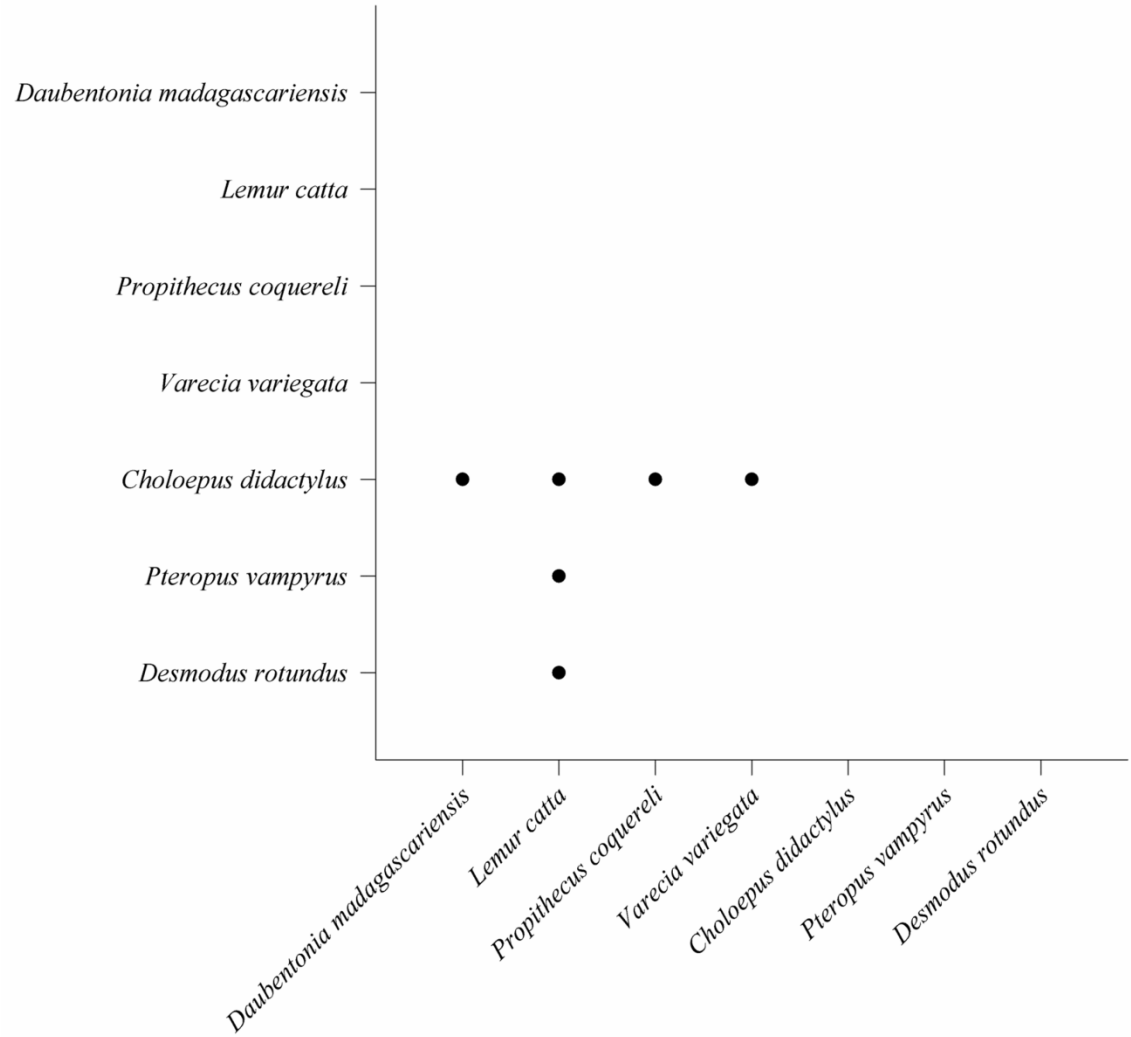

Figure 54: Multiple statistical comparisons between the timing of propulsive to braking transition in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

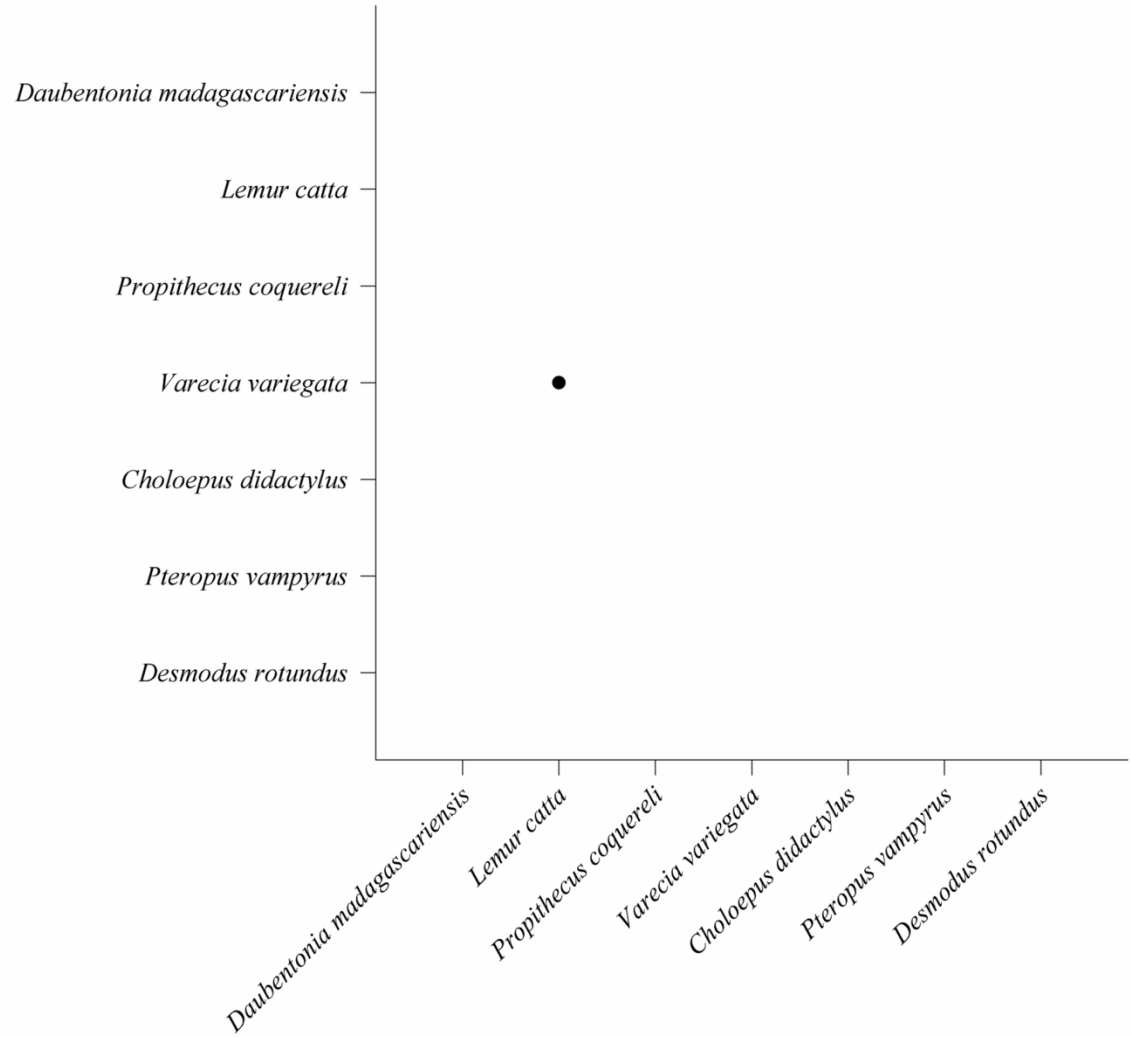

Figure 55: Multiple statistical comparisons between the timing of propulsive to braking transition in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

During below branch quadrupedal walking, all species displayed a positive net HI in the forelimbs and negative net HI in the hindlimbs, meaning that the forelimbs were net propulsive whereas the hindlimbs were net braking (Figure 56). The only significant differences observed between any of the species was the forelimb and hindlimb impulses observed in *C. didactylus*, which were quite large due to the tendency for extremely slow and careful movement in this species (Figures 57-58).

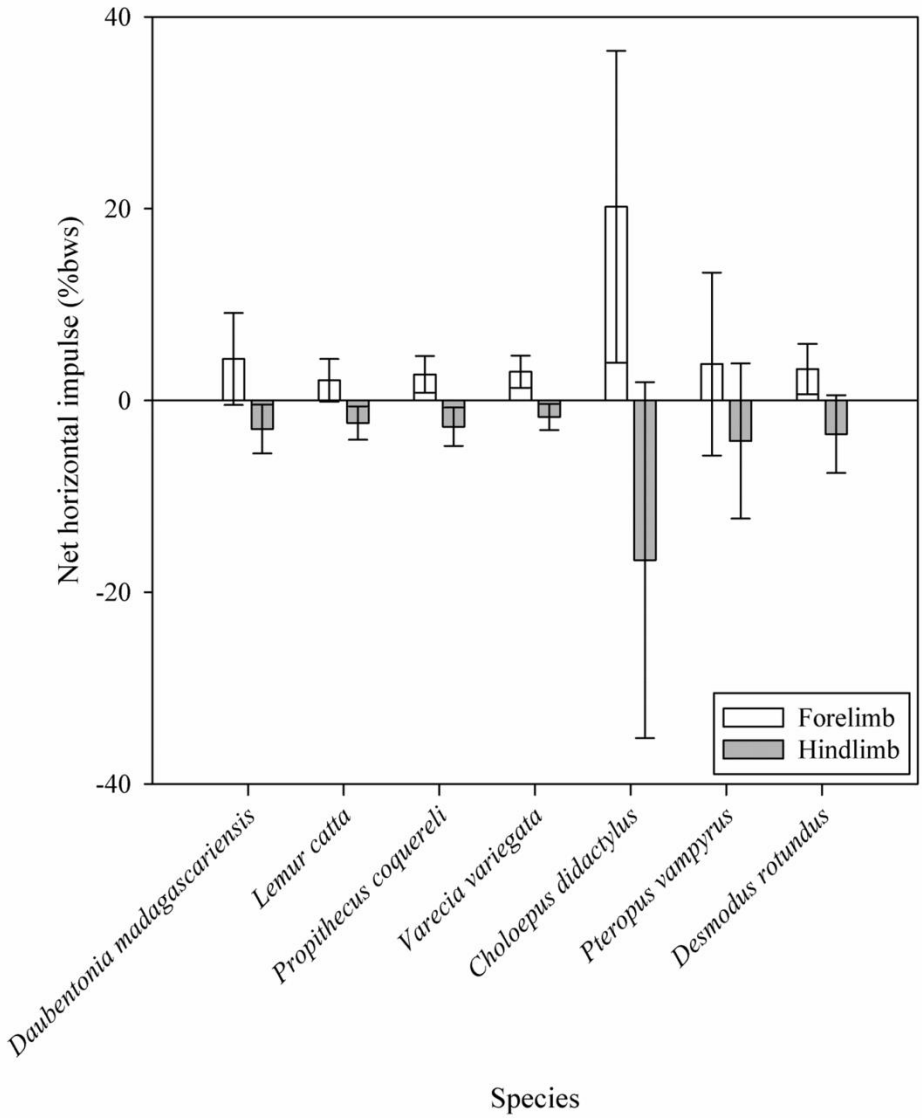

Figure 56: Mean and standard deviation values of the net horizontal impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

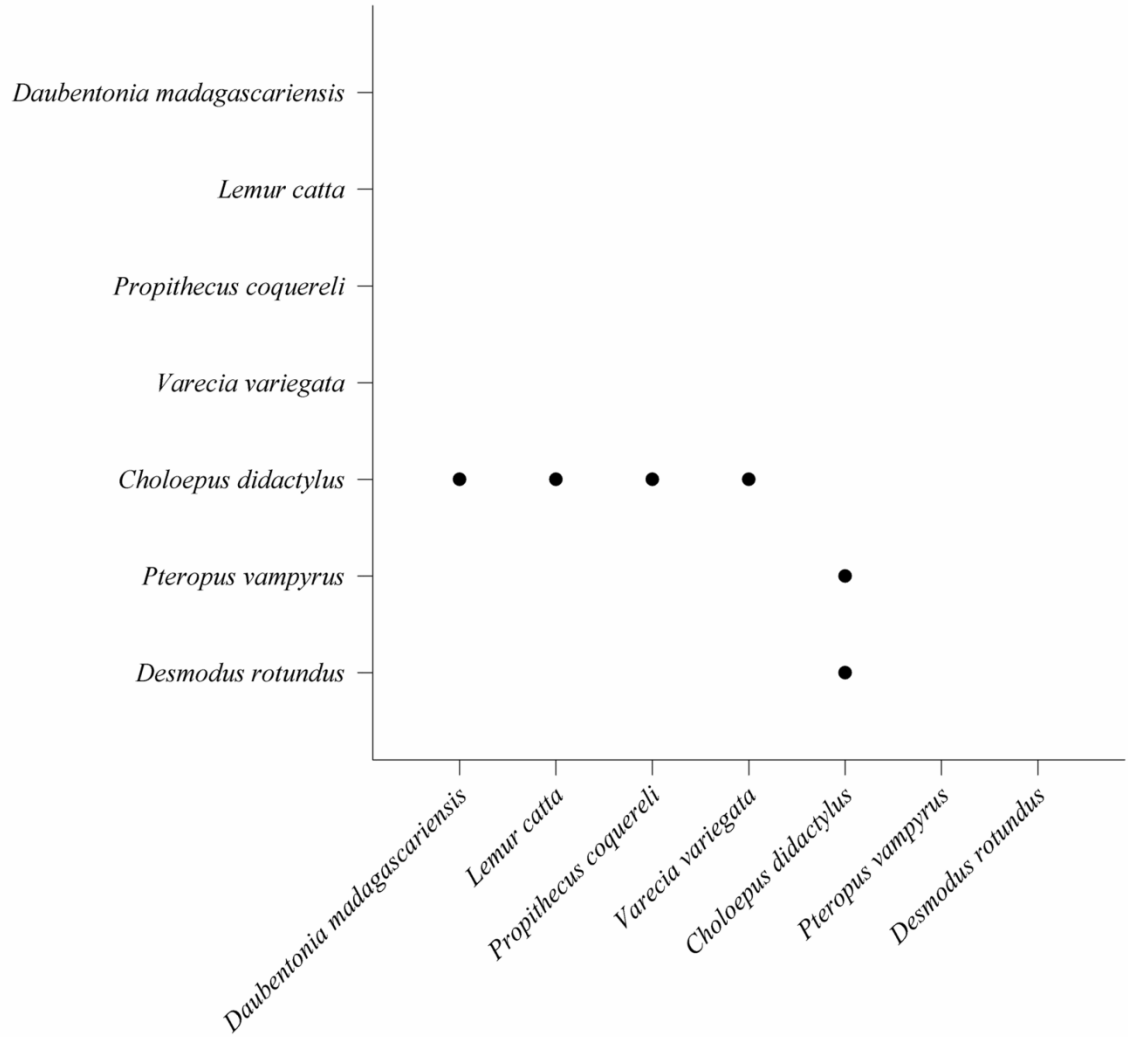

Figure 57: Multiple statistical comparisons between the horizontal impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

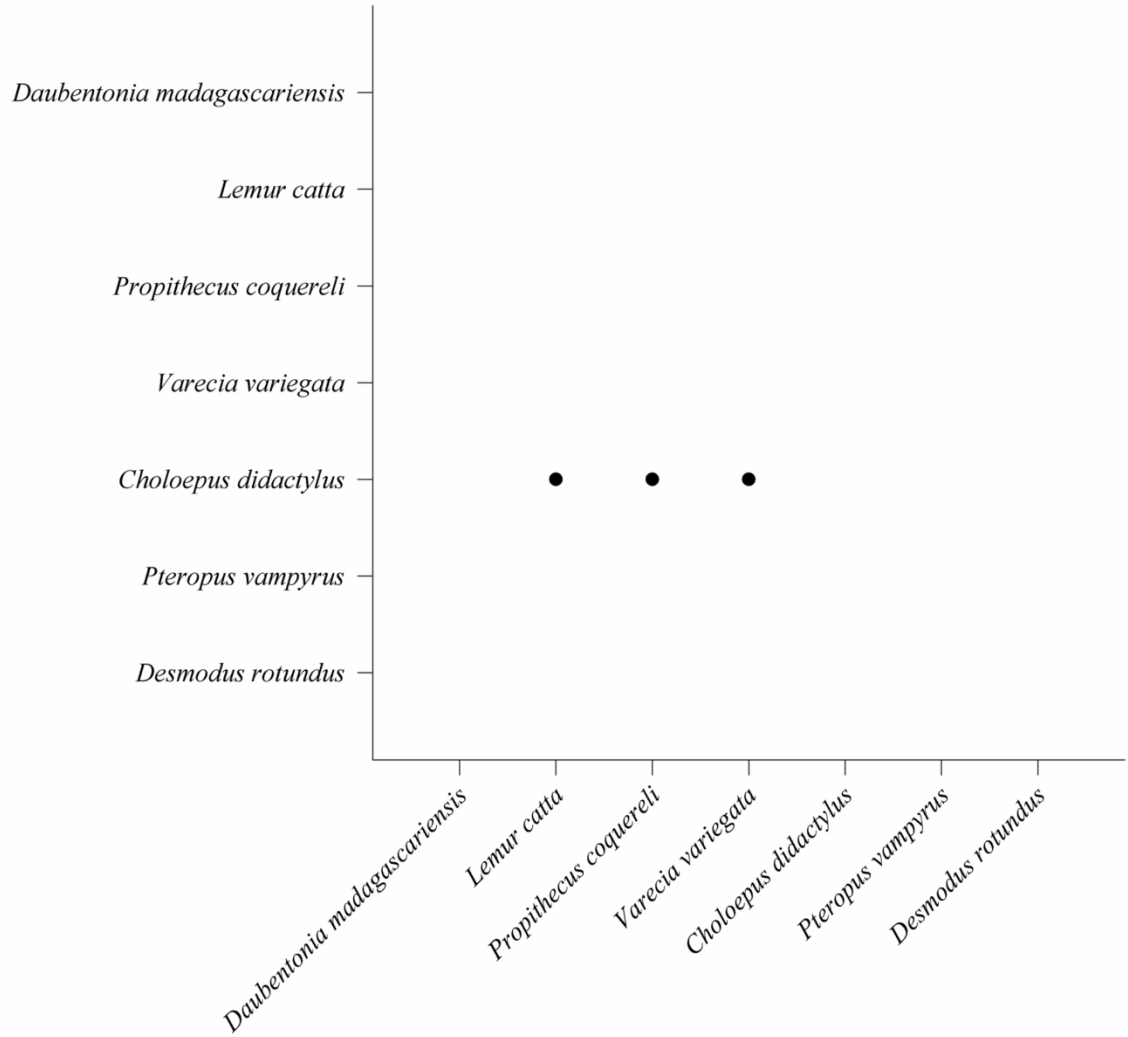

Figure 58: Multiple statistical comparisons between the horizontal impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

The analysis of the first occurring horizontal impulse (Figure 59) and the second occurring horizontal impulse (Figure 60) separately for each limb showed that during below branch quadrupedal walking, the first occurring horizontal impulse was associated with a propulsive force in both limbs, and was significantly greater in the forelimb when compared to the hindlimb for all species. The second occurring horizontal impulse was associated with a braking impulse in both limbs, and was significantly greater in the hindlimb than the forelimb in all species. As with HI, most differences between FHI and SHI were between *C. didactylus* and the other species, but other notable distinctions were present. In regards to FHI, significant differences between species were only present in the forelimb (Figure 61). *Choloepus didactylus* showed a significantly greater FHI than all other species, and *D. madagascariensis* showed a significantly greater FHI than *L. catta* and *D. rotundus*. In regards to SHI, significant differences between species were present in both limbs. In the forelimb, *D. madagascariensis* showed a significantly greater SHI than *D. rotundus*, *C. didactylus*, and *V. variegata*, and *D. rotundus* showed a significantly greater FHI than *L. catta* and *P. coquereli* (Figure 62). In the hindlimb, *C. didactylus* showed a significantly greater FHI than all other species except *D. rotundus* (Figure 63).

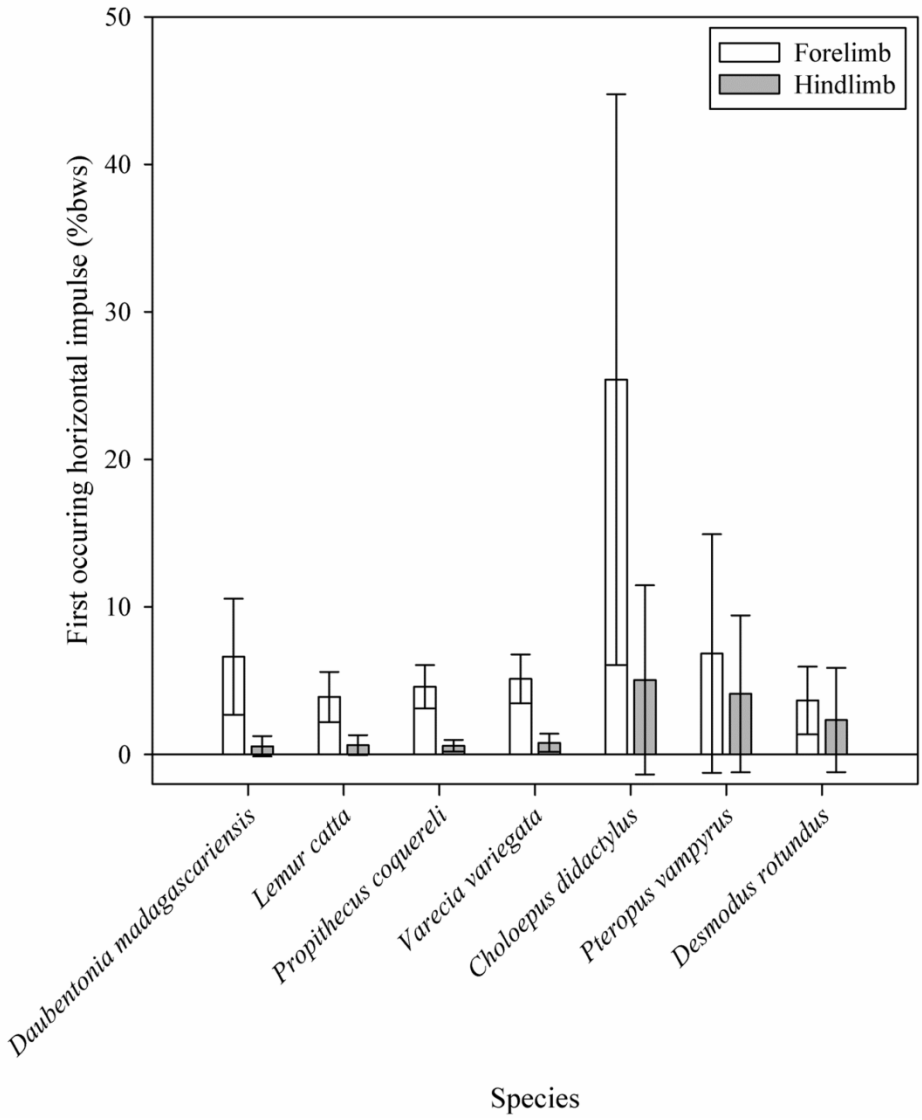

Figure 59: Mean and standard deviation values of the first occurring horizontal impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

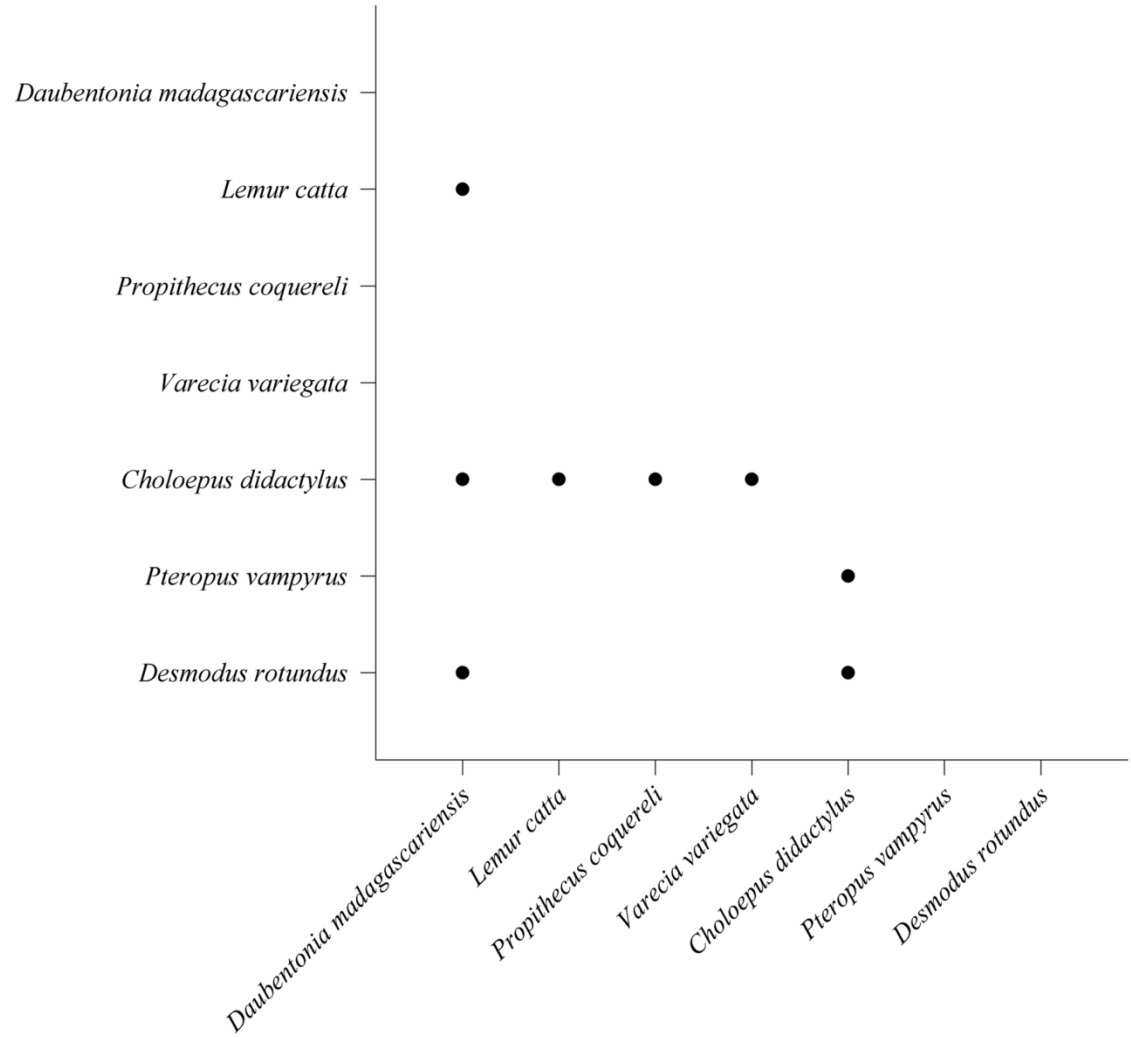

Figure 60: Multiple statistical comparisons between the first occurring horizontal impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

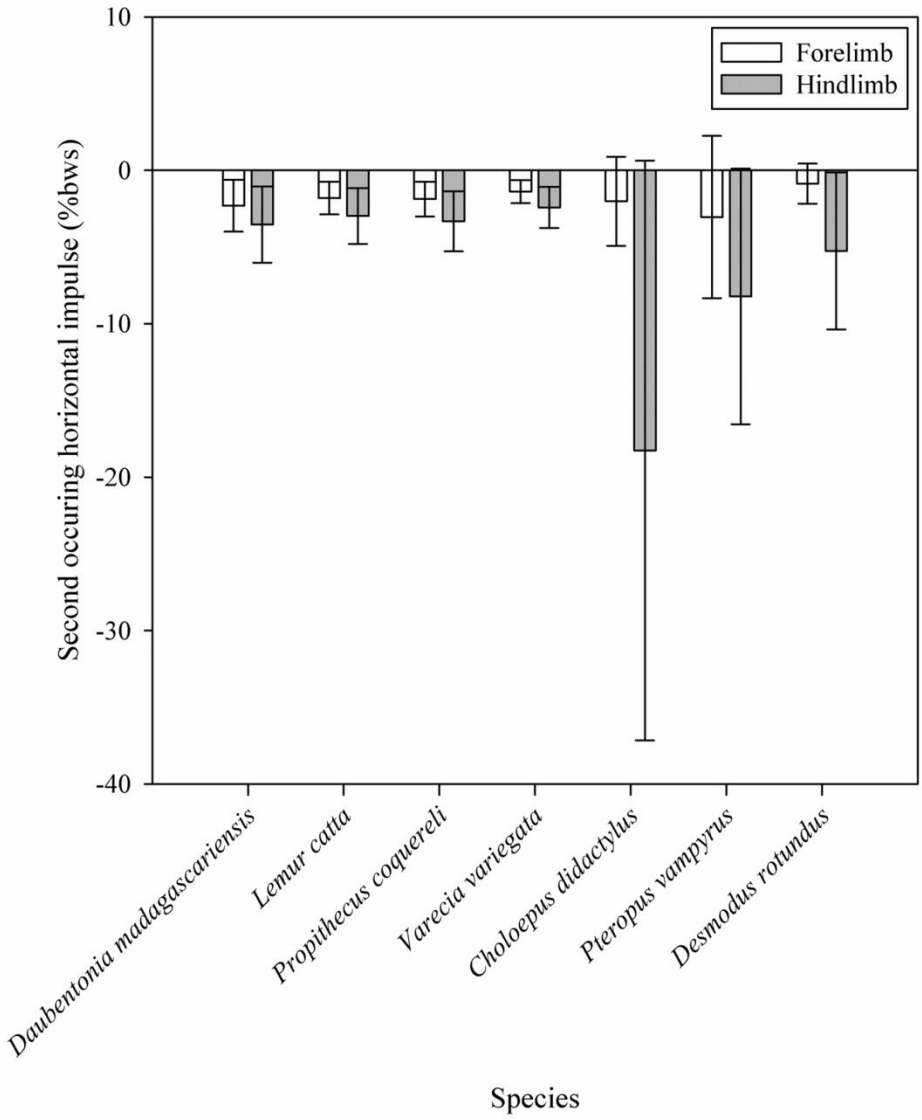

Figure 61: Mean and standard deviation values of the second occurring horizontal impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

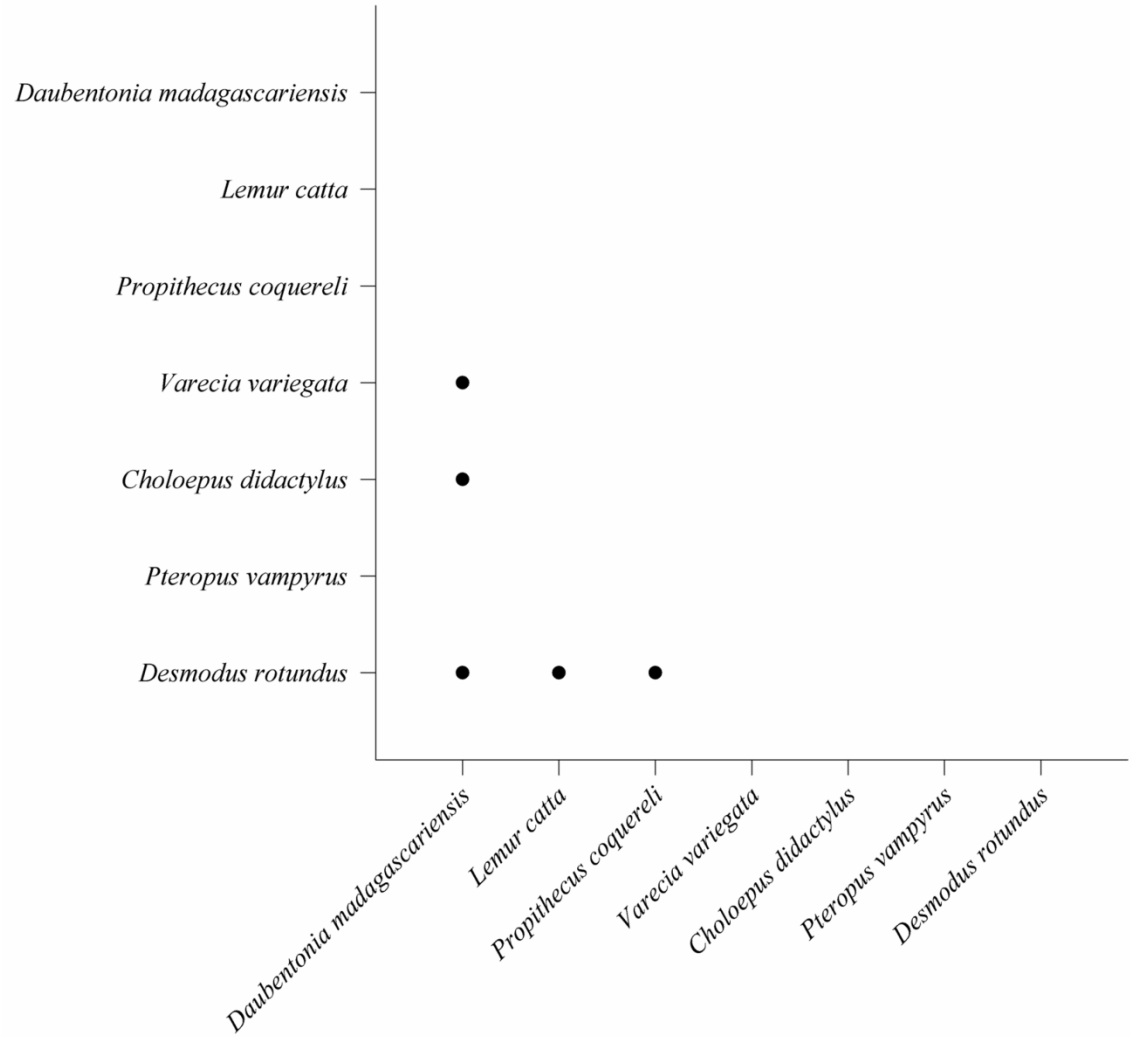

Figure 62: Multiple statistical comparisons between the second occurring horizontal impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

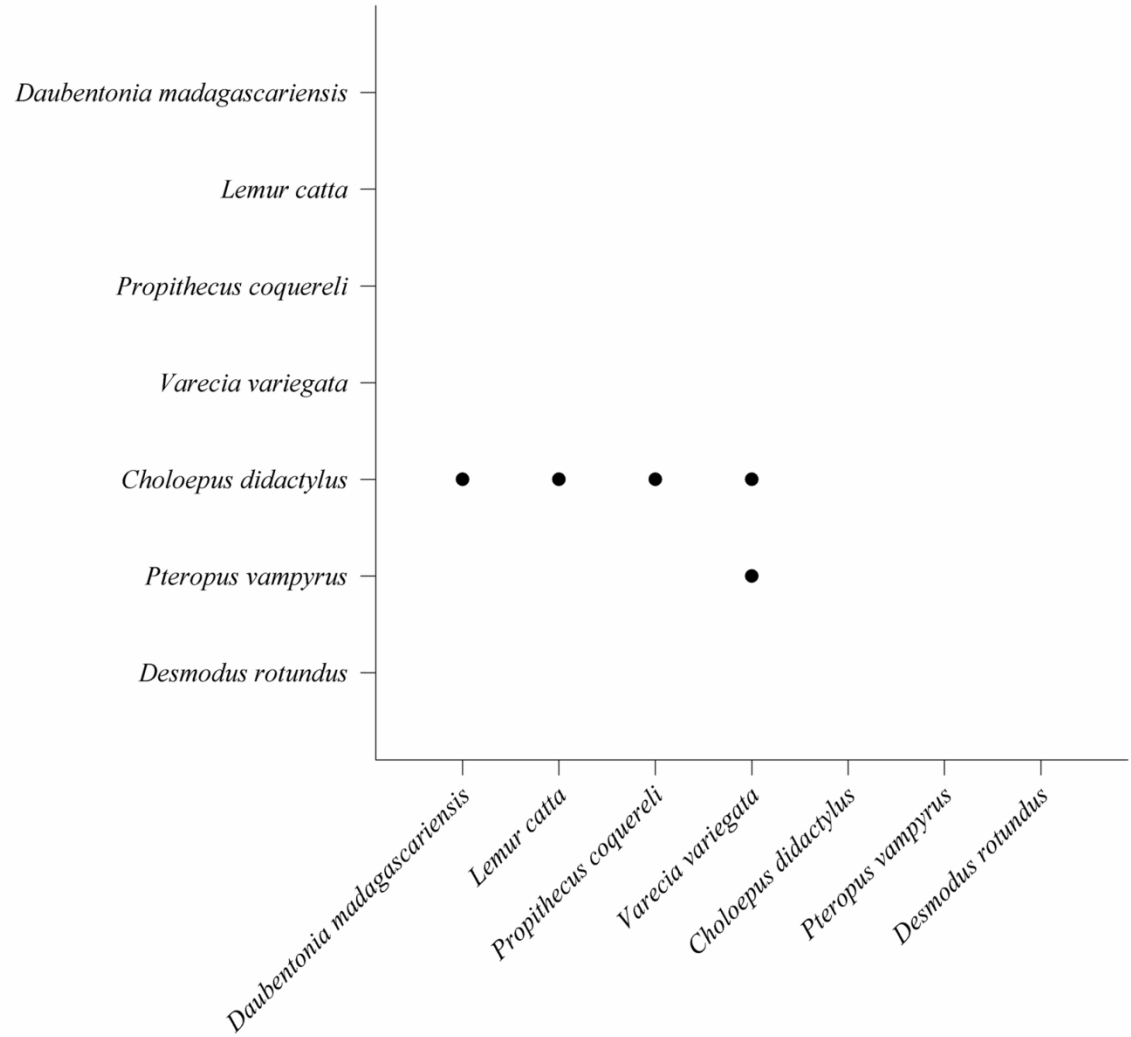

Figure 63: Multiple statistical comparisons between the second occurring horizontal impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

In all species, the mediolateral force component was dominated by medially directed forces. This means that animals applied a medially directed force to the substrate during support phase. These forces were highly variable and low in comparison to vertical and horizontal forces (Figures 64-77). In general Mpk and Lpk were highly variable, but some significant differences between species were observed. Similarly, mediolateral impulse measures were also highly variable, but there was a tendency for greater MI, LI, and MLI in non-primate mammals. Most of the observed statistical differences observed between taxa were driven by the unusually slow movement of the *C. didactylus*. The timings associated with Lpk and Mpk were inconsistent and did not demonstrate any identifiable patterns, and only one significant difference was observed between any of the species and limbs (Figure 78).

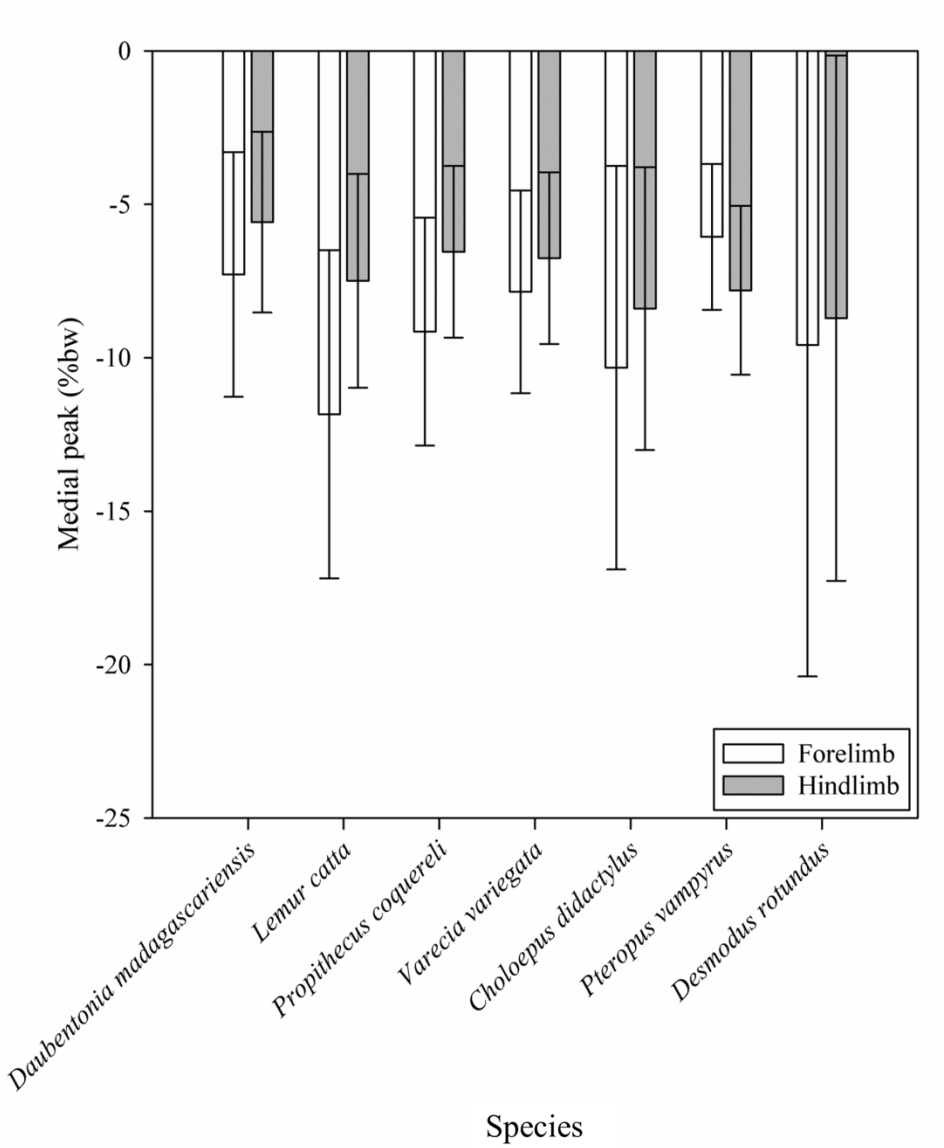

Figure 64: Mean and standard deviation values of peak medial forces in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

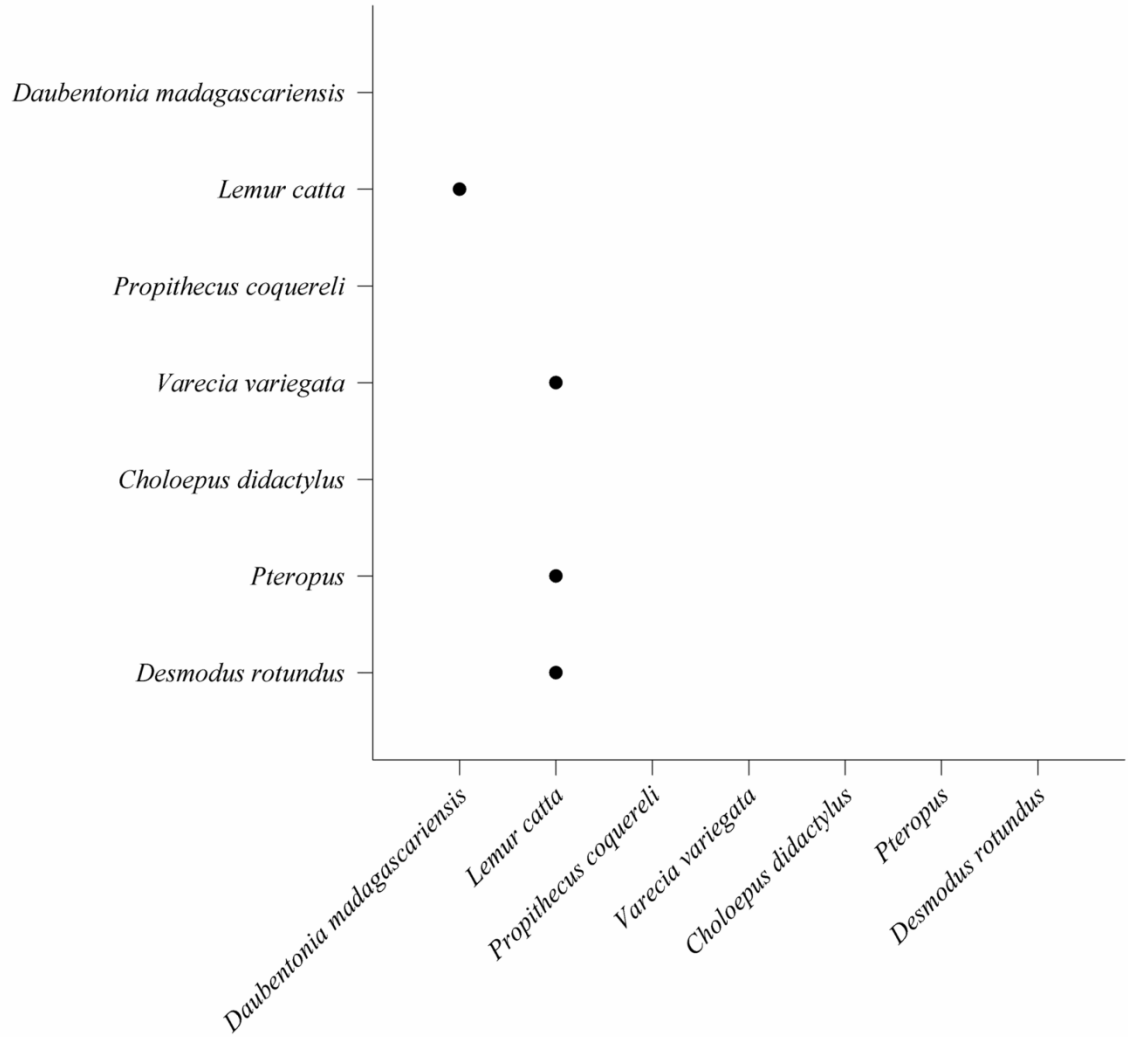

Figure 65: Multiple statistical comparisons between the medial peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

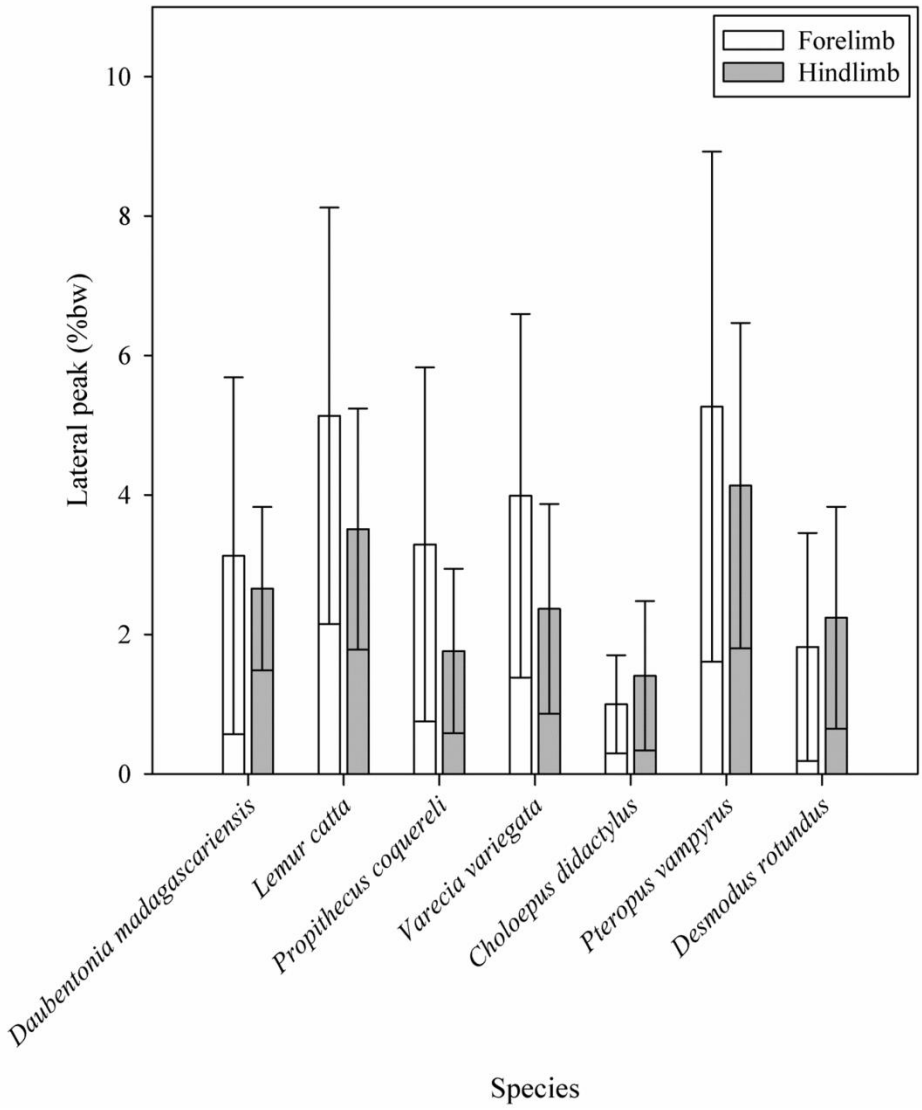

Figure 66: Mean and standard deviation values of lateral peak in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

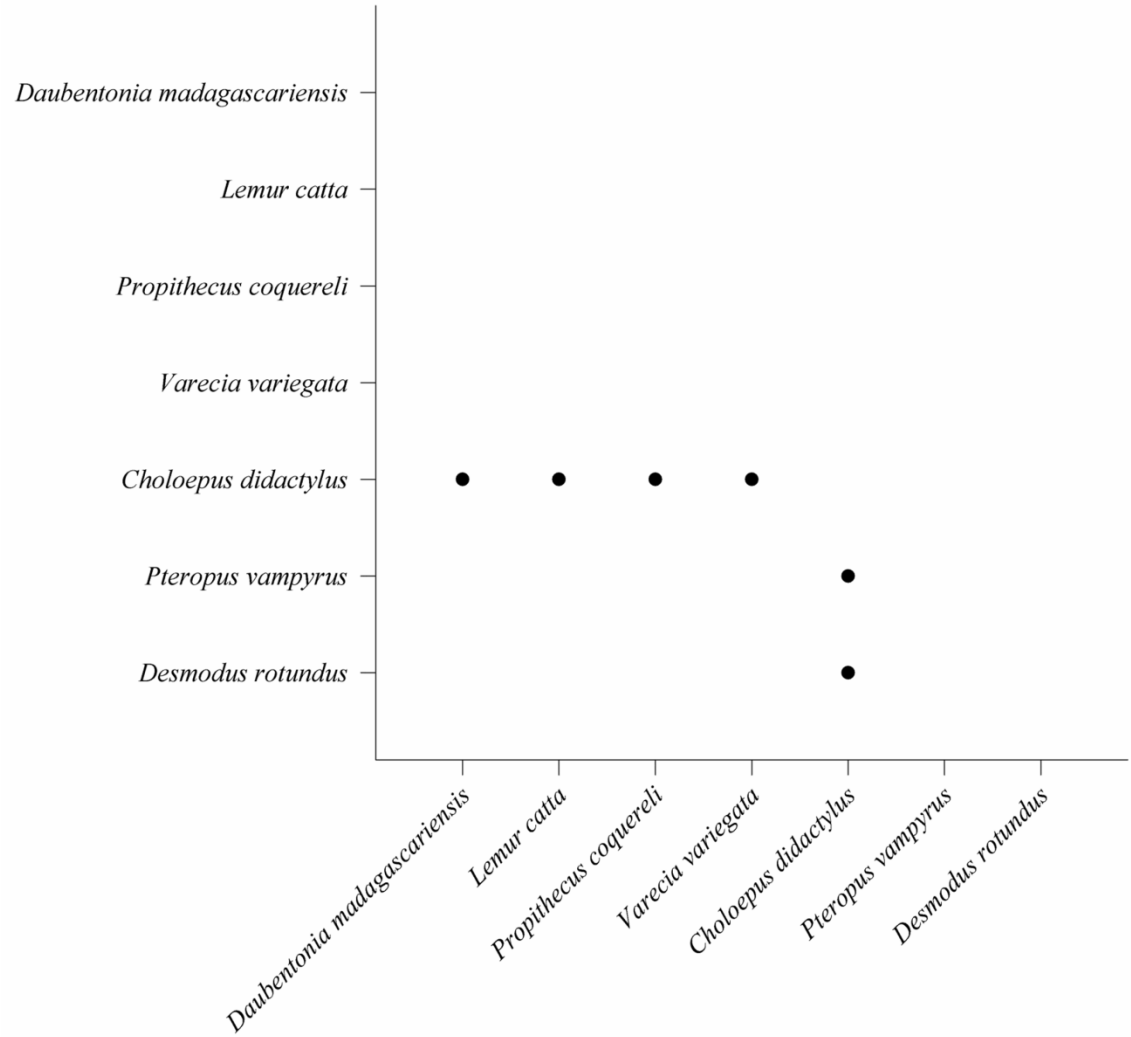

Figure 67: Multiple statistical comparisons between the lateral peak in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

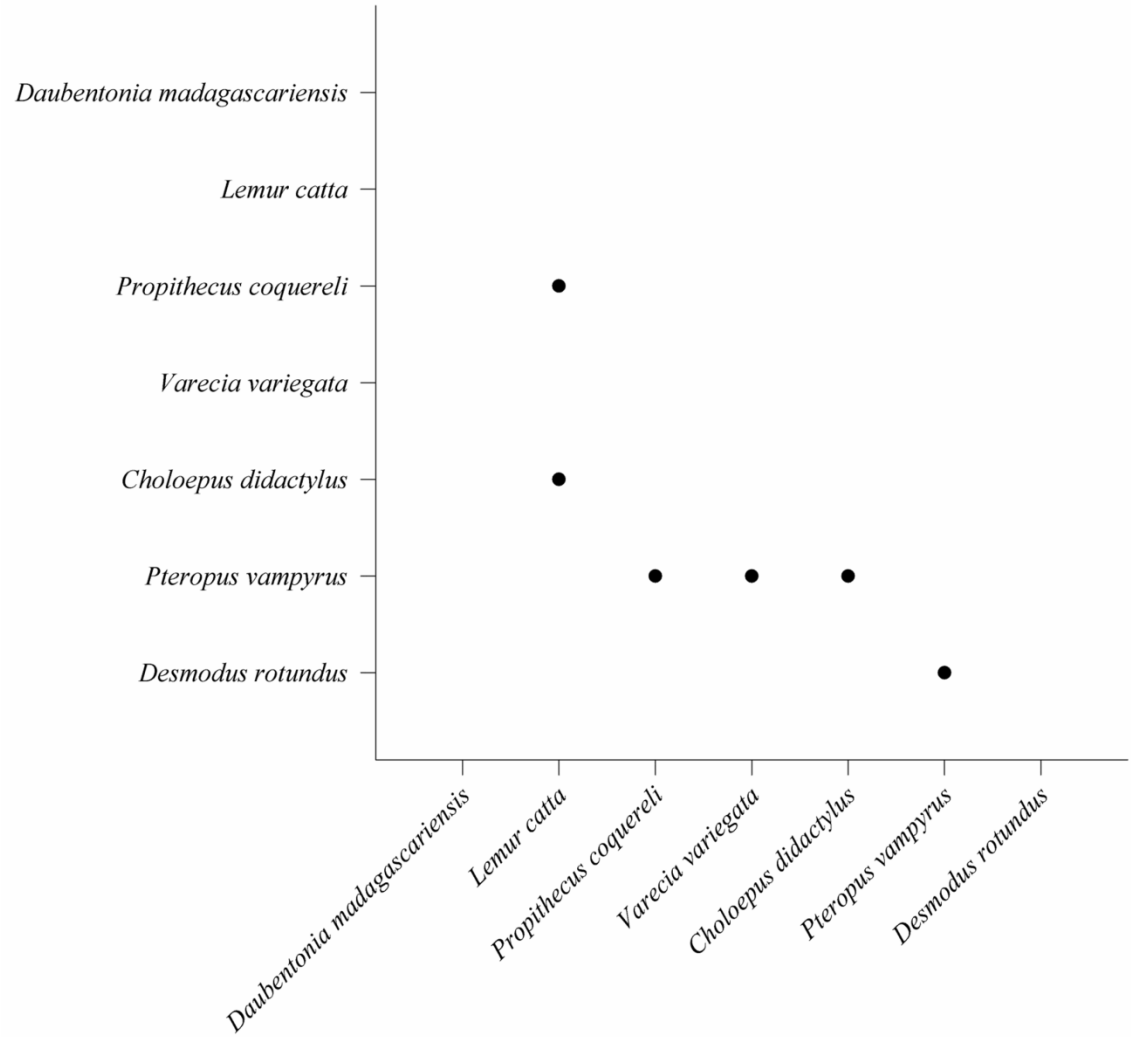

Figure 68: Multiple statistical comparisons between the lateral peak in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

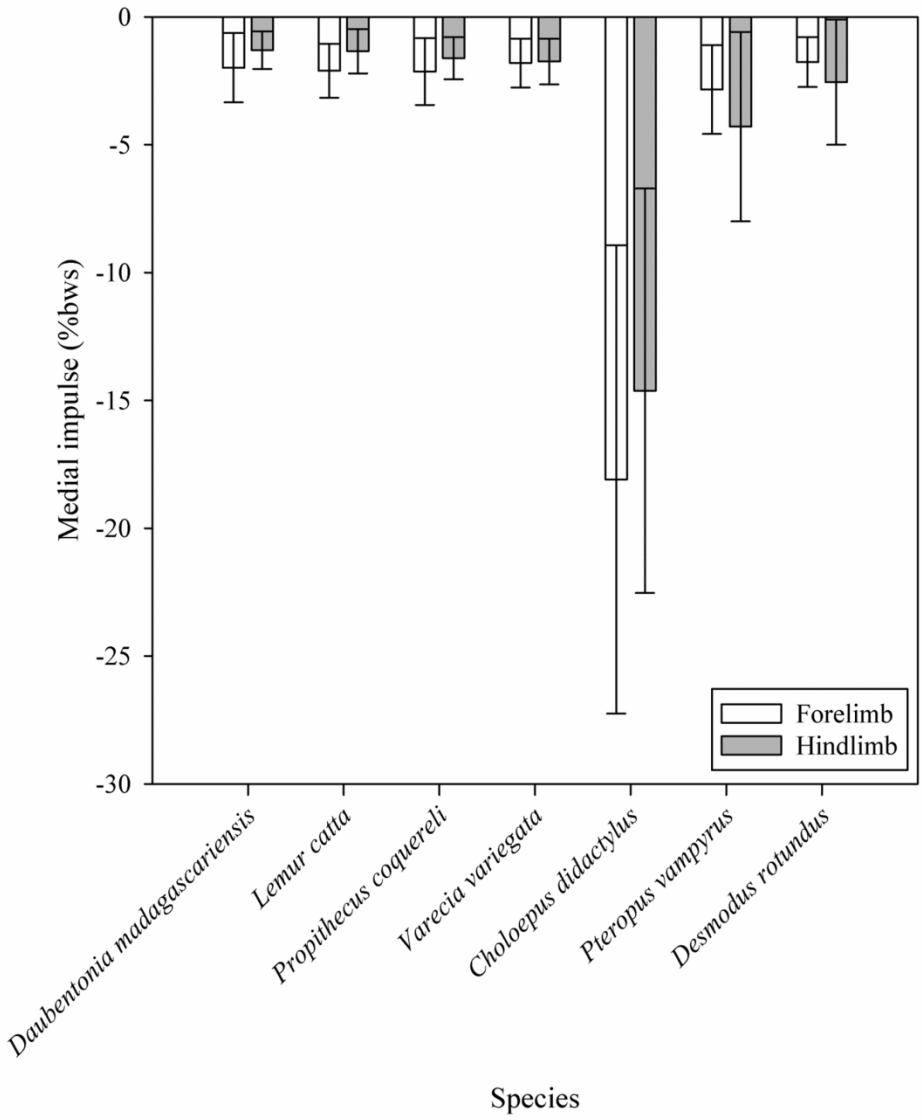

Figure 69: Mean and standard deviation values of the medial impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

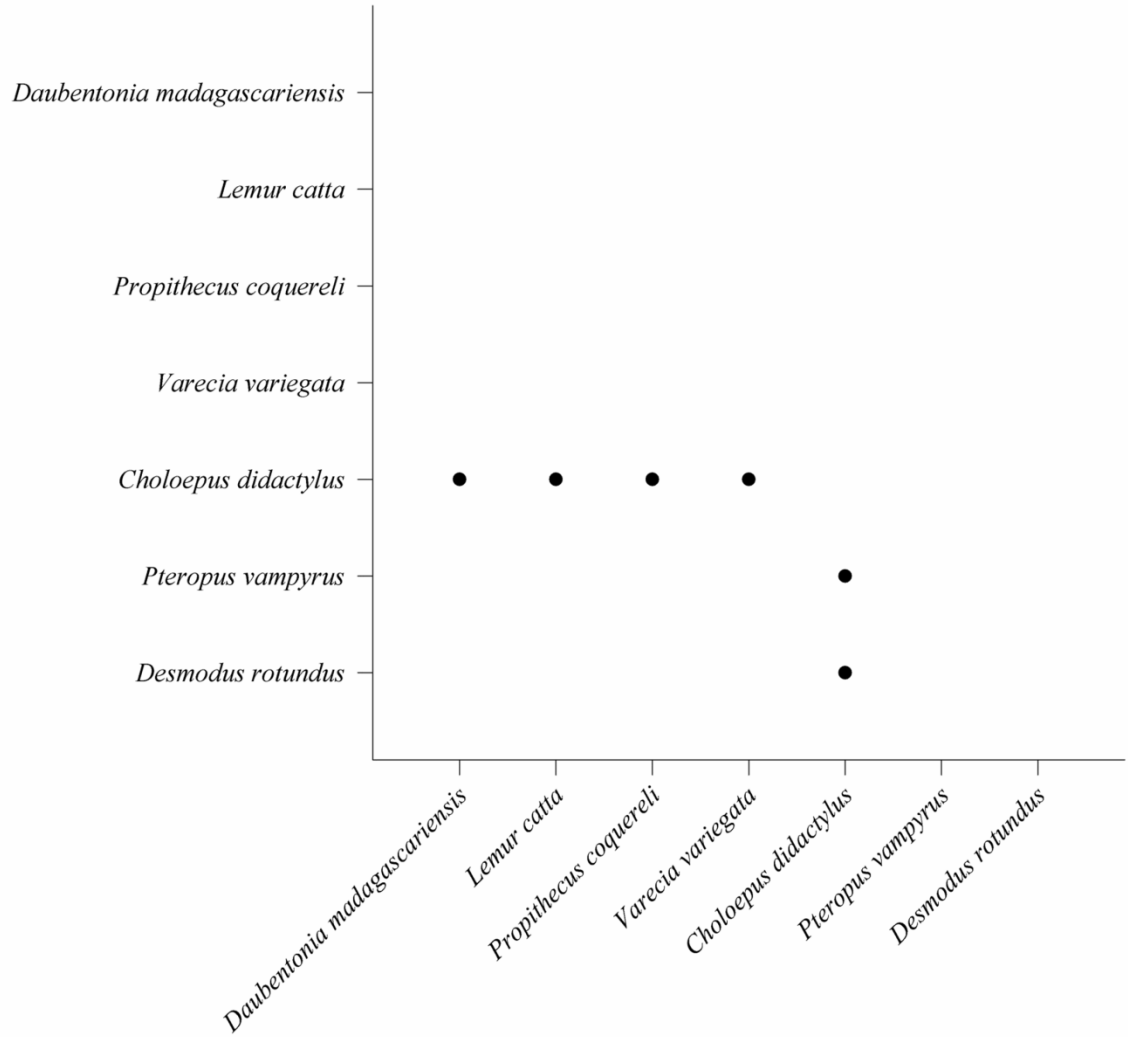

Figure 70: Multiple statistical comparisons between the medial impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

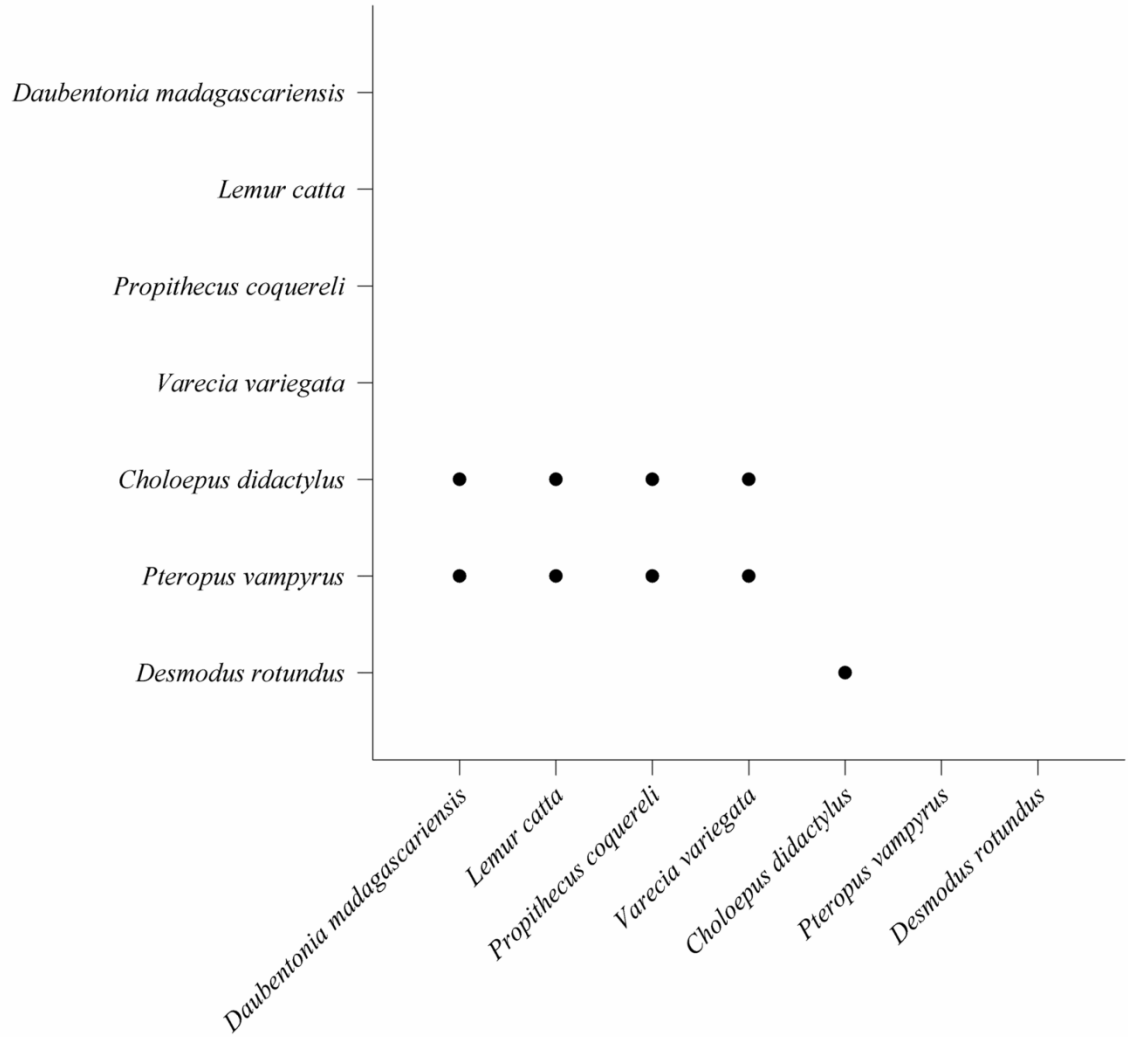

Figure 71: Multiple statistical comparisons between the medial impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

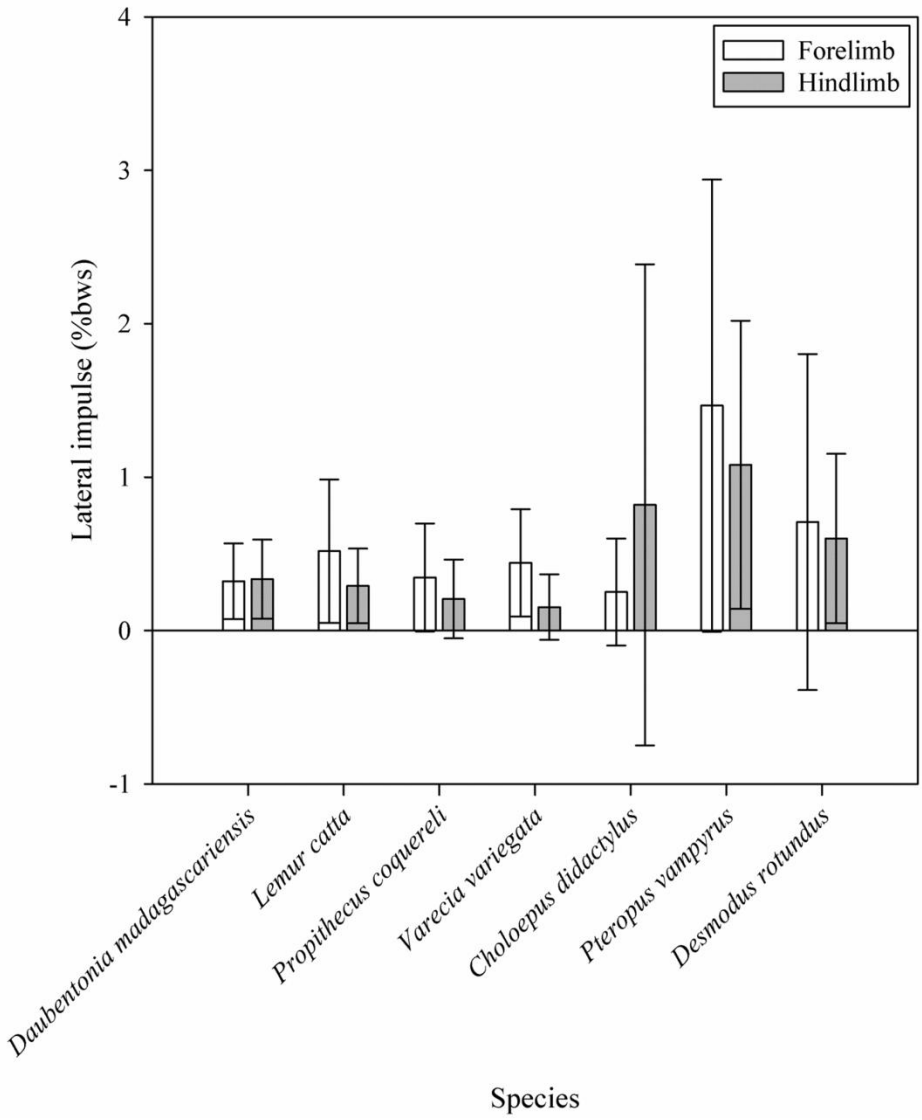

Figure 72: Mean and standard deviation values of the lateral impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

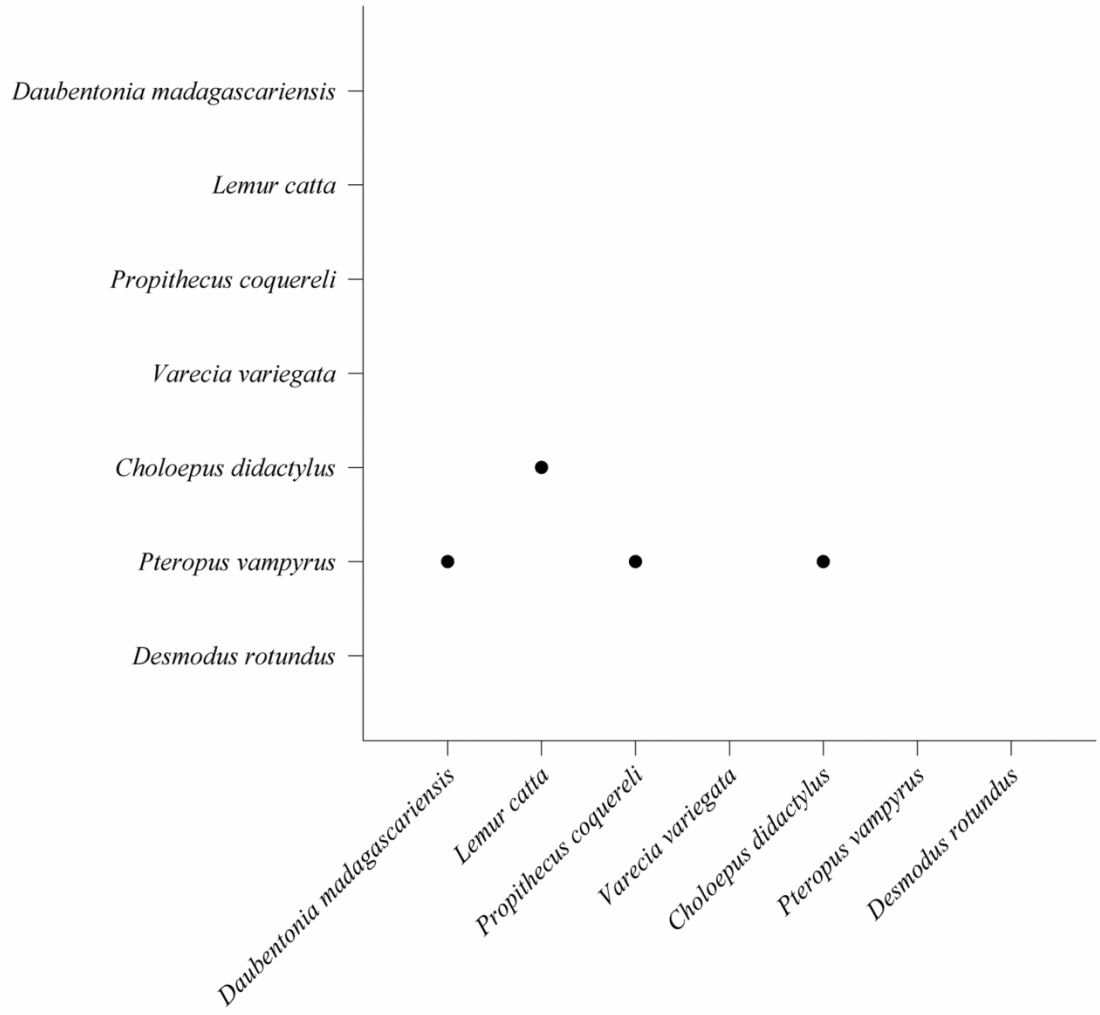

Figure 73: Multiple statistical comparisons between the lateral impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

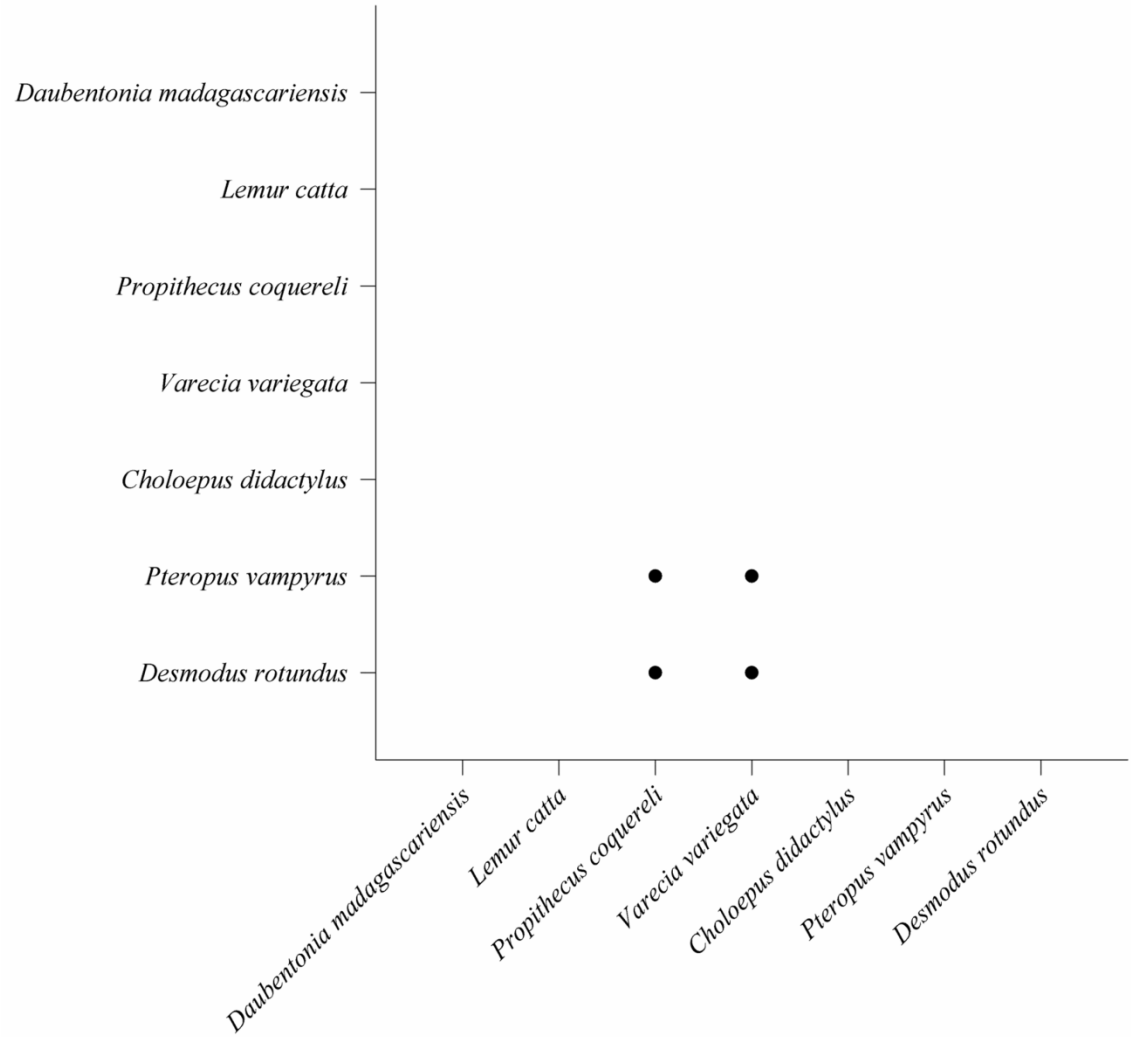

Figure 74: Multiple statistical comparisons between the lateral impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

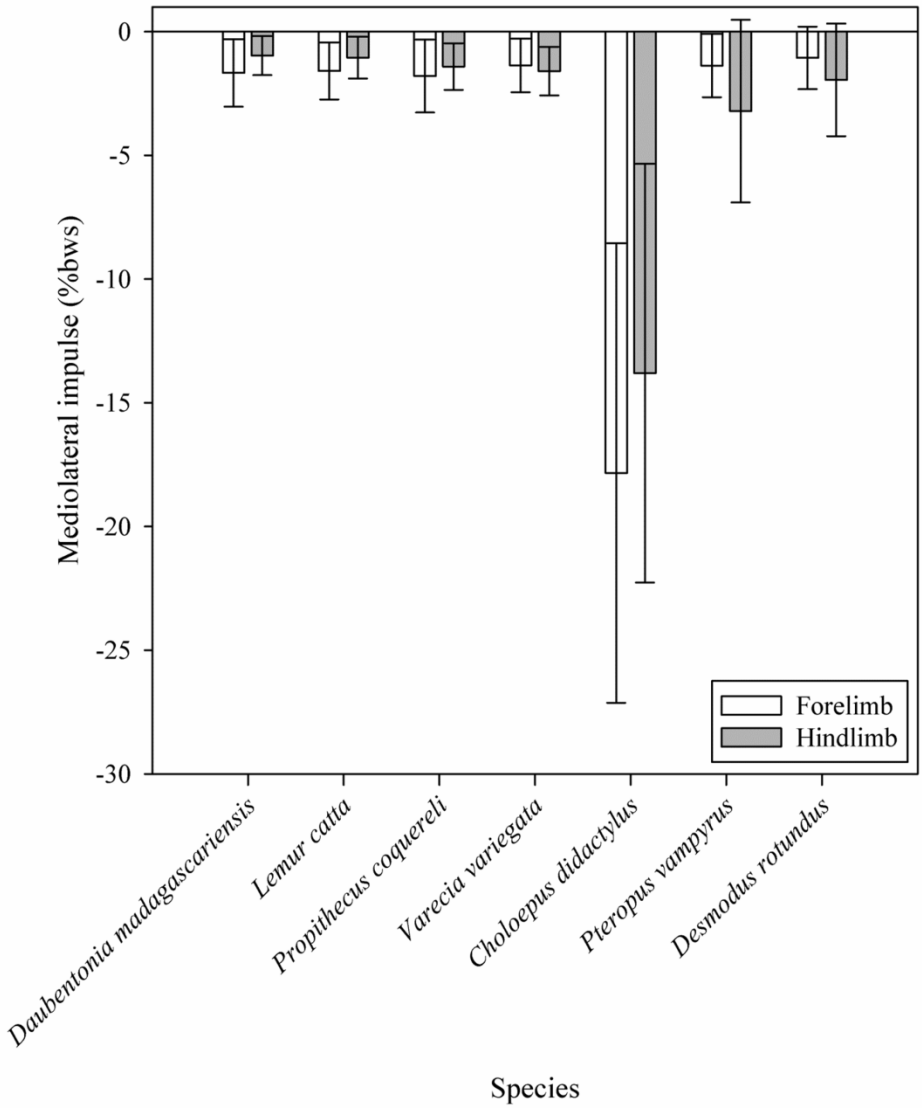

Figure 75: Mean and standard deviation values of the mediolateral impulse in the forelimbs and hindlimbs in primate and non-primate mammals during below branch quadrupedal locomotion. All data presented as a percentage of the animals body weight (%bw).

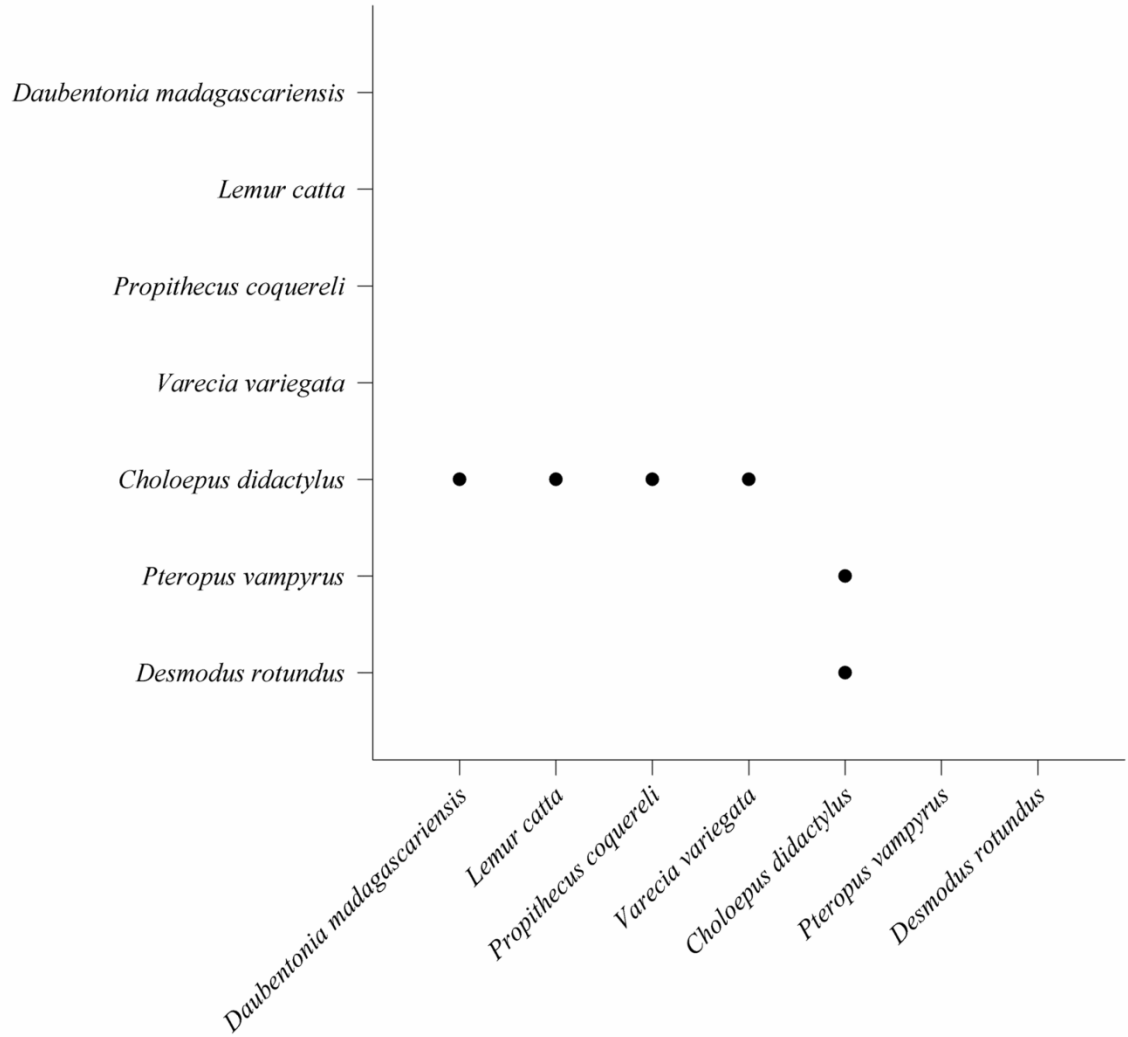

Figure 76: Multiple statistical comparisons between the mediolateral impulse in the forelimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

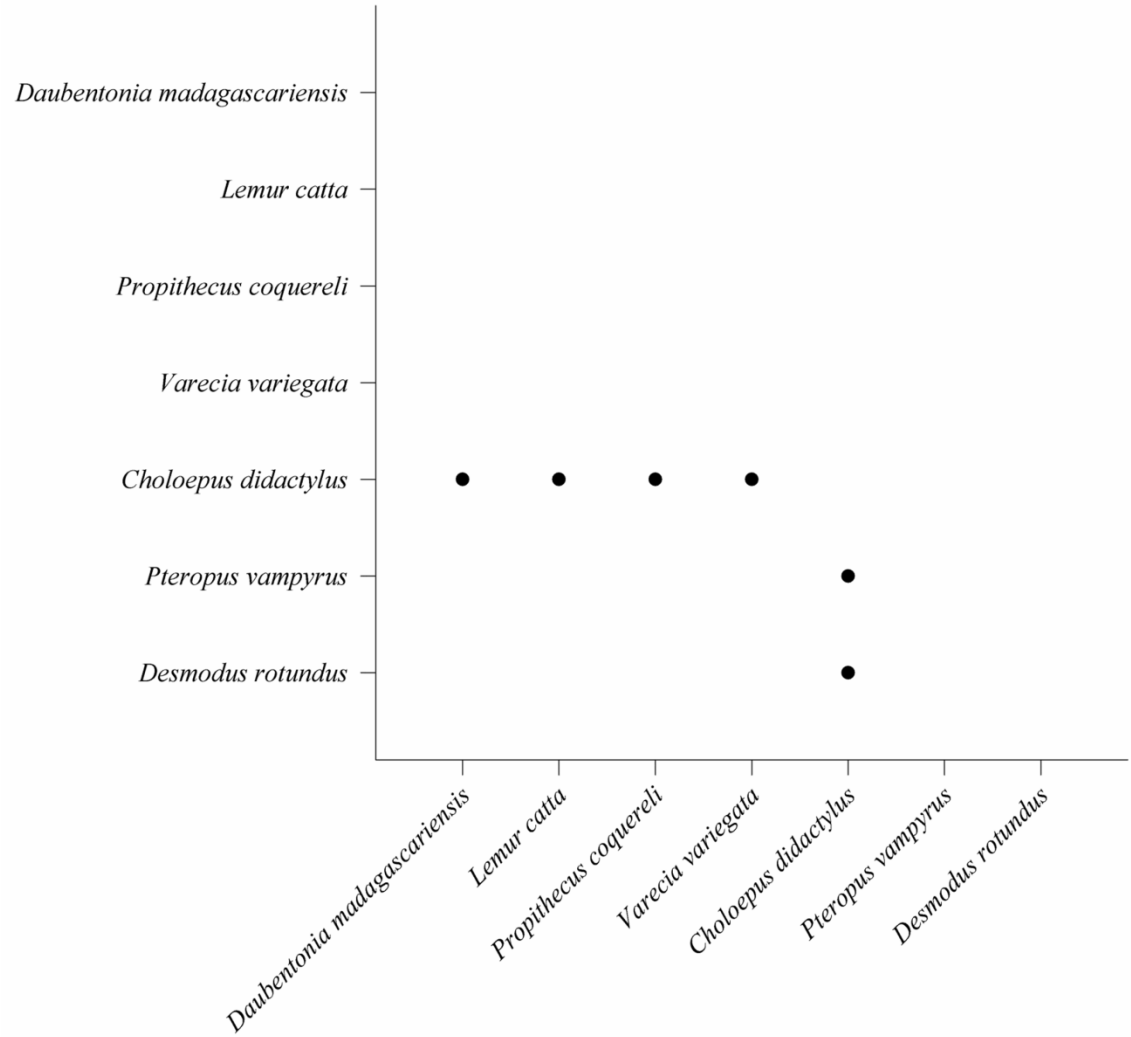

Figure 77: Multiple statistical comparisons between the mediolateral impulse in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

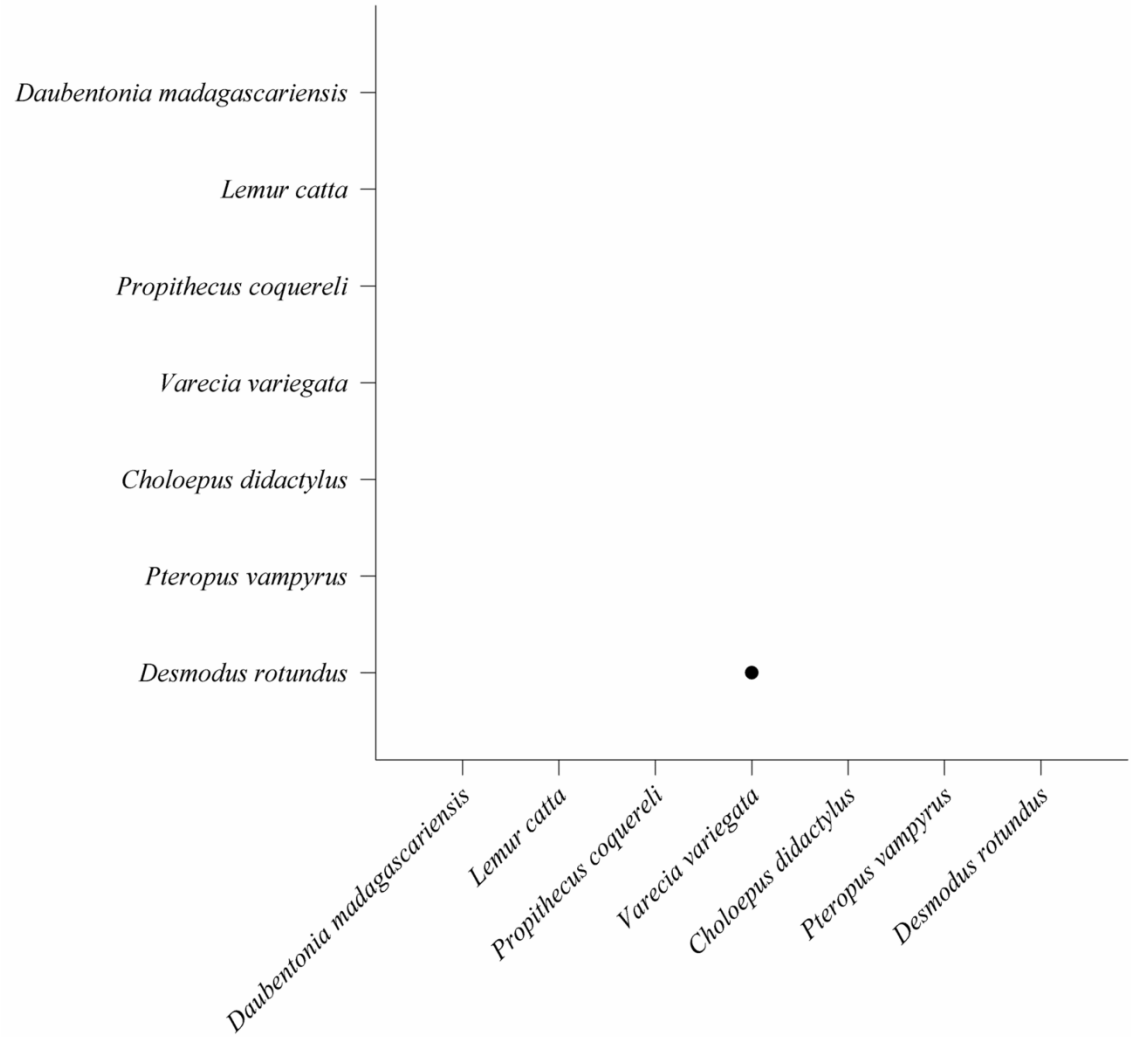

Figure 78: Multiple statistical comparisons between the timing of the lateral peak in the hindlimbs of primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

3.2.2 Kinematics

In total, 178 strides were used for kinematic analysis. Table 9 summarizes the number of strides collected per limb for each species, and data for touchdown angle, mid-support angle, end of support phase angle, and joint excursion. Overall, kinematic movements of the all measured joints, and the overall excursion observed at those joints, tended to be fairly similar across all species during below branch quadrupedal locomotion, although there were exceptions.

Table 9: Mean and standard deviation values for kinematic gait variables collected during above below branch quadrupedal locomotion in primate and non-primate mammals.

Species	Joint	N	Touchdown angle (°)	Mid-support angle (°)	End of support phase angle (°)	Joint excursion (°)
Cebus capucinus	Shoulder	6	-3.27 ± 5.92	-56.75 ± 12.33	-70.38 ± 5.35	80.39 ± 4.25
	Elbow	6	128.54 ± 9.70	104.67 ± 10.23	132.84 ± 7.43	41.51 ± 7.78
	Wrist	6	171.97 ± 7.26	185.59 ± 5.11	178.33 ± 7.03	29.89 ± 5.61
	Hip	6	54.07 ± 4.83	31.25 ± 3.46	-12.41 ± 3.98	67.69 ± 4.31
	Knee	6	107.91 ± 8.84	90.12 ± 6.17	121.51 ± 4.23	35.00 ± 10.33
	Ankle	6	236.67 ± 5.75	254.86 ± 6.57	240.21 ± 11.43	27.59 ± 5.91
Daubentonia madagascariensis	Shoulder	30	4.35 ± 10.23	-48.37 ± 10.25	-80.04 ± 9.42	85.57 ± 11.17
	Elbow	30	121.86 ± 17.90	102.06 ± 13.94	119.76 ± 10.37	32.25 ± 13.54
	Wrist	30	175.11 ± 13.17	192.43 ± 11.08	206.07 ± 11.53	36.23 ± 11.30
	Hip	30	60.04 ± 8.84	27.92 ± 11.17	-28.68 ± 7.78	90.04 ± 11.10
	Knee	30	90.88 ± 11.19	92.43 ± 10.68	137.33 ± 9.26	55.34 ± 10.96
	Ankle	30	237.42 ± 9.38	241.93 ± 5.15	238.00 ± 7.06	15.90 ± 6.31
Lemur catta	Shoulder	30	1.36 ± 15.99	-48.41 ± 15.73	-77.98 ± 5.54	80.59 ± 18.32
	Elbow	30	122.89 ± 16.39	112.82 ± 12.81	126.12 ± 8.27	27.45 ± 15.20
	Wrist	30	172.35 ± 11.08	192.72 ± 7.62	190.63 ± 6.57	30.61 ± 11.35
	Hip	30	51.49 ± 7.13	25.59 ± 8.55	-6.32 ± 12.43	58.07 ± 9.71
	Knee	30	83.84 ± 9.96	87.64 ± 12.41	117.96 ± 18.42	40.53 ± 16.19
	Ankle	30	261.82 ± 7.85	263.38 ± 6.82	239.85 ± 10.90	27.96 ± 7.70
Propithecus coquereli	Shoulder	30	-18.57 ± 13.16	-65.91 ± 10.87	-85.34 ± 5.65	68.96 ± 11.86
	Elbow	30	95.84 ± 15.03	90.35 ± 11.10	107.00 ± 11.87	23.24 ± 10.26
	Wrist	30	160.79 ± 7.11	184.57 ± 6.22	194.35 ± 7.17	37.57 ± 8.17
	Hip	30	48.45 ± 6.52	16.76 ± 8.05	-15.30 ± 11.97	64.32 ± 15.36
	Knee	30	68.82 ± 5.99	79.10 ± 8.36	115.78 ± 15.41	51.87 ± 17.77
	Ankle	30	272.60 ± 6.59	271.54 ± 7.61	238.39 ± 11.86	41.50 ±14.55
Varecia variegata	Shoulder	30	4.82 ± 18.29	-53.78 ± 14.08	-67.78 ± 10.11	87.00 ± 15.62
	Elbow	30	127.94 ± 18.97	104.26 ± 12.59	134.15 ± 11.72	48.84 ± 14.13

	Wrist	30	169.45 ± 12.68	183.73 ± 12.39	176.85 ± 9.01	36.88 ± 14.04
	Hip	30	57.92 ± 6.48	34.78 ± 7.11	-8.22 ± 5.74	67.95 ± 8.04
	Knee	30	109.47 ± 13.65	94.48 ± 13.36	124.08 ± 8.00	35.38 ± 11.92
	Ankle	30	228.74 ± 20.26	245.85 ± 19.03	233.37 ± 17.65	30.01 ± 10.48
Choloepus didactylus	Shoulder	21	-10.57 ± 22.01	-56.48 ± 27.92	-83.05 ± 11.02	79.47 ± 20.50
	Elbow	21	114.06 ± 23.69	92.71 ± 20.28	103.10 ± 13.09	42.53 ± 22.31
	Wrist	21	156.71 ± 14.92	160.22 ± 7.89	173.22 ± 5.93	26.81 ± 8.91
	Hip	21	52.29 ± 10.79	39.59 ± 13.38	-7.58 ± 16.43	63.46 ± 15.30
	Knee	21	135.63 ± 13.11	118.45 ± 13.41	148.45 ± 17.98	39.40 ± 11.85
	Ankle	21	197.23 ± 13.76	203.10 ± 13.34	208.45 ± 11.47	27.82 ± 8.48
Pteropus vampyrus	Shoulder	28	-18.49 ± 10.69	-44.00 ± 15.48	-64.18 ± 19.54	51.42 ± 16.18
	Elbow	28	101.33 ± 12.63	90.60 ± 16.82	84.39 ± 16.59	31.98 ± 9.38
	Wrist	28	124.18 ± 9.73	131.74 ± 7.43	137.38 ± 11.23	23.85 ± 9.09
	Hip	28	65.73 ± 7.07	17.84 ± 17.94	-53.11 ± 8.76	126.68 ± 9.43
	Knee	28	141.05 ± 11.18	156.06 ± 12.14	138.17 ± 11.45	45.35 ± 10.60
	Ankle	28	162.76 ± 14.63	166.17 ± 11.42	176.72 ± 13.04	22.69 ± 5.41

The basic movement at the shoulder was overall quite similar for all species during below branch quadrupedal locomotion (Figure 79). At touchdown, humeral position was either only slightly protracted (*L. catta*, *D. madagascariensis*, and *V. variegata*) or retracted (*C. capucinus*, *P. coquereli*, *C. didactylus*, and *P. vampyrus*) (Figure 80). As support phase continued, the humerus was retracted substantially and even passed beyond the horizontal axis of the body (i.e., shoulder angle below -90°) in some species. At mid-support (Figure 81) and at the end of support phase (Figure 82), the position of the humerus was generally similar for all species, although there were exceptions. Most notable was *P. coquereli*, which showed the greatest level of humeral retraction throughout the stride compared to any other species. Levels of excursion at the shoulder joint were largely similar for most species, with the exception of *P. vampyrus* and *P. coquereli* (Figures 83 and 84), which showed relatively little actual movement of the shoulder compared to the other species.

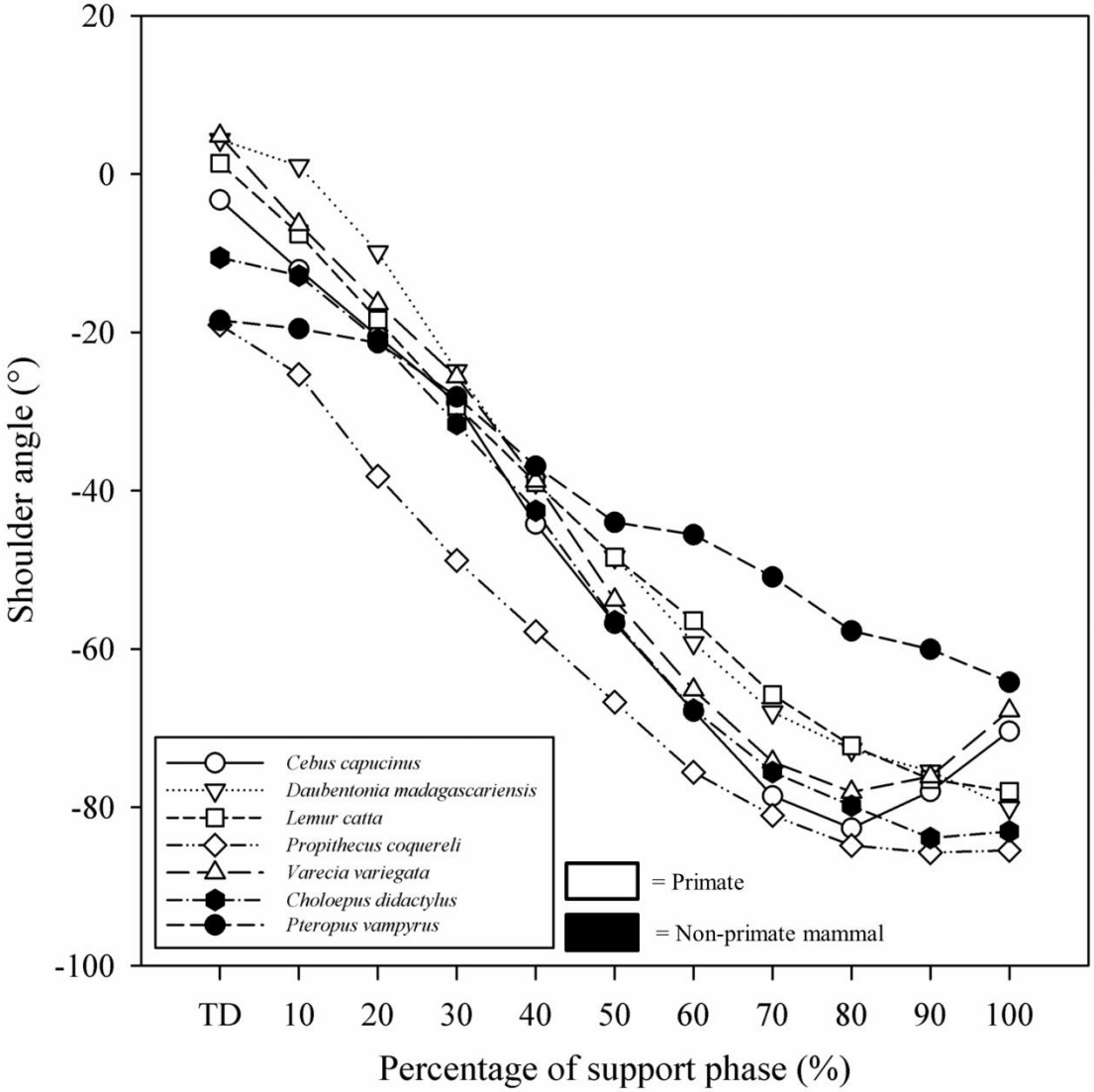

Figure 79: Patterns of mean shoulder movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals.

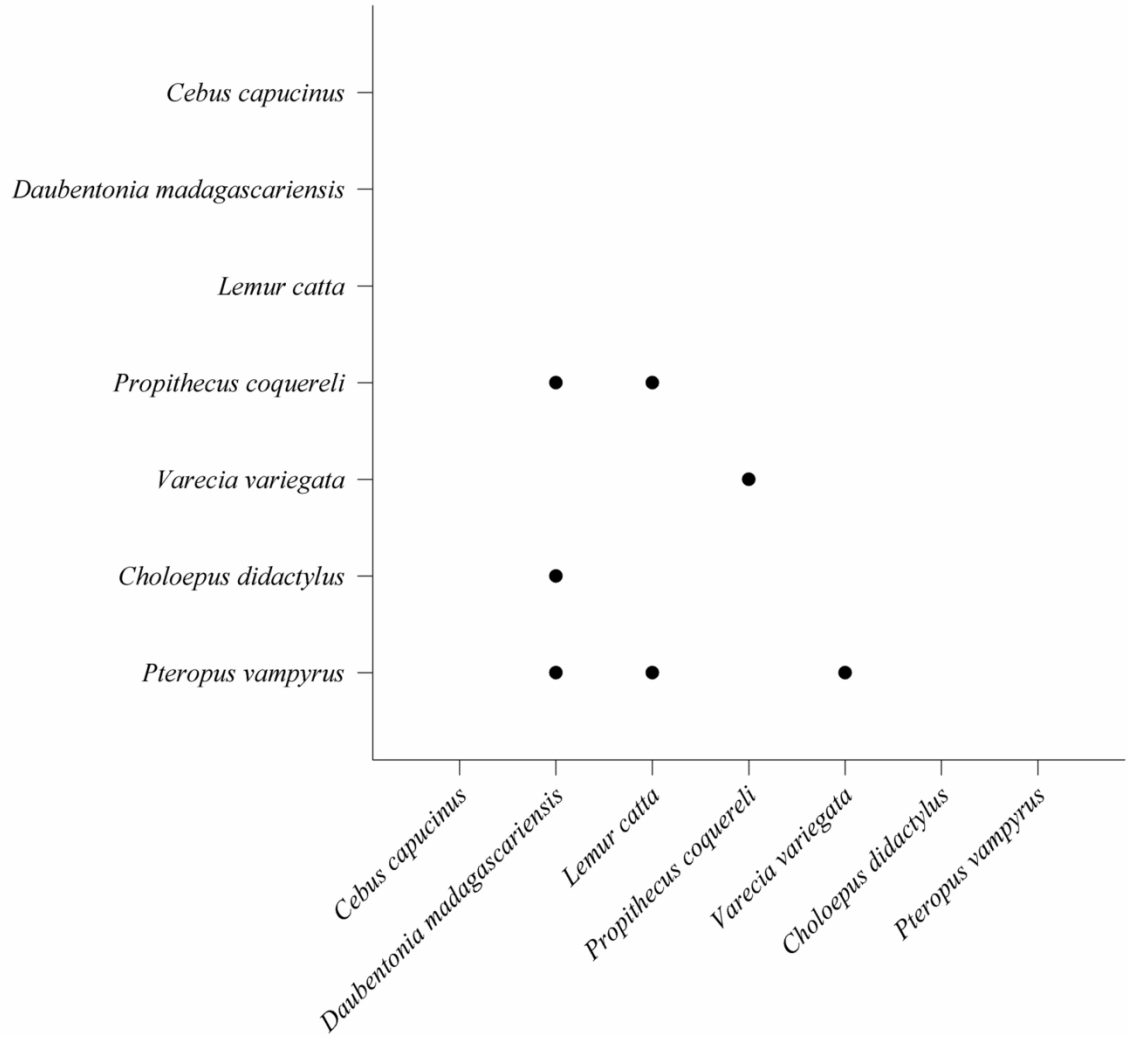

Figure 80: Multiple statistical comparisons between shoulder angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

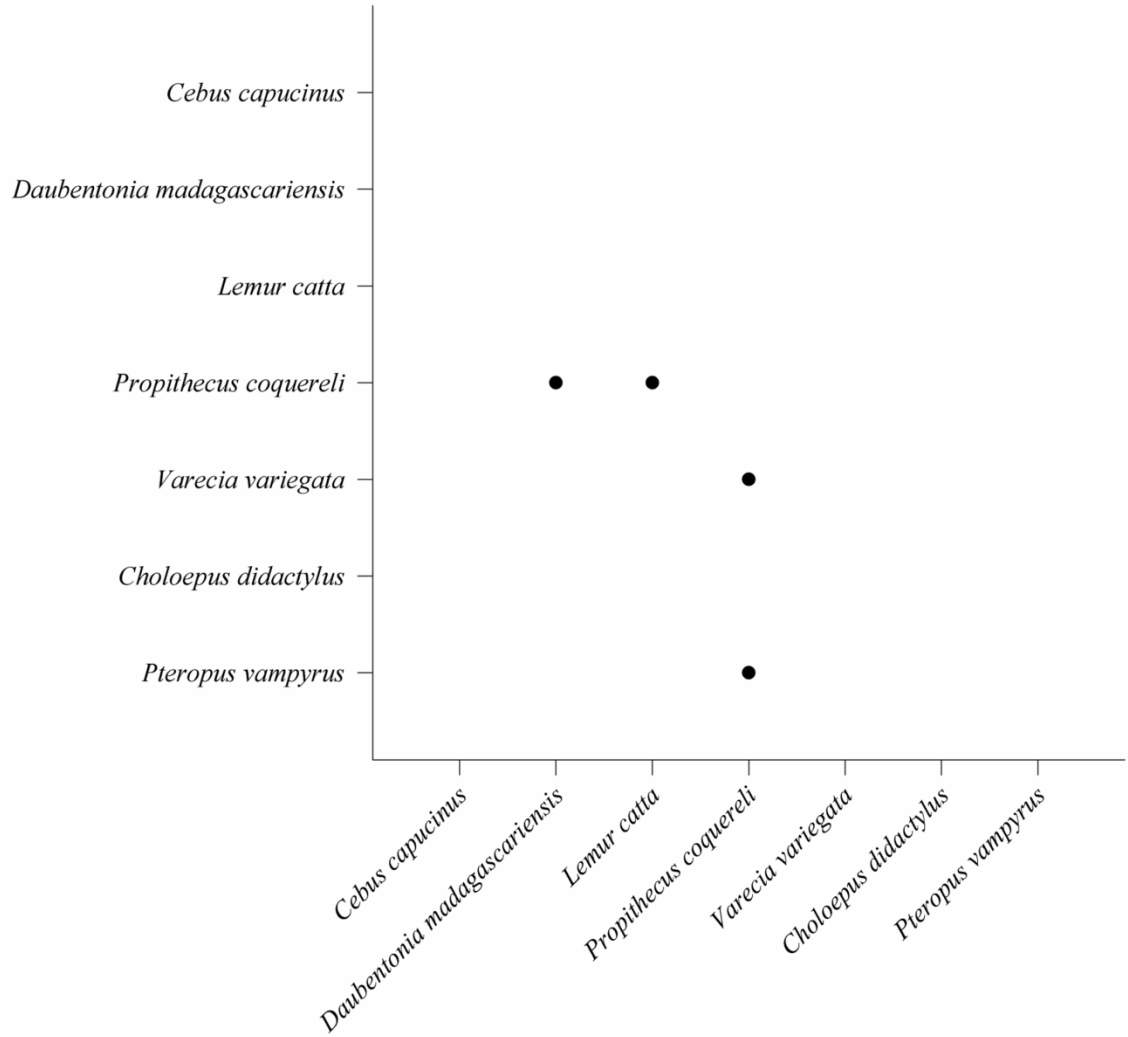

Figure 81: Multiple statistical comparisons between shoulder angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

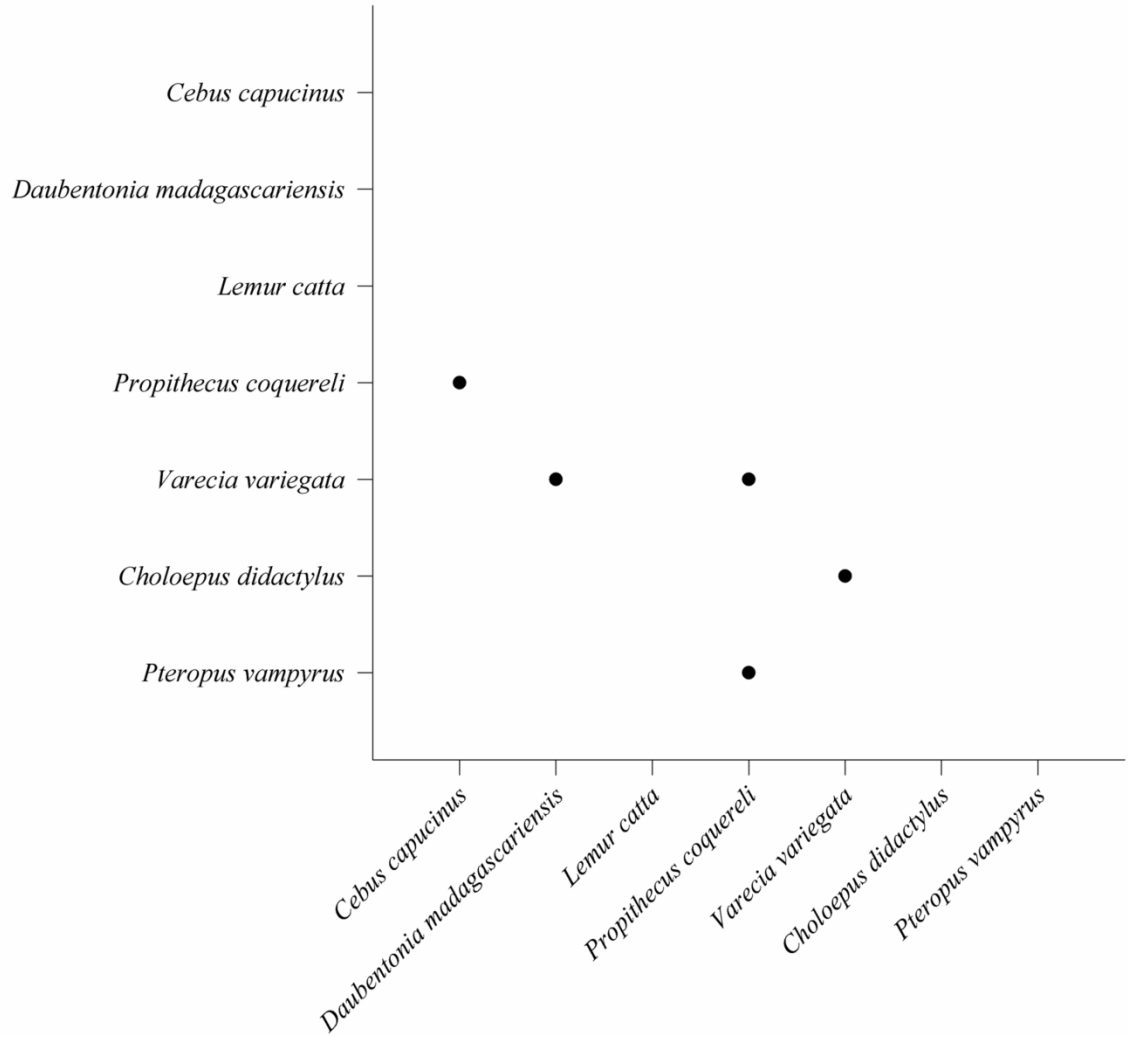

Figure 82: Multiple statistical comparisons between shoulder angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

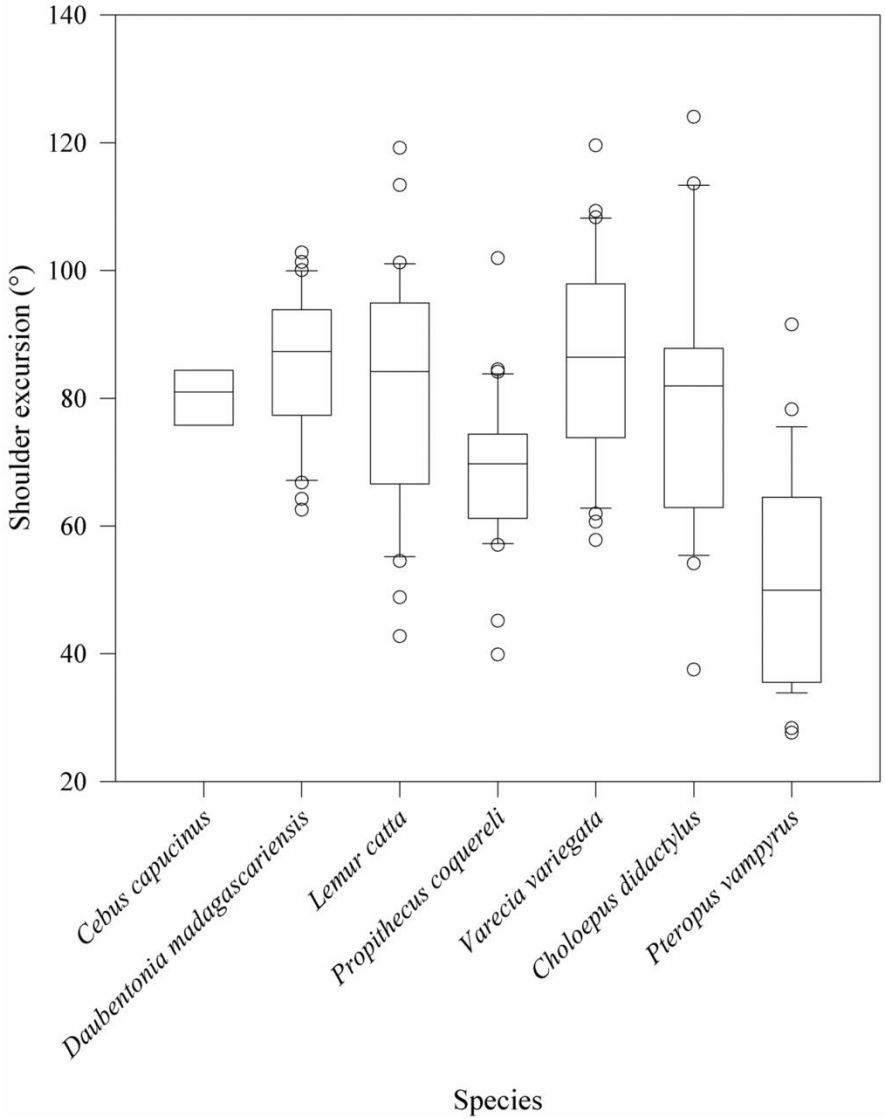

Figure 83: Mean and standard deviation values of shoulder excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals.

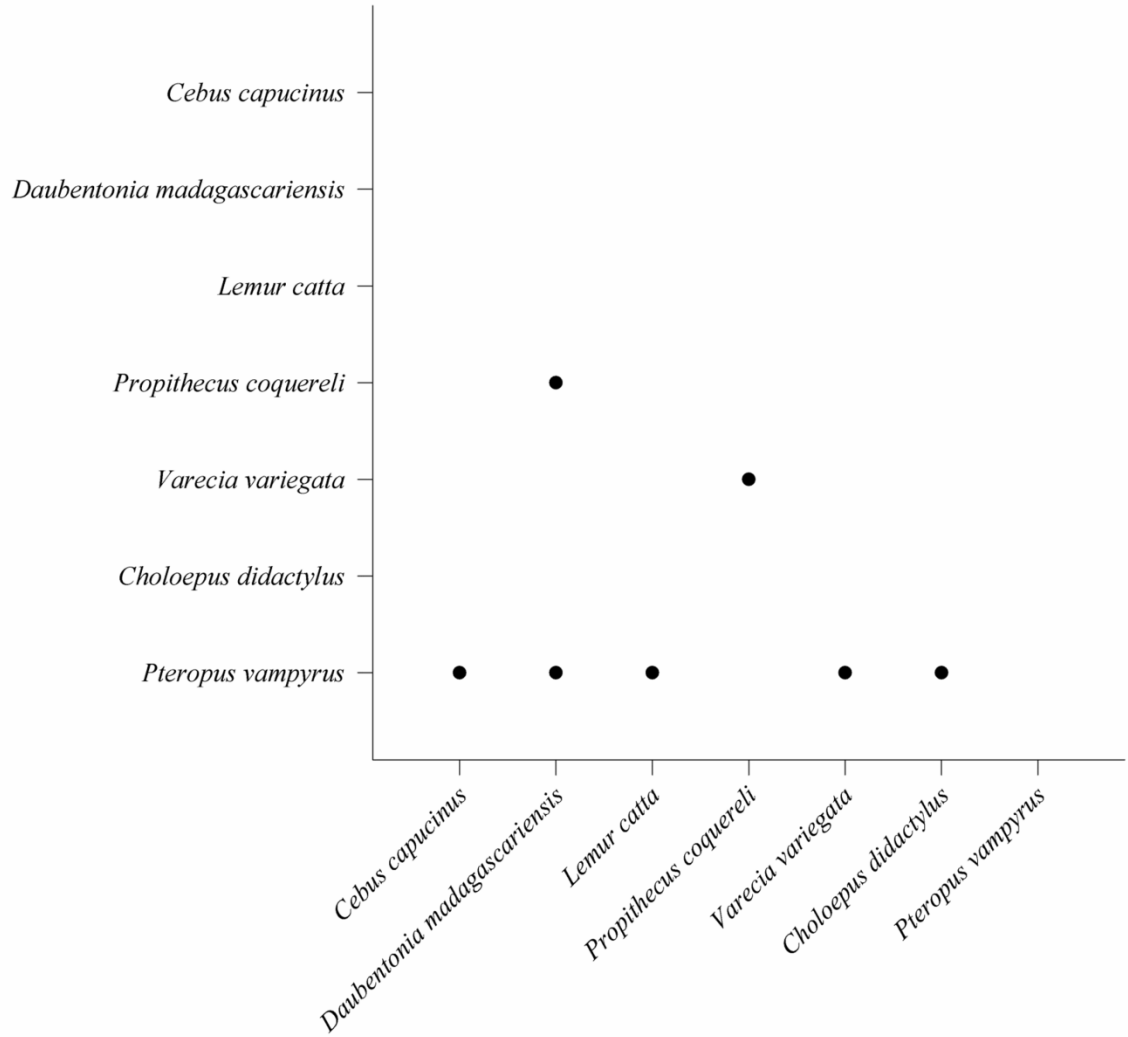

Figure 84: Multiple statistical comparisons between shoulder excursion in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

The basic pattern of movement at the elbow was similar for all species during below branch quadrupedal locomotion (Figure 85). In all species, the elbow positon at touchdown began in a relatively extended (the level of extension was quite variable between primate species) position (Figure 86), and subsequently flexed until approximately mid-support (Figure 87). The elbow then began to re-extend until the end support phase (Figure 88). It should be noted, that while this basic pattern of movement was similar for all species, levels of flexion and extension varied significantly between taxa throughout support phase. For *P. vampyrus* and *P. coquereli* both species began support phase with relatively flexed elbow joints, and maintained that flexion through the remainder of support phase. While all species actively flexed their elbow joint throughout support phase, the level of flexion varied significantly across taxa. Movement and overall excursion of the elbow was relatively high for *P. vampyrus*, *C. capucinus*, *D. madagascariensis*, *V. variegata*, and *C. didactylus* compared to *L. catta*, and *P. coquereli* (Figures 89 and 90).

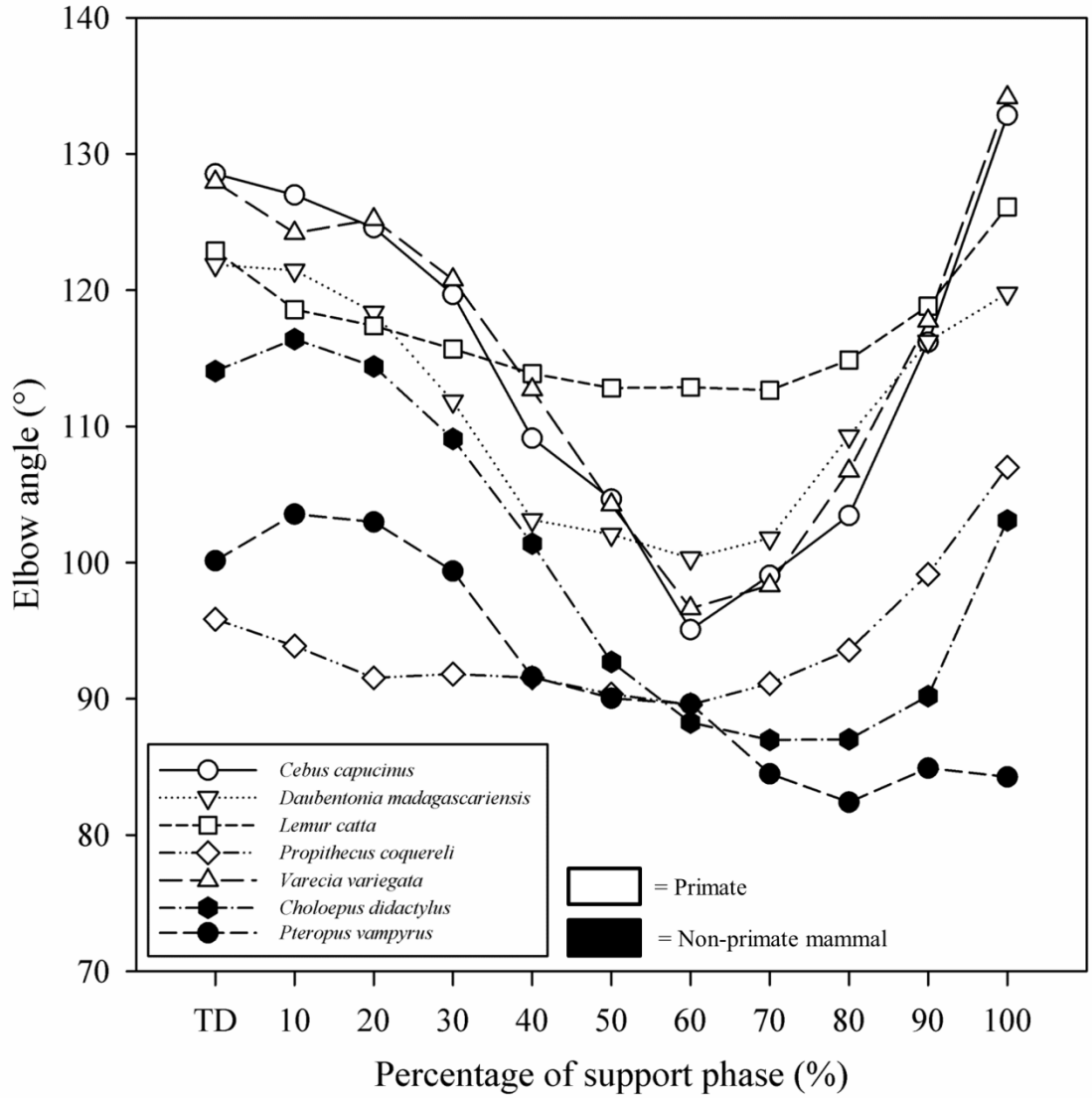

Figure 85: Patterns of mean elbow movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals.

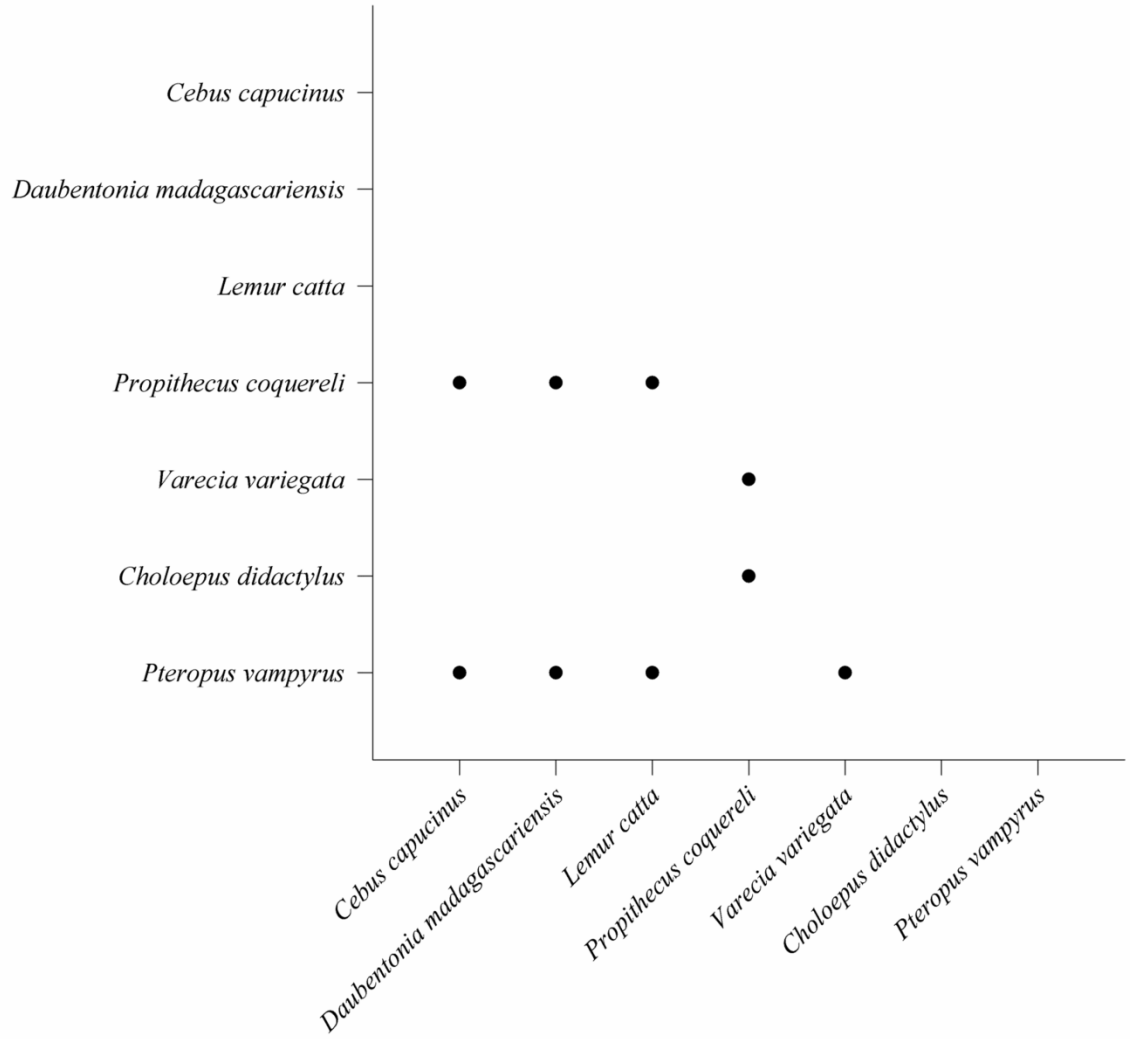

Figure 86: Multiple statistical comparisons between elbow angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (P < 0.001) between the different species.

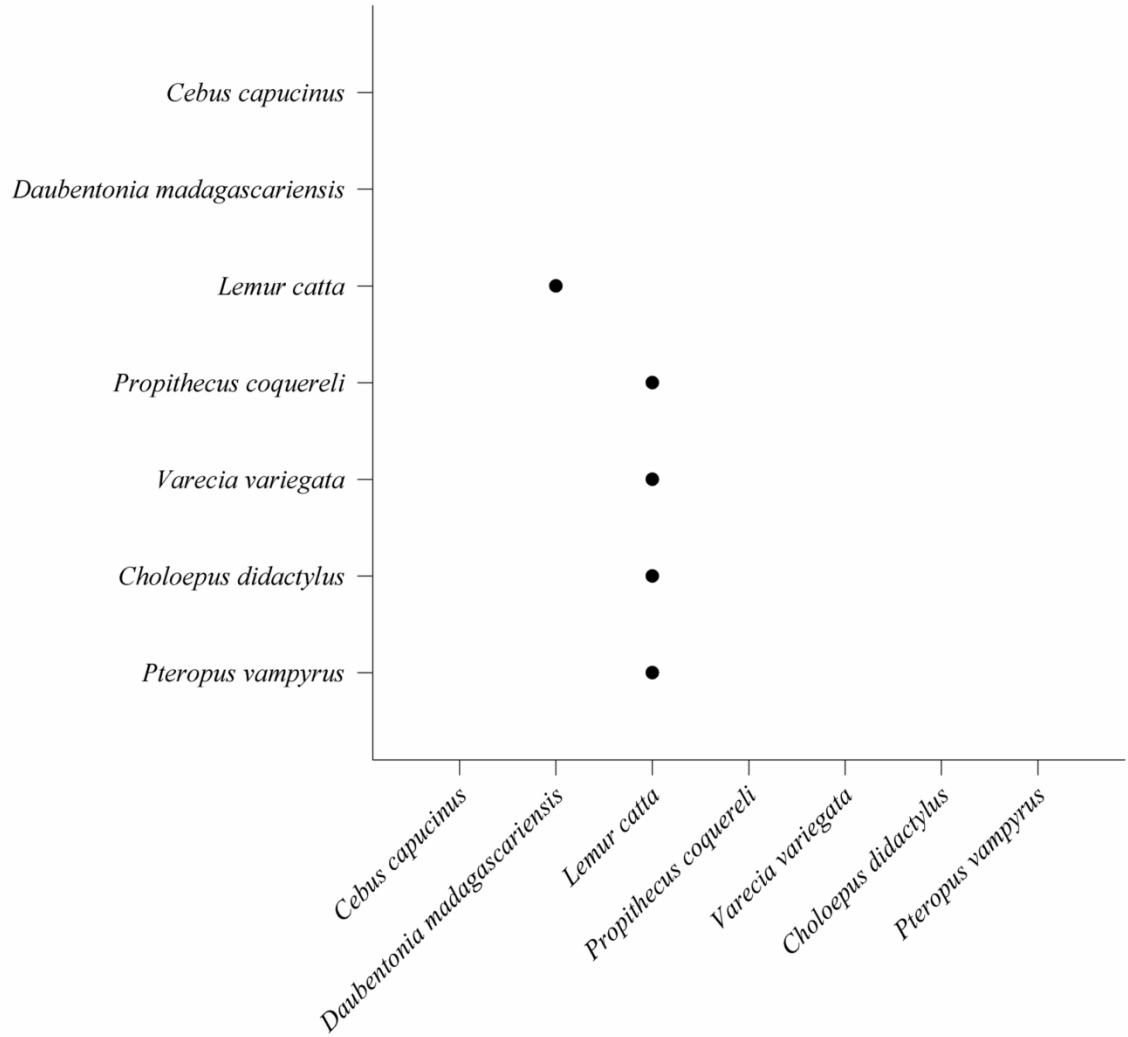

Figure 87: Multiple statistical comparisons between elbow angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (P < 0.001) between the different species.

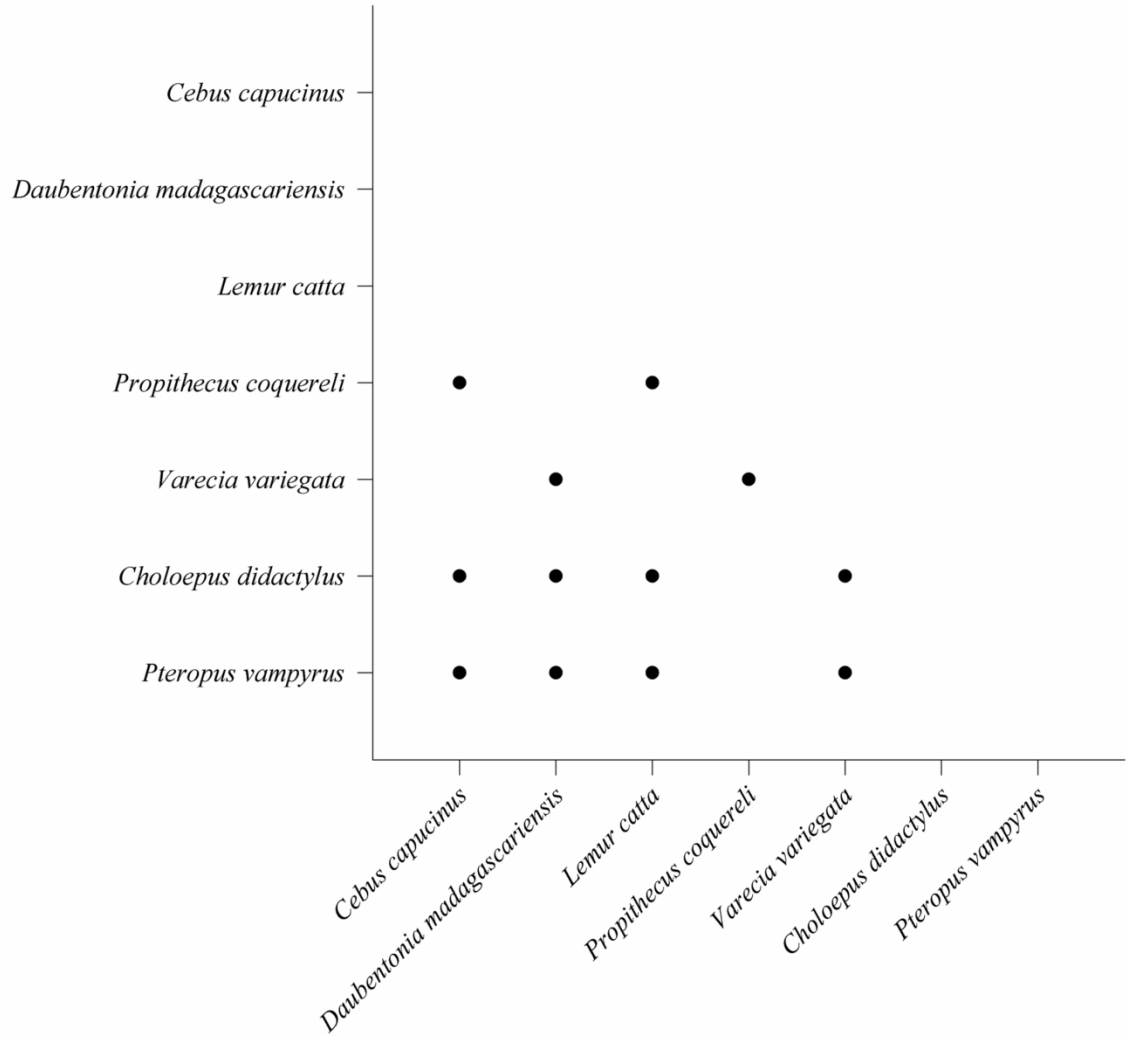

Figure 88: Multiple statistical comparisons between elbow angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

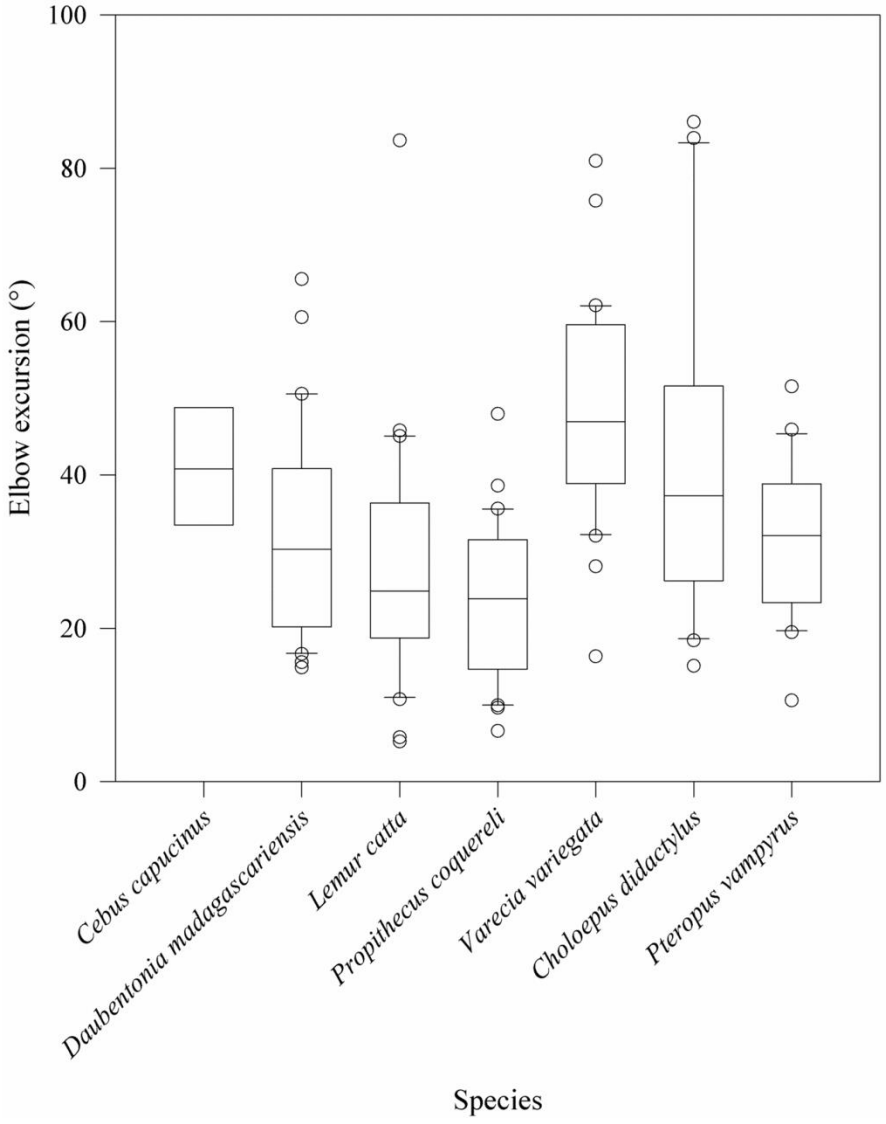

Figure 89: Mean and standard deviation values of elbow excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals.

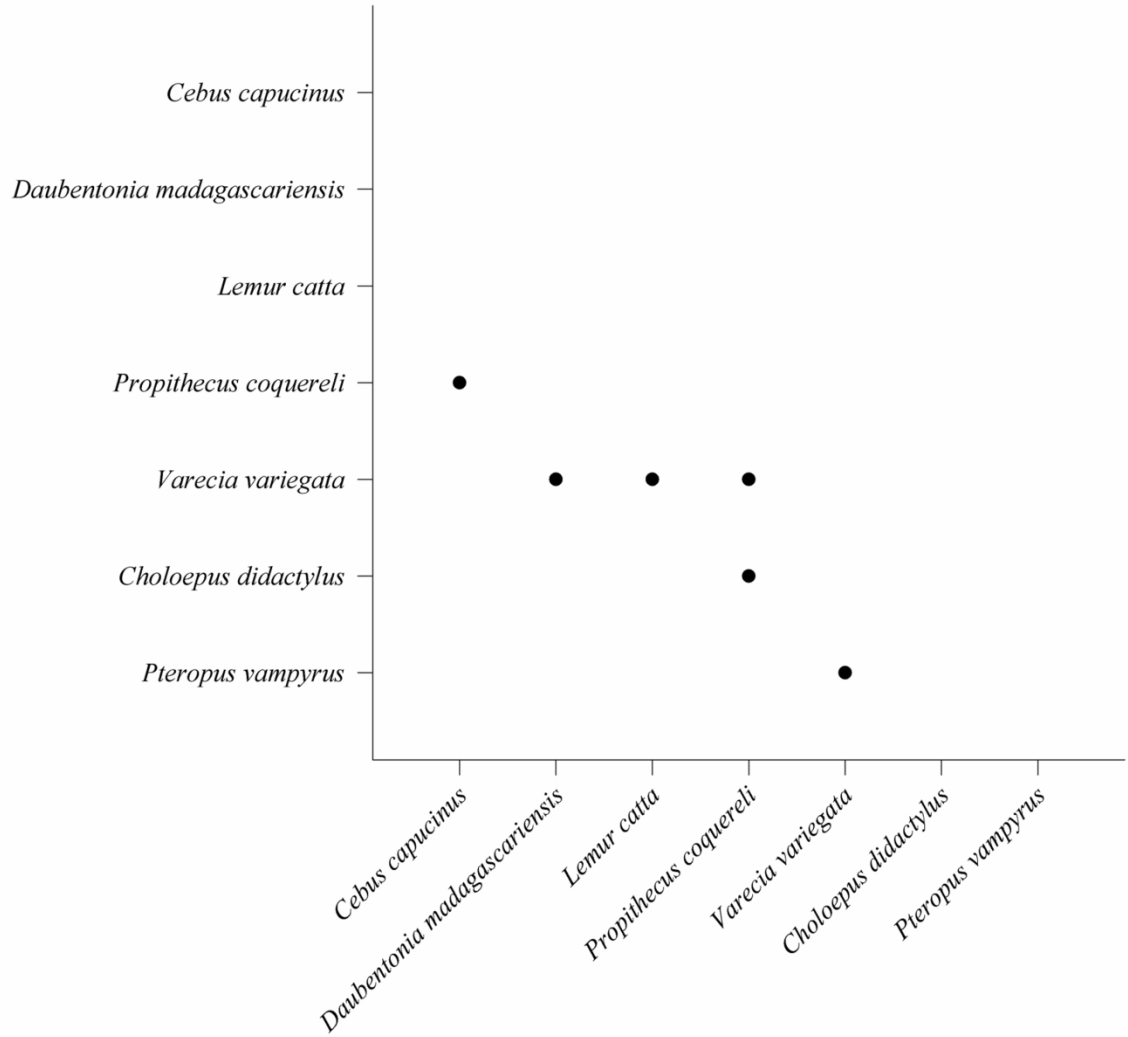

Figure 90: Multiple statistical comparisons between elbow excursion in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

During below branch quadrupedal locomotion all species used supinated hook grasps, but the movement of the wrist displayed a marked distinction between primate and non-primate mammals (Figure 91). During supinated hook grasps in primates, movements of the wrist are largely confined to ulnar and radial deviation. For animals that use this grasp type, the wrist is slightly ulnarly deviated during touchdown (Figure 92), and then subsequently radially deviates throughout the remainder of support phase (Figure 93). Just prior to lift-off, the wrist ulnarly deviates once again and enters a more neutral position (Figure 94). In *C. didactylus* and *P. vampyrus* the wrist is ulnarly deviated throughout support phase, and in both species there is a tendency for the wrist to reach a slightly more neutral position near the end of support phase. The overall level of joint excursion tends to be lower in these non-primate species compared to the primates (Figure 95 and 96).

Of all the species, *P. vampyrus* shows the most unusual movement at the wrist. This may be because of the highly derived wrist and hand anatomy that results from powered-flight and the fact that only the thumb is used to contact to the support. This likely forces the wrist to maintain an ulnarly deviated position throughout support phase.

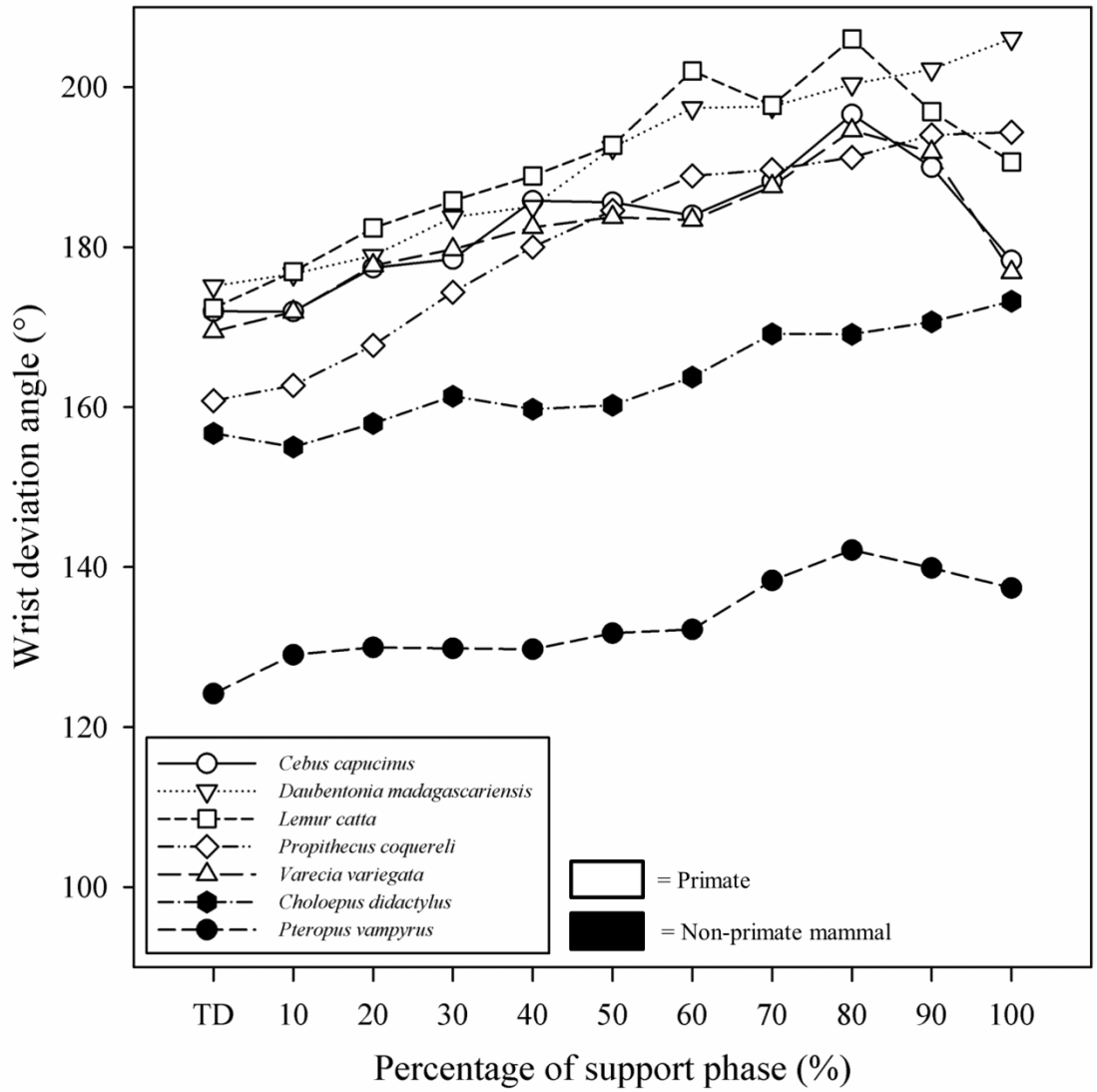

Figure 91: Patterns of mean wrist movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals.

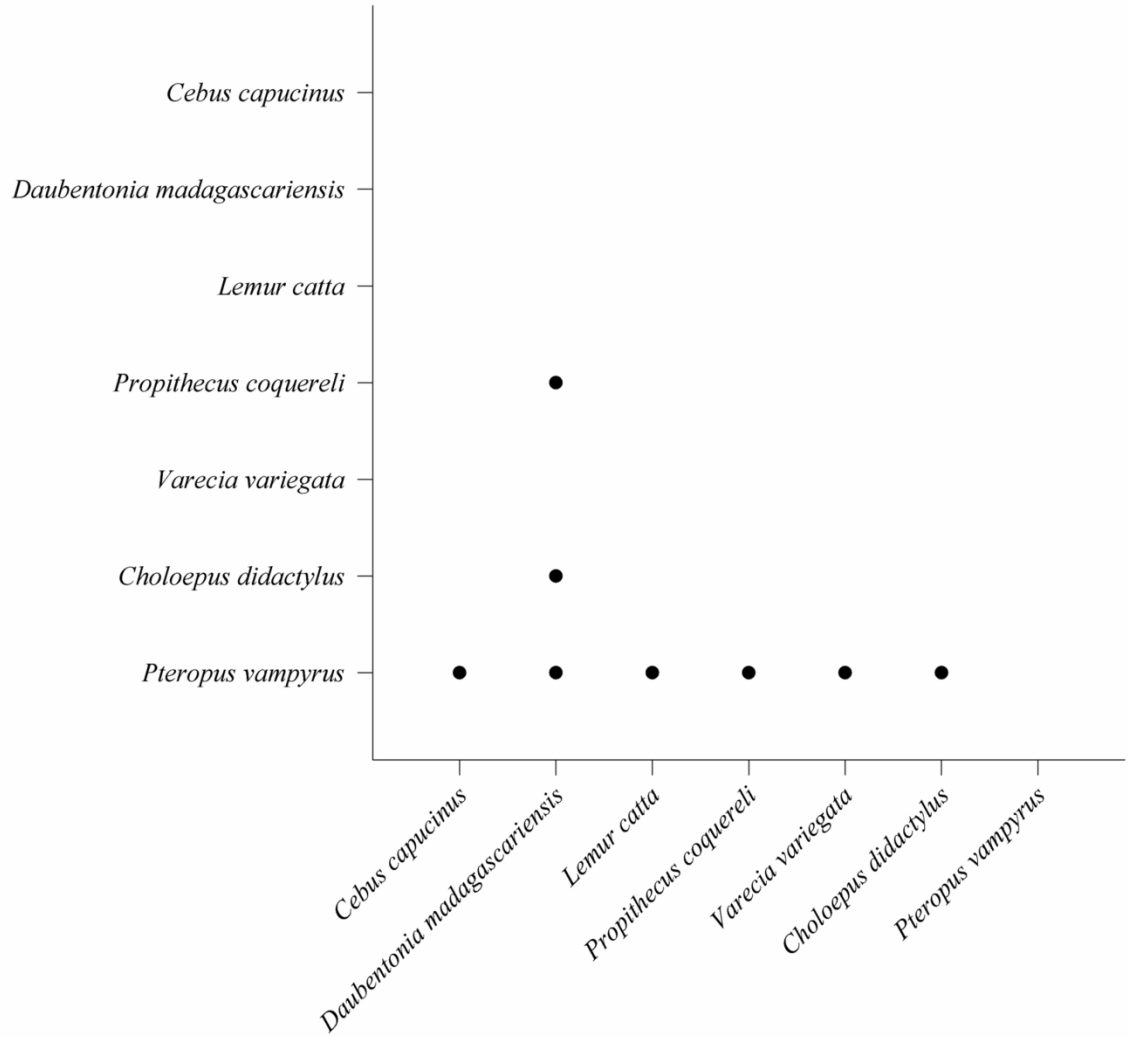

Figure 92: Multiple statistical comparisons between wrist angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

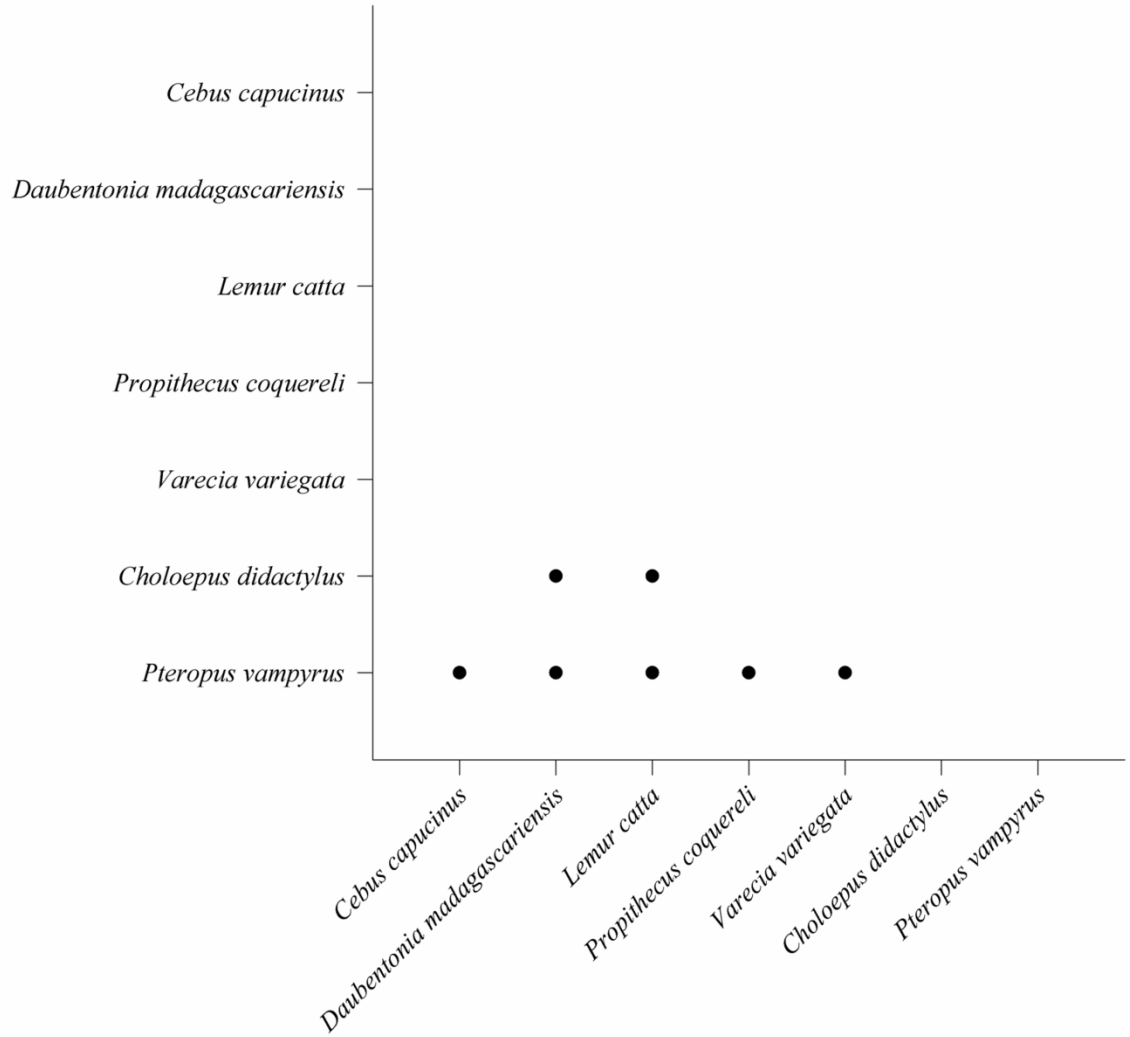

Figure 93: Multiple statistical comparisons between wrist angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

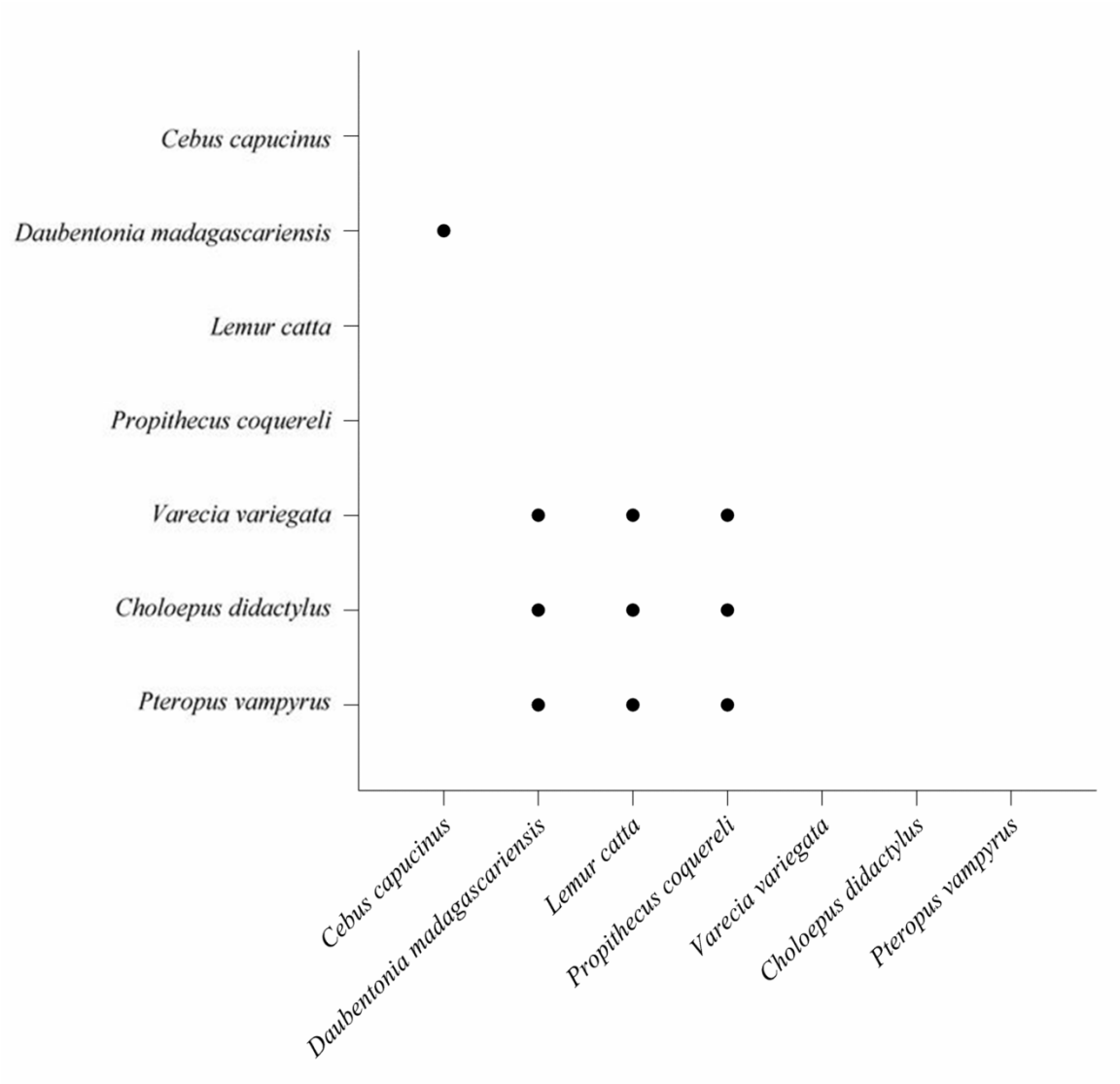

Figure 94: Multiple statistical comparisons between wrist angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

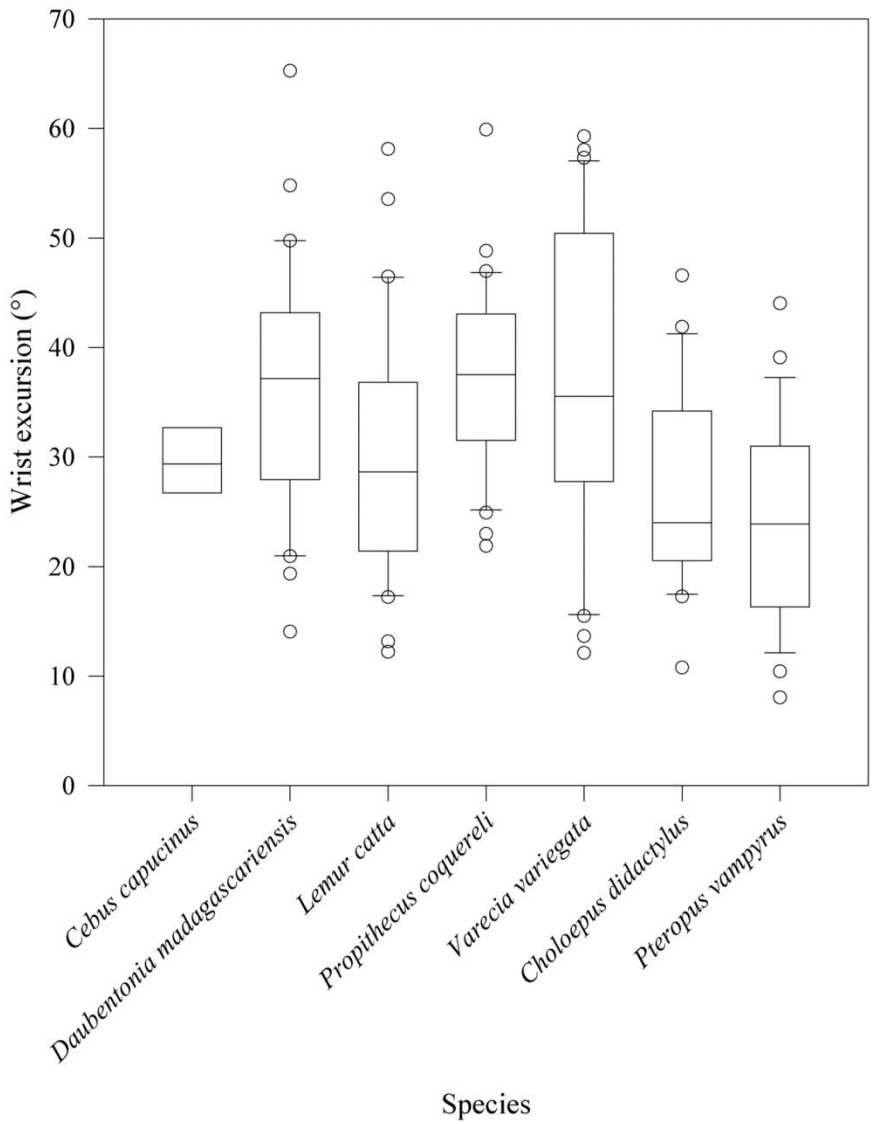

Figure 95: Mean and standard deviation values of wrist excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals.

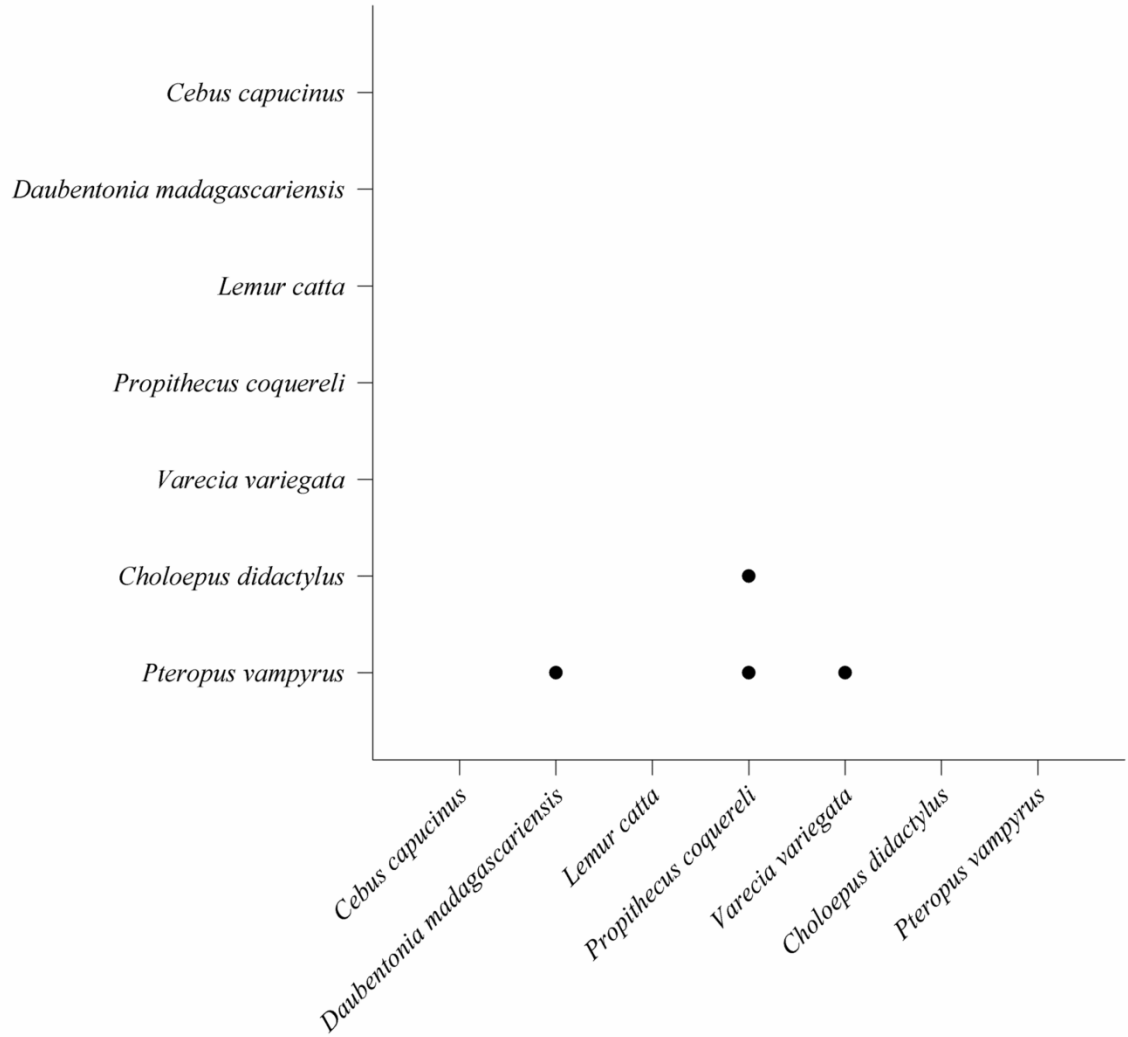

Figure 96: Multiple statistical comparisons between wrist excursion in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

The overall movement of the hip was largely similar for all species during below branch quadrupedal locomotion except for *P. vampyrus* and *D. madagascariensis* (Figure 97). For most species, at touchdown (Figure 98), the femur was placed in a protracted position and then was subsequently retracted throughout the remainder of support phase (Figures 99 and 100). Femoral angle did not enter into a truly retracted position until relatively late in support phase. Compared to most other species, hip movement of *P. vampyrus* and of *D. madagascariensis* was characterized by a sigmoidal path that began with a significantly greater degree of protraction at touchdown and ended with a significantly greater degree of retraction near limb lift-off. Accordingly, hip excursion for these species was significantly greater than what was observed in other taxa (Figure 101 and 102).

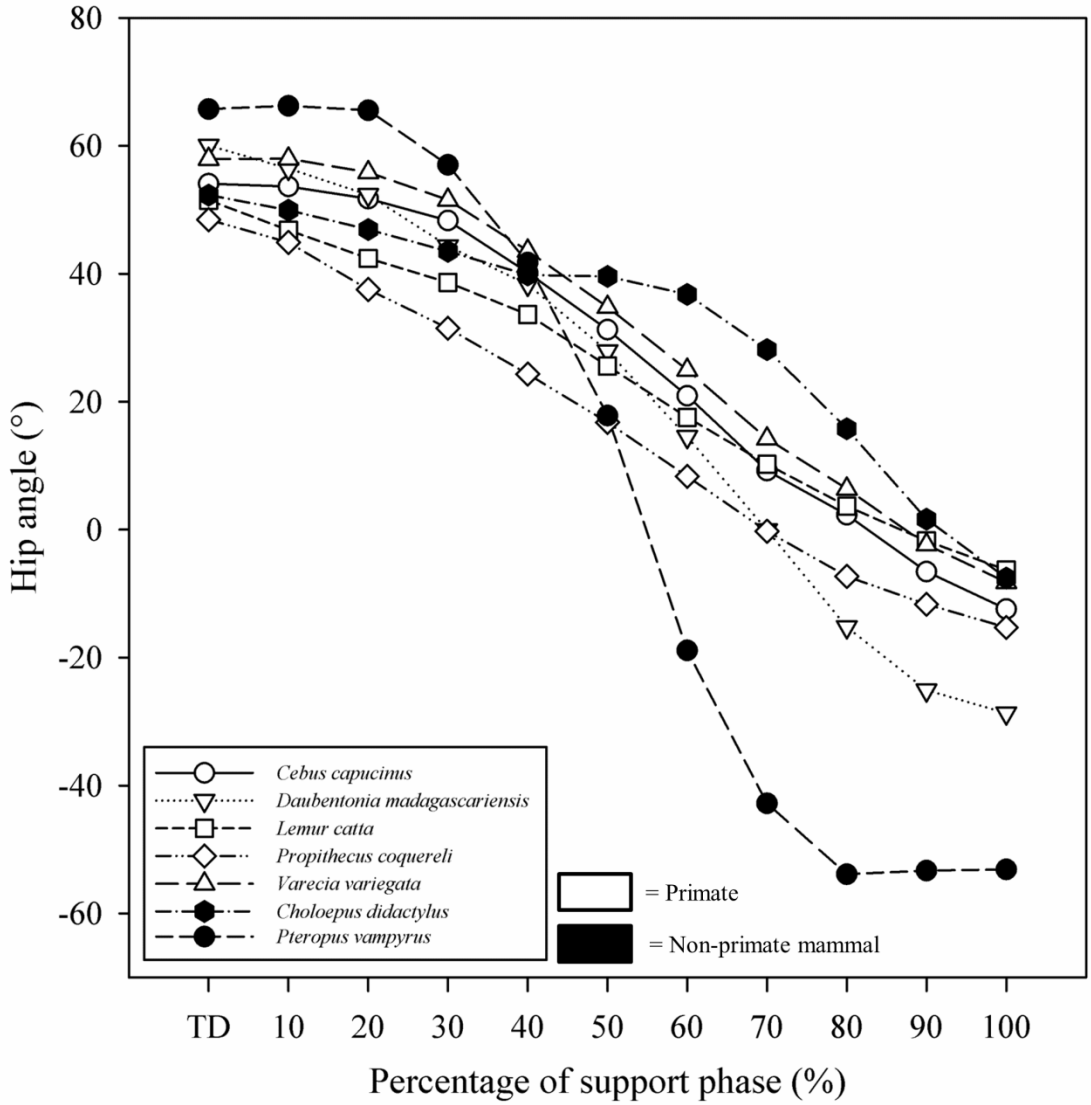

Figure 97: Patterns of mean hip movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals.

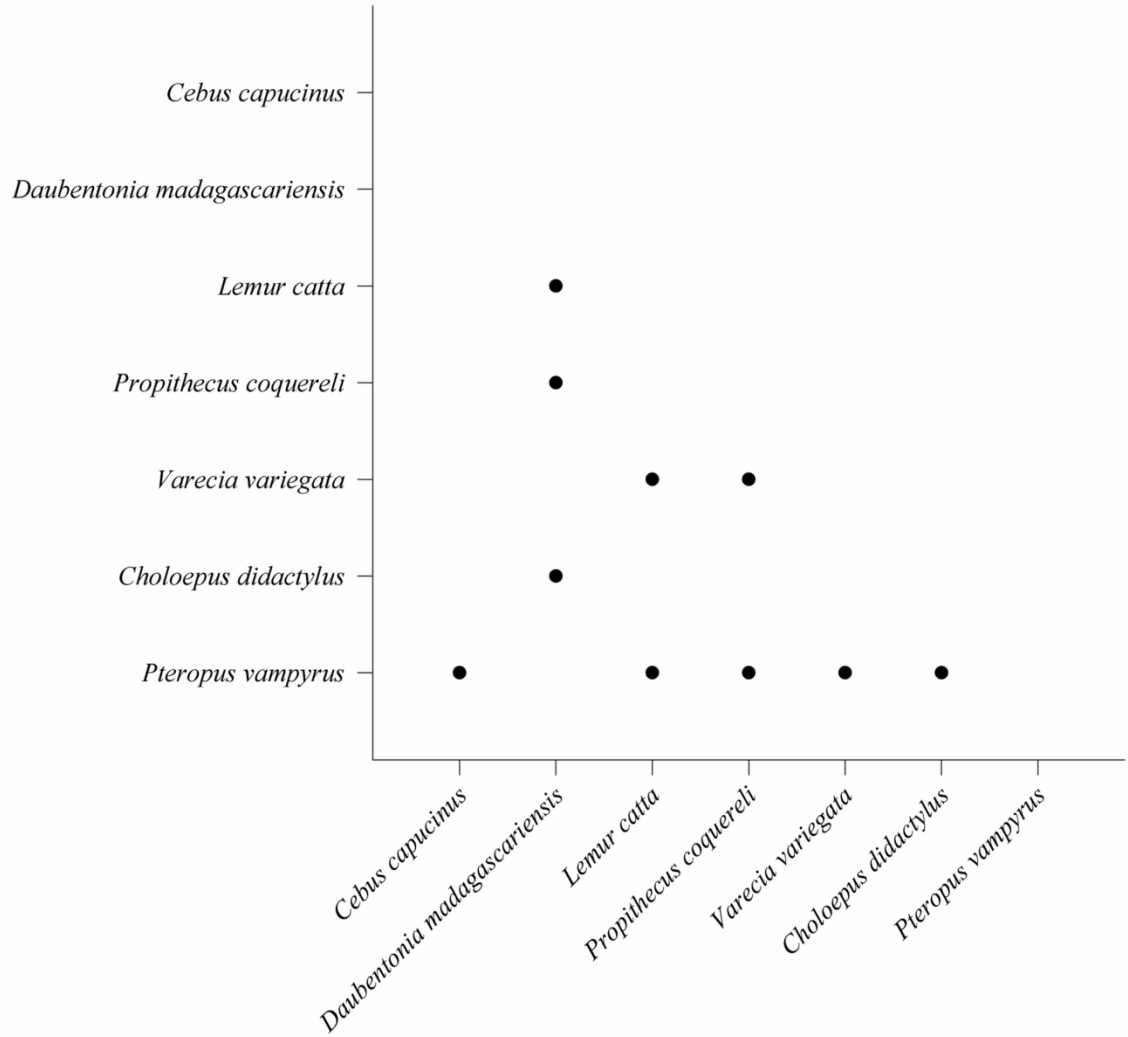

Figure 98: Multiple statistical comparisons between hip angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

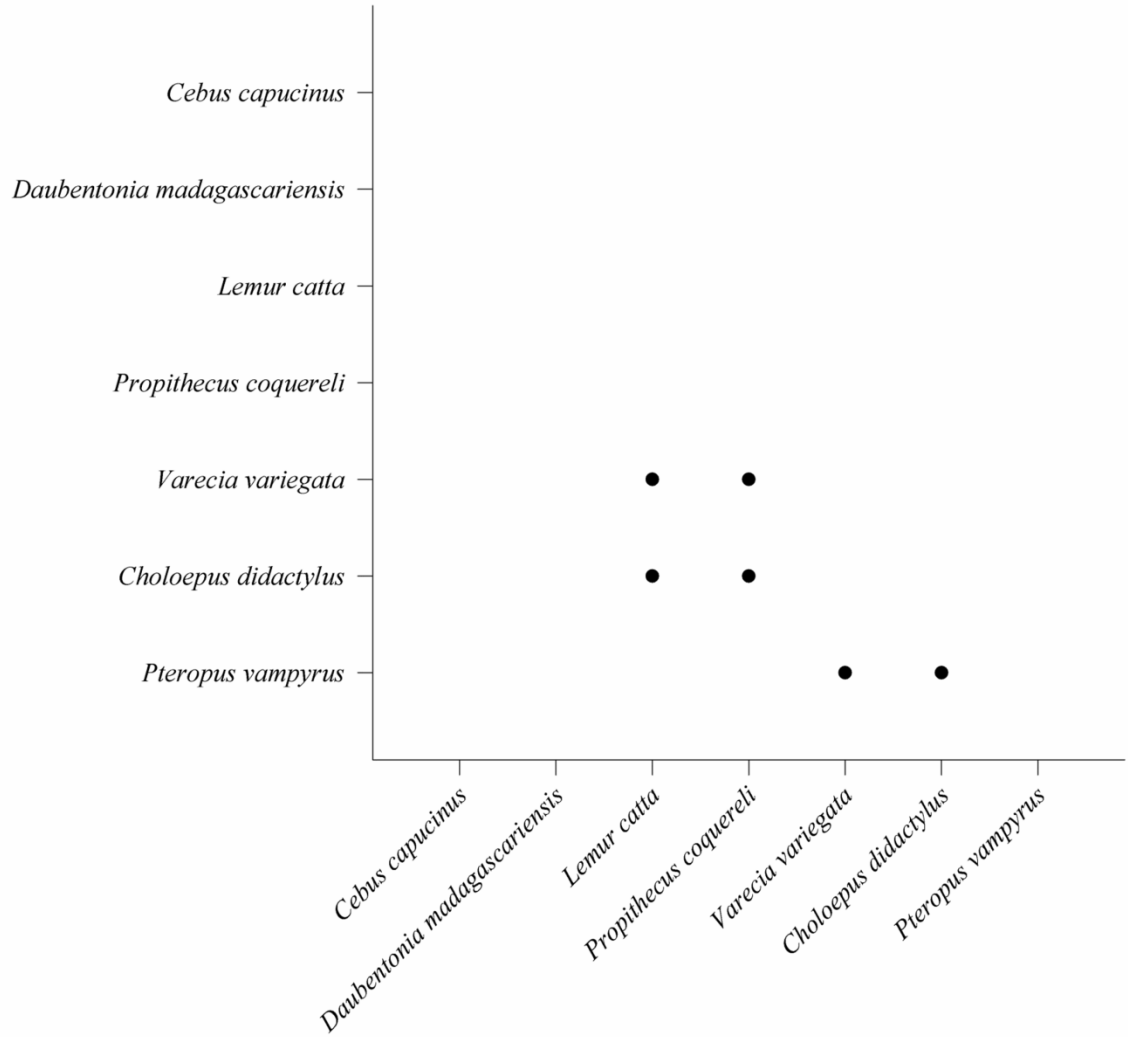

Figure 99: Multiple statistical comparisons between hip angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

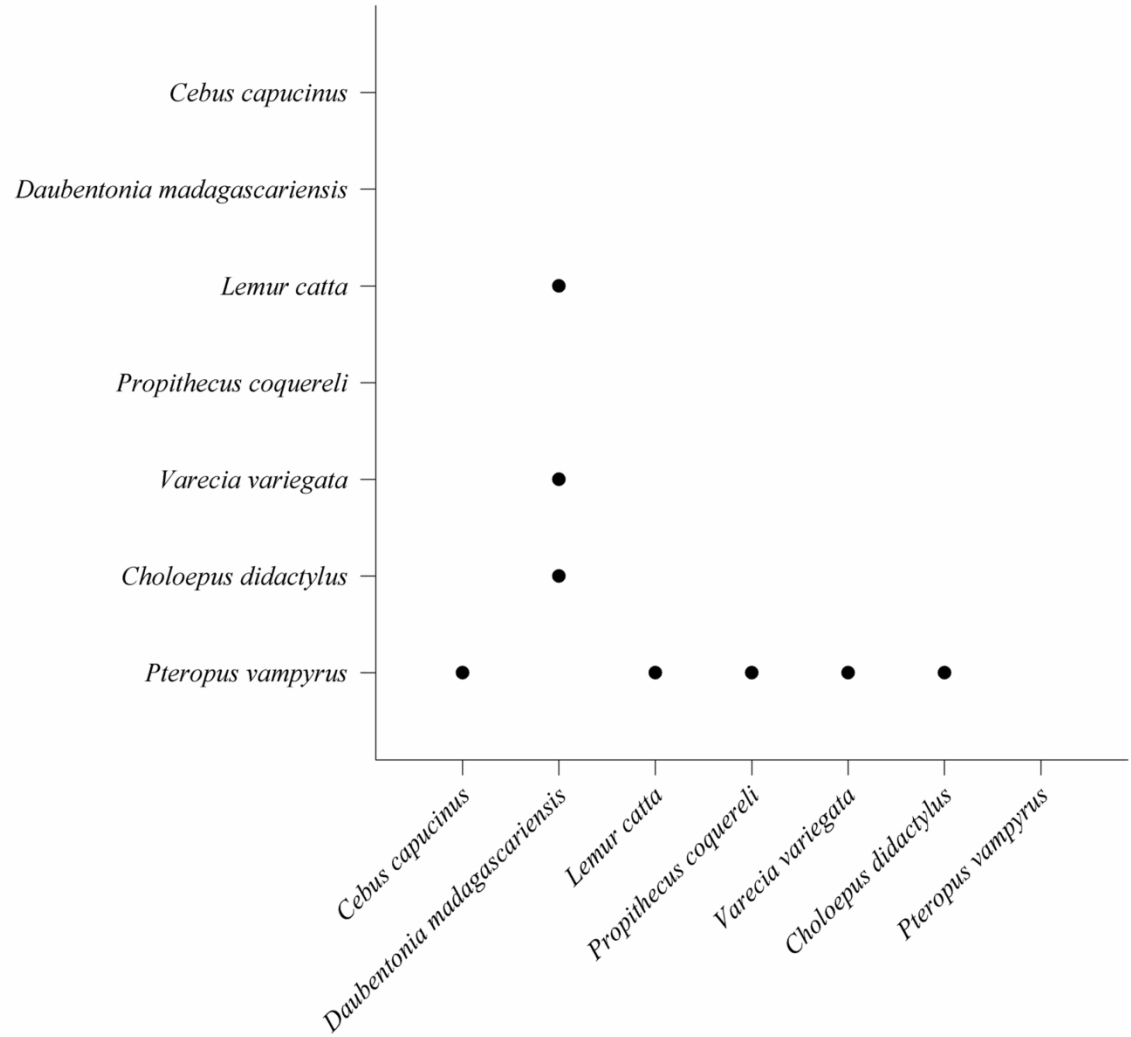

Figure 100: Multiple statistical comparisons between hip angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

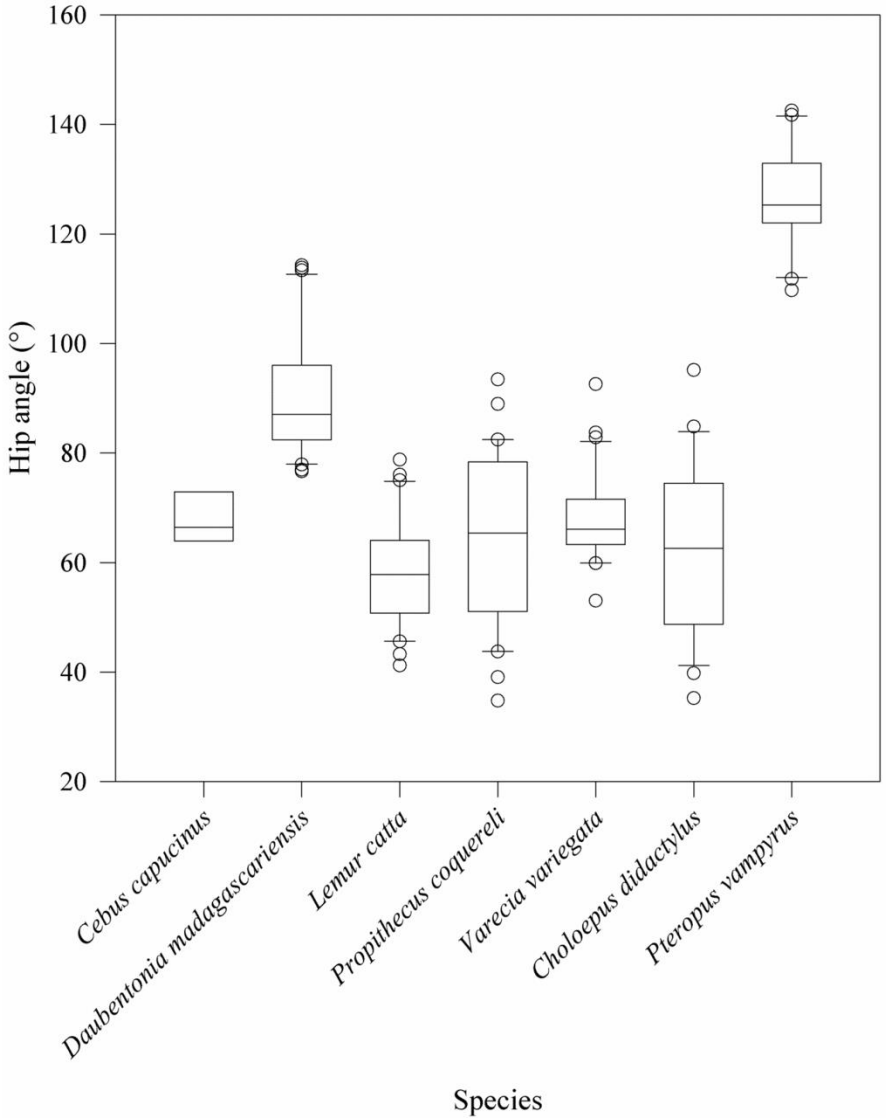

Figure 101: Mean and standard deviation values of hip excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals.

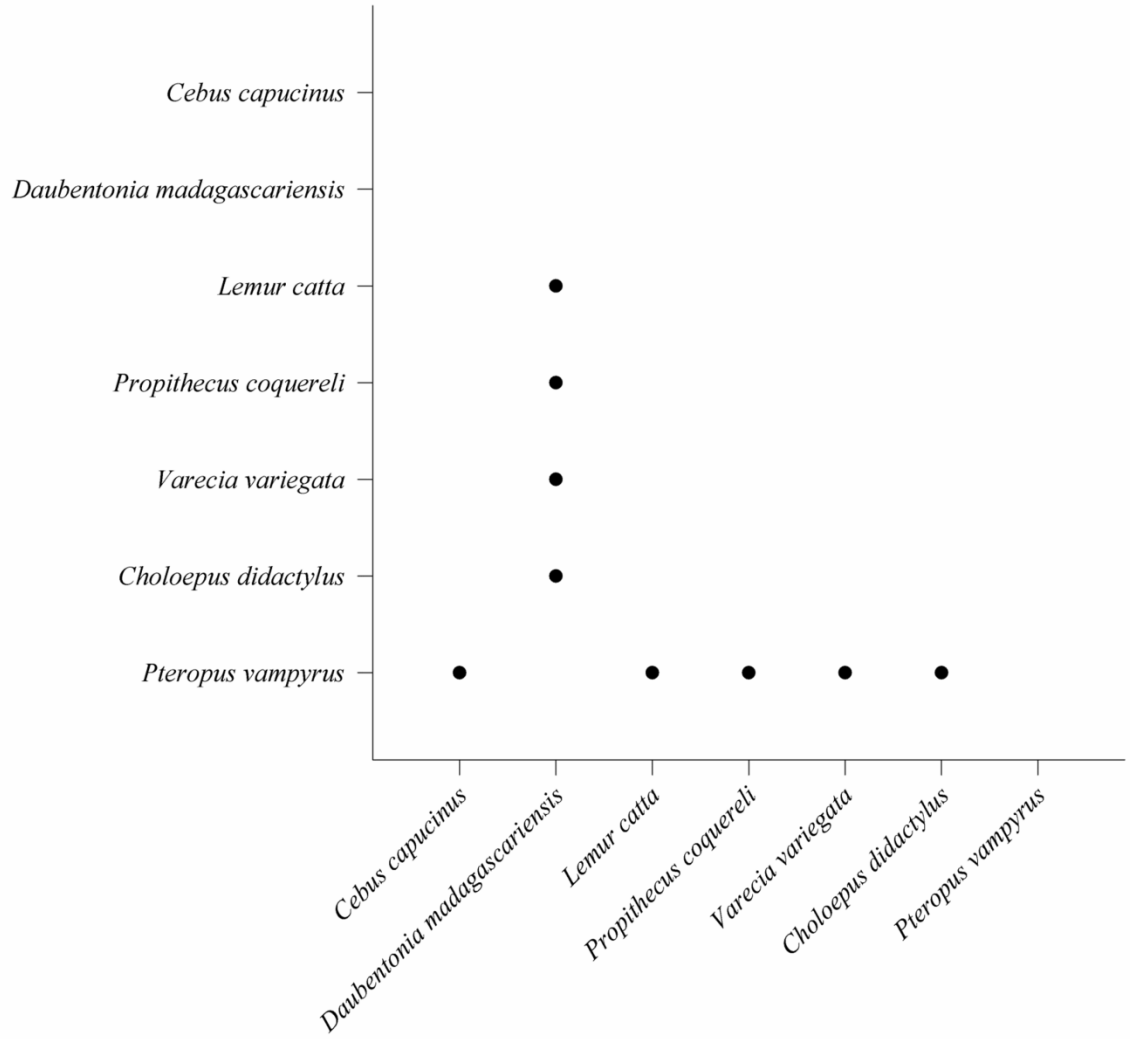

Figure 102: Multiple statistical comparisons between hip excursion in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

Kinematic patterns of knee movement were significantly different between primates and non-primate mammals during below branch quadrupedal locomotion (Figure 103). In primates, the knee remained in a relatively flexed position until mid-support (Figure 104 and 105), at which time the knee extended until lift-off (Figure 106). The level of knee extension at the end of support phase was greatest in *D. madagascariensis*. In the non-primate mammals, the knee was kept in a relatively extended position throughout support phase compared to primate taxa. *Choloepus didactylus* tended to flex the knee slightly near mid-support, but then re-extended it prior to lift-off. In contrast, *P. vampyrus* extended its knee near mid-support, but then flexed it before lift-off. Levels of knee excursion were largely similar across taxa with the exception of *D. madagascariensis*, which demonstrated greater knee excursion than most species (Figures 107 and 108). It should be noted that based on the data, knee extension indicated different things for different taxa. In all species except of *P. vampyrus*, knee excursion indicated flexion at the knee joint. In *P. vampyrus*, knee excursion indicated that the knee extended throughout support phase.

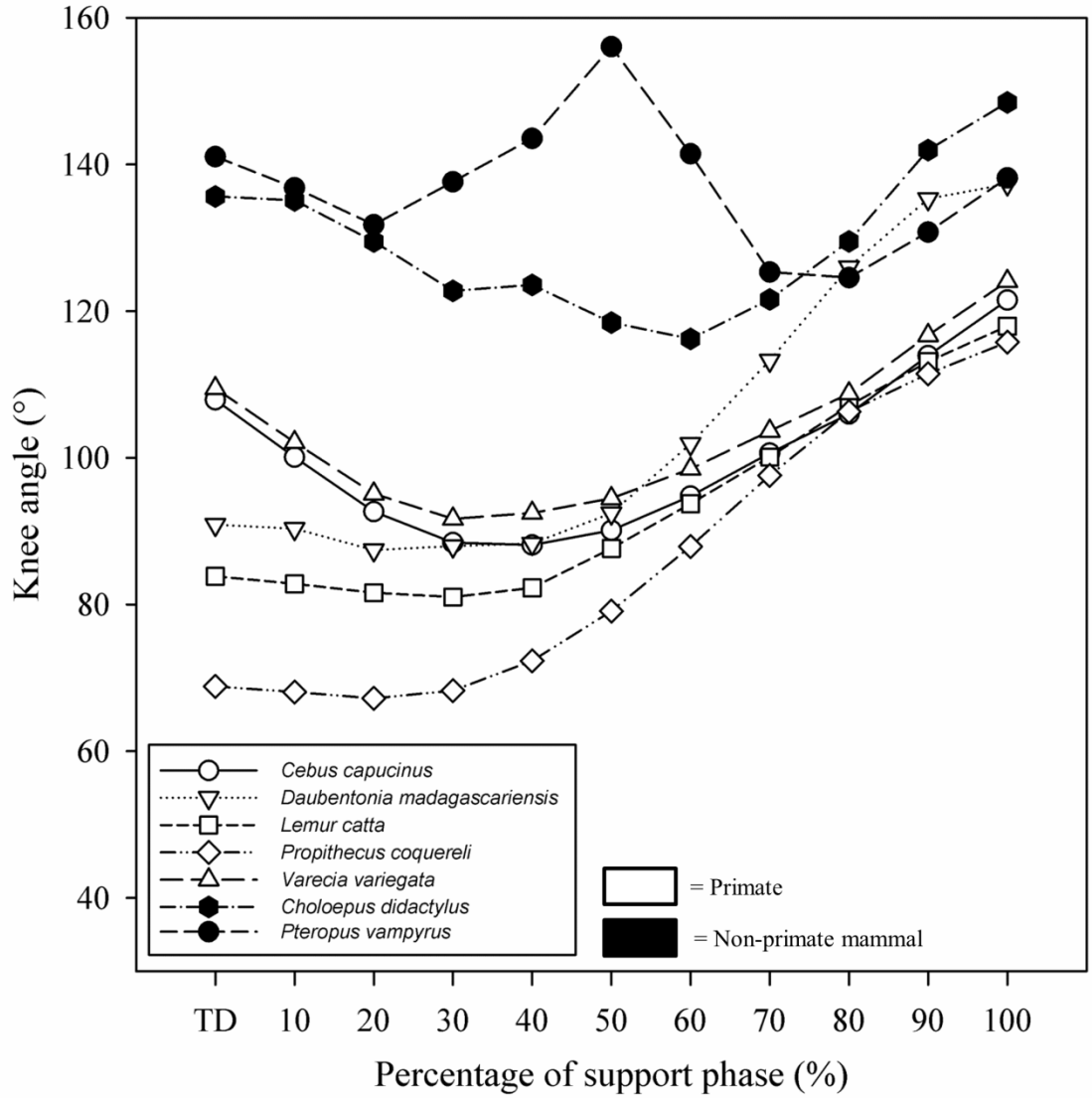

Figure 103: Patterns of mean knee movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals.

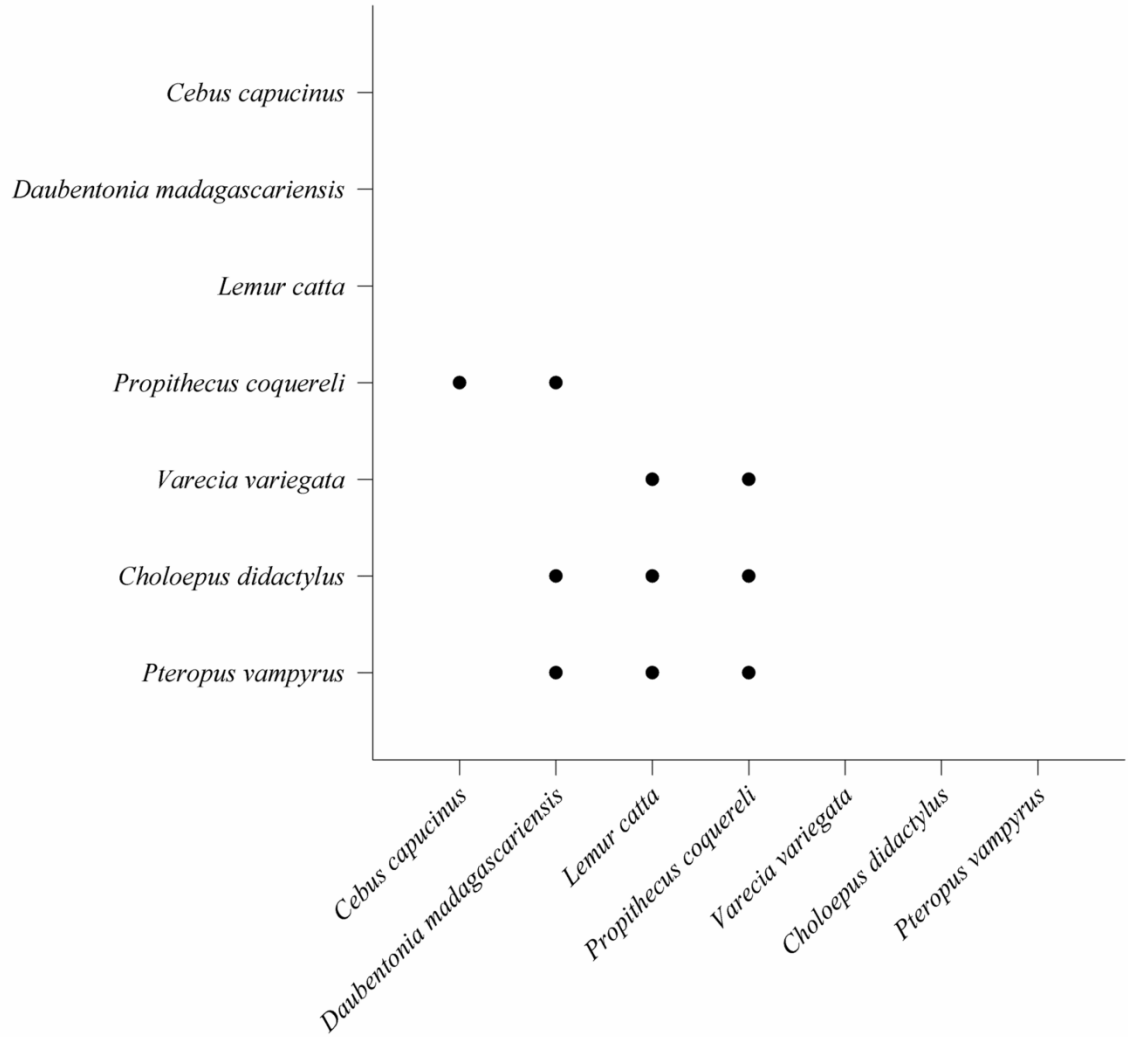

Figure 104: Multiple statistical comparisons between knee angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

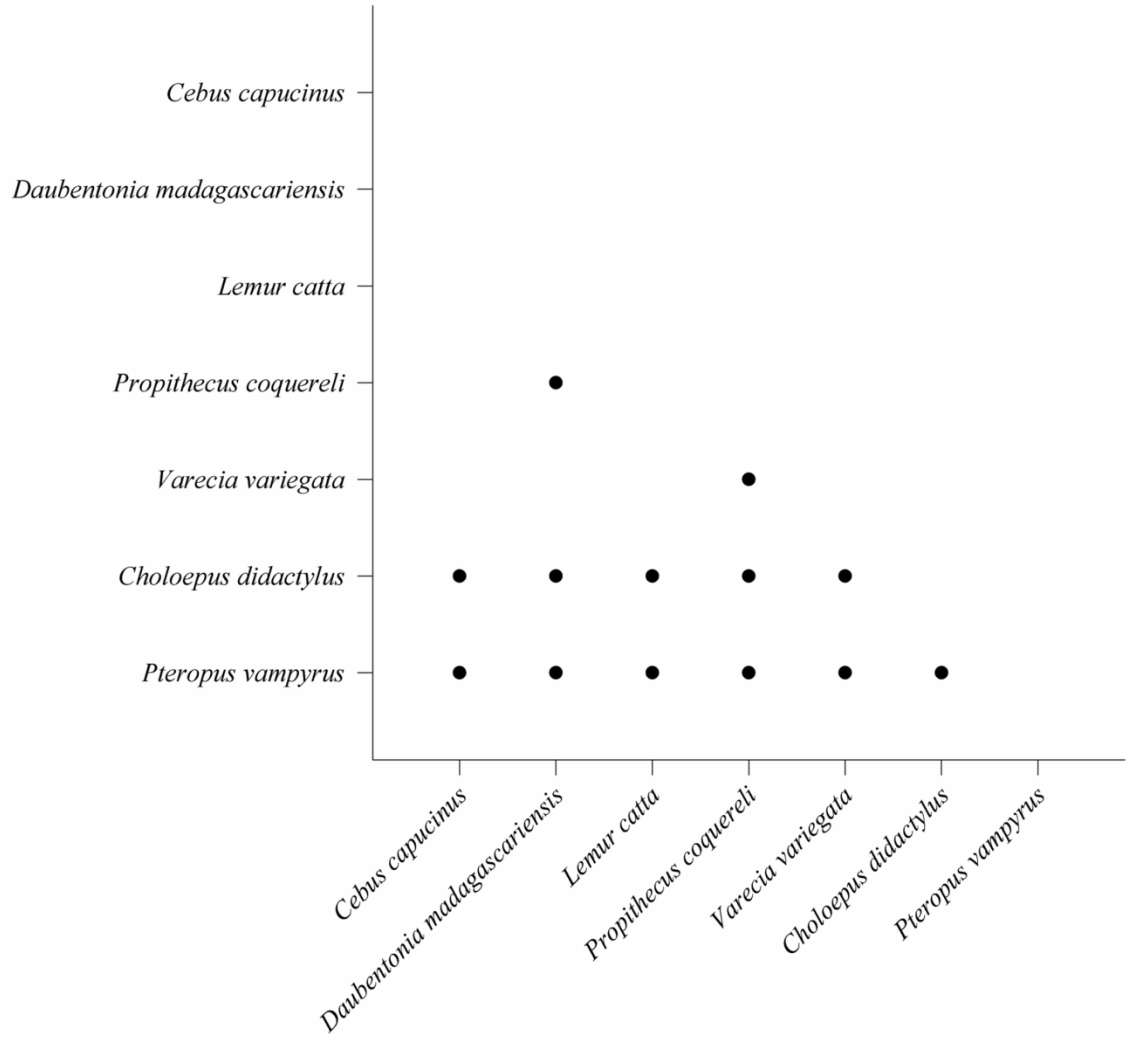

Figure 105: Multiple statistical comparisons between knee angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

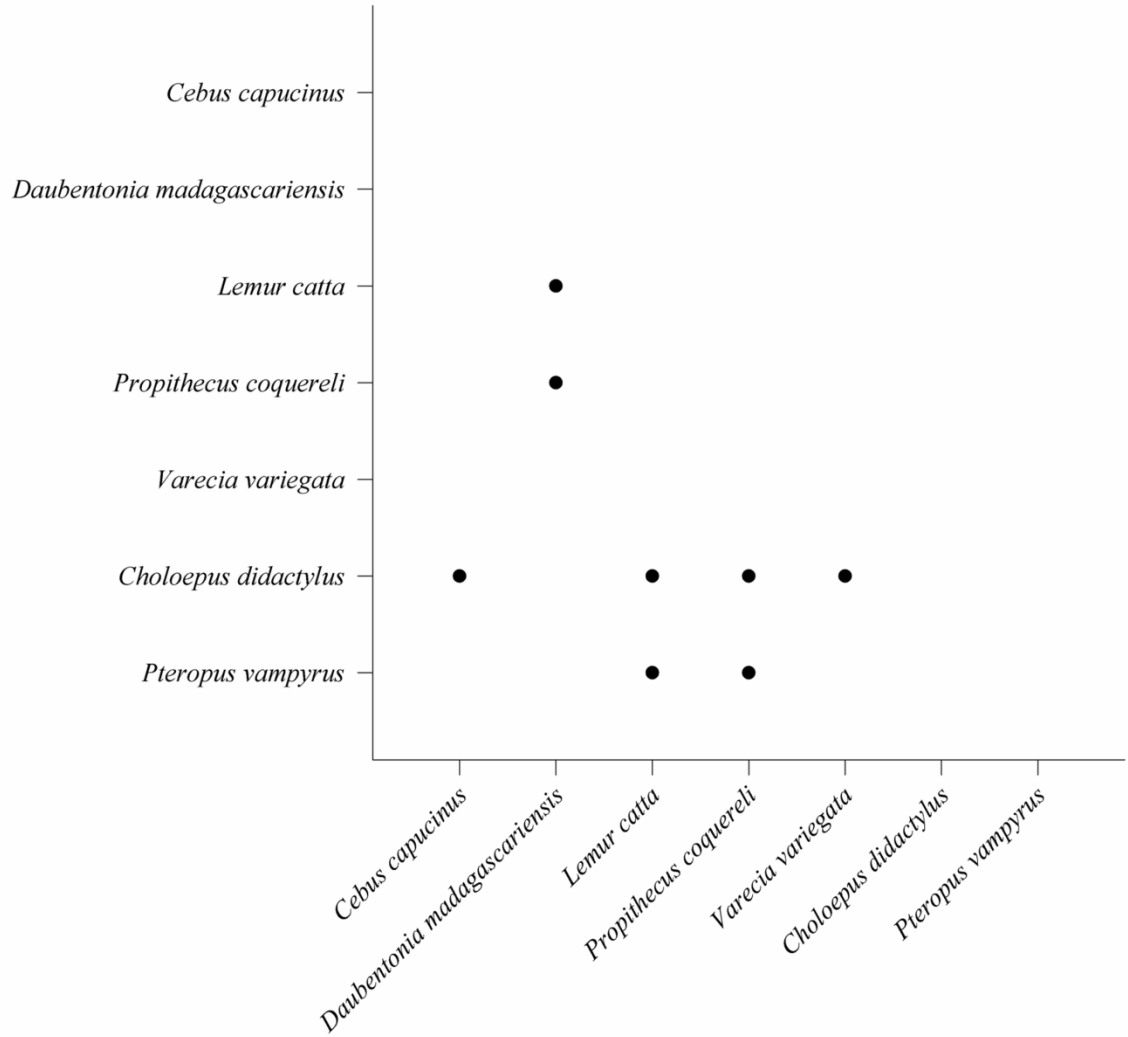

Figure 106: Multiple statistical comparisons between knee angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

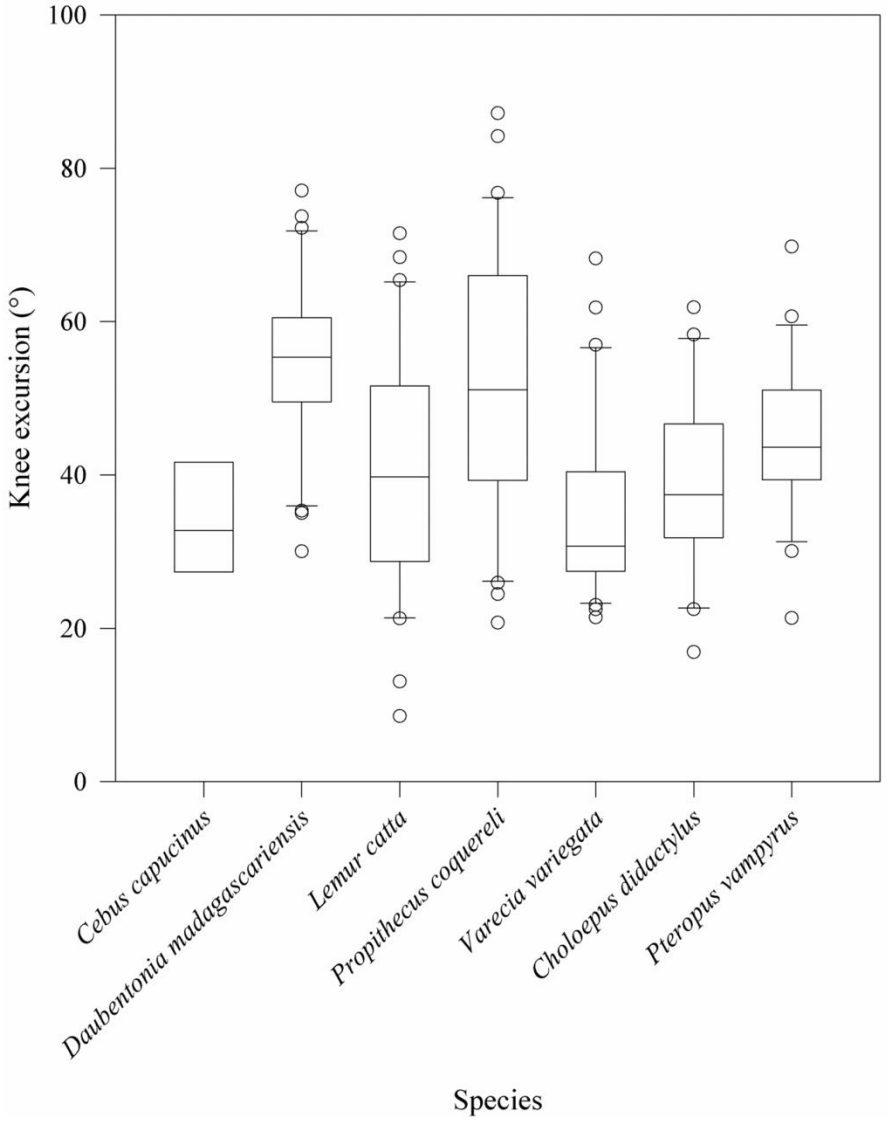

Figure 107: Mean and standard deviation values of knee excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals.

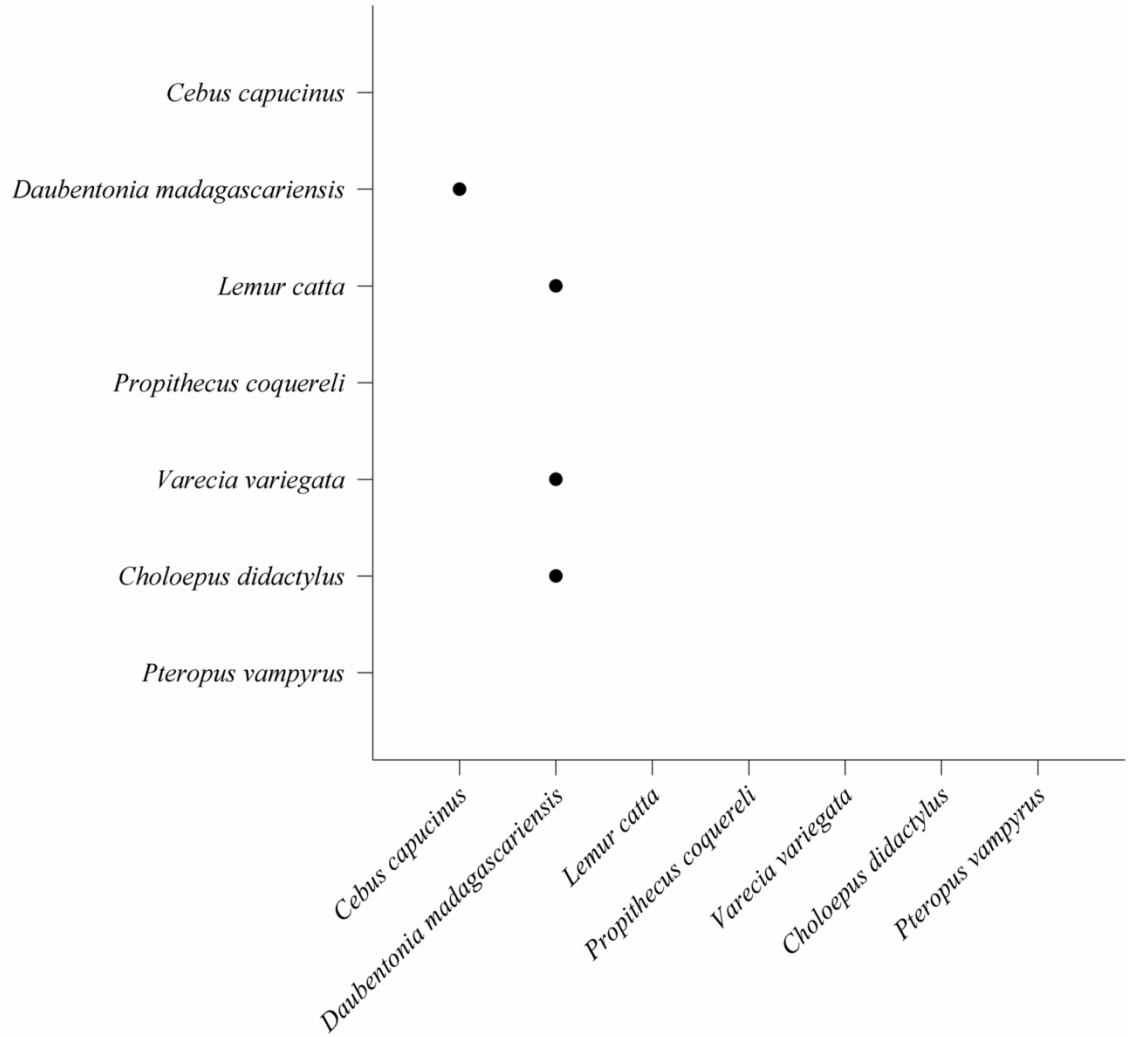

Figure 108: Multiple statistical comparisons between knee excursion in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

In respects to the ankle, all species used a hook grasp during below branch quadrupedal locomotion, but as with the wrist a clear primate and non-primate distinction emerged (Figure 109). As mention in section 3.1.2, ankle movements in primates during below branch quadrupedal locomotion were characterized by two general patterns. In *C. capucinus*, *V. variegata*, and *D. madagascariensis*, the position of the ankle was cranially oriented at touchdown. The ankle was then further cranially oriented until close to the end of support phase, and at this point the ankle was caudally deviated to slightly more neutral position until lift-off. In *L. catta* and *P. coquereli* the ankle was placed in a highly cranially oriented position at touchdown, and throughout the remainder of support phase the ankle was caudally deviated into a more neutral position. All primate species walking below branches demonstrated a similar cranially-deviated ankle angle near the end of support phase.

In the non-primate species, the position of the ankle was kept in a more neutral position throughout support phase, with only slight cranial deviation observed in *C. didactylus*, and slight caudal deviation observed in *P. vampyrus* (Figures 110-112). Overall levels of ankle excursion were similar between most species; with the exception that *P. coquereli* demonstrated a relatively large amount of ankle excursion, while *D. madagascariensis* and *P. vampyrus* showed relatively little (Figures 113 and 114).

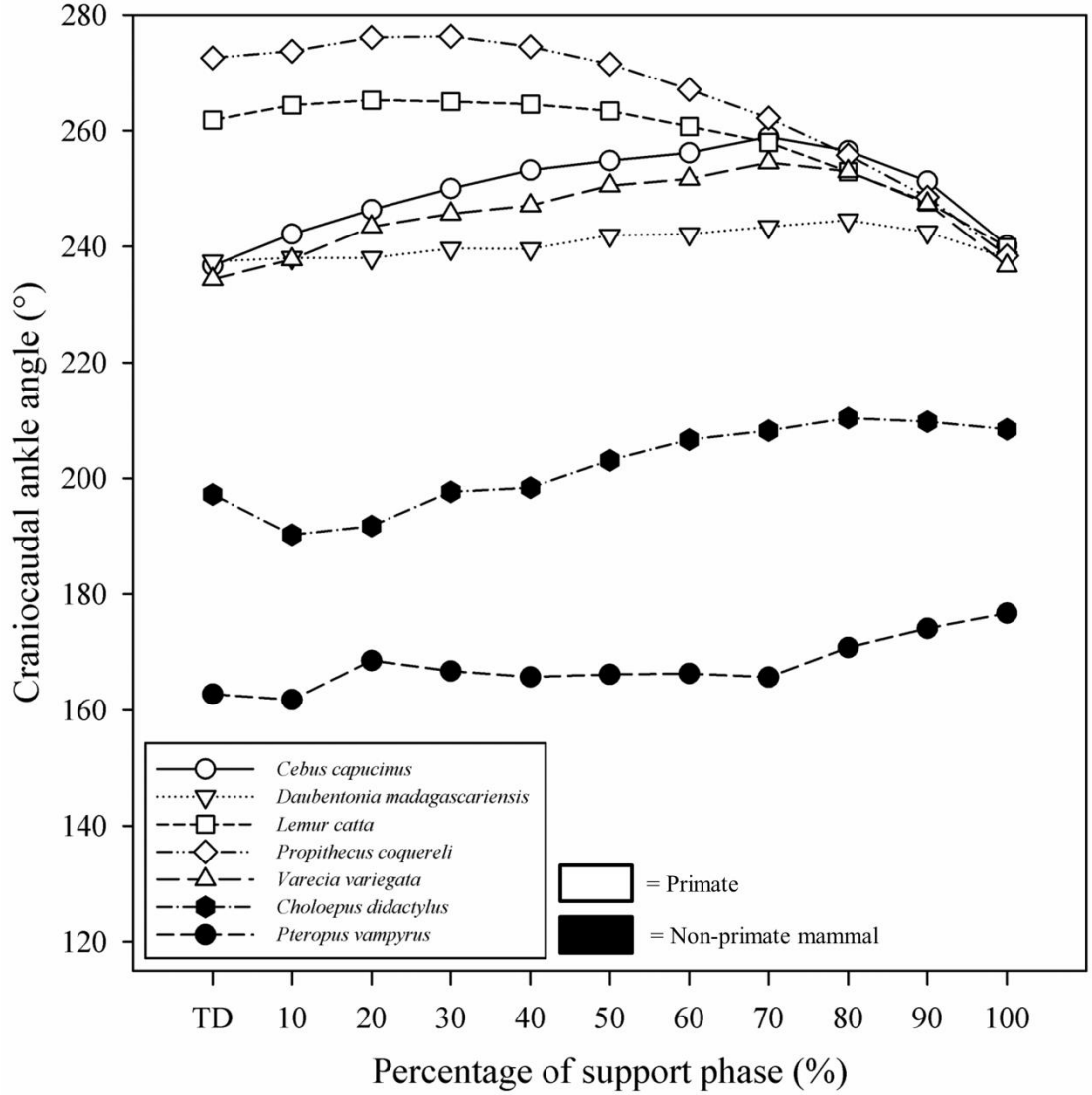

Figure 109: Patterns of mean ankle movement (°) observed during below branch quadrupedal locomotion in primates and non-primate mammals.

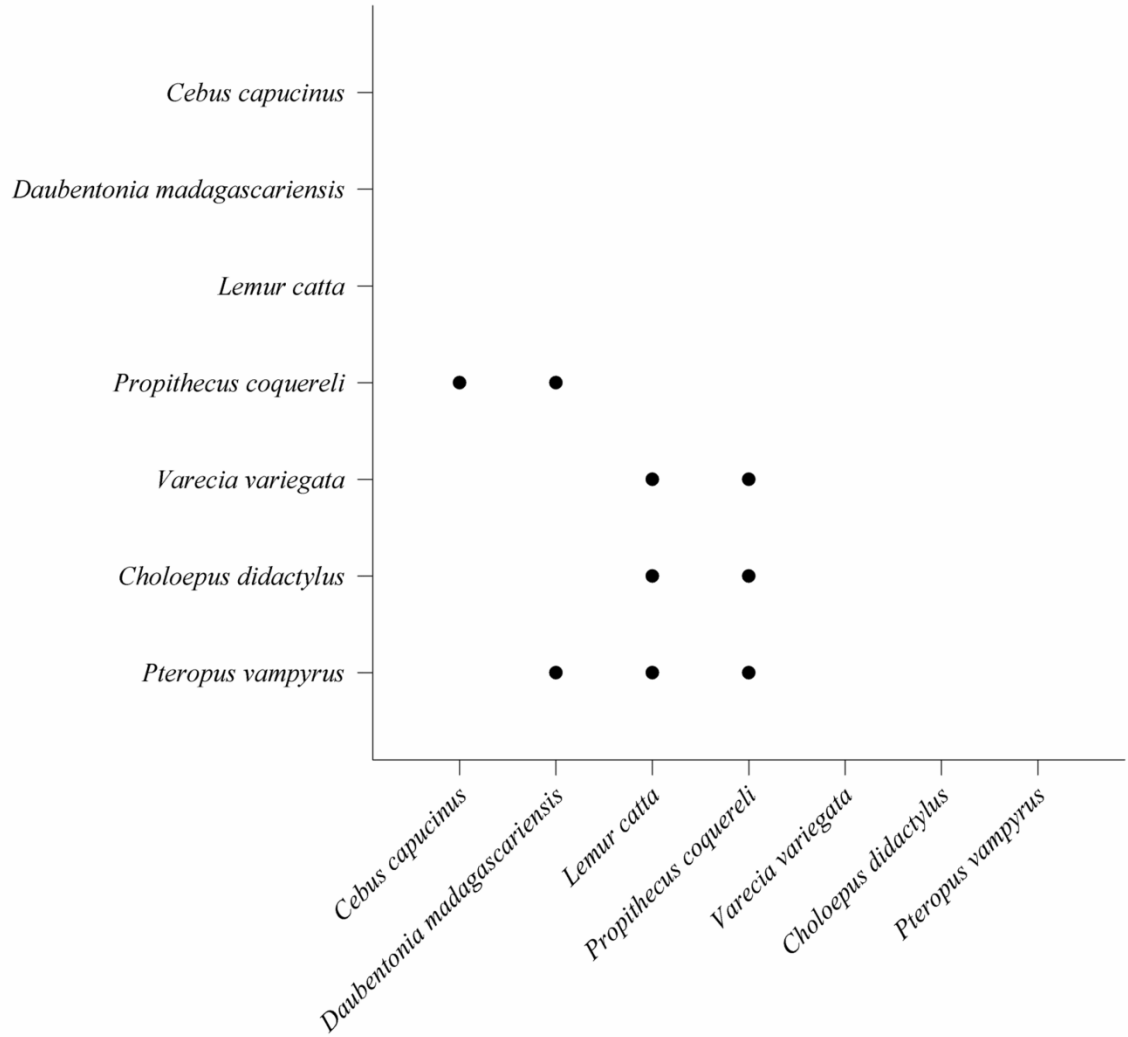

Figure 110: Multiple statistical comparisons between ankle angle at touchdown in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

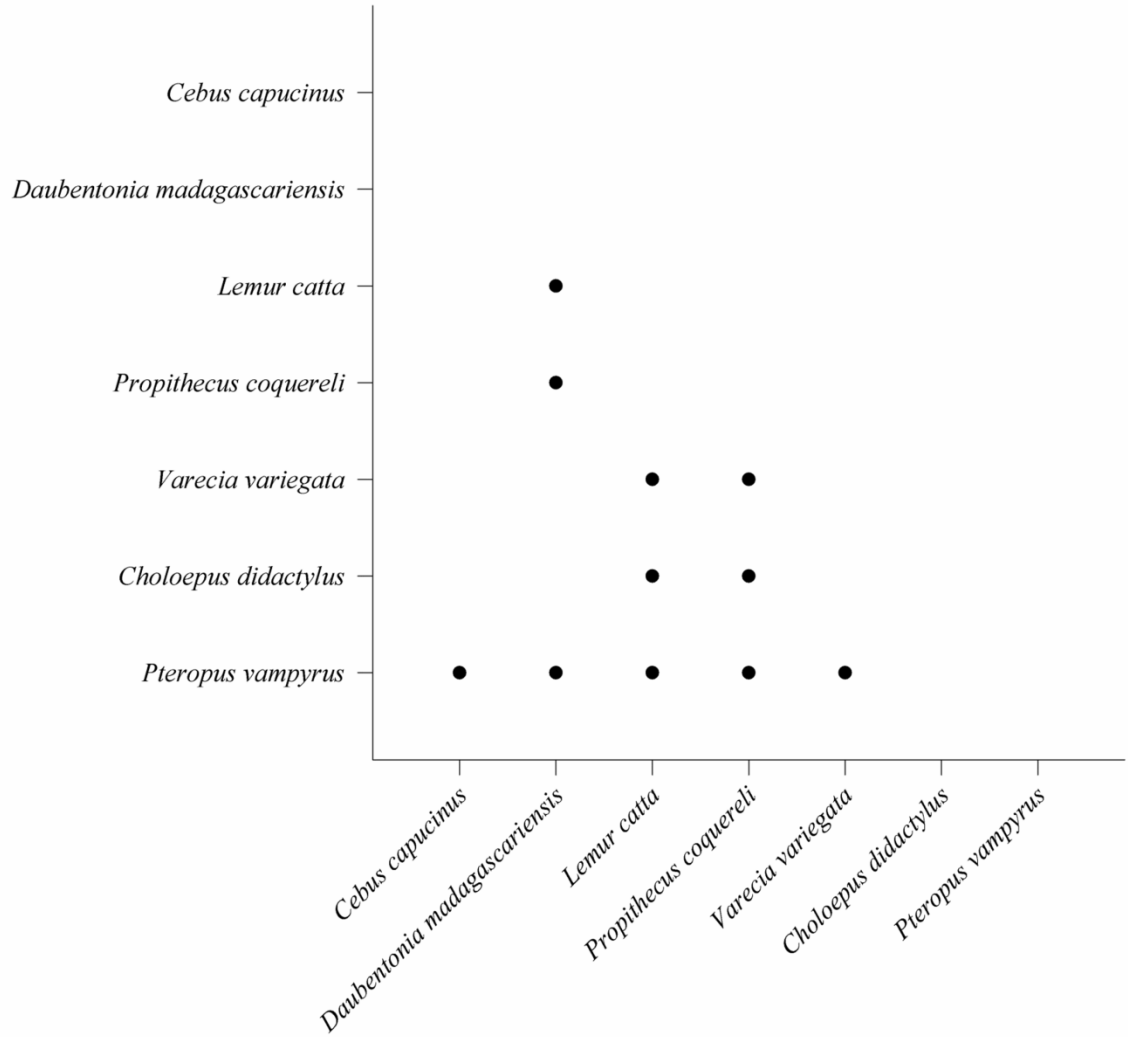

Figure 111: Multiple statistical comparisons between ankle angle at mid-support in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

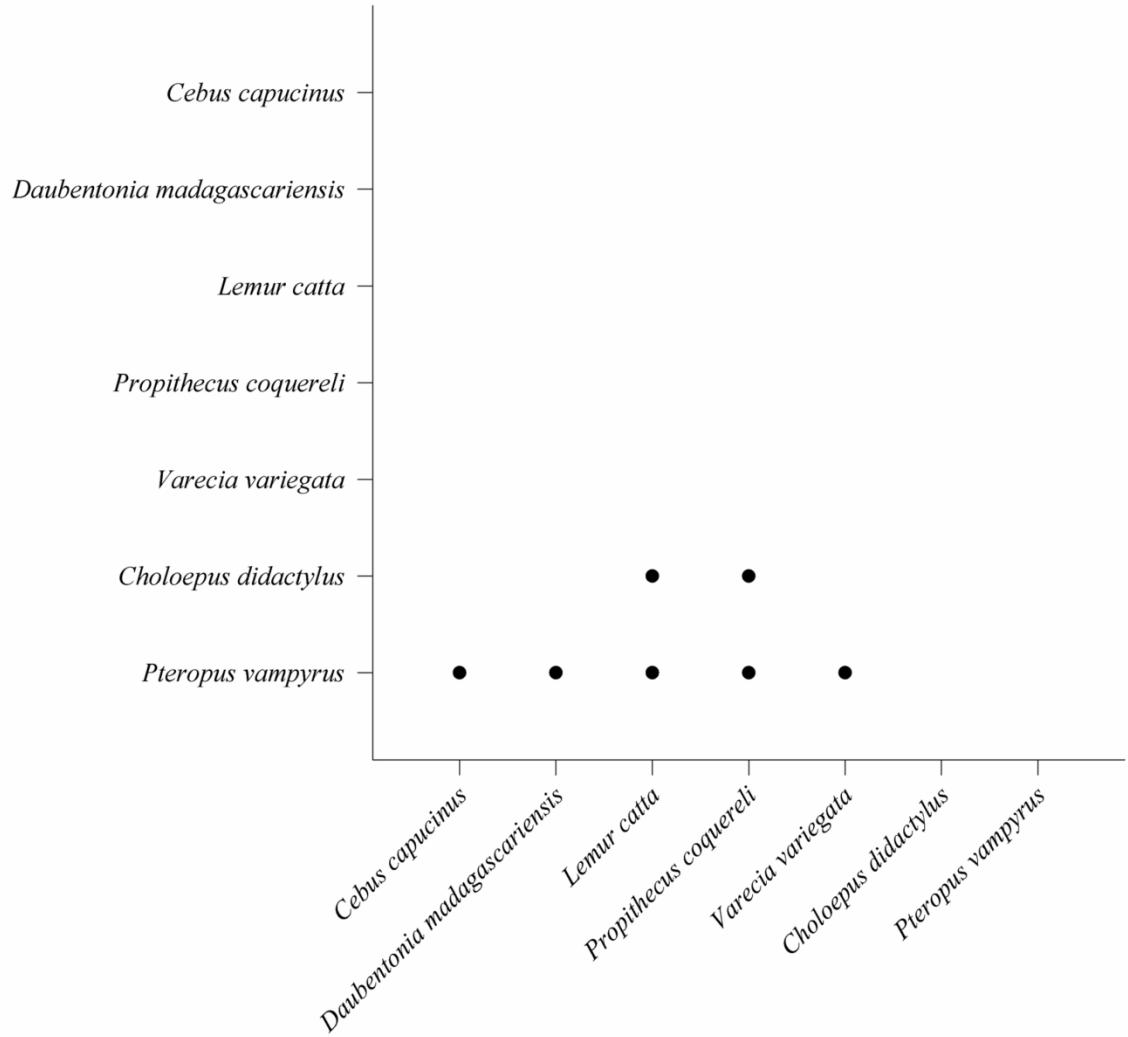

Figure 112: Multiple statistical comparisons between ankle angle at the end of support phase in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

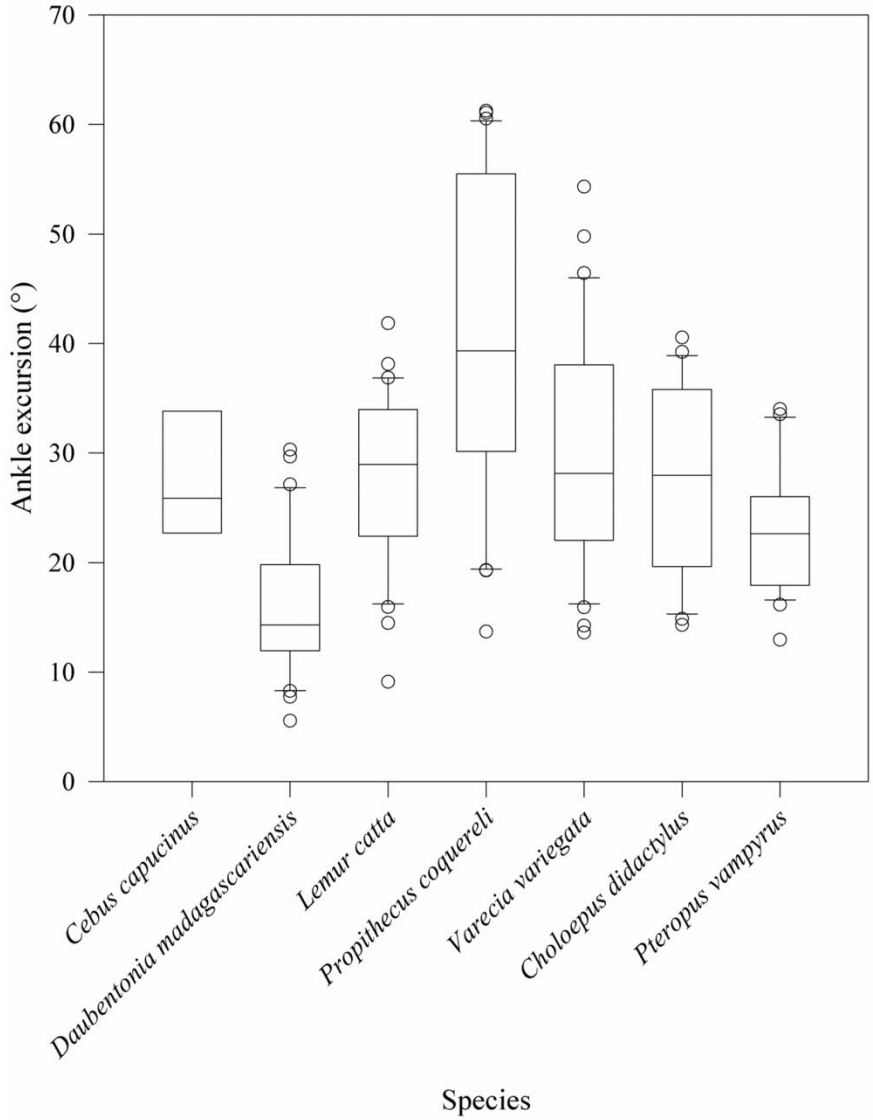

Figure 113: Mean and standard deviation values of ankle excursion (°) observed during below branch quadrupedal locomotion in primate and non-primate mammals.

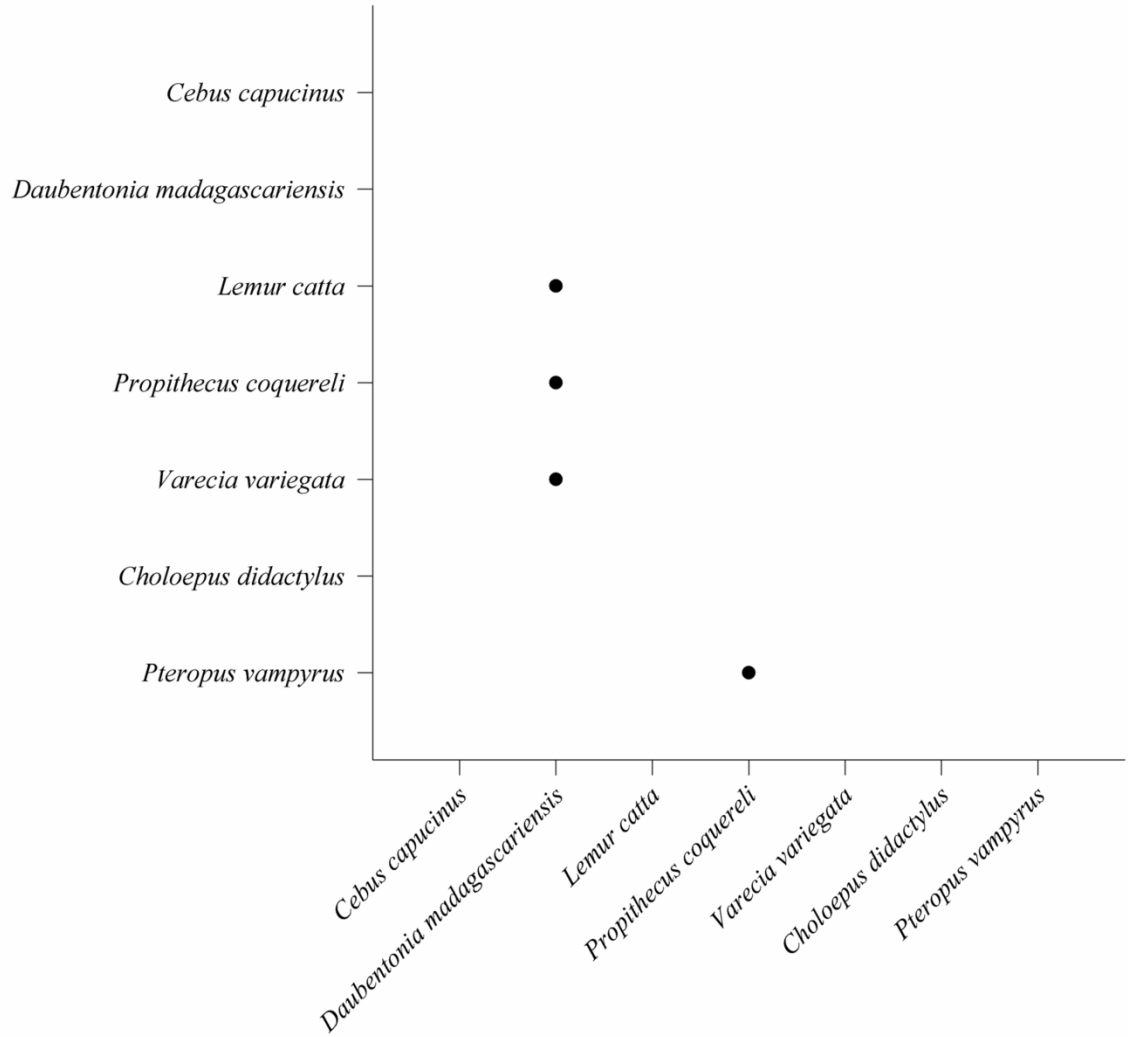

Figure 114: Multiple statistical comparisons between ankle excursion in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

3.2.3 Spatiotemporal gait variables

In total, 398 strides were used for spatiotemporal gait analysis. Table 10 summarizes the number of steps collected per limb for each species, and data for diagonality, stride duration, stride length, and forelimb and hindlimb duty factor and relative swing proportion. All data displayed a non-normal distribution and unequal variances, therefore non-parametric statistics were used for all comparisons. A significant ($P \leq 0.001$) positive association was observed between stride duration and stride length. No significant relationship between normalized speed and the other spatiotemporal gait variables collected were observed.

Table 10: Mean and standard deviation values for spatiotemporal gait variables collected during below branch quadrupedal locomotion in primate and non-primate mammals.

Species	N	Velocity (m/s)	Diagonality	Relative forelimb swing	Relative hindlimb swing	Forelimb duty factor	Hindlimb duty factor	Stride distance (m)	Stride duration (sec)
Cebus capucinus	6	0.59 ± 0.07	0.54 ± 0.07	0.43 ± 0.07	0.43 ± 0.05	0.57 ± 0.07	0.57 ± 0.05	0.57 ± 0.05	0.83 ± 0.13
Daubentonia madagascariensis	49	0.47 ± 0.15	0.56 ± 0.07	0.45 ± 0.11	0.40 ± 0.08	0.56 ± 0.14	0.60 ± 0.08	0.53 ± 0.10	1.29 ± 0.43
Lemur catta	76	0.54 ± 0.18	0.49 ± 0.08	0.36 ± 0.10	0.32 ± 0.05	0.65 ± 0.11	0.68 ± 0.05	0.39 ± 0.11	0.75 ± 0.12
Propithecus coquereli	84	0.51 ± 0.08	0.41 ± 0.12	0.44 ± 0.12	0.36 ± 0.06	0.56 ± 0.14	0.64 ± 0.06	0.52 ± 0.09	1.05 ± 0.23
Varecia variegata	52	0.60 ± 0.08	0.53 ± 0.05	0.42 ± 0.02	0.41 ± 0.05	0.59 ± 0.09	0.57 ± 0.5	0.57 ± 0.07	0.97 ± 0.10
Choloepus didactylus	51	0.11 ± 0.04	0.50 ± 0.16	0.34 ± 0.11	0.30 ± 0.10	0.72 ± 0.31	0.70 ± 0.10	0.87 ± 0.32	1.25 ± 0.43
Pteropus vampyrus	46	0.17 ± 0.05	0.38 ± 0.36	0.38 ± 0.12	0.27± 0.09	0.71 ± 0.26	0.73 ± 0.09	0.34 ± 0.10	2.04 ± 0.34
Desmodus rotundus	34	0.18 ± 0.06	0.39 ± 0.16	0.44 ± 0.20	0.26 ± 0.09	0.62 ± 0.18	0.74 ± 0.09	0.23 ± 0.01	1.29 ± 0.68

277

In regards to stride duration and distance, significant differences were observed between species during below branch quadrupedal locomotion (Figures 115-118). Stride duration demonstrated a negative association with normalized speed, and although significant differences were observed between species no appreciable patterns were detected as a whole. For *C. capucinus* and *L. catta* stride duration was significantly shorter than observed in most other species. Stride distance was positively correlated with normalized speed, and varied greatly between species. After accounting for variation in normalized speed between species, *C. didactylus* demonstrated significantly greater stride distance, and *D. rotundus* demonstrated significantly shorter stride distance than what was observed in other species.

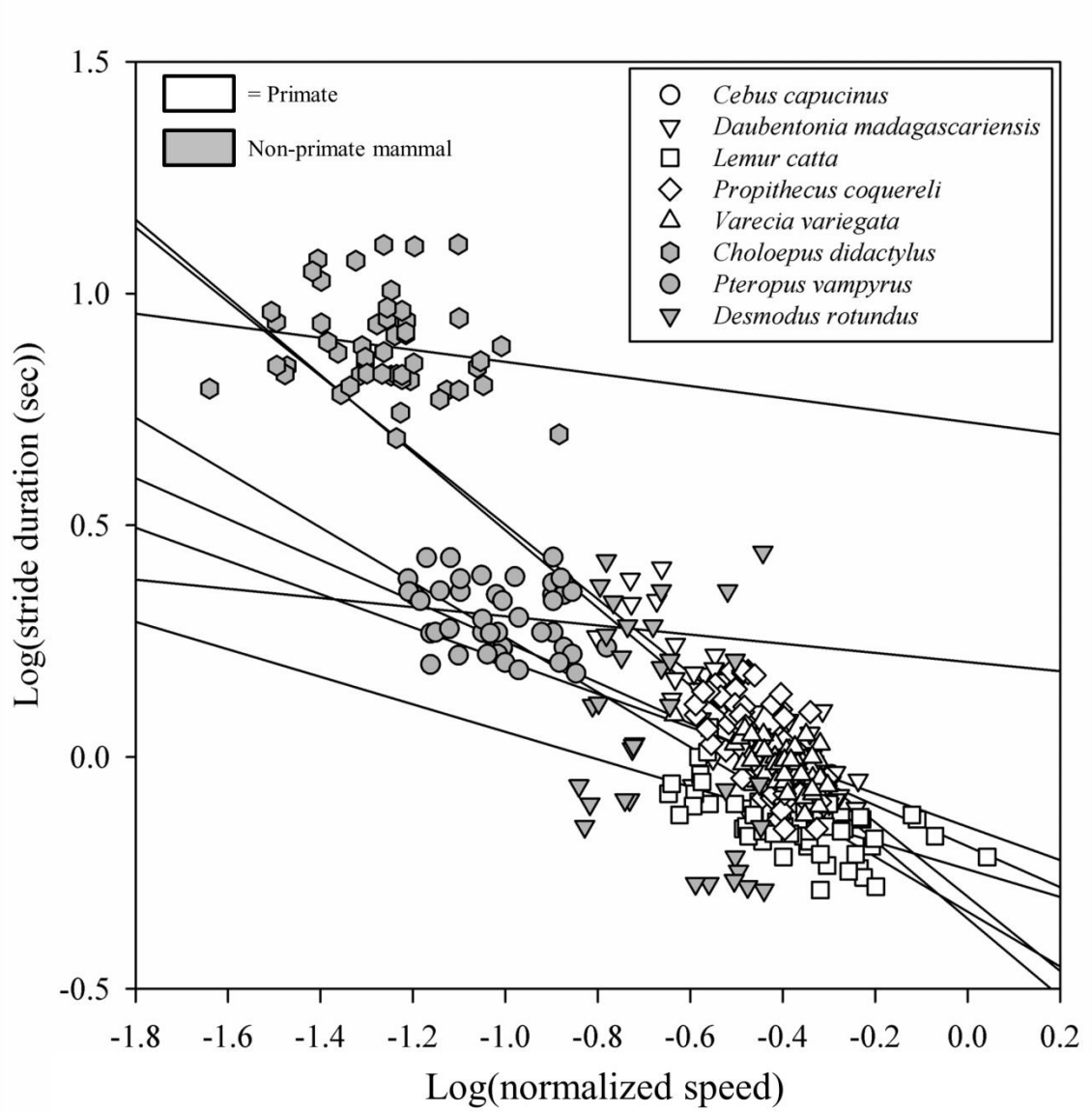

Figure 115: The relationship between log-transformed normalized speed and stride duration (sec) during below branch quadrupedal locomotion in primate and non-primate mammals.

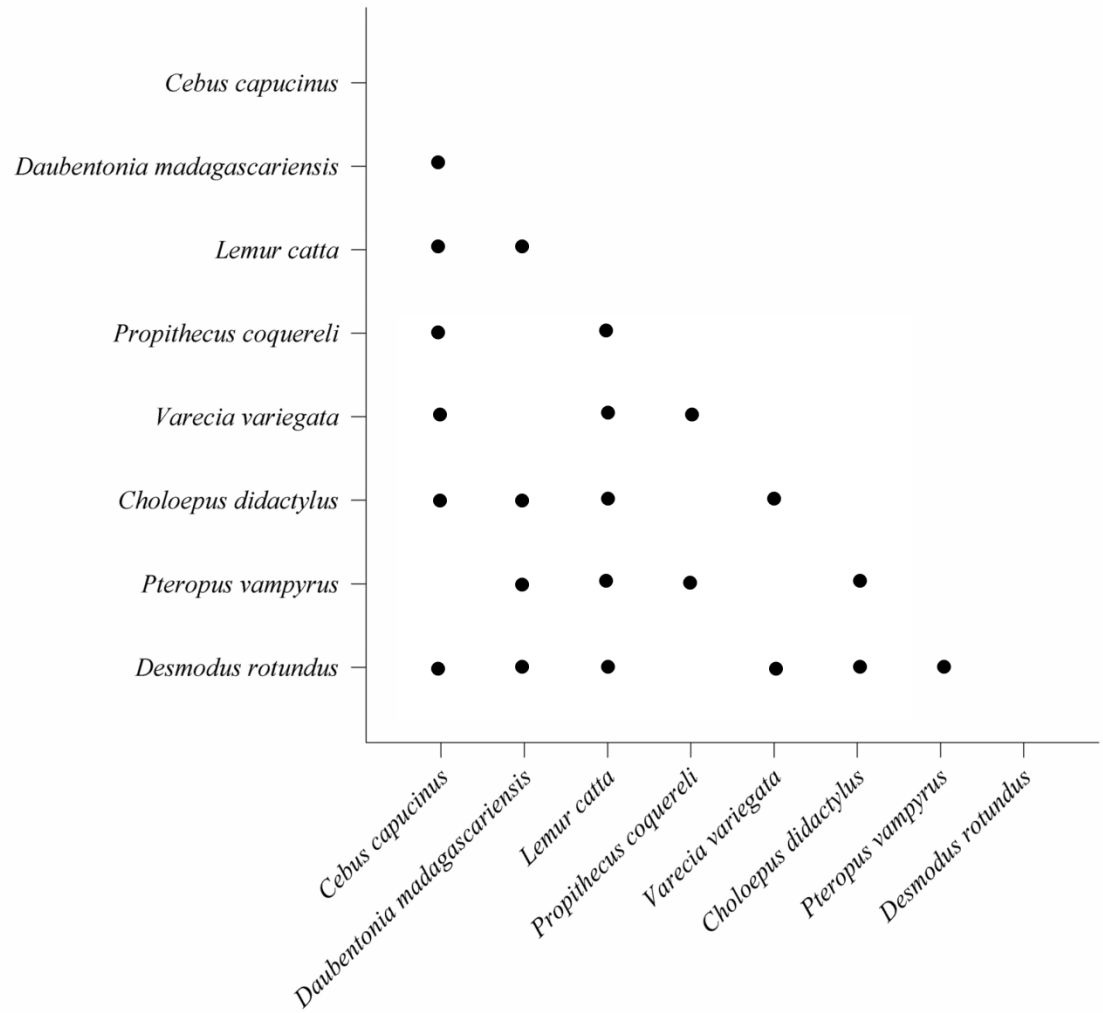

Figure 116: Multiple statistical comparisons between stride duration in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

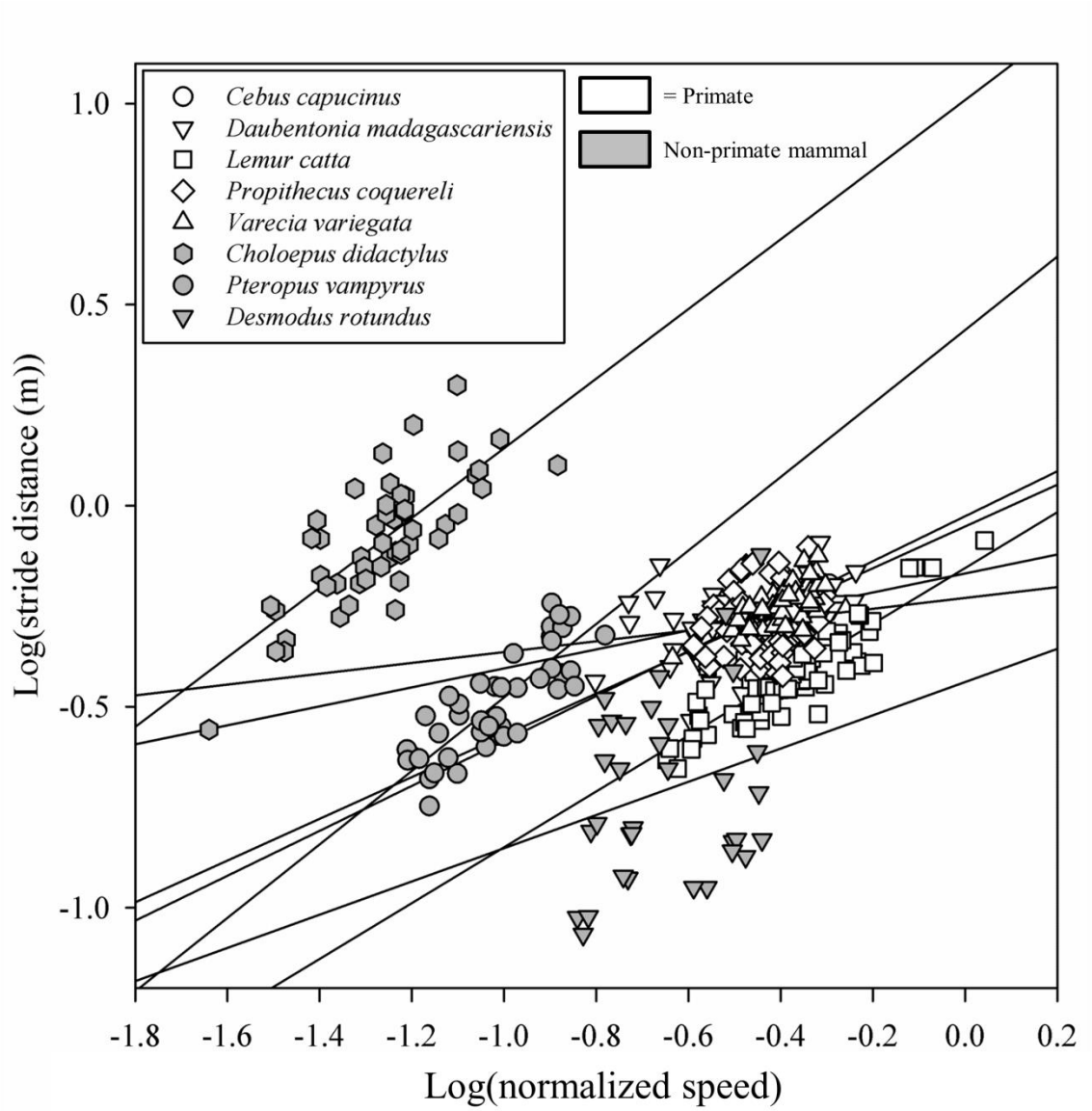

Figure 117: The relationship between log-transformed normalized speed and stride distance (m) during below branch quadrupedal locomotion in primate and non-primate mammals.

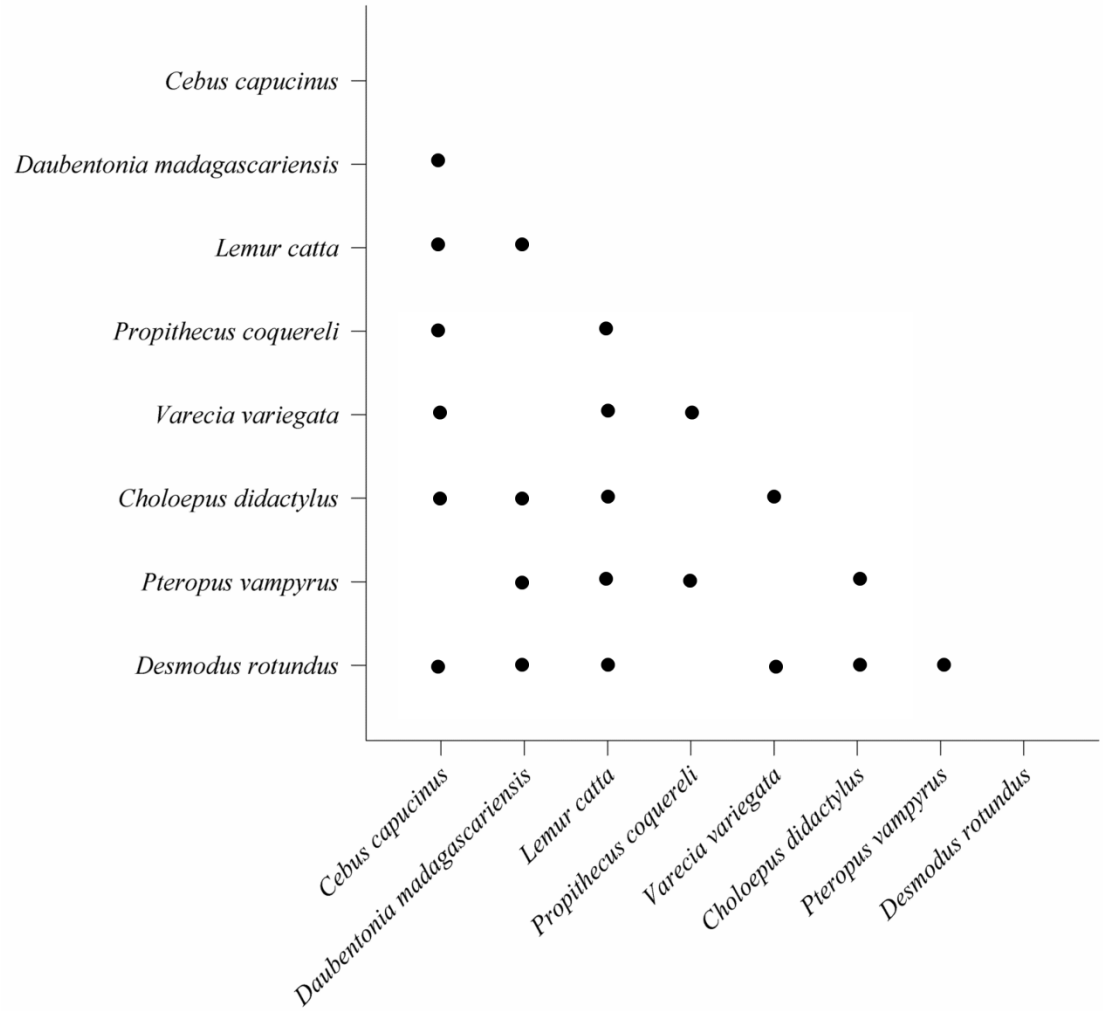

Figure 118: Multiple statistical comparisons between stride duration in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

Patterns of forelimb and hindlimb duty factor and relative swing phase largely showed the same pattern across all species, although some exceptions were present (Figures 119-126). In general, forelimb and hindlimb duty factor tended to be slightly longer, and forelimb and hindlimb relative swing phase tended to be slightly shorter in the non-primates species, but clear taxonomic differences were not observed.

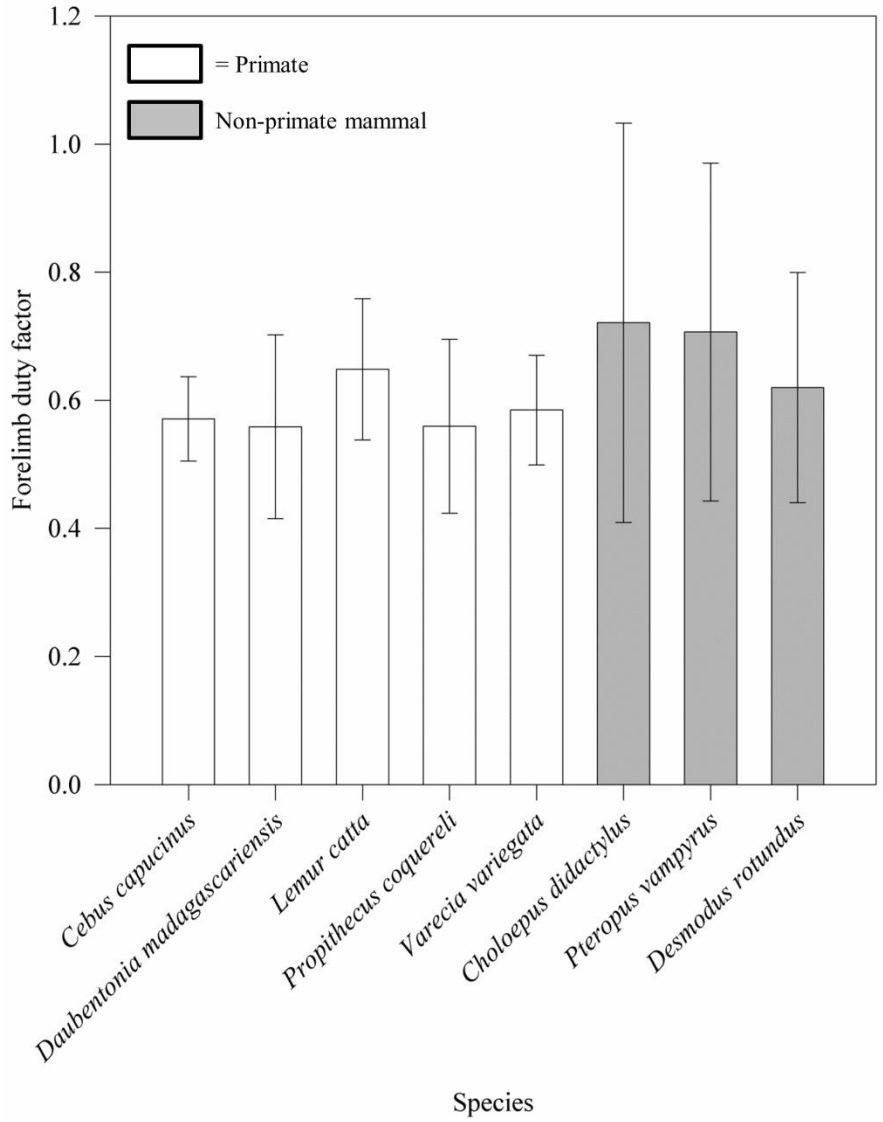

Figure 119: Forelimb duty factor (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals.

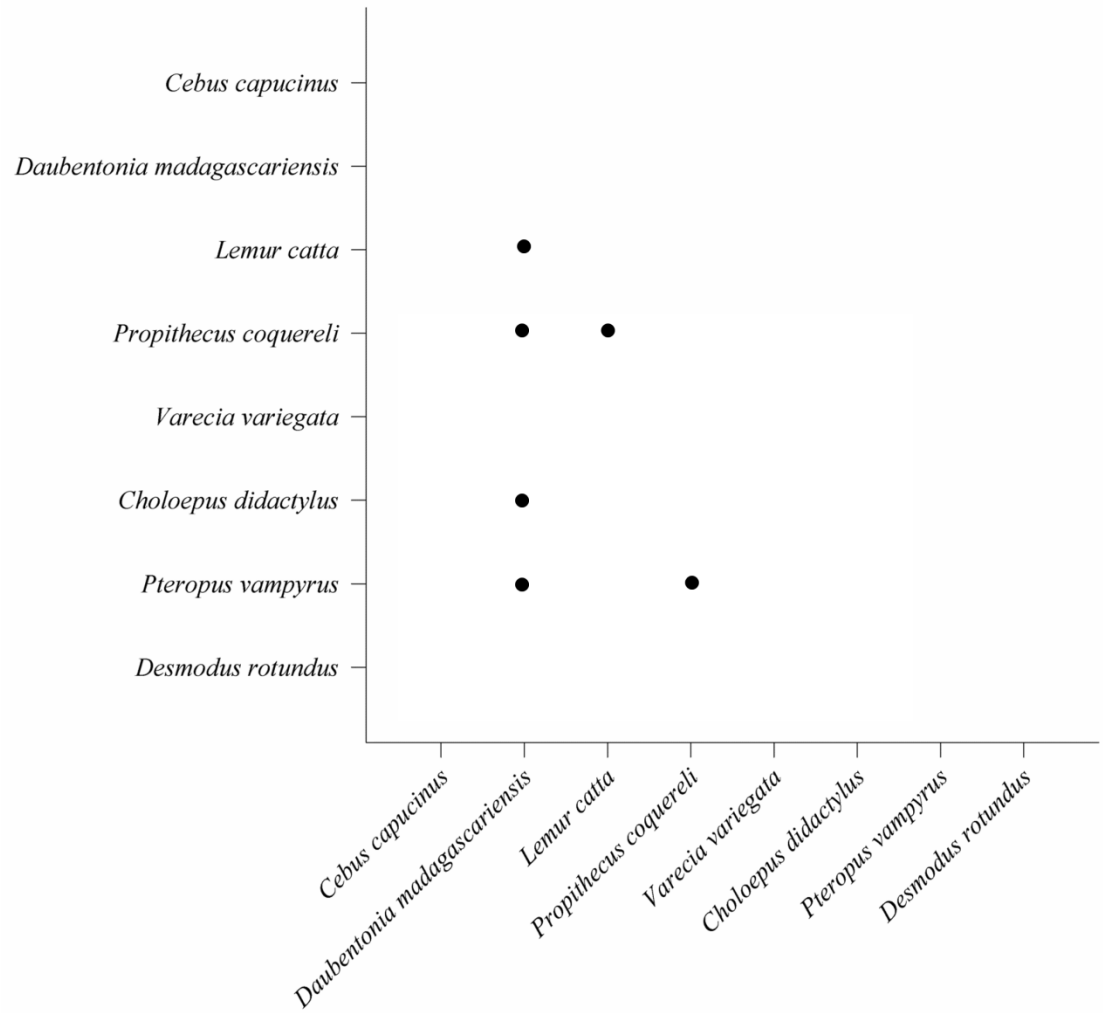

Figure 120: Multiple statistical comparisons between forelimb duty factor in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

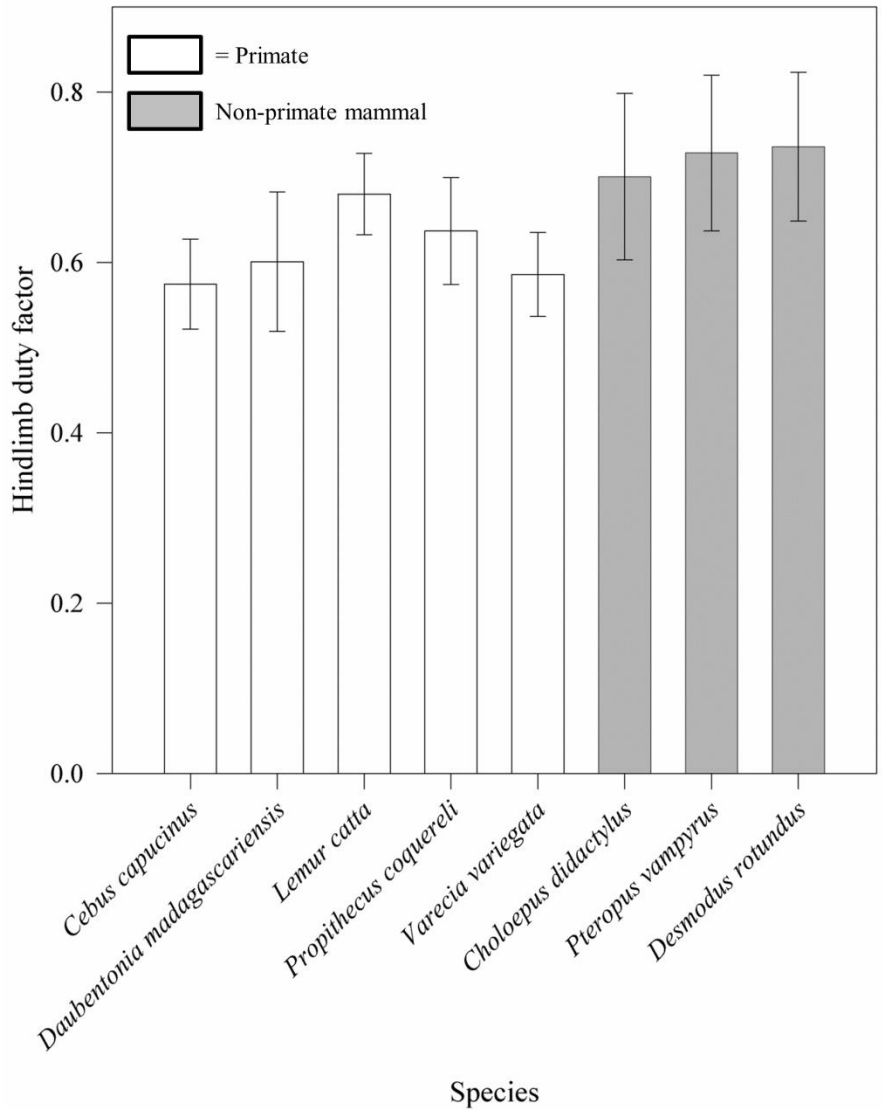

Figure 121: Hindlimb duty factor (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals.

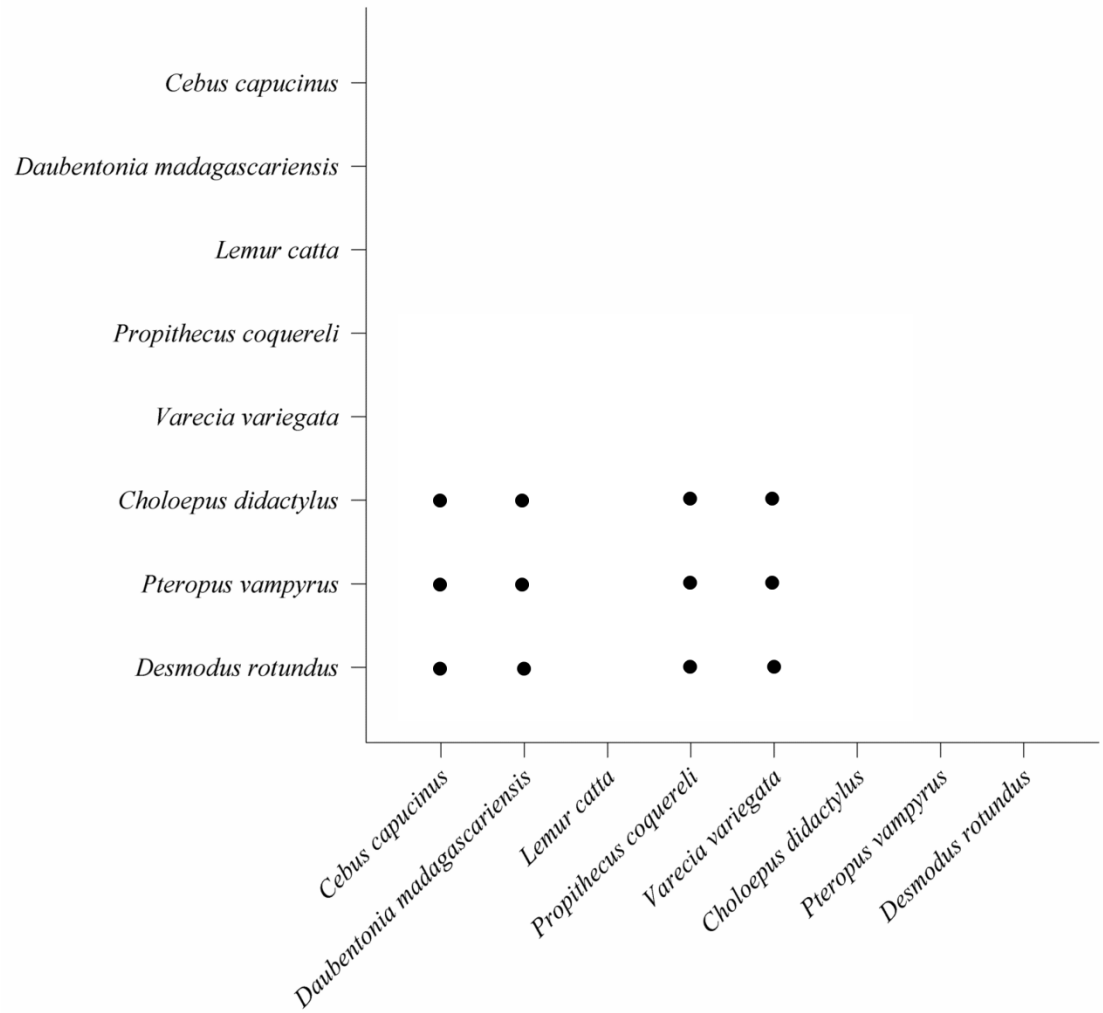

Figure 122: Multiple statistical comparisons between hindlimb duty factor in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* ≤ 0.001) between the different species.

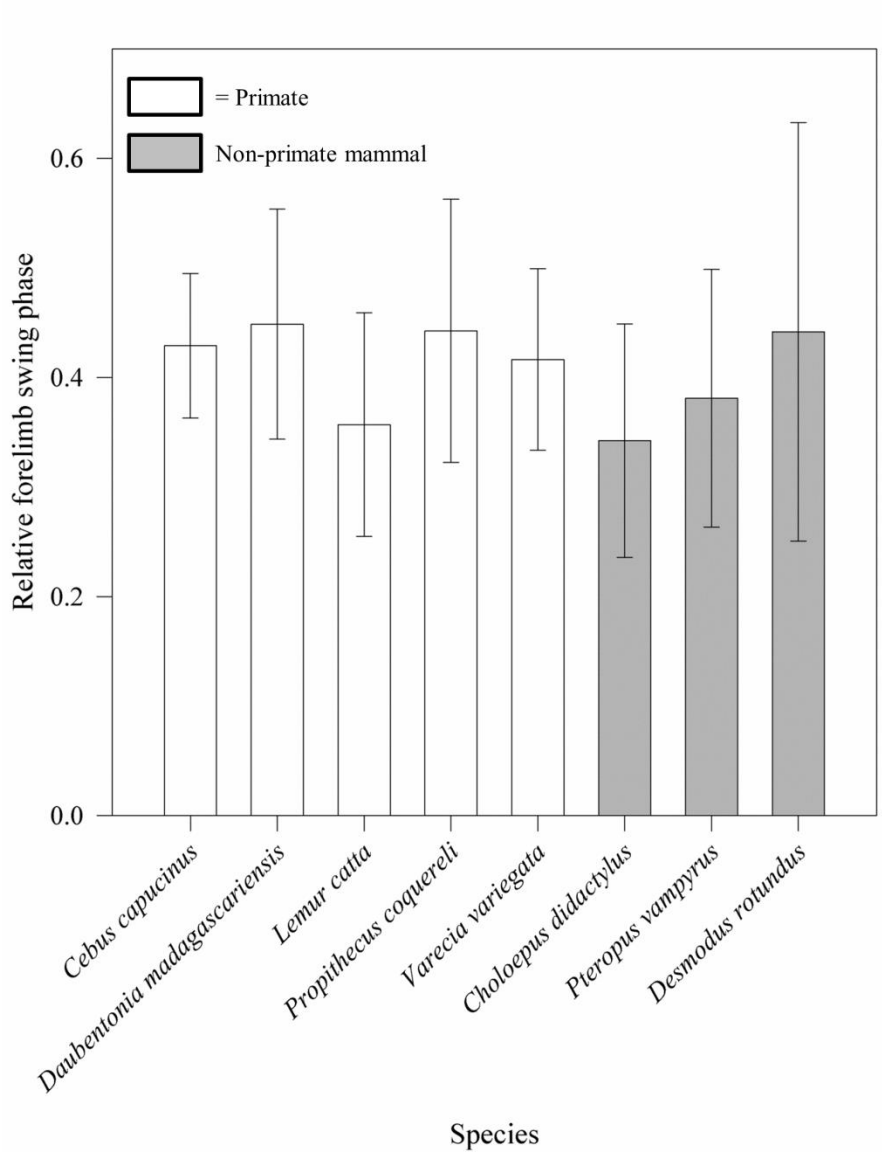

Figure 123: Relative forelimb swing phase (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals.

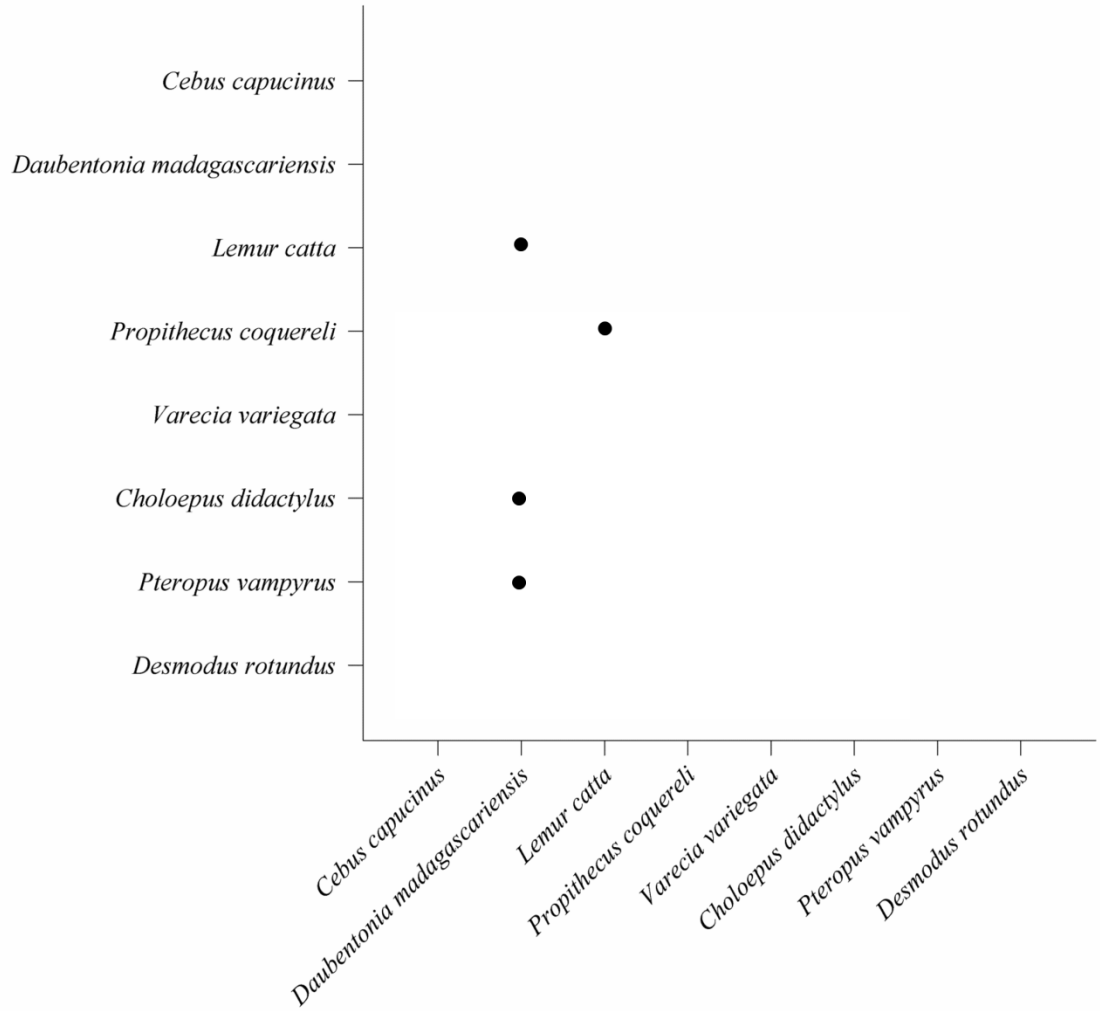

Figure 124: Multiple statistical comparisons between hindlimb duty factor in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* ≤ 0.001) between the different species.

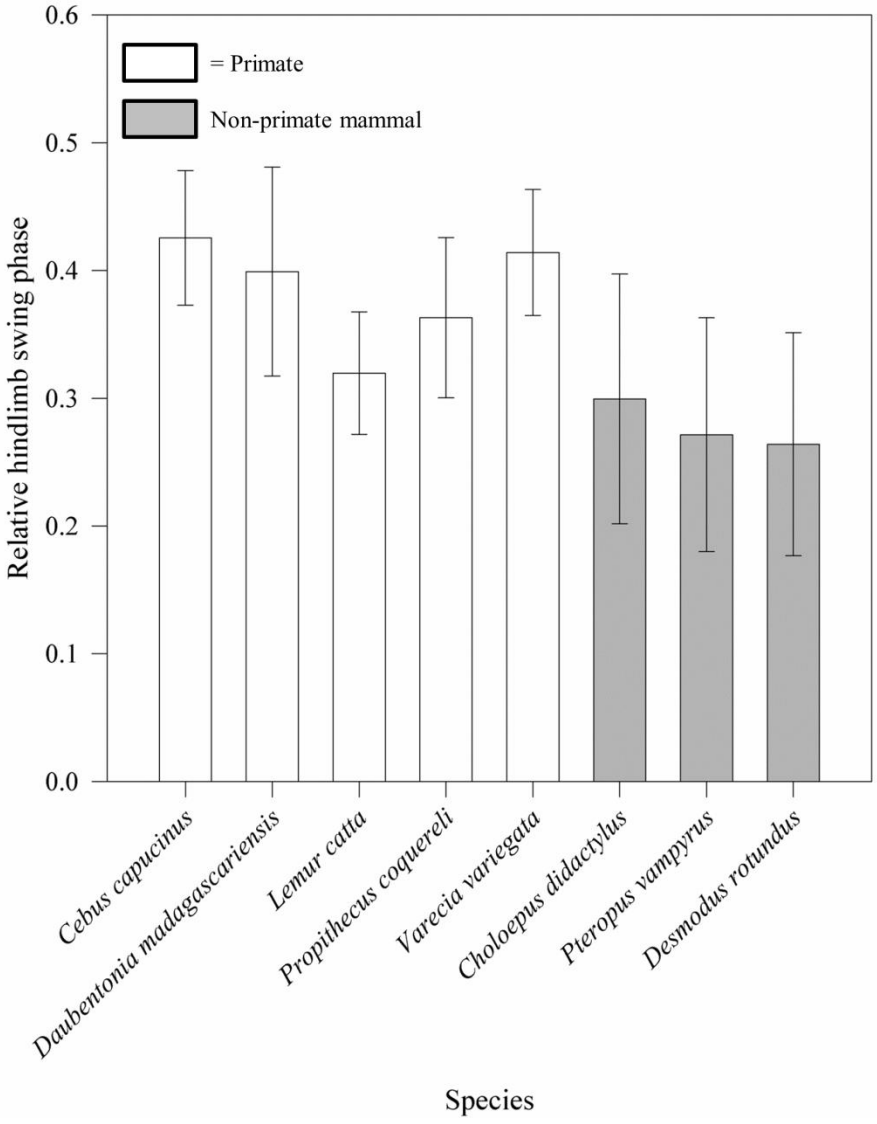

Figure 125: Relative hindlimb swing phase (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals.

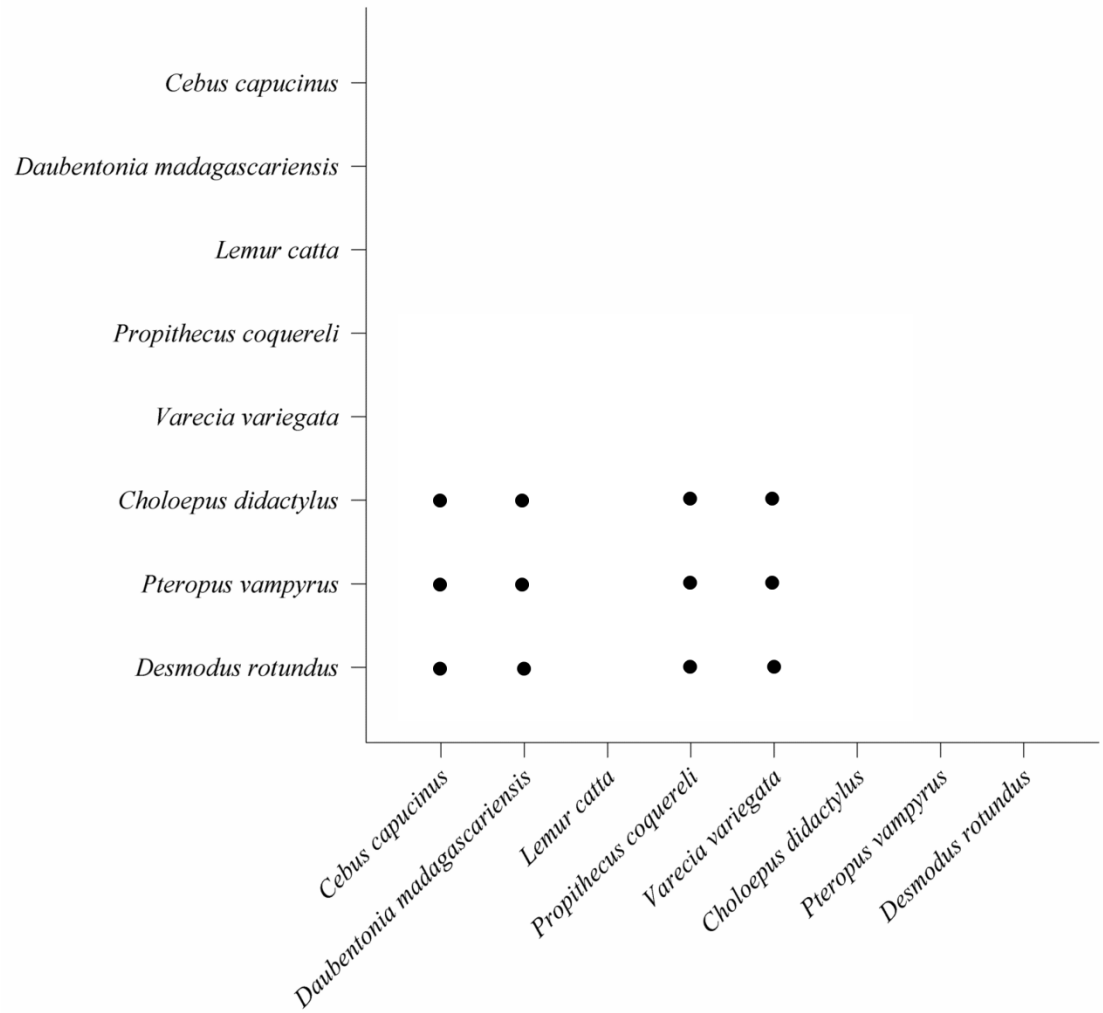

Figure 126: Multiple statistical comparisons between hindlimb duty factor in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* ≤ 0.001) between the different species.

Interlimb coordination demonstrated wide variability among taxa especially among the non-primate mammals (Figure 127), and accordingly significant variation between taxa was limited (Figure 128). In general, all the primates (except *P. coquereli*) and *C. didactylus* demonstrated a tendency for DSDC gaits, although LSDC AND LSLC gaits were also common. In *P. coquereli* and the two chiropterans, LSDC gaits were most prevalent. Gaits patterns did not follow the predicated relationship between diagonality and hindlimb duty factor proposed by Cartmill et al. (2002).

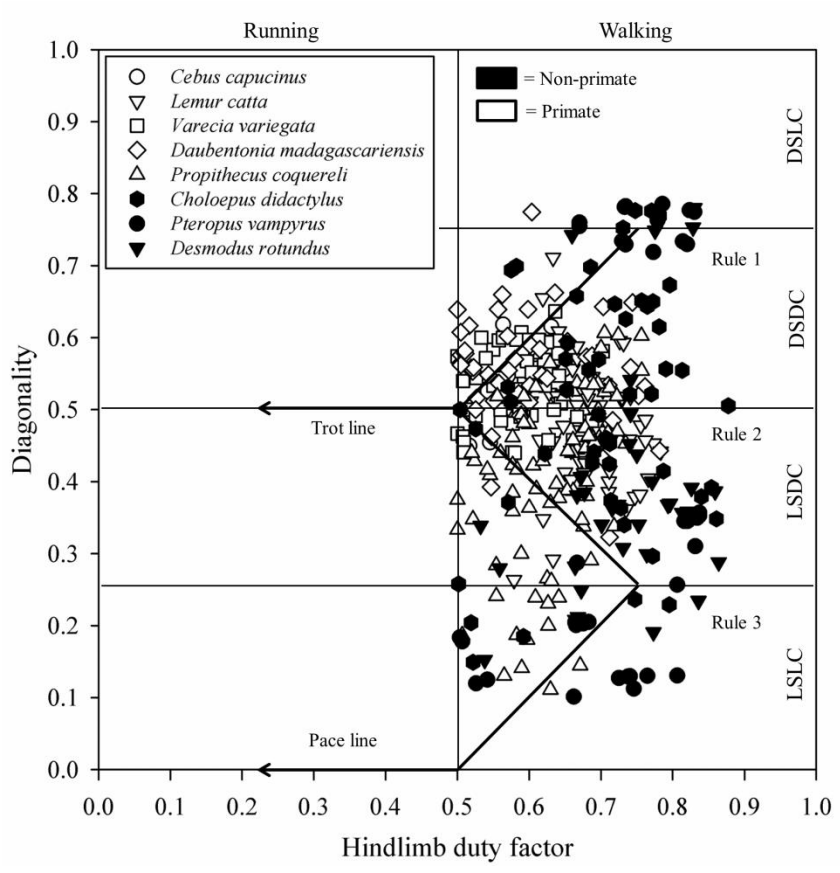

Figure 127: A modified "Hildebrand" plot (following the approach of Cartmill et al. 2002) displaying diagonality for multiple strides of each of the study species over hindlimb duty factor during below branch quadrupedal locomotion.

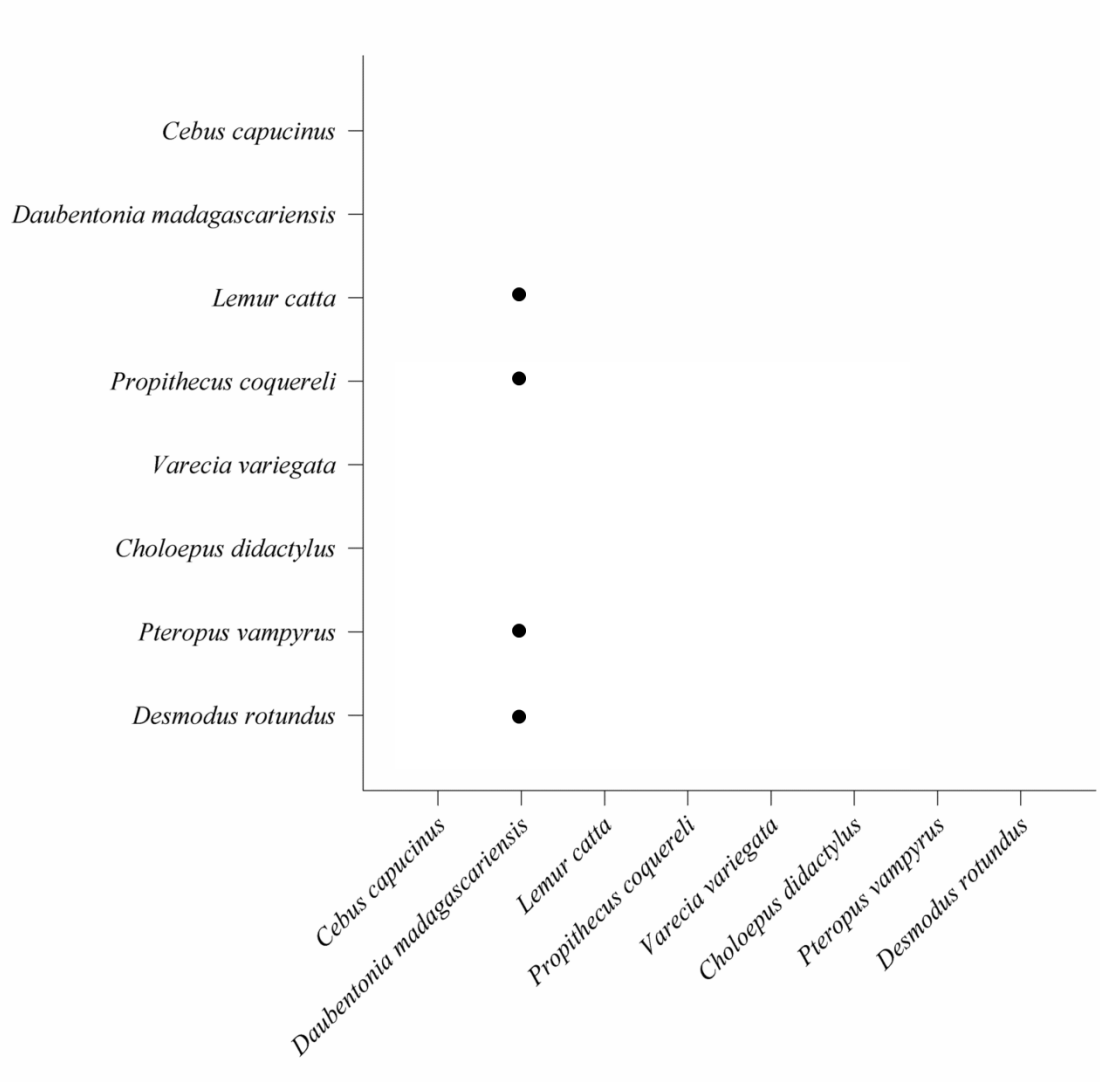

Figure 128: Multiple statistical comparisons between diagonality in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

3.3 An interspecific comparison of the mechanics of below branch quadrupedal locomotion and arm-swinging

3.3.1 Kinetics

In total, 251 single contact forelimb forces were collected and analyzed. Table 11 and 12 summarizes the number of steps collected for each species, data for FHpk, SHpk, FHI, SHI, HI, Mpk, Lpk, MI, LI, MLI, and Zpk, and the timing associated with FHpk, SHpk, B/P, Mpk, Lpk, and Zpk. All data displayed a non-normal distribution and unequal variances, therefore non-parametric statistics were used for all comparisons. A significant ($P \leq 0.001$) positive association was observed between Vpk and normalized speed. No significant relationship between normalized speed and the other kinetic variables collected were observed.

Table 11. Limb loading data (mean ± standard deviation) for below branch quadrupedal locomotion and arm-swinging in primate and non-primate mammals.

Species	Orientation	Limb	N	FHpk (%bw)	SHpk (%bw)	FHI (%bws)	SHI (%bws)	HI (%bws)	Mpk (%bw)	Lpk (%bw)	MI (%bws)	LI (%bws)	MLI (%bws)	Vpk (%bw)
Daubentonia madagascariensis	Below	Forelimb	26	23.34 ± 7.45	-13.64 ± 6.42	6.63 ± 3.94	-2.31 ± 1.69	4.32 ± 4.80	-7.29 ± 3.99	3.13 ± 2.56	-1.99 ± 1.35	0.32 ± 0.25	-1.67 ± 1.36	66.96 ± 8.33
Lemur catta	Below	Forelimb	52	23.14 ± 7.09	-14.79 ± 6.90	3.90 ± 1.70	-1.81 ± 1.07	2.09 ± 2.23	-11.84 ± 5.35	5.14 ± 2.99	-2.11 ± 1.06	0.52 ± 0.47	-1.59 ± 1.15	70.12 ± 9.32
Propithecus coquereli	Below	Forelimb	59	22.21 ± 5.59	-13.56 ± 6.86	4.59 ± 1.47	-1.88 ± 1.13	2.71 ± 1.92	-9.15 ± 3.71	3.29 ± 2.54	-2.14 ± 1.31	0.35 ± 0.35	-1.80 ± 1.47	79.90 ± 10.71
Varecia variegata	Below	Forelimb	38	25.54 ± 7.70	-10.85 ± 4.27	5.12 ± 1.65	-1.39 ± 0.74	2.99 ± 1.67	-7.85 ± 3.30	3.99 ± 2.61	-1.81 ± 0.96	0.44 ± 0.35	-1.36 ± 1.08	82.54 ± 14.95
Choloepus didactylus	Below	Forelimb	25	10.24 ± 4.88	-2.49 ± 2.20	25.41 ± 19.35	-2.02 ± 2.90	20.20 ± 16.26	-10.33 ± 6.58	1.00 ± 0.70	-18.09 ± 9.16	0.25 ± 0.35	-17.84 ± 9.29	61.64 ± 15.74
Pteropus vampyrus	Below	Forelimb	16	9.83 ± 6.54	-6.99 ± 6.14	6.84 ± 8.09	-3.05 ± 5.29	3.79 ± 9.54	-6.06 ± 2.38	5.27 ± 3.66	-2.84 ± 1.74	1.47 ± 1.47	-1.37 ± 1.28	42.28 ± 12.40
Desmodus rotundus	Arm-swinging	Forelimb	21	13.45 ± 6.05	-5.20 ± 2.85	3.66 ± 2.29	-0.87 ± 1.30	3.27 ± 2.63	-9.58 ± 10.80	1.82 ± 1.64	-1.77 ± 0.98	0.71 ± 1.10	-1.06 ± 1.26	59.74 ± 20.70
Hylobates moloch	Arm-swinging	Forelimb	13	45.59 ± 10.19	-46.27 ±14.89	12.71 ± 6.98	-12.73 ± 7.92	-0.02 ± 4.62	-15.48 ± 6.67	5.98 ± 3.39	-4.53 ± 2.44	0.88 ± 1.01	-3.65 ± 2.70	167.51 ± 6.42
Pygathrix nemaeus	Arm-swinging	Forelimb	14	30.34 ± 6.80	-26.59 ± 12.83	7.65 ± 4.16	-7.29 ± 5.66	0.36 ± 3.97	-19.39 ± 7.17	7.47 ± 4.91	-6.06 ± 3.16	1.06 ± 1.18	-5.00 ± 3.58	130.86 ± 20.55

[*] Significant difference observed ($P \leq 0.05$)
[ns] No significant difference observed ($P > 0.05$)
[FHpk] First horizontal peak force
[SHpk] Second horizontal peak force
[FHI] First horizontal impulse
[SHI] Second horizontal impulse
[Mpk] Medial peak
[Lpk] Lateral peak
[MI] Medial impulse
[LI] Lateral impulse
[MLI] Mediolateral impulse
[Vpk] Vertical peak

Table 12: The timing of limb loading events throughout support phase (mean ± standard deviation) during below branch quadrupedal locomotion and arm-swinging in primate and non-primate mammals.

Species	Orientation	Limb	N	FHpk	SHpk	B/P	Mpk	Lpk	Vpk
Daubentonia madagascariensis	Below	Forelimb	26	0.21 ± 0.10	0.78 ± 0.15	0.60 ± 0.11	0.52 ± 0.26	0.64 ± 0.34	0.60 ± 0.11
Lemur catta	Below	Forelimb	52	0.21 ± 0.07	0.76 ± 0.08	0.56 ± 0.10	0.47 ± 0.20	0.53 ± 0.38	0.55 ± 0.11
Propithecus coquereli	Below	Forelimb	59	0.25 ± 0.07	0.77 ± 0.05	0.58 ± 0.09	0.48 ± 0.20	0.41 ± 0.39	0.53 ± 0.12
Varecia variegata	Below	Forelimb	38	0.19 ± 0.08	0.74 ± 0.08	0.58 ± 0.08	0.45 ± 0.20	0.38 ± 0.35	0.54 ± 0.10
Choloepus didactylus	Below	Forelimb	25	0.42 ± 0.15	0.89 ± 0.12	0.77 ± 0.18	0.56 ± 0.17	0.69 ± 0.44	0.56 ± 0.11
Pteropus vampyrus	Below	Forelimb	16	0.27 ± 0.21	0.72 ± 0.24	0.65 ± 0.26	0.45 ± 0.29	0.46 ± 0.28	0.49± 0.20
Desmodus rotundus	Arm-swinging	Forelimb	21	0.32 ± 0.18	0.80 ± 0.11	0.66 ± 0.19	0.57 ± 0.26	0.46 ± 0.43	0.50 ± 0.21
Hylobates moloch	Arm-swinging	Forelimb	13	0.25 ± 0.08	0.72 ± 0.08	0.50 ± 0.07	0.40 ± 0.20	0.55 ± 0.39	0.43 ± 0.06
Pygathrix nemaeus	Arm-swinging	Forelimb	14	0.24 ± 0.08	0.73 ± 0.08	0.49 ± 0.07	0.41 ± 0.20	0.58 ± 0.38	0.42 ± 0.07

[*] Significant difference observed ($P \leq 0.05$)
[ns] No significant difference observed ($P > 0.05$)
[FHpk] First horizontal peak force
[SHpk] Second horizontal peak force
[B/P] Braking to propulsive transition during above branch quadrupedal locomotion and/or propulsive to braking transition during below branch quadrupedal locomotion
[Mpk] Medial peak
[Lpk] Lateral peak
[Vpk] Vertical peak

In large part, forelimb loading patterns for animals walking quadrupedally below branches were more similar to each other than to species that use arm-swinging locomotion. Vertical peak forces were much higher in arm-swinging primates than in animals that walk quadrupedally below branches, although the differences were greater between arm-swinging primates and non-primate mammals (Figures 129-131). For all species, forelimb vertical force traces were represented by a single peak. During below branch quadrupedal locomotion, this peak occurred approximately at 54% of support phase, and no significant difference was observed between the timing of the Vpk in the forelimb between species. During arm-swinging, this peak occurred approximately at 43% of support phase, and while no significant differences between the timing of the Vpk were observed amongst the two species of arm-swinging primate, some differences were observed when compared to animals that walk quadrupedally below branches (Figure 132).

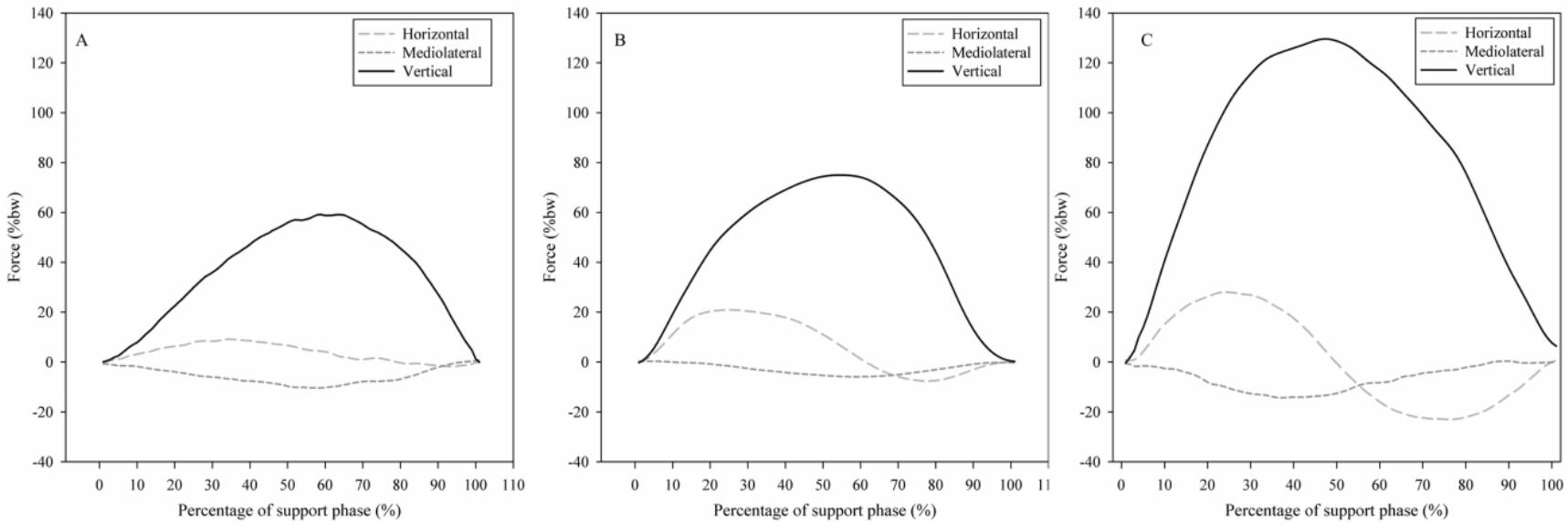

Figure 129: Representative forelimb force traces for *Choloepus didactylus* (A) and *Propithecus coquereli* (B) during below branch quadrupedal locomotion and *Pygathrix nemaeus* (C) during arm-swinging. All data are presented as a percentage of the animal's body weight (%bw).

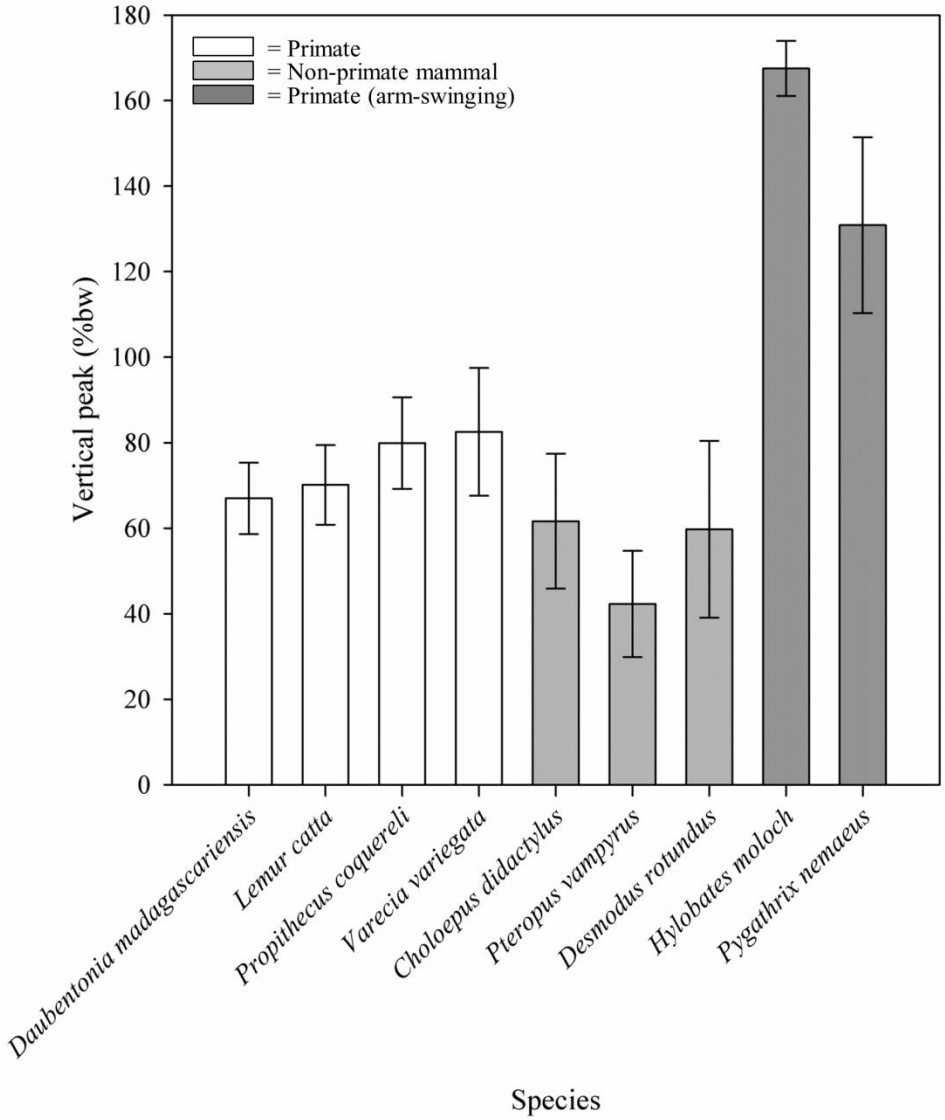

Figure 130: Mean and standard deviation values of peak vertical forces in the forelimb of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

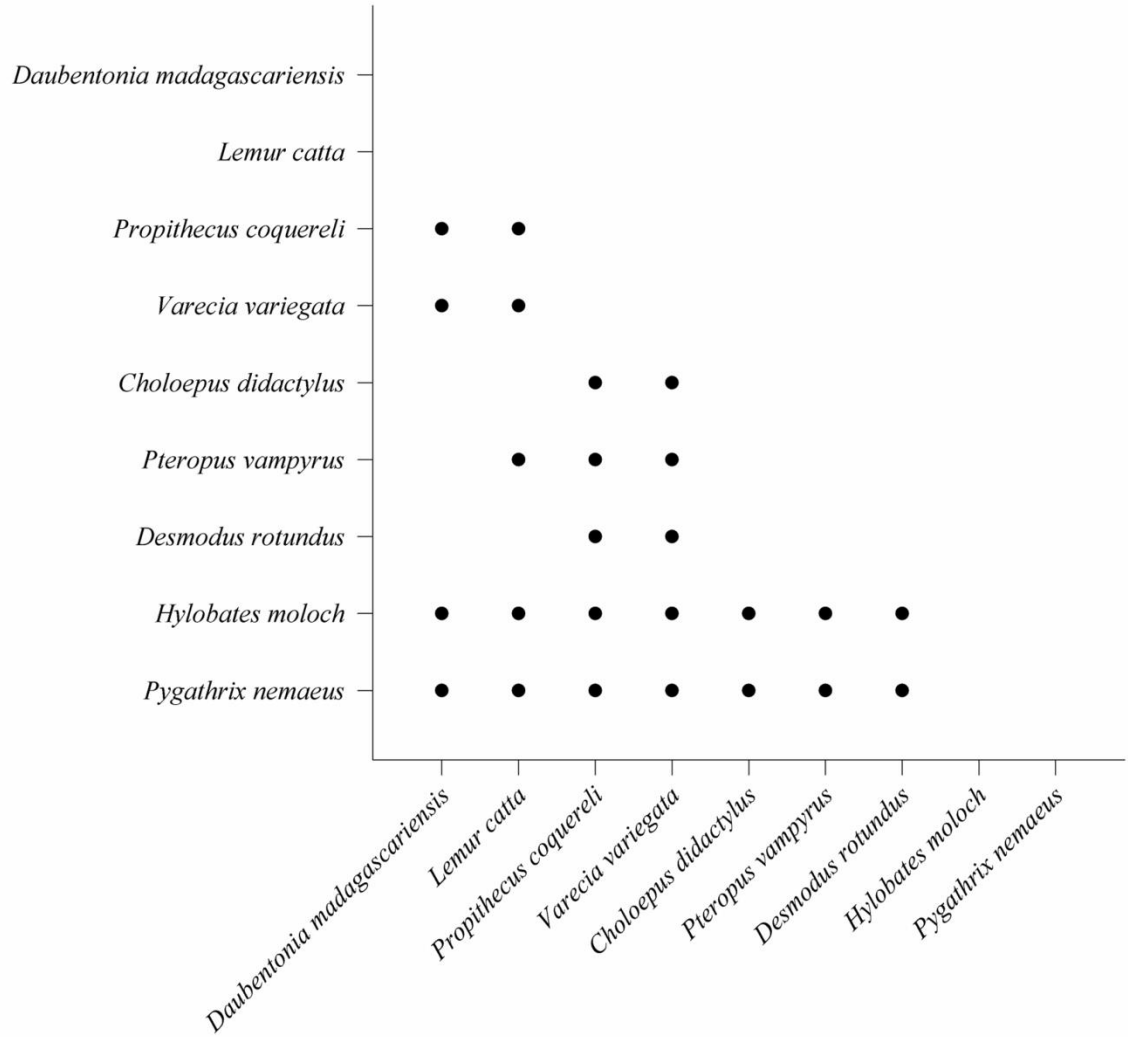

Figure 131: Multiple statistical comparisons between peak vertical forces in the forelimb of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

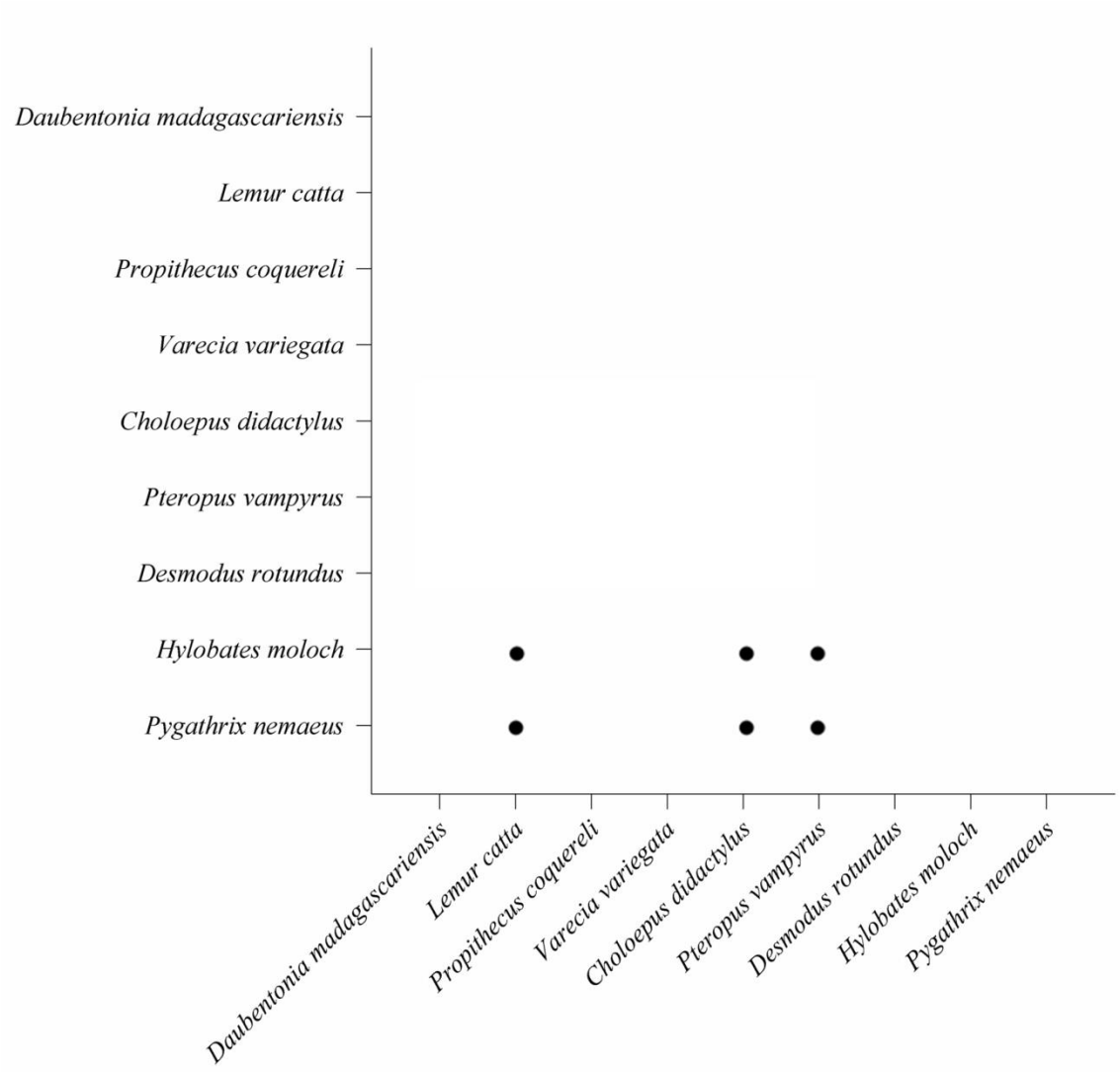

Figure 132: Multiple statistical comparisons between the timing of the peak vertical force in the forelimb if the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

During below branch quadrupedal locomotion and arm-swinging, a consistent limb loading pattern was observed for all species, in which as the forelimb touches down, it first applies a propulsive force to the substrate (Figure 133) followed by a braking force prior to lift-off (Figure 134). In all primates (both during below branch quadrupedal locomotion and arm-swinging), the magnitude of the first occurring horizontal peak in the forelimb was significantly greater than what was observed in non-primate mammals. The magnitude of the first occurring horizontal peak was significantly greater in *H. moloch* compared to all other species except *P. nemaeus* (Figure 135). In regards to the second occurring horizontal peak, interspecific comparisons revealed that in most primates, the magnitude of the second occurring horizontal peak in the forelimb was significantly greater than what was observed in most non-primate mammals. The magnitude of the second occurring horizontal peak was significantly greater in *H. moloch* compared to all other species except *P. nemaeus* (Figure 136). In all species, the first occurring horizontal peak occurred within the first 45% of support phase. The timing of the first occurring horizontal peak tended to be somewhat later in the forelimb of *C. didactylus* and *D. rotundus*, and quite early in the hindlimb of *V. variegata* compared to most of the other species. This resulted in some significant differences between the timing of this event in each limb amongst the sample species (Figure 137). In all species, the second occurring horizontal peak occurred within the latter 70% of support phase. The late occurrence of this second occurring horizontal peak in the forelimb of *C. didactylus* was significantly different from most of the primates (Figure 138). During below branch quadrupedal locomotion, the B/P transition always occurred during the

latter 55% of support phase in the forelimb. The occurrence of the B/P tended to occur later in the forelimb of non-primate species than in primates. This resulted in significant differences between the timing of the B/P in the forelimb between *C. didactylus* and all of the primates. During arm-swinging the B/P tended to occur approximately 50% of support phase. The timing of the B/P during arm-swinging did not vary significantly between the timing of the B/P during below branch quadrupedal locomotion in primates, but did vary significantly between the timing of the B/P during below branch quadrupedal locomotion in non-primate mammals (Figure 139).

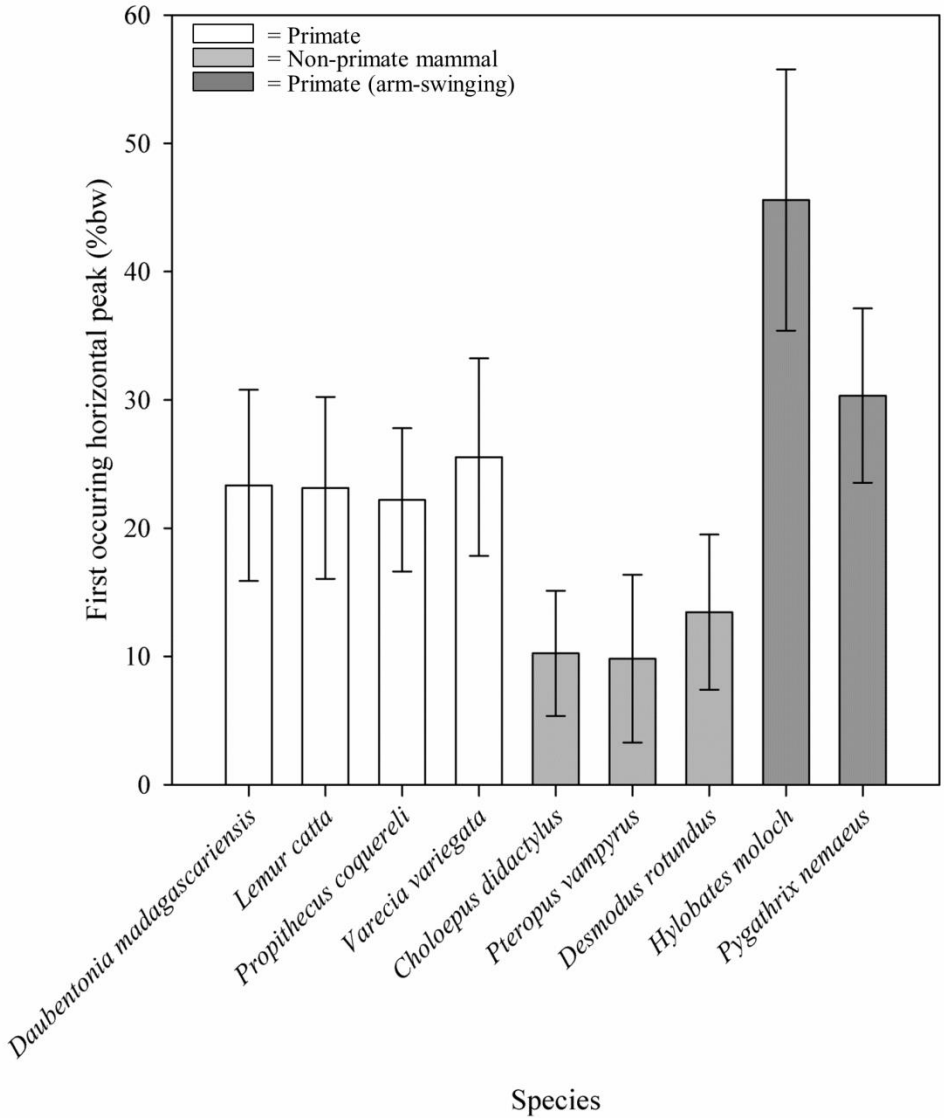

Figure 133: Mean and standard deviation values of the first occurring horizontal peak in the forelimb of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

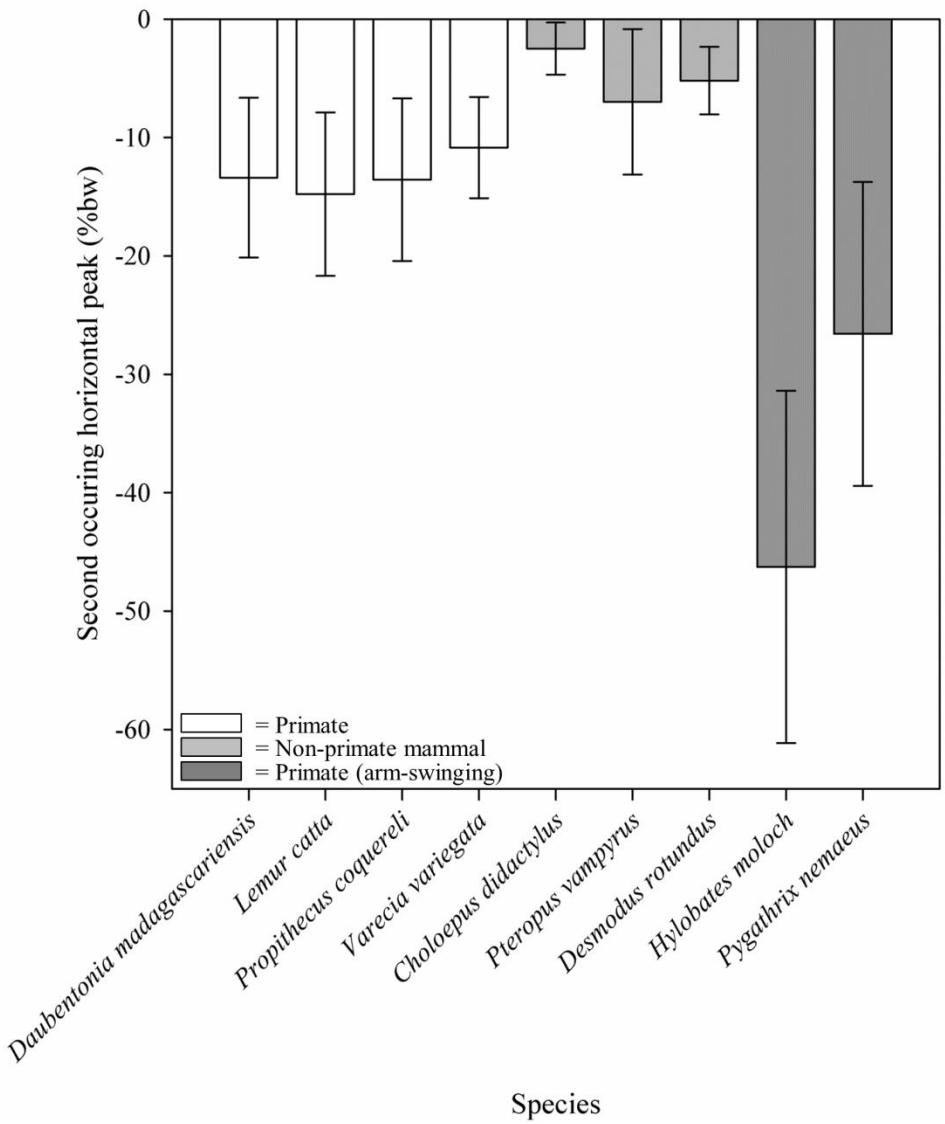

Figure 134: Mean and standard deviation values of the second occurring horizontal peak in the forelimb of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

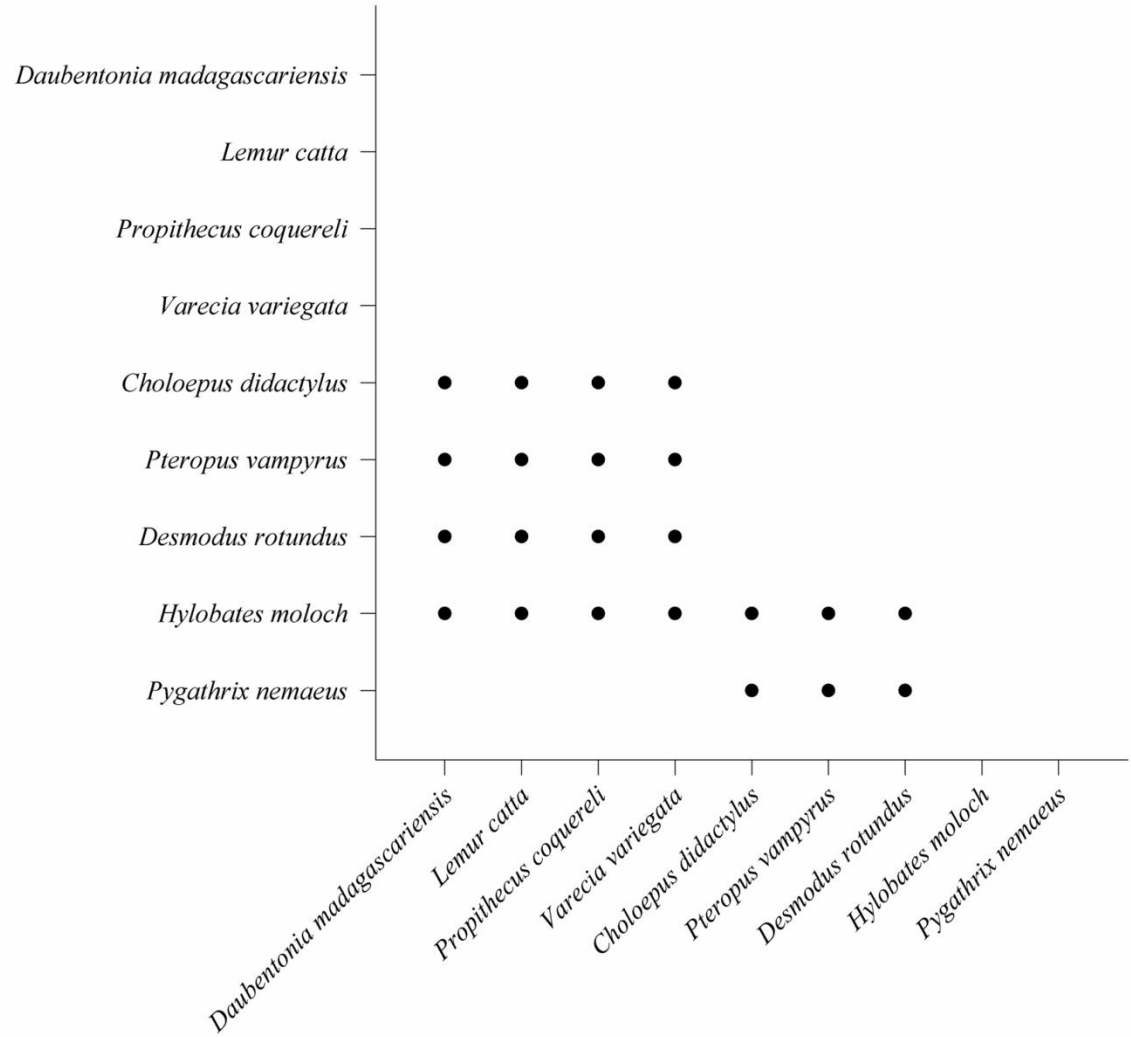

Figure 135: Multiple statistical comparisons between the first occurring horizontal peak in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

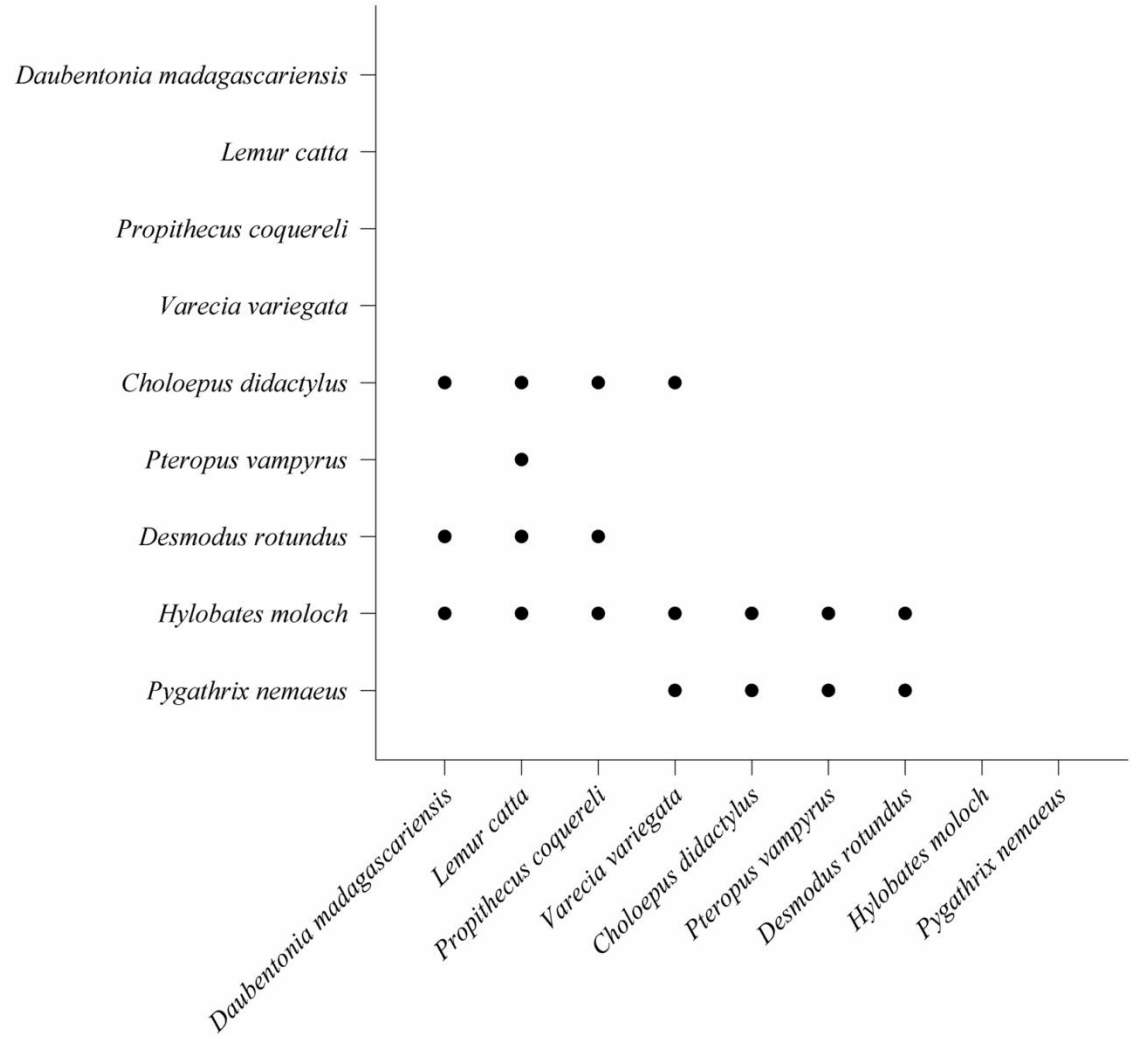

Figure 136: Multiple statistical comparisons between the second occurring horizontal peak in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

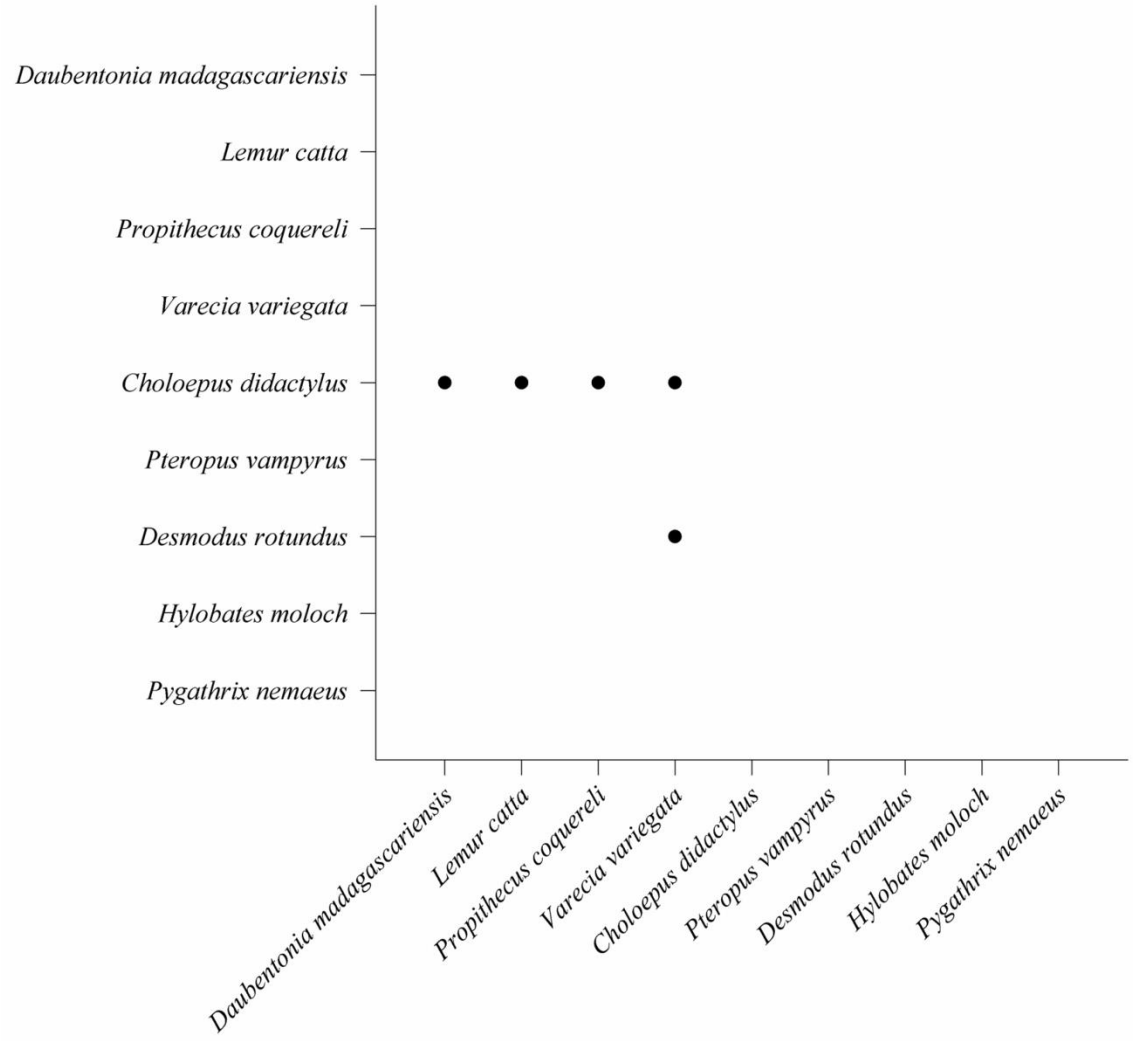

Figure 137: Multiple statistical comparisons between the timing of the first occurring horizontal peak in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

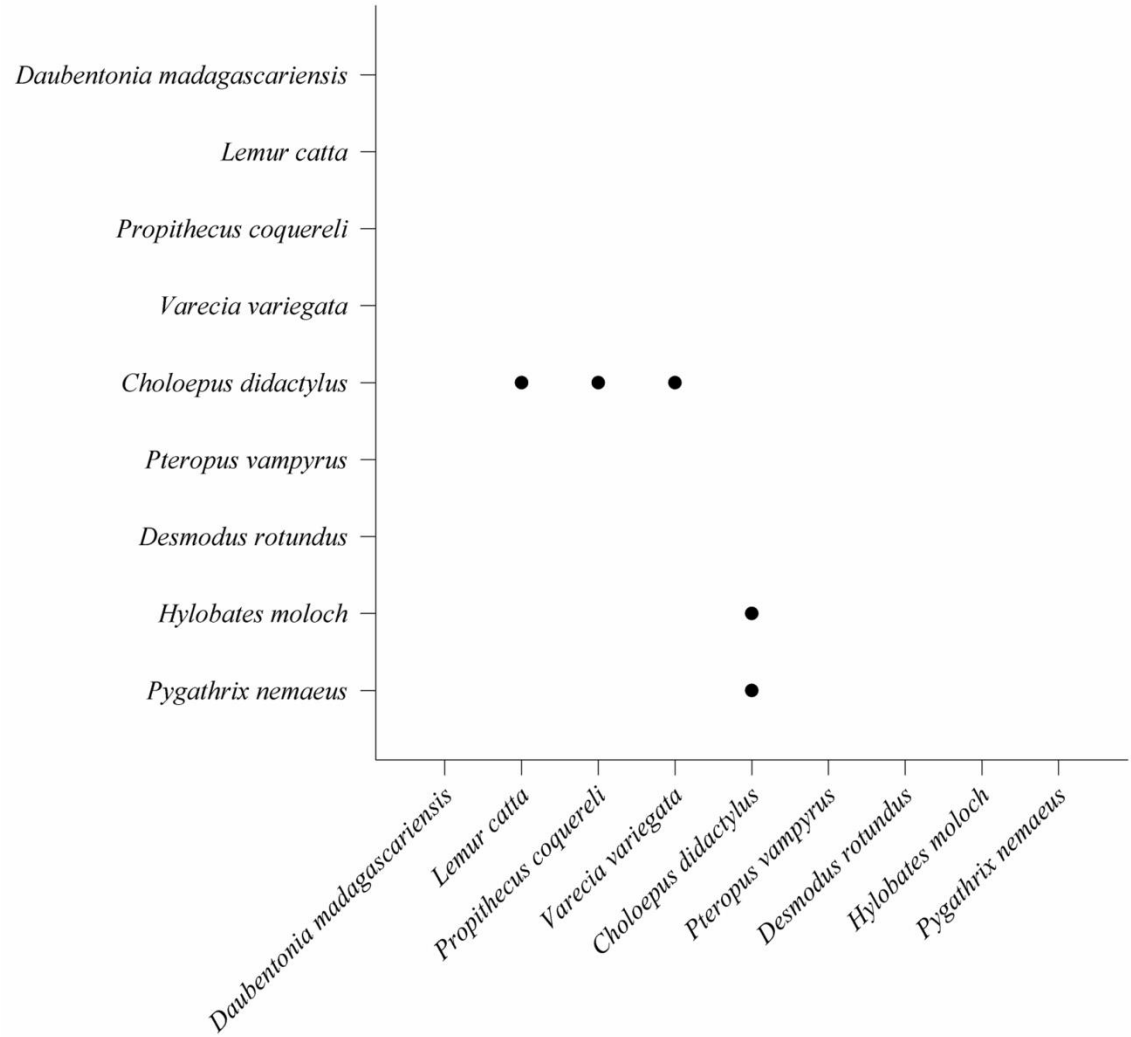

Figure 138: Multiple statistical comparisons between the timing of the second occurring horizontal peak in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

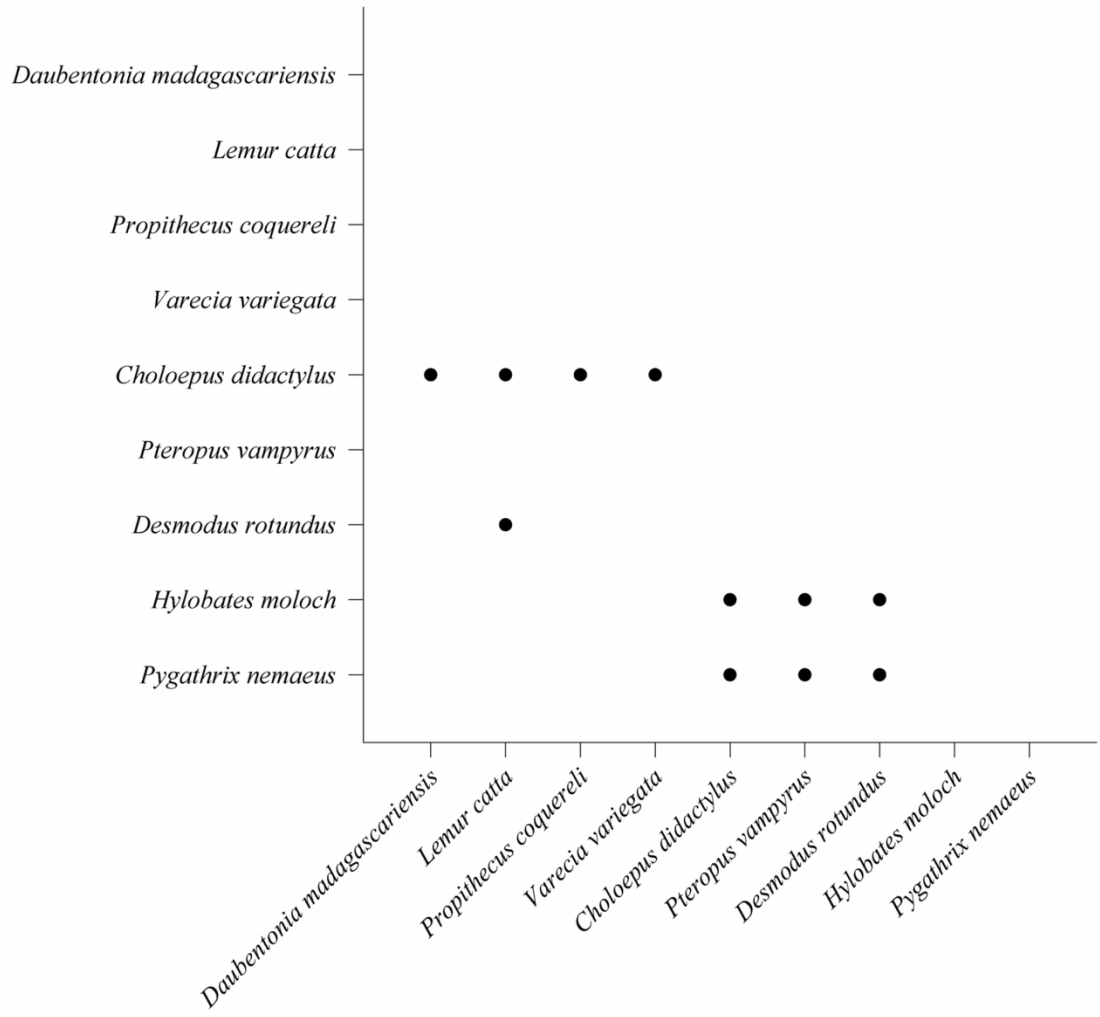

Figure 139: Multiple statistical comparisons between the timing of the propulsive to braking transition in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (P < 0.001) between the different species.

During below branch quadrupedal walking, all species displayed a positive net HI in the forelimbs, meaning that the forelimbs were net propulsive. During arm-swinging HI was close to zero indicating an even exchange of propulsive and braking forces (Figure 140). The only significant differences observed between any of the species was the forelimb impulses observed in *C. didactylus*, which were quite large due to the tendency for extremely slow and careful movement in this species (Figure 141).

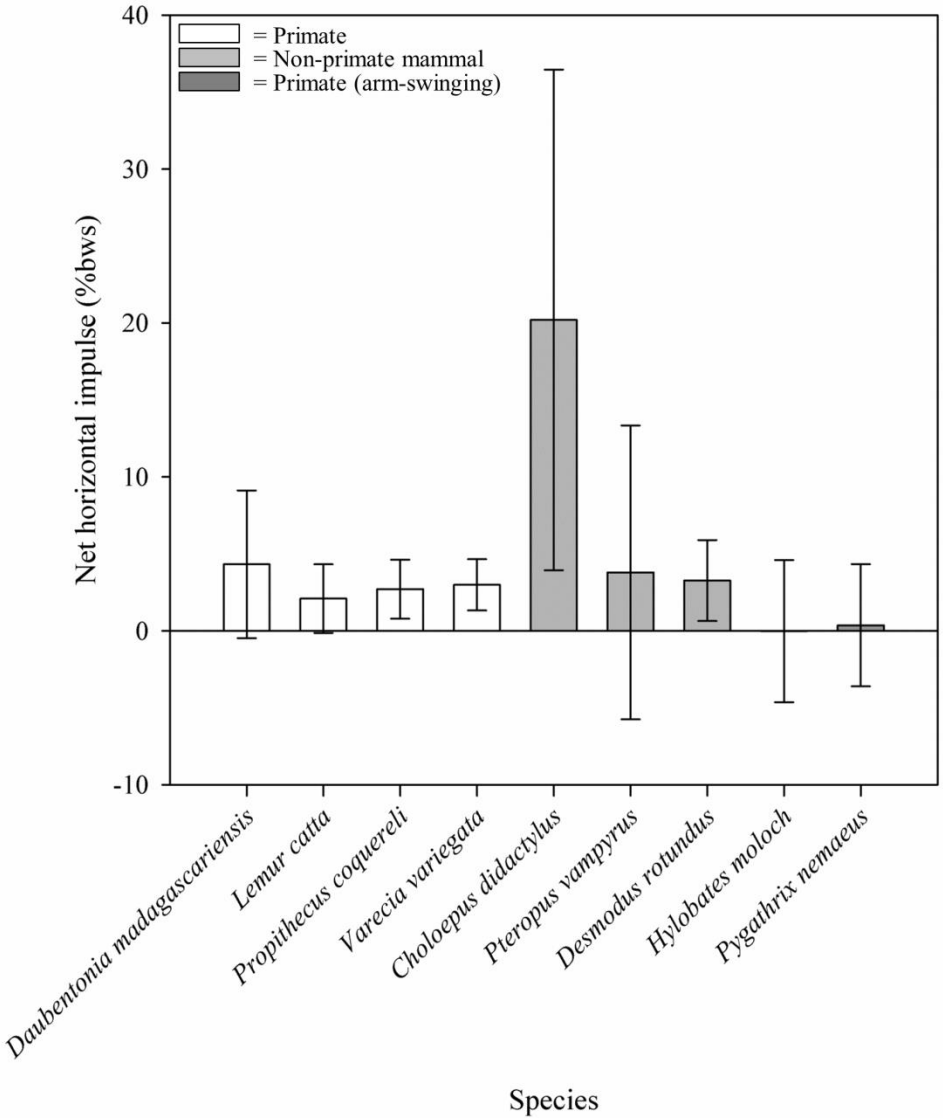

Figure 140: Mean and standard deviation values of the net horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bws).

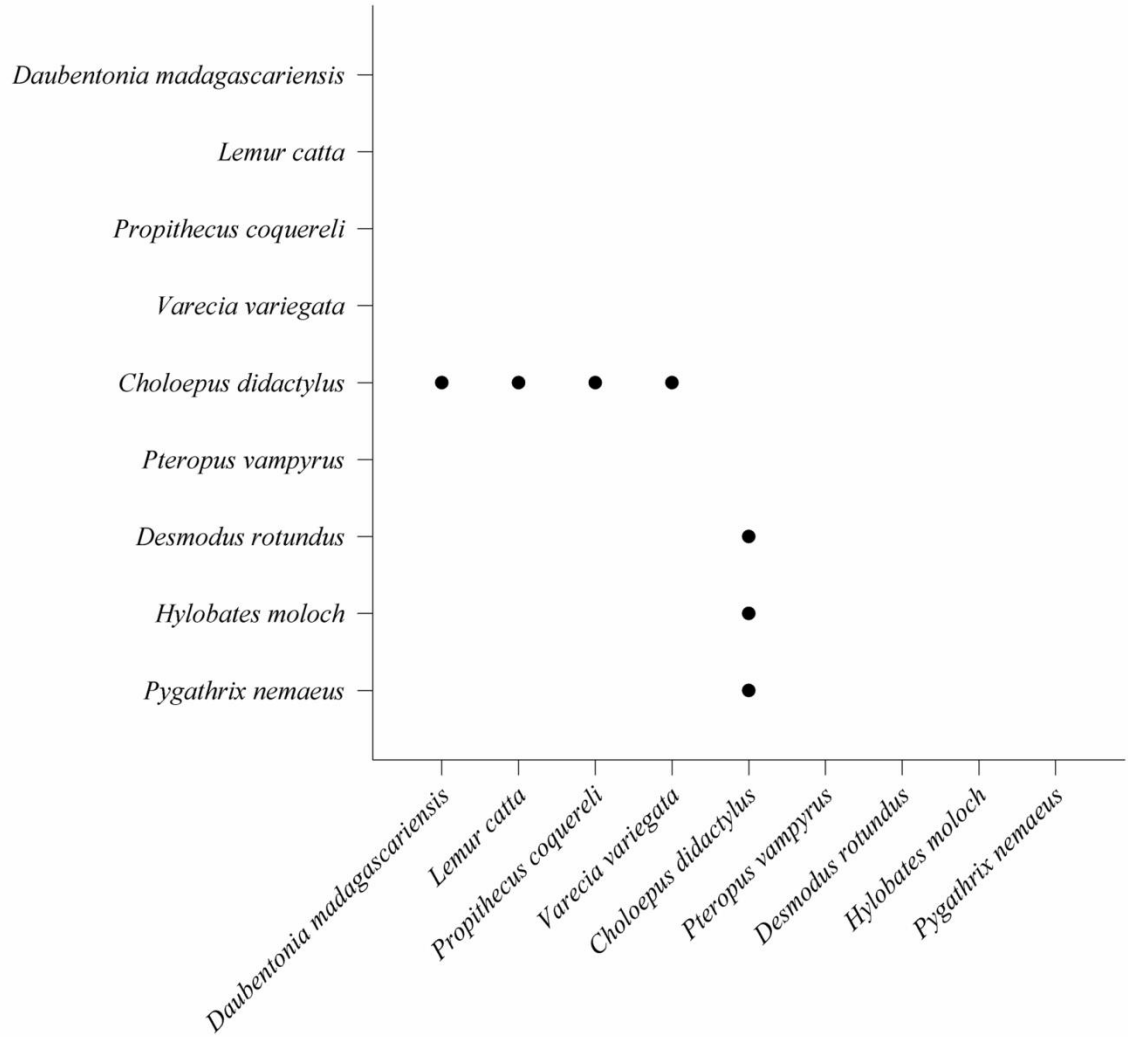

Figure 141: Multiple statistical comparisons between the horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

The analysis of the first occurring horizontal impulse (Figure 142) and the second occurring horizontal impulse (Figure 143) separately for the forelimb showed that during below branch quadrupedal walking and arm-swinging the first occurring horizontal impulse is associated with a propulsive force, while the second occurring horizontal impulse is associated with a braking impulse. As with HI, most differences between FHI and SHI are between *C. didactylus* and the other species, but other notable distinctions are present (Figures 144 and 145).

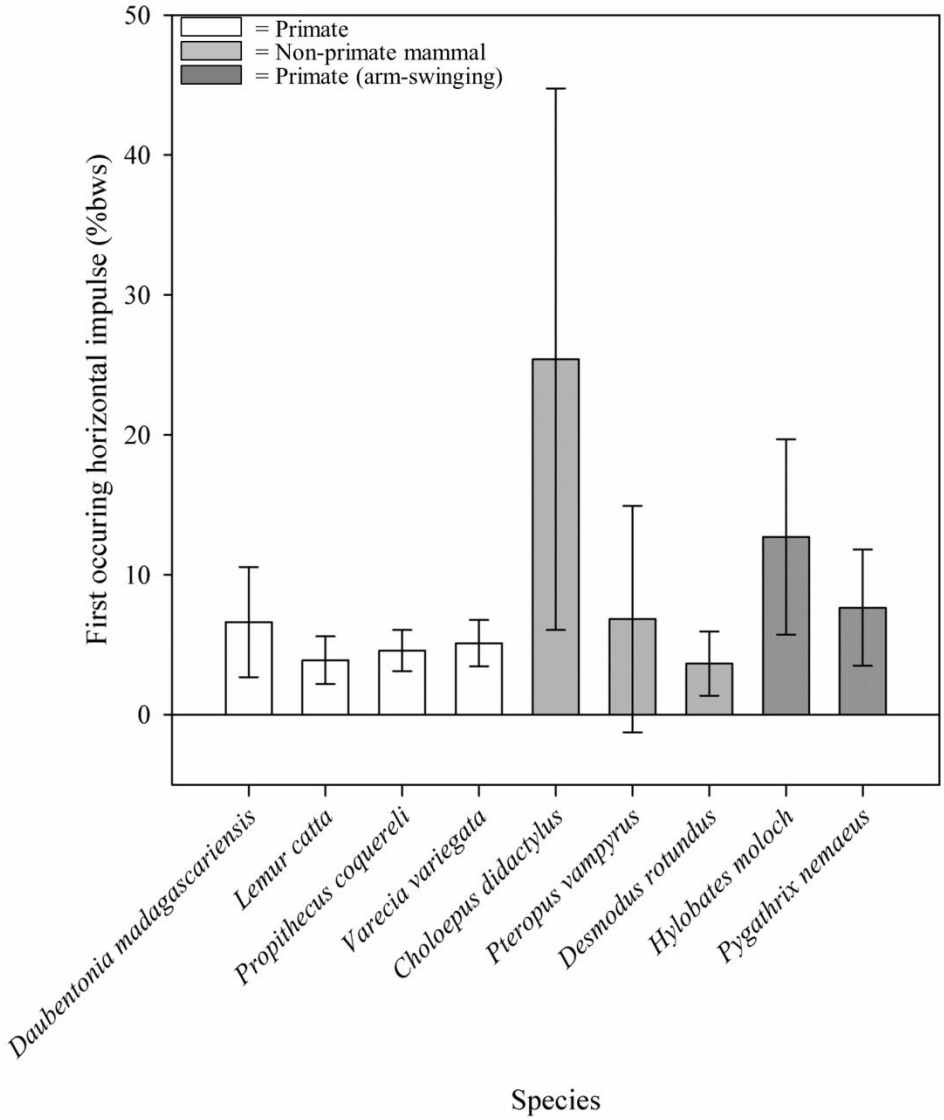

Figure 142: Mean and standard deviation values of the first occurring horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

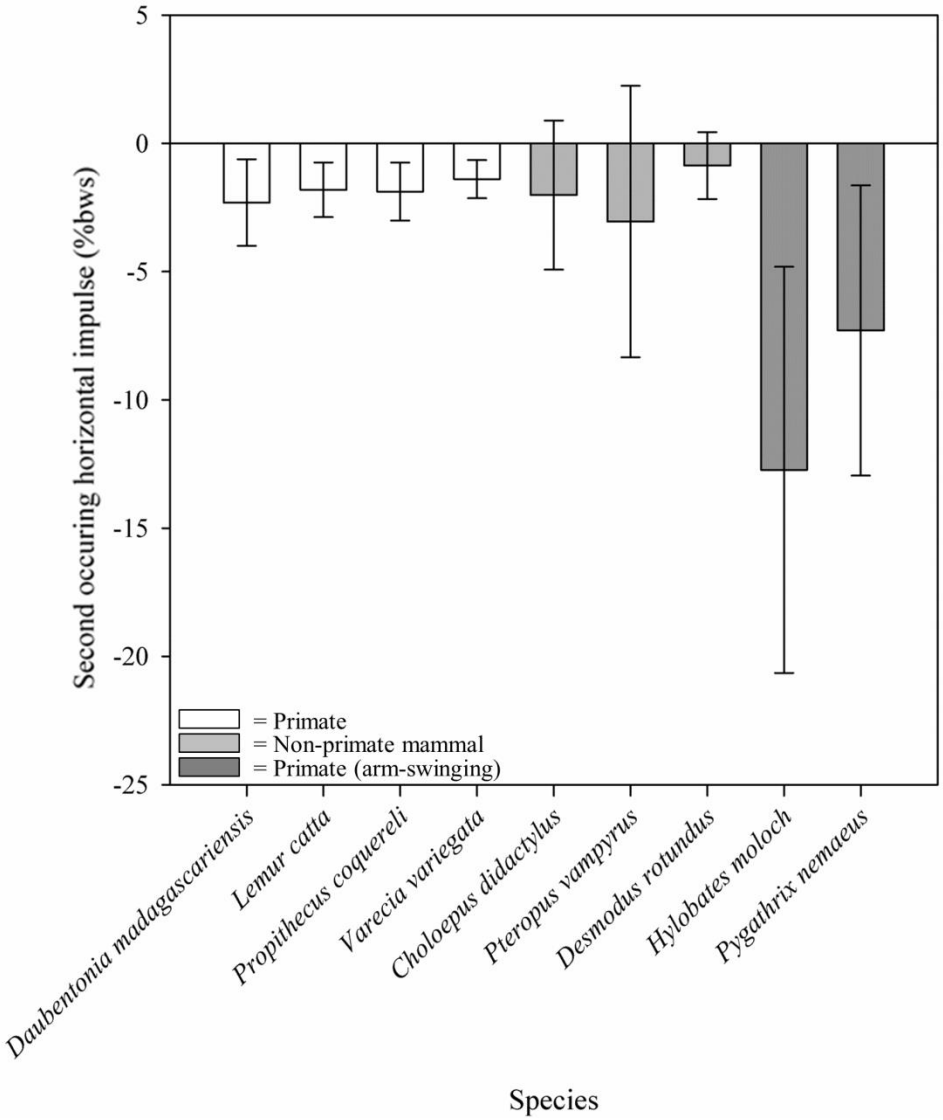

Figure 143: Mean and standard deviation values of the second occurring horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

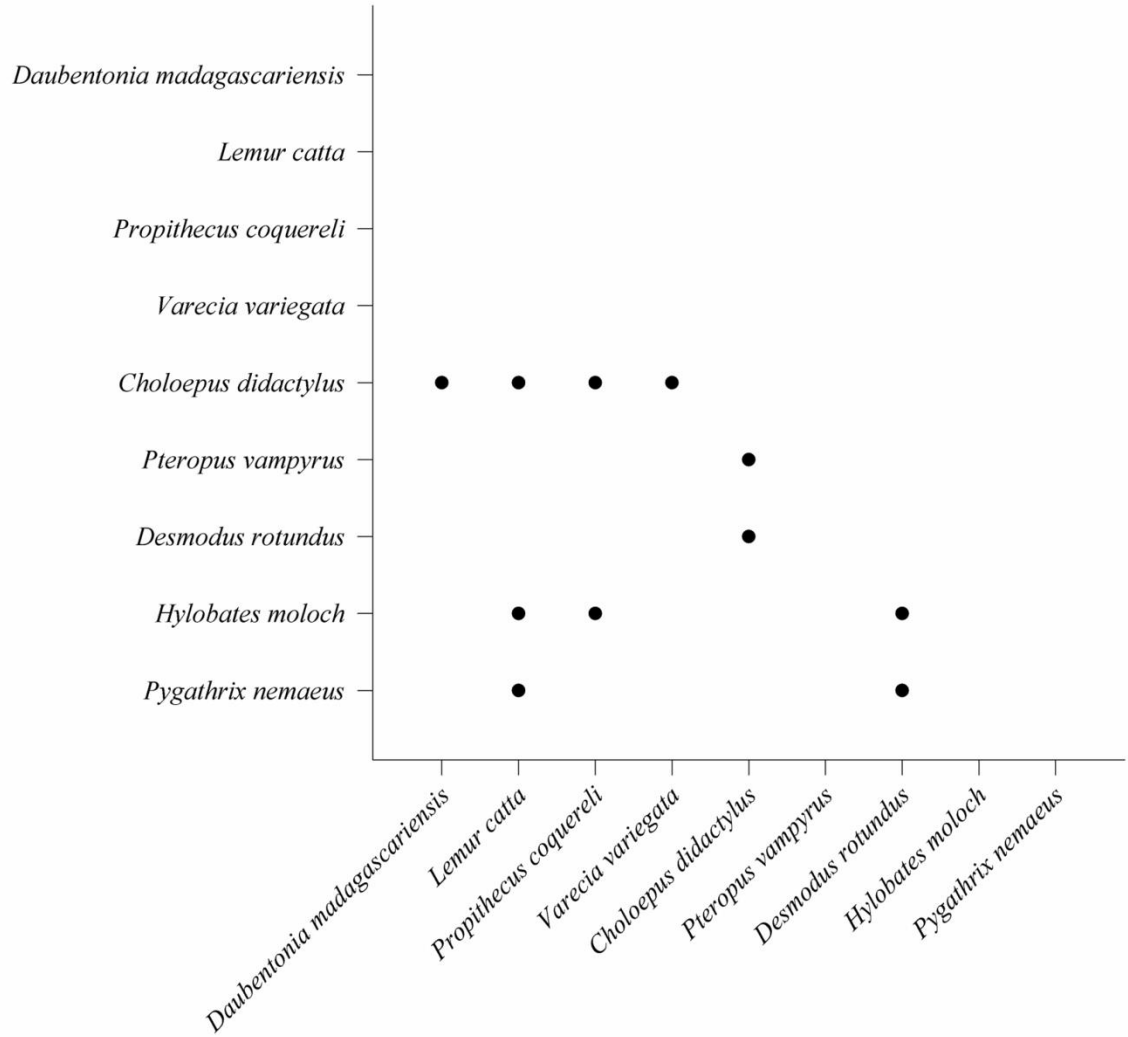

Figure 144: Multiple statistical comparisons between the first occurring horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

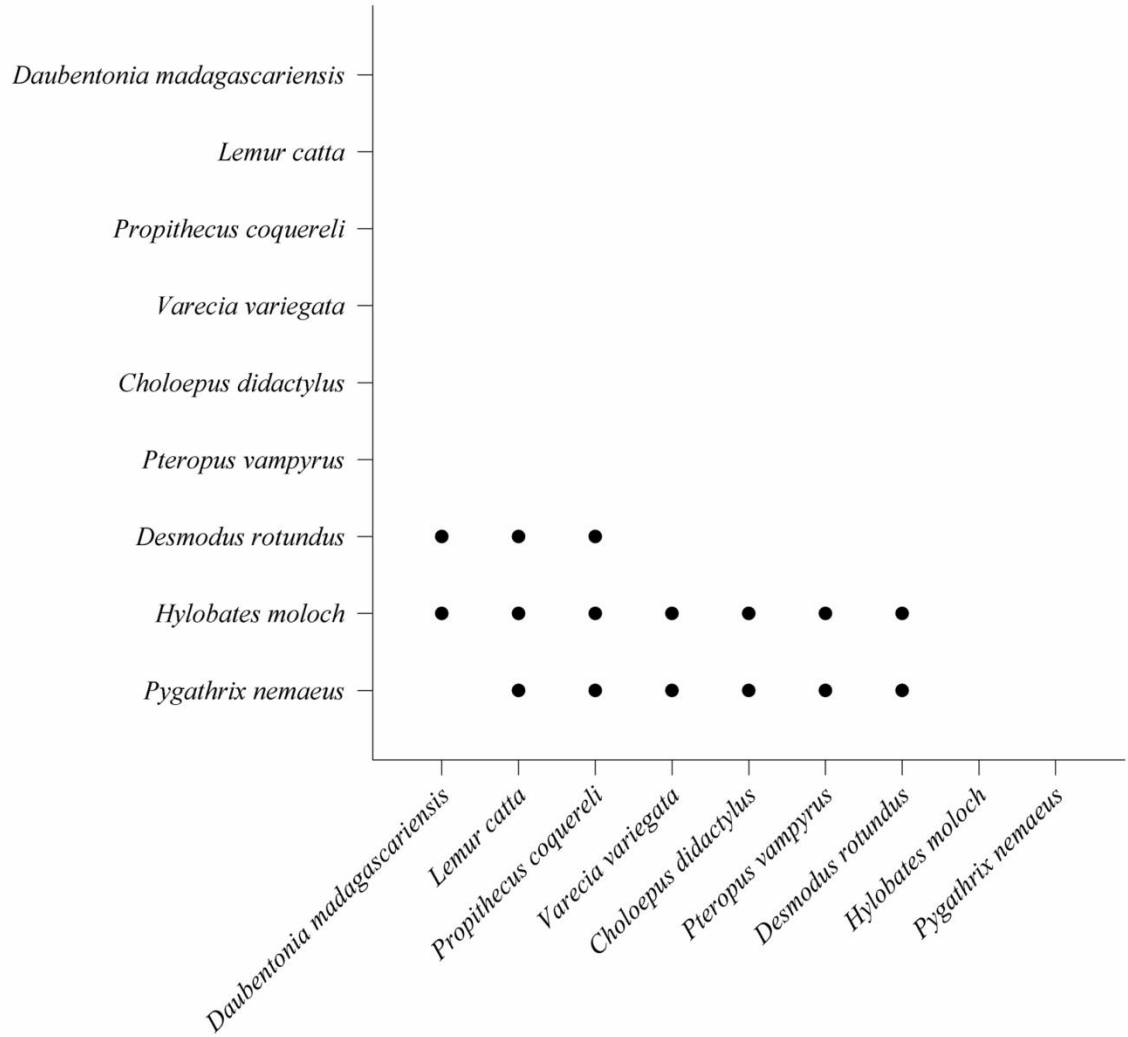

Figure 145: Multiple statistical comparisons between the second occurring horizontal impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

In all species, the mediolateral force component was dominated by medially directed forces. This means that the animal applied a medially directed force to the substrate during support phase. These forces were highly variable and low in comparison to vertical and horizontal forces. In general Mpk and Lpk were highly variable, but some significant differences between species were observed (Figures 146-155). Similarly, mediolateral impulse measures were also highly variable, but there was a tendency for greater MI, LI, and MLI in non-primate mammals compared to the primates during below branch quadrupedal locomotion. Many of the statistical differences observed were due to the slow movement of *C. didactylus*. *Choloepus didactylus* notwithstanding, mediolateral forces tended to be higher during arm-swinging compared to below branch quadrupedal locomotion, and among the arm-swinging primates mediolateral forces were relatively higher during arm-swing in *P. nemaeus* compared to *H. moloch*. The timings associated with Lpk and Mpk were inconsistent and did not demonstrate any significant differences between species.

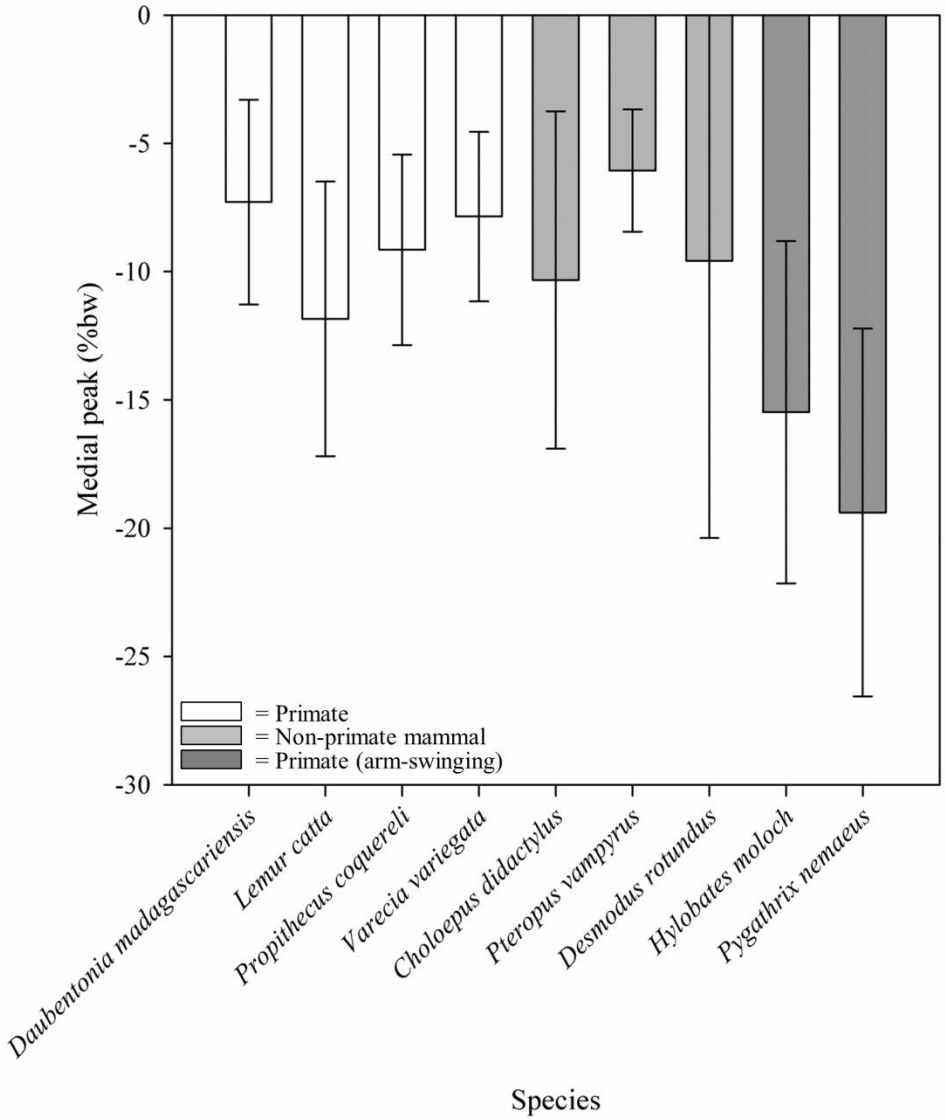

Figure 146: Mean and standard deviation values of peak medial force in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

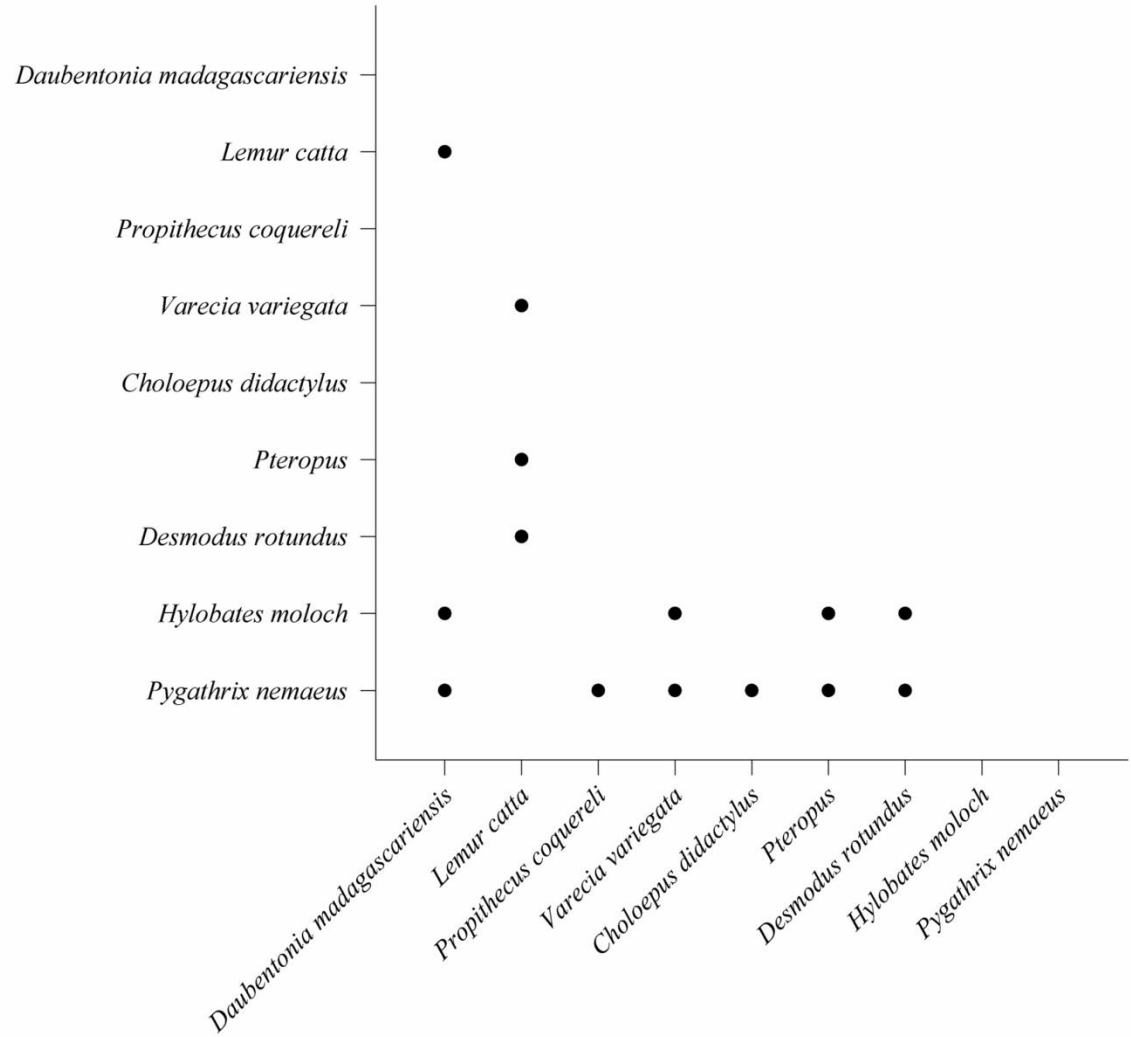

Figure 147: Multiple statistical comparisons between the medial peak force in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

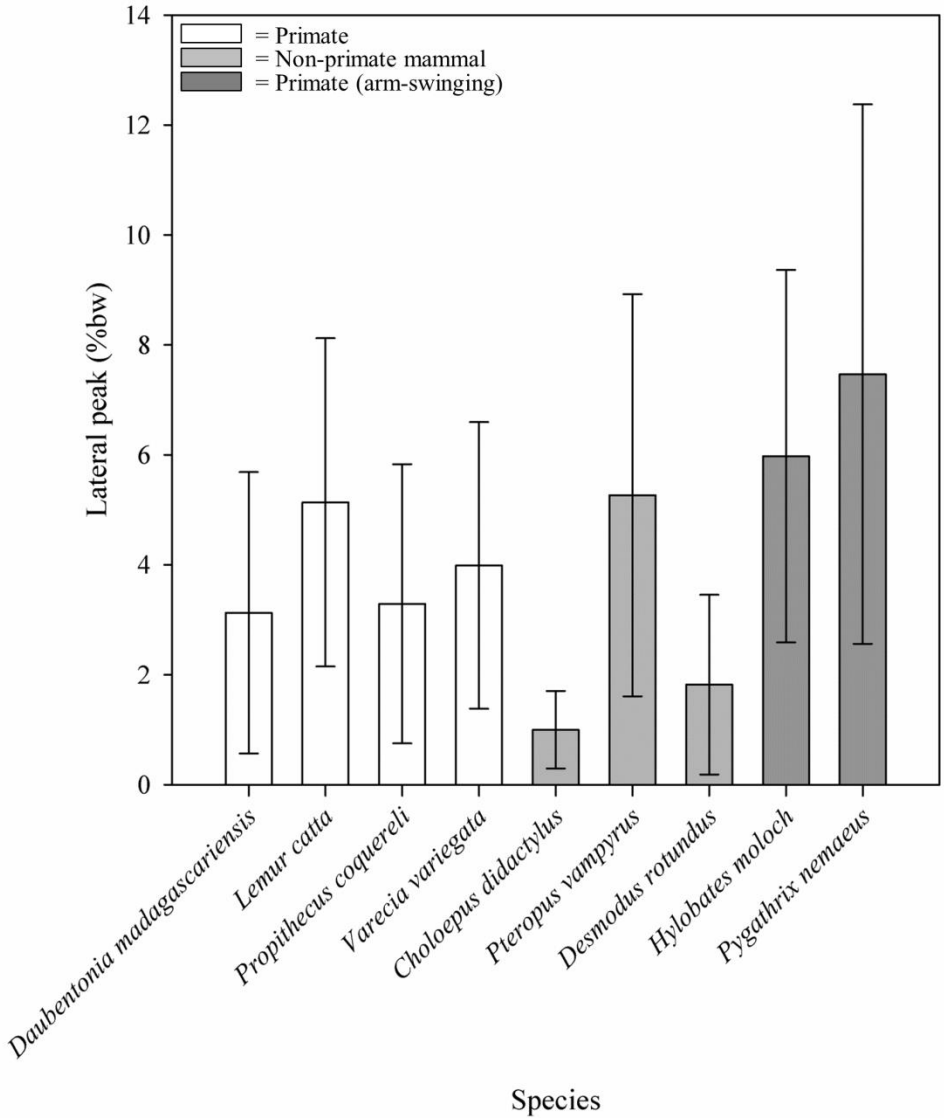

Figure 148: Mean and standard deviation values of peak lateral force in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

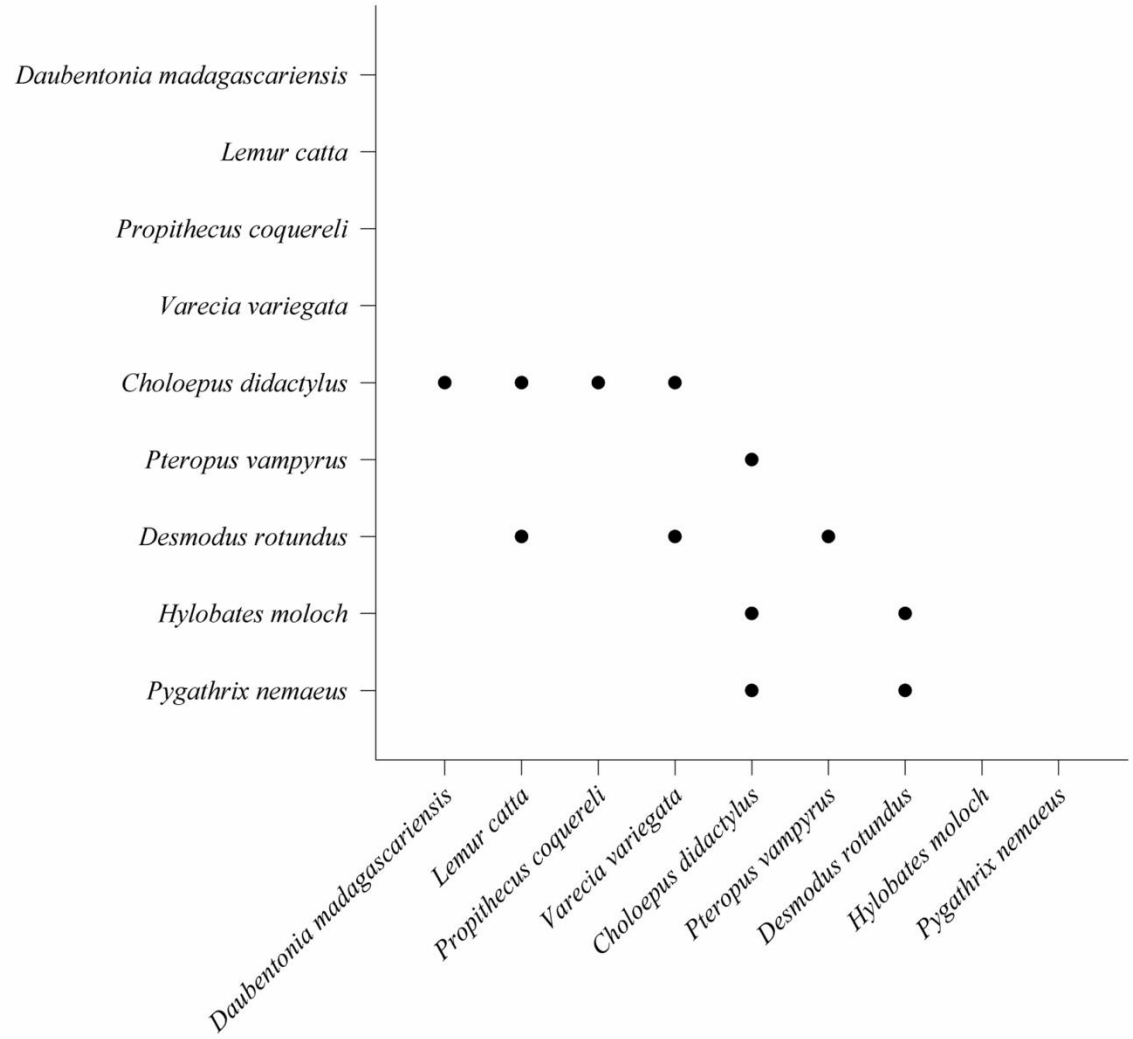

Figure 149: Multiple statistical comparisons between the lateral peak force in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

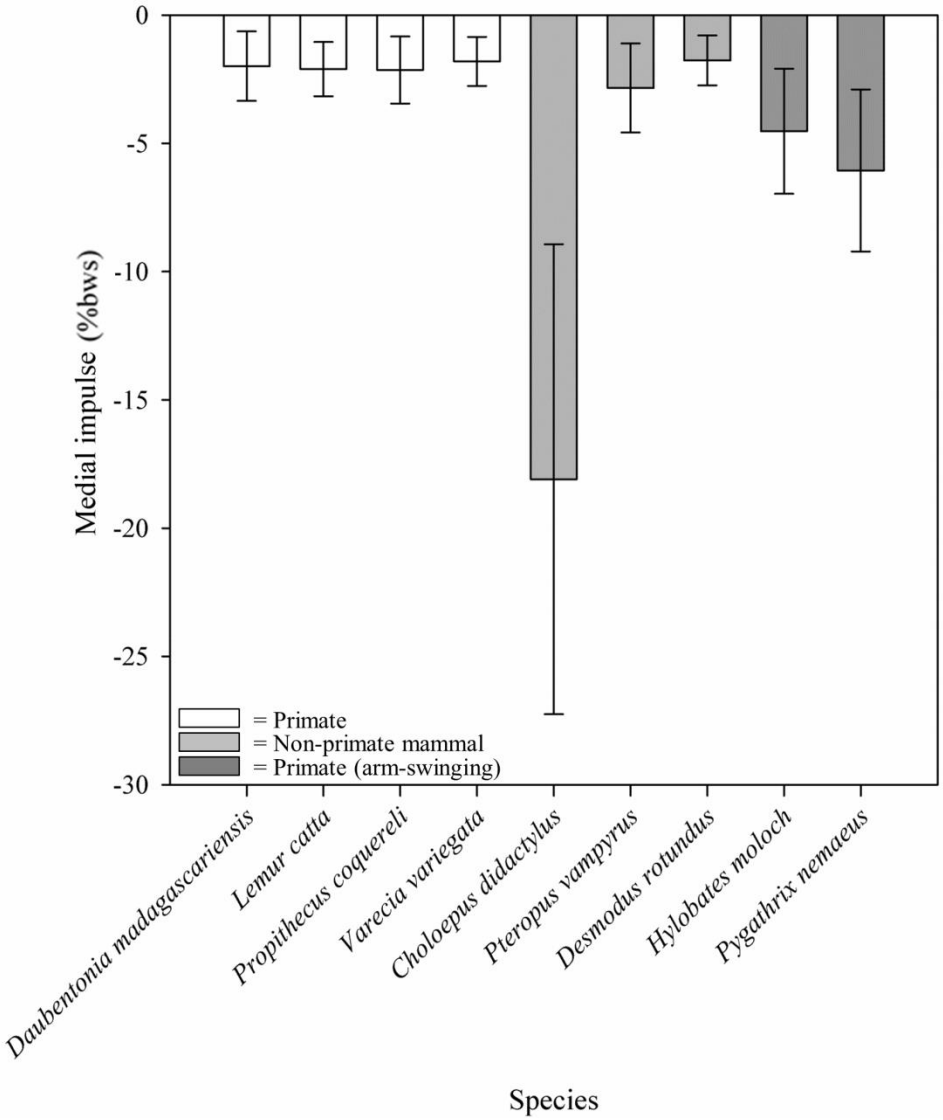

Figure 150: Mean and standard deviation values of medial impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

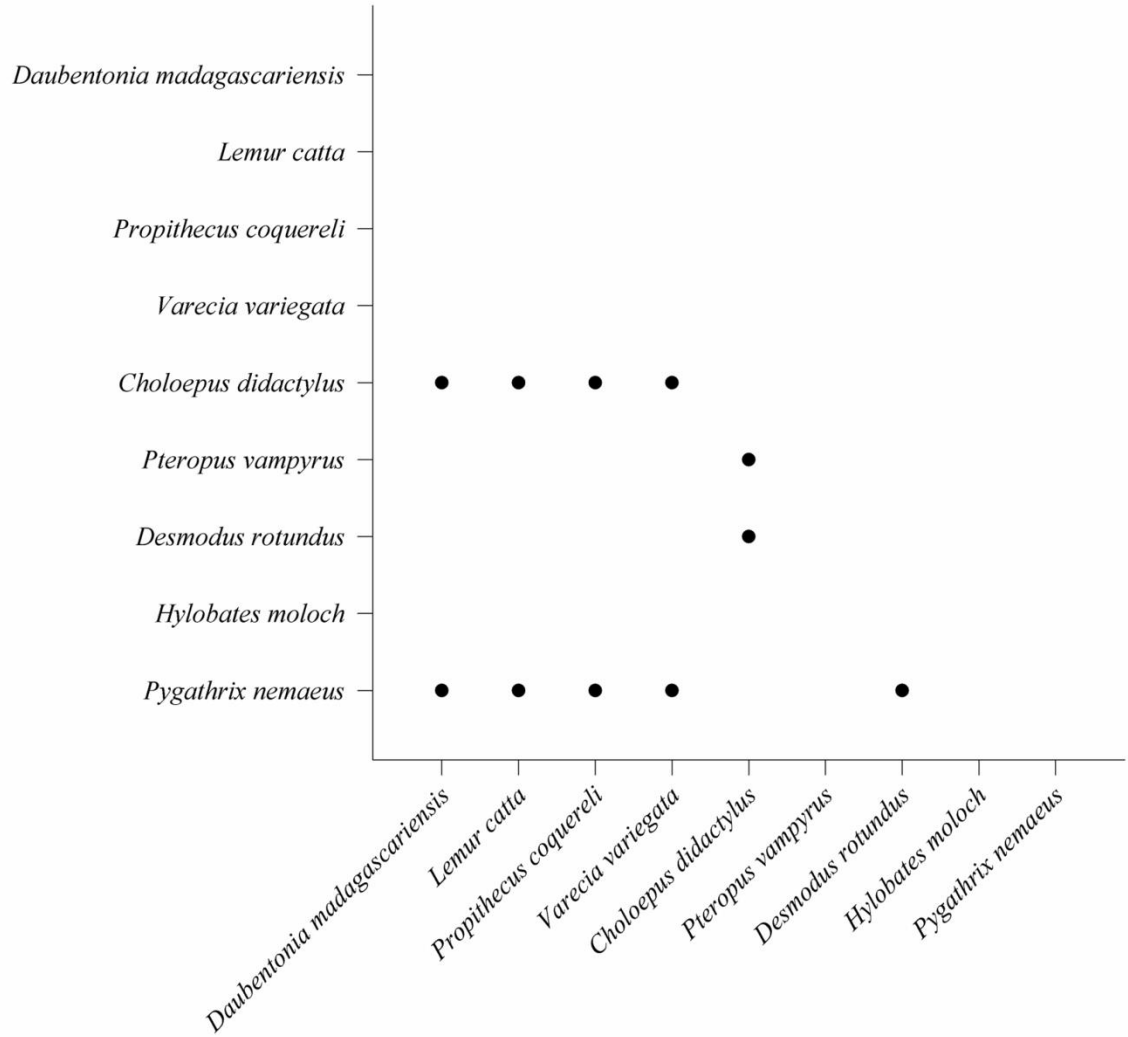

Figure 151: Multiple statistical comparisons between the medial impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

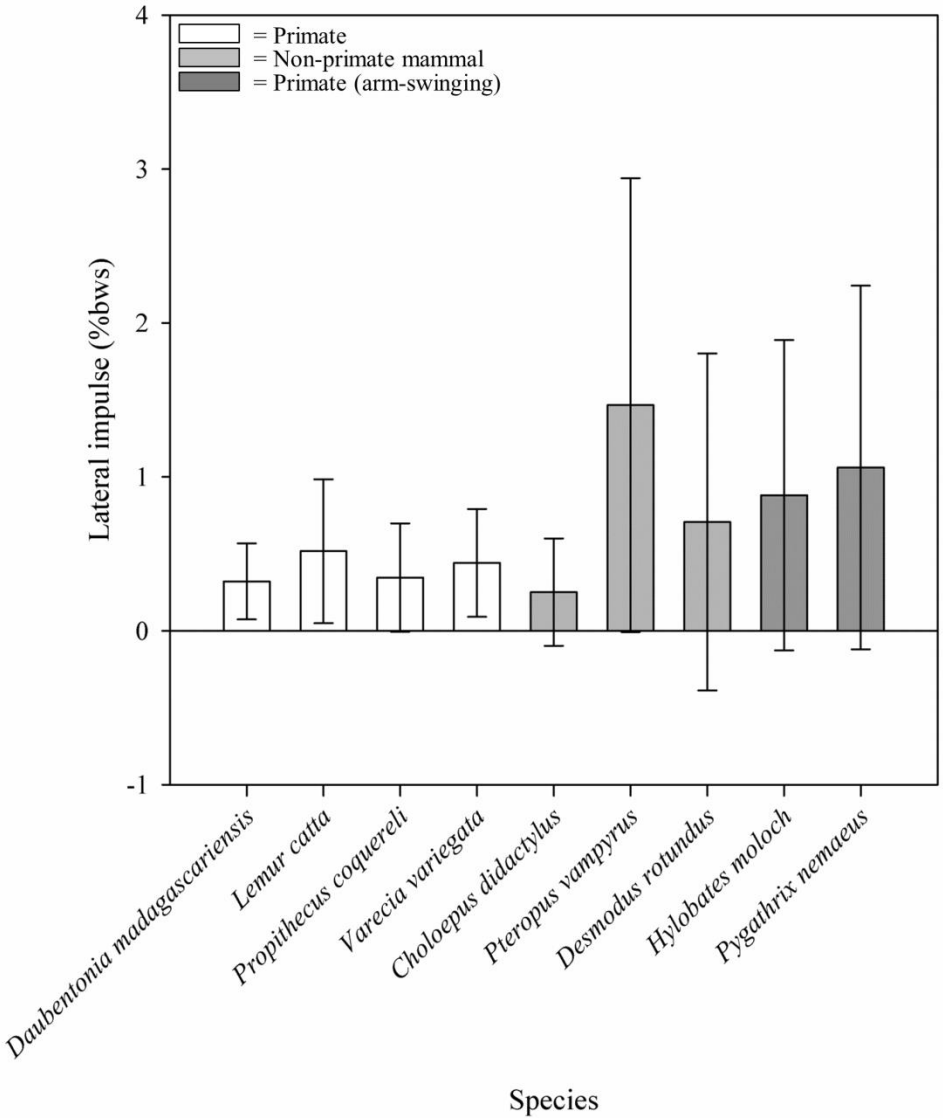

Figure 152: Mean and standard deviation values of lateral impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

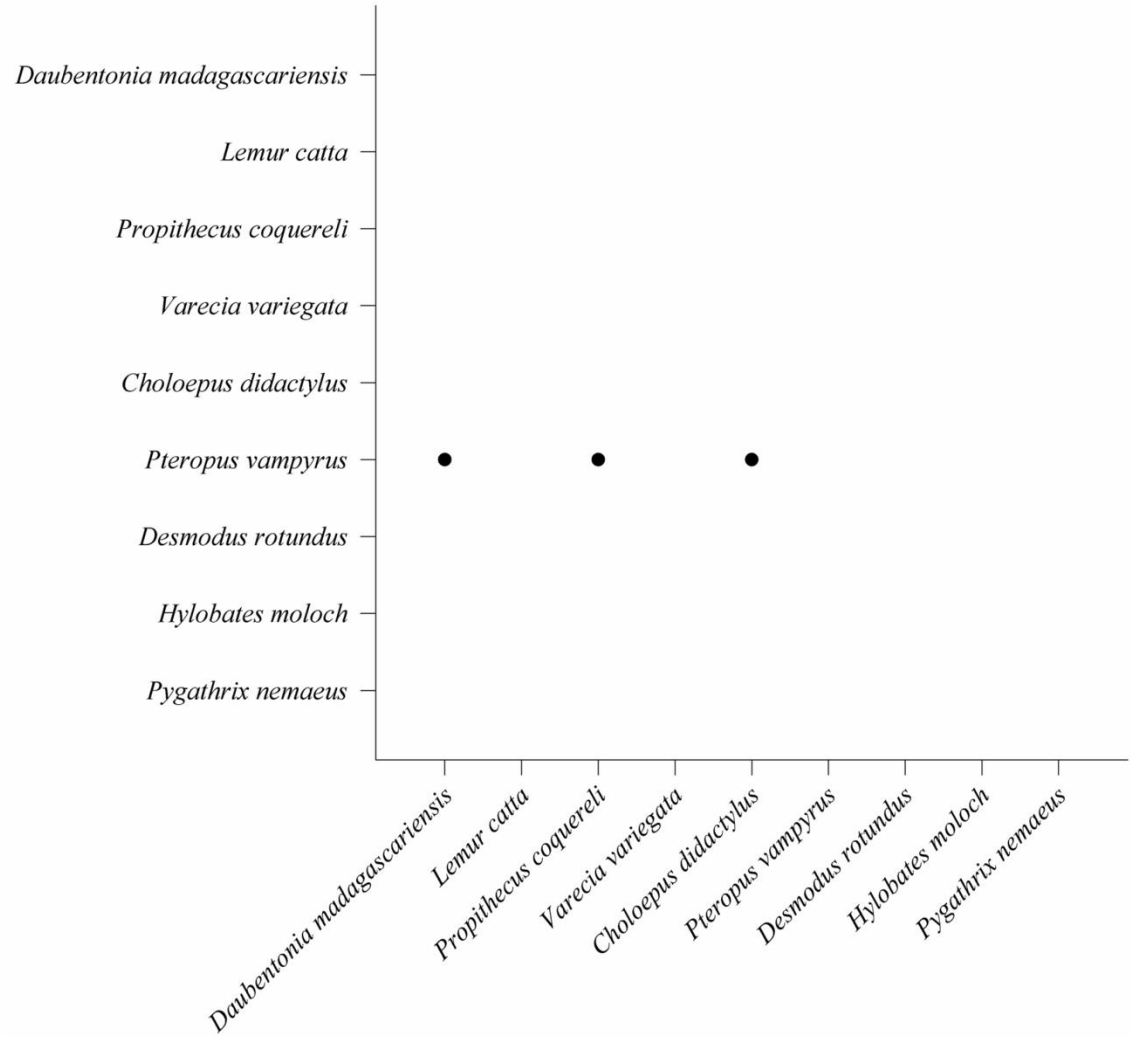

Figure 153: Multiple statistical comparisons between the lateral impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

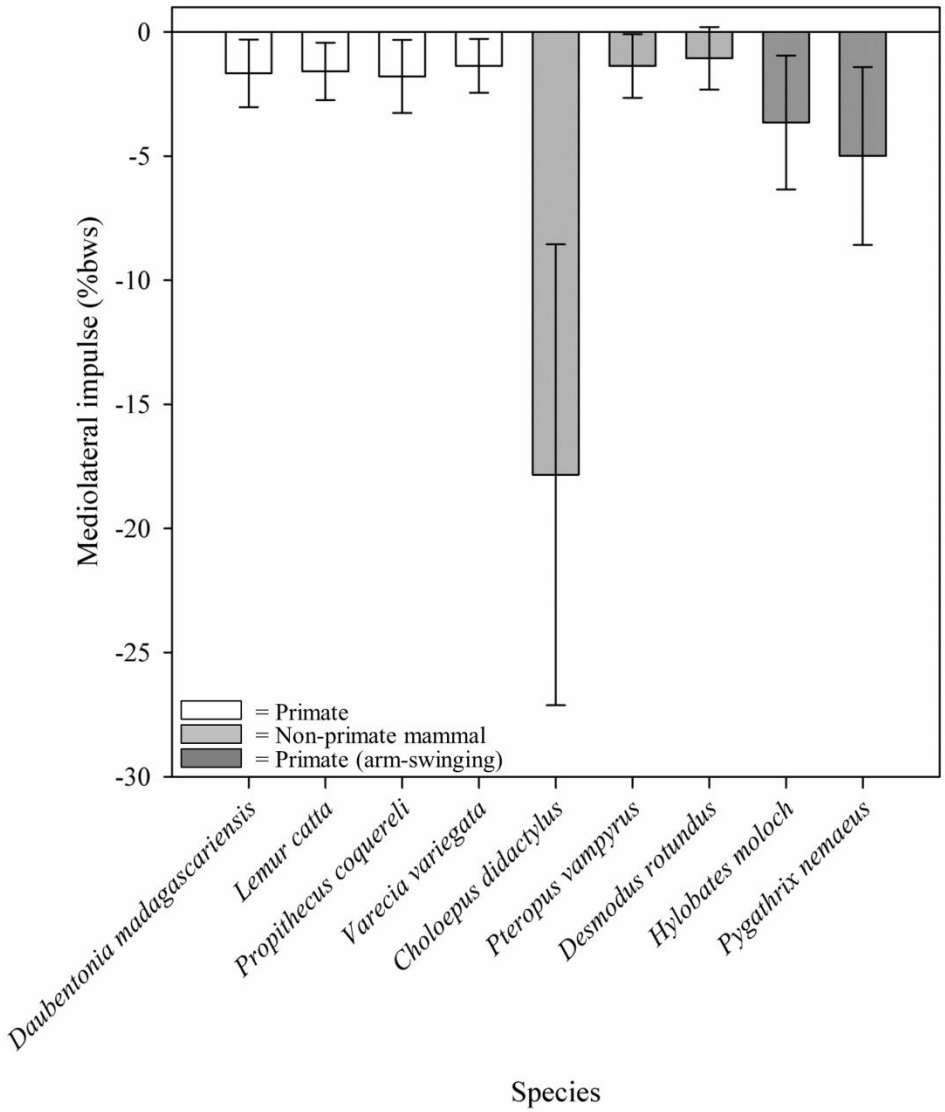

Figure 154: Mean and standard deviation values of mediolateral impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. All data presented as a percentage of the animals body weight (%bw).

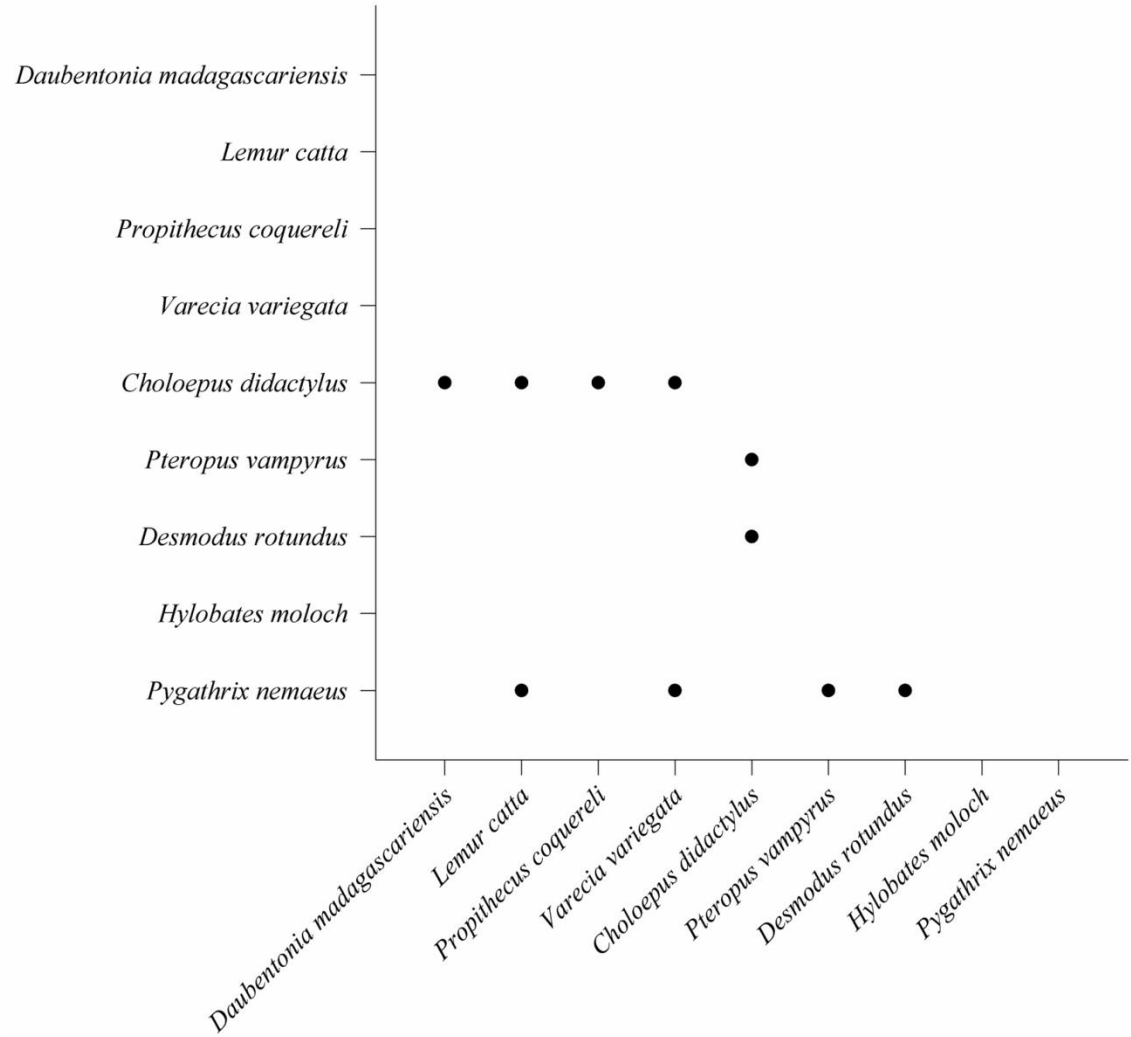

Figure 155: Multiple statistical comparisons between the mediolateral impulse in the forelimbs of the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

3.2.2 Kinematics

In total, 235 strides were used for kinematic analysis. Table 13 summarizes the number of strides collected per limb for each orientation, and data for touchdown angle, mid-support angle, end of support phase angle, and joint excursion. Overall, kinematic movements of the all measured joints, and the overall excursion observed at those joints, tended to be fairly similar across all species during below branch quadrupedal locomotion. Similarly, kinematic movements of the all measured joints, and the overall excursion observed at those joints, tended to be fairly similar across all species during arm-swinging. Patterns of joint movement appeared to vary substantially between arm-swinging and below branch quadrupedal locomotion in most instances.

Table 13: Mean and standard deviation values for kinematic gait variables collected during above below branch quadrupedal locomotion and arm-swinging in primate and non-primate mammals.

Species	Joint	Orientation	N	Touchdown angle (°)	Mid-stance angle (°)	End of support phase angle (°)	Joint excursion (°)
Cebus capucinus	Shoulder	Below	6	-3.27 ± 5.92	-56.75 ± 12.33	-70.38 ± 5.35	80.39 ± 4.25
	Elbow	Below	6	128.54 ± 9.70	104.67 ± 10.23	132.84 ± 7.43	41.51 ± 7.78
	Wrist	Below	6	171.97 ± 7.26	185.59 ± 5.11	178.33 ± 7.03	29.89 ± 5.61
Daubentonia madagascariensis	Shoulder	Below	30	4.35 ± 10.23	-48.37 ± 10.25	-80.04 ± 9.42	85.57 ± 11.17
	Elbow	Below	30	121.86 ± 17.90	102.06 ± 13.94	119.76 ± 10.37	32.25 ± 13.54
	Wrist	Below	30	175.11 ± 13.17	192.43 ± 11.08	206.07 ± 11.53	36.23 ± 11.30
Lemur catta	Shoulder	Below	30	1.36 ± 15.99	-48.41 ± 15.73	-77.98 ± 5.54	80.59 ± 18.32
	Elbow	Below	30	122.89 ± 16.39	112.82 ± 12.81	126.12 ± 8.27	27.45 ± 15.20
	Wrist	Below	30	172.35 ± 11.08	192.72 ± 7.62	190.63 ± 6.57	30.61 ± 11.35
Propithecus coquereli	Shoulder	Below	30	-18.57 ± 13.16	-65.91 ± 10.87	-85.34 ± 5.65	68.96 ± 11.86
	Elbow	Below	30	95.84 ± 15.03	90.35 ± 11.10	107.00 ± 11.87	23.24 ± 10.26
	Wrist	Below	30	160.79 ± 7.11	184.57 ± 6.22	194.35 ± 7.17	37.57 ± 8.17
Varecia variegata	Shoulder	Below	30	4.82 ± 18.29	-53.78 ± 14.08	-67.78 ± 10.11	87.00 ± 15.62
	Elbow	Below	30	127.94 ± 18.97	104.26 ± 12.59	134.15 ± 11.72	48.84 ± 14.13
	Wrist	Below	30	169.45 ± 12.68	183.73 ± 12.39	176.85 ± 9.01	36.88 ± 14.04
Choloepus didactylus	Shoulder	Below	21	-10.57 ± 22.01	-56.48 ± 27.92	-83.05 ± 11.02	79.47 ± 20.50
	Elbow	Below	21	114.06 ± 23.69	92.71 ± 20.28	103.10 ± 13.09	42.53 ± 22.31
	Wrist	Below	21	156.71 ± 14.92	160.22 ± 7.89	173.22 ± 5.93	26.81 ± 8.91
Pteropus vampyrus	Shoulder	Below	28	-18.49 ± 10.69	-44.00 ± 15.48	-64.18 ± 19.54	51.42 ± 16.18
	Elbow	Below	28	101.33 ± 12.63	90.60 ± 16.82	84.39 ± 16.59	31.98 ± 9.38
	Wrist	Below	28	124.18 ± 9.73	131.74 ± 7.43	137.38 ± 11.23	23.85 ± 9.09
Ateles fusciceps	Shoulder	Arm-swinging	19	53.92 ± 13.62	-2.60 ± 9.42	-69.73 ± 7.23	124.97 ± 15.55
	Elbow	Arm-swinging	19	174.10 ± 5.52	163.94 ± 6.10	157.58 ± 6.29	26.45 ± 4.39
	Wrist	Arm-swinging	19	191.40 ± 14.63	179.55 ± 10.83	155.23 ± 17.68	55.89 ± 16.67
Hylobates moloch	Shoulder	Arm-swinging	13	38.27 ± 10.10	-4.93 ± 15.75	-44.31 ± 8.41	89.00 ± 13.56
	Elbow	Arm-swinging	13	166.17 ± 5.64	169.61 ± 3.38	153.81 ± 4.81	25.41 ± 3.48
	Wrist	Arm-swinging	13	184.59 ± 8.61	180.58 ± 9.56	176.27 ± 2.42	23.34 ± 4.65
Pygathrix nemaeus	Shoulder	Arm-swinging	28	50.34 ± 10.43	-2.53 ± 5.42	-50.59 ± 8.23	101.36 ± 10.62
	Elbow	Arm-swinging	28	168.56 ± 9.90	173.09 ± 3.76	166.13 ± 7.28	18.54 ± 6.47
	Wrist	Arm-swinging	28	170.94 ± 14.92	192.78 ± 15.44	202.16 ± 27.24	53.64 ± 13.42

The basic movement at the shoulder was quite similar for all species during below branch quadrupedal locomotion. At touchdown, humeral position was either slightly protracted (*L. catta*, *D. madagascariensis*, and *V. variegata*) or retracted (*C. capucinus*, *P. coquereli*, *C. didactylus*, and *P. vampyrus*). As support phase continued, position of the humerus was generally positioned similarly for all species at mid-support and near the end of support phase with some exceptions. Levels of excursion at the shoulder joint were largely similar for most species, with the exception of *P. vampyrus* and *P. coquereli.* During arm-swinging, shoulder movements demonstrate relatively equal levels of protraction and retraction, and the shoulder reached its neutral position approximately midway throughout support phase (Figures 156-159). Shoulder excursion tended to be greater during arm-swinging than during below branch quadrupedal locomotion (Figures 160 and 161).

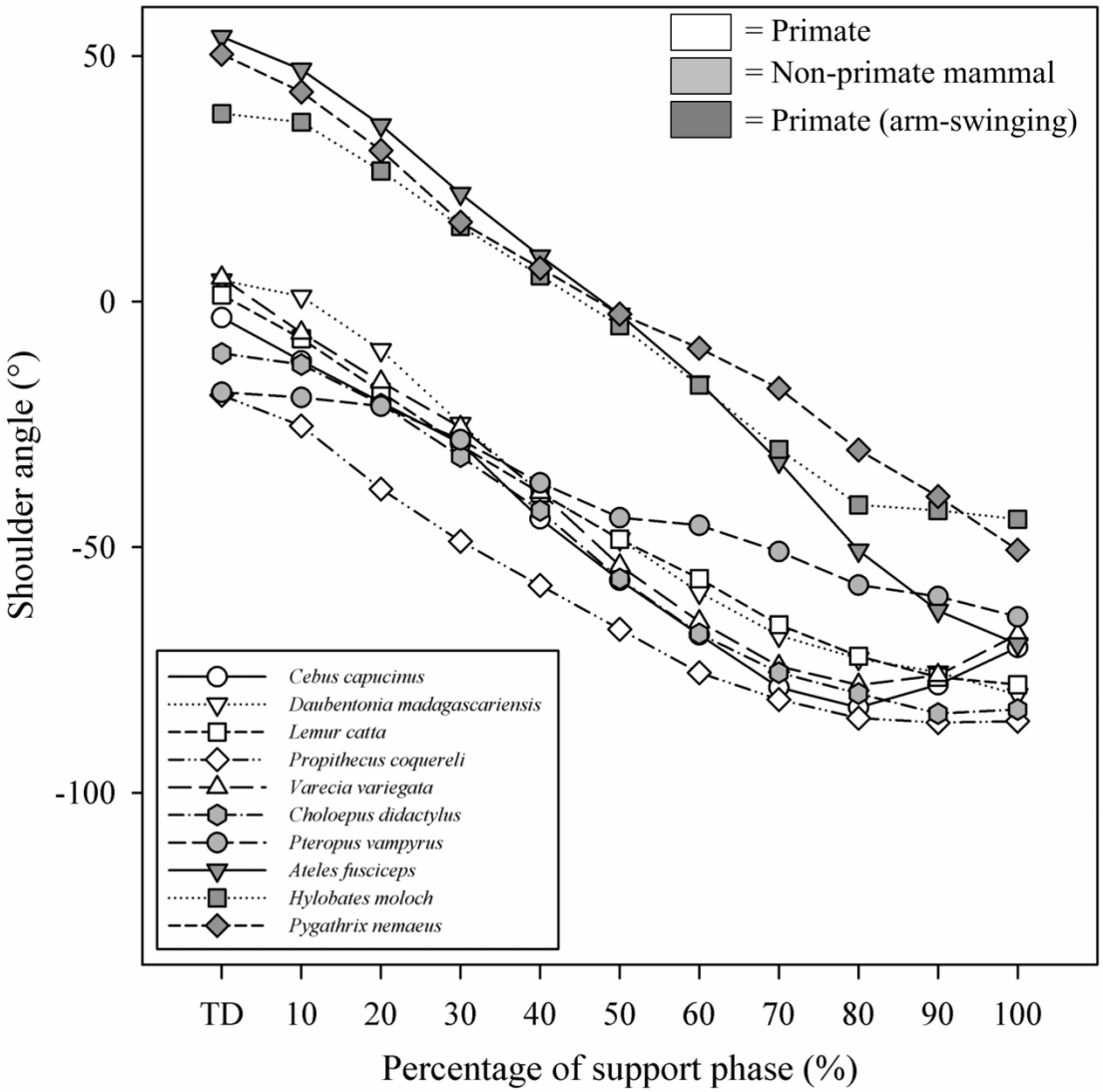

Figure 156: Patterns of mean shoulder movement (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species.

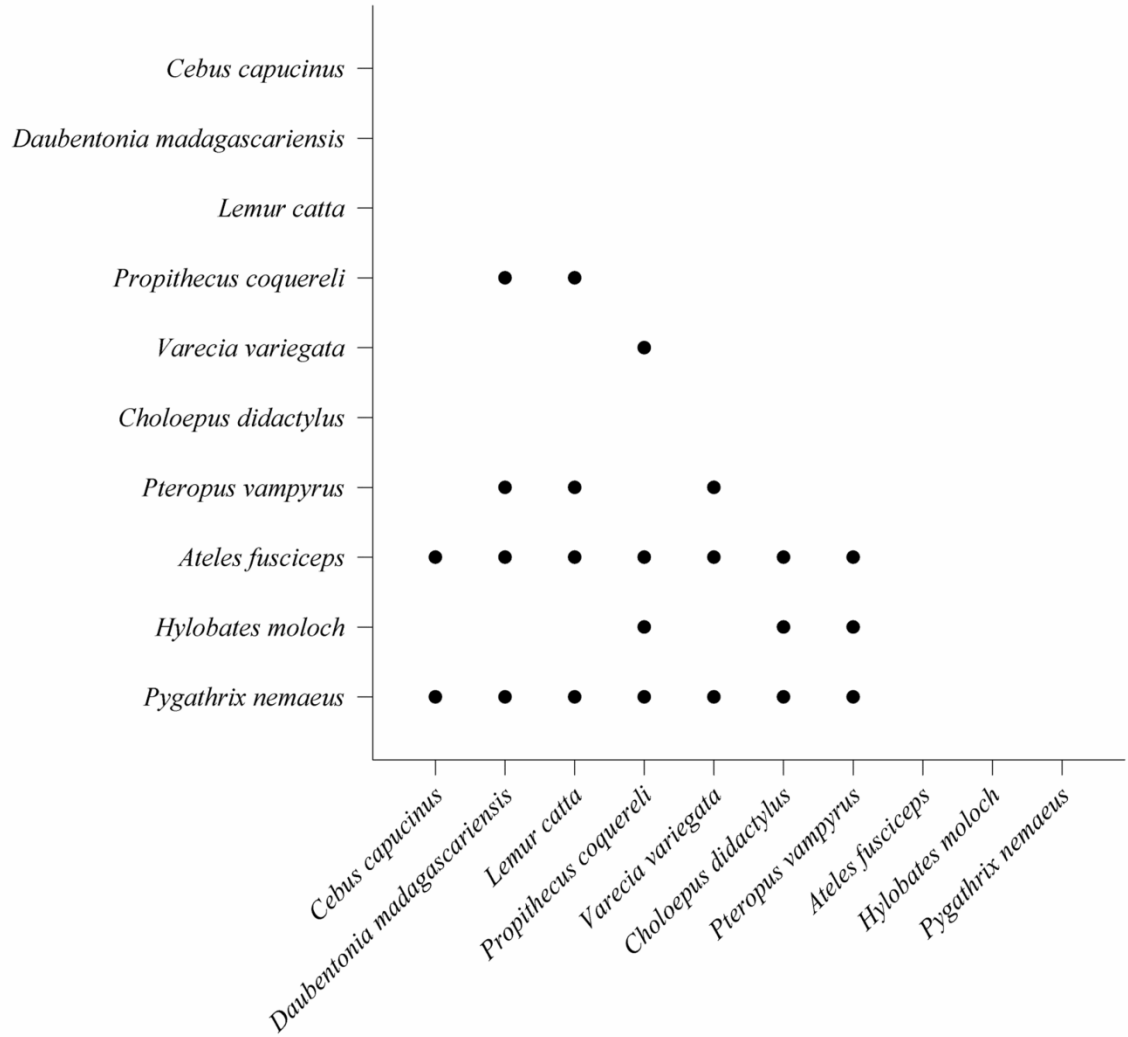

Figure 157: Multiple statistical comparisons between shoulder angle at touchdown in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

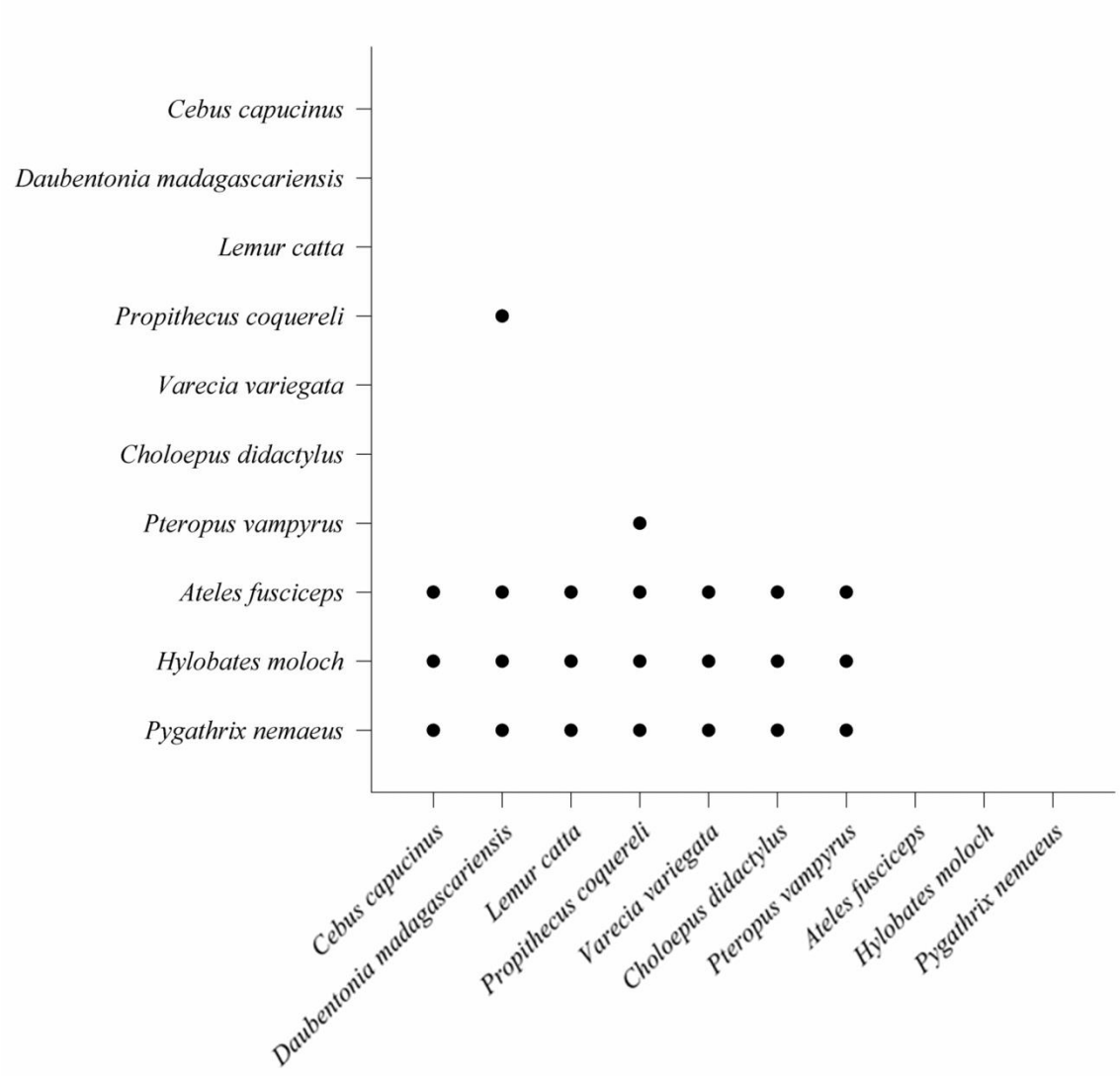

Figure 158: Multiple statistical comparisons between shoulder angle at mid-support in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* < 0.001) between the different species.

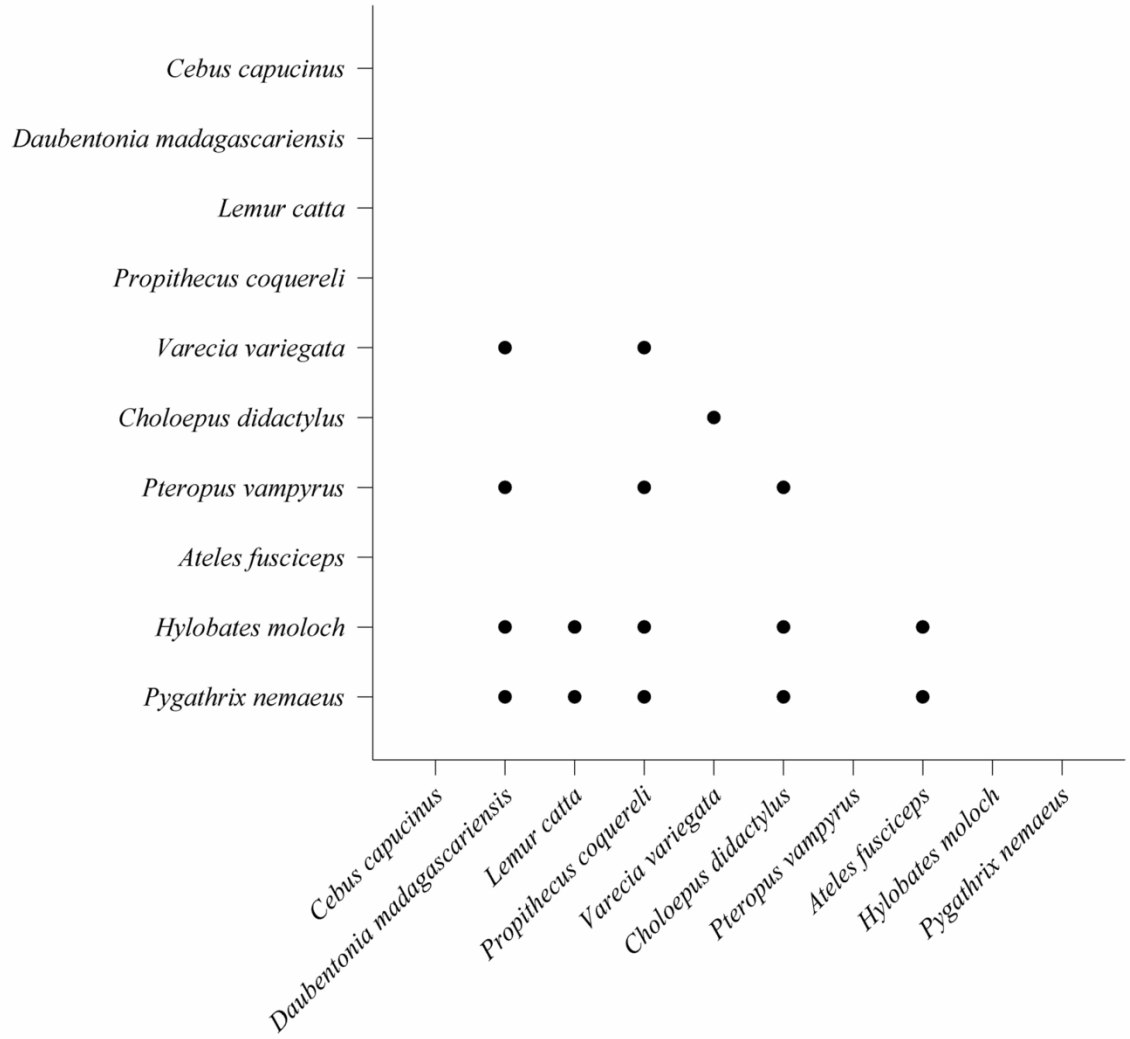

Figure 159: Multiple statistical comparisons between shoulder angle at the end of support phase in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

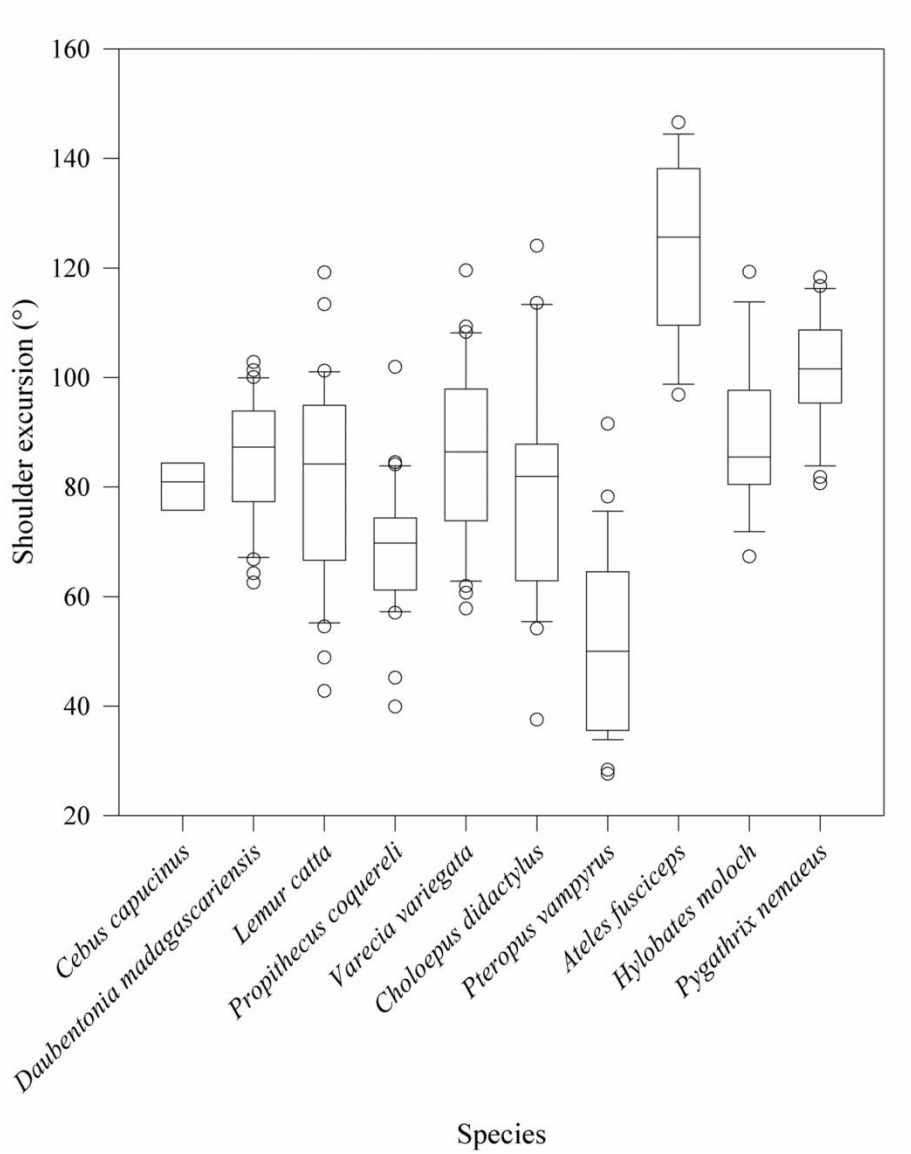

Figure 160: Mean and standard deviation values of shoulder excursion (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species.

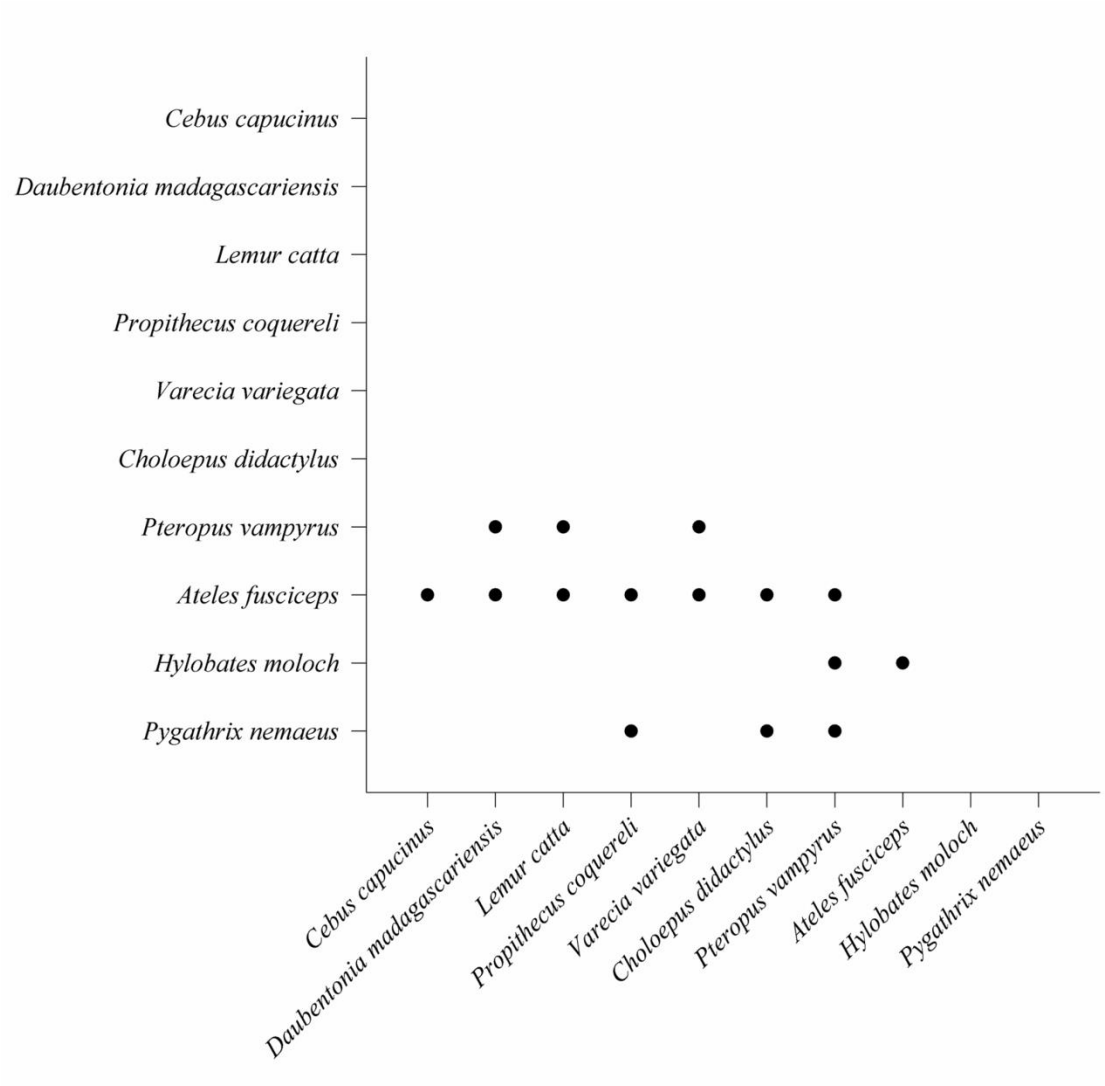

Figure 161: Multiple statistical comparisons between shoulder excursion in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

The basic pattern of movement at the elbow was similar for all species during below branch quadrupedal locomotion (Figure 162). In all species, the elbow begins at touchdown in a relatively extended (the level of extension was quite variable between primate species) position (Figure 163), and subsequently flexes until approximately mid-support (Figure 164). The elbow then begins to re-extend until the end support phase (Figure 165). It should be noted, that while this basic pattern of movement was similar for all species, levels of flexion and extension varied significantly between taxa throughout support phase. For *P. vampyrus* and *P. coquereli* both species began support phase with relatively flexed elbow joints, and maintained that flexion through the remainder of support phase. While all species actively flexed their elbow joint throughout support phase, the level of flexion varied significantly across taxa.

Elbow movements during arm-swinging were characterized by somewhat flexed positions at touchdown, followed by extension until late in support phase at which point the joint was flexed again. The extended position of elbow throughout support phase was drastically different during arm-swinging compared to below branch quadrupedal locomotion (Figures 162-165). Movement and overall excursion of the elbow was relatively high for *P. vampyrus, C. capucinus*, *D. madagascariensis*, *V. variegata*, and *C. didactylus* compared to the arm-swinging primates, *L. catta*, and *P. coquereli* (Figures 166 and 167).

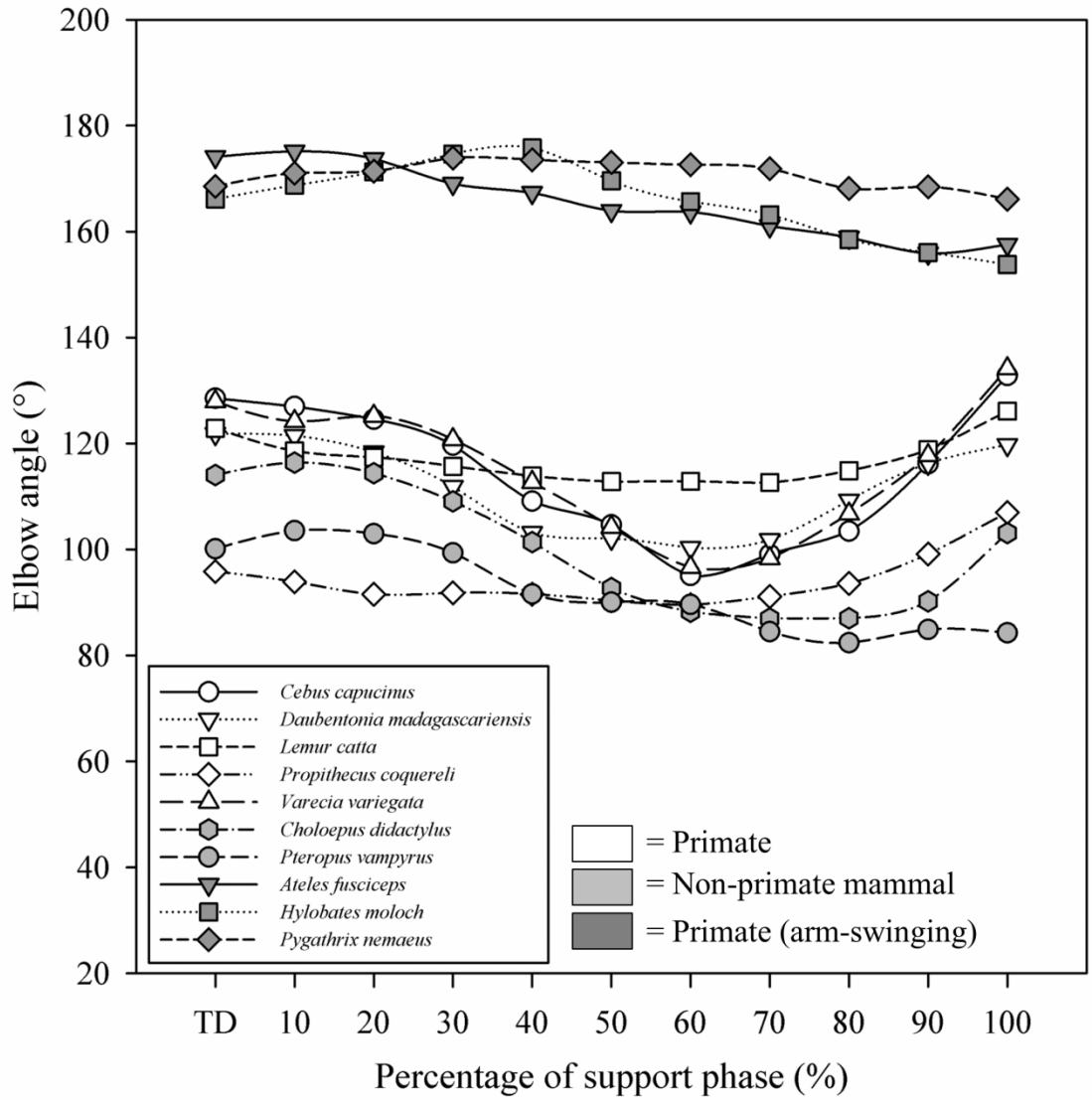

Figure 162: Patterns of mean elbow movement (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species.

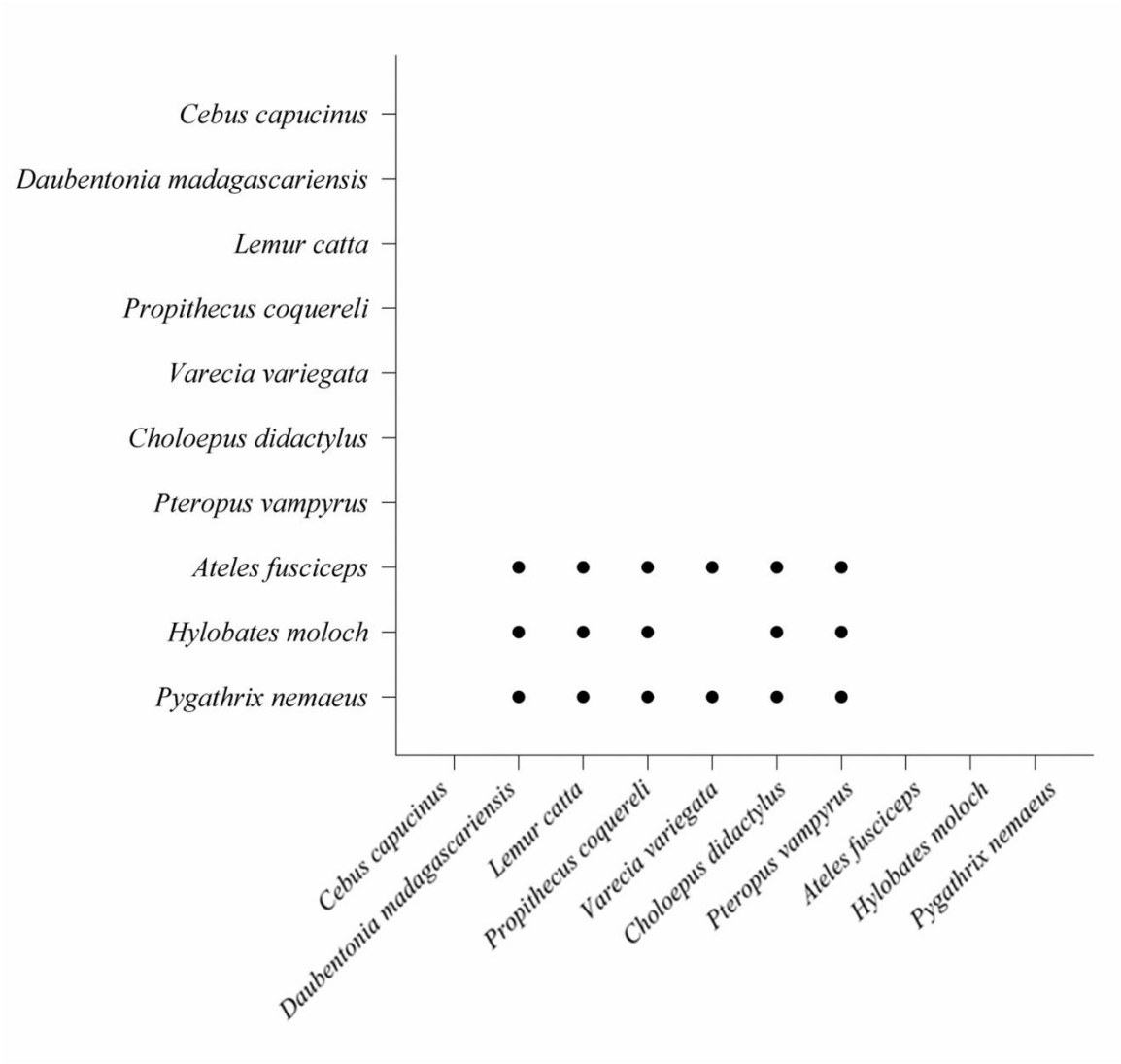

Figure 163: Multiple statistical comparisons between elbow angle at touchdown in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

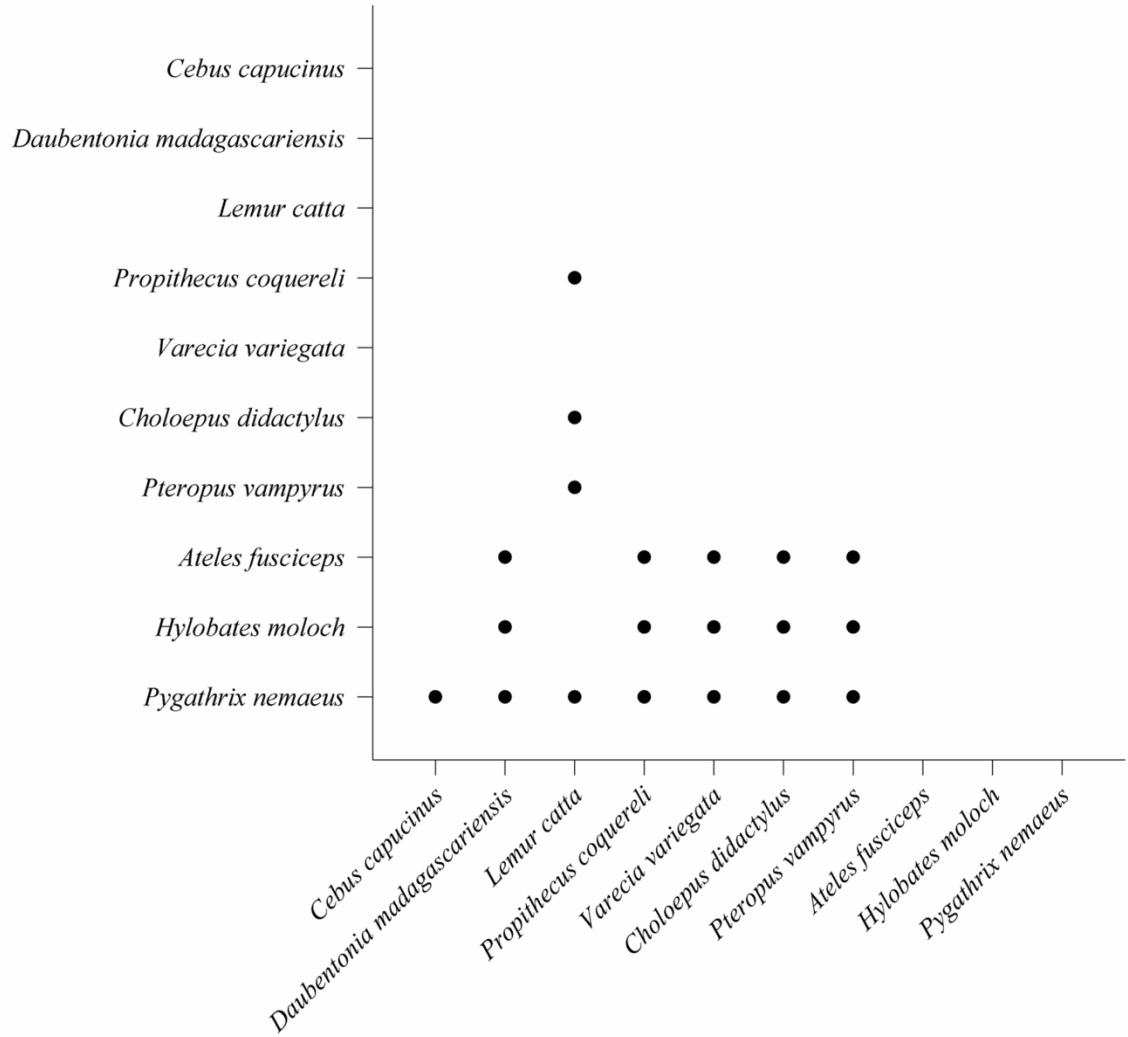

Figure 164: Multiple statistical comparisons between elbow angle at mid-support in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

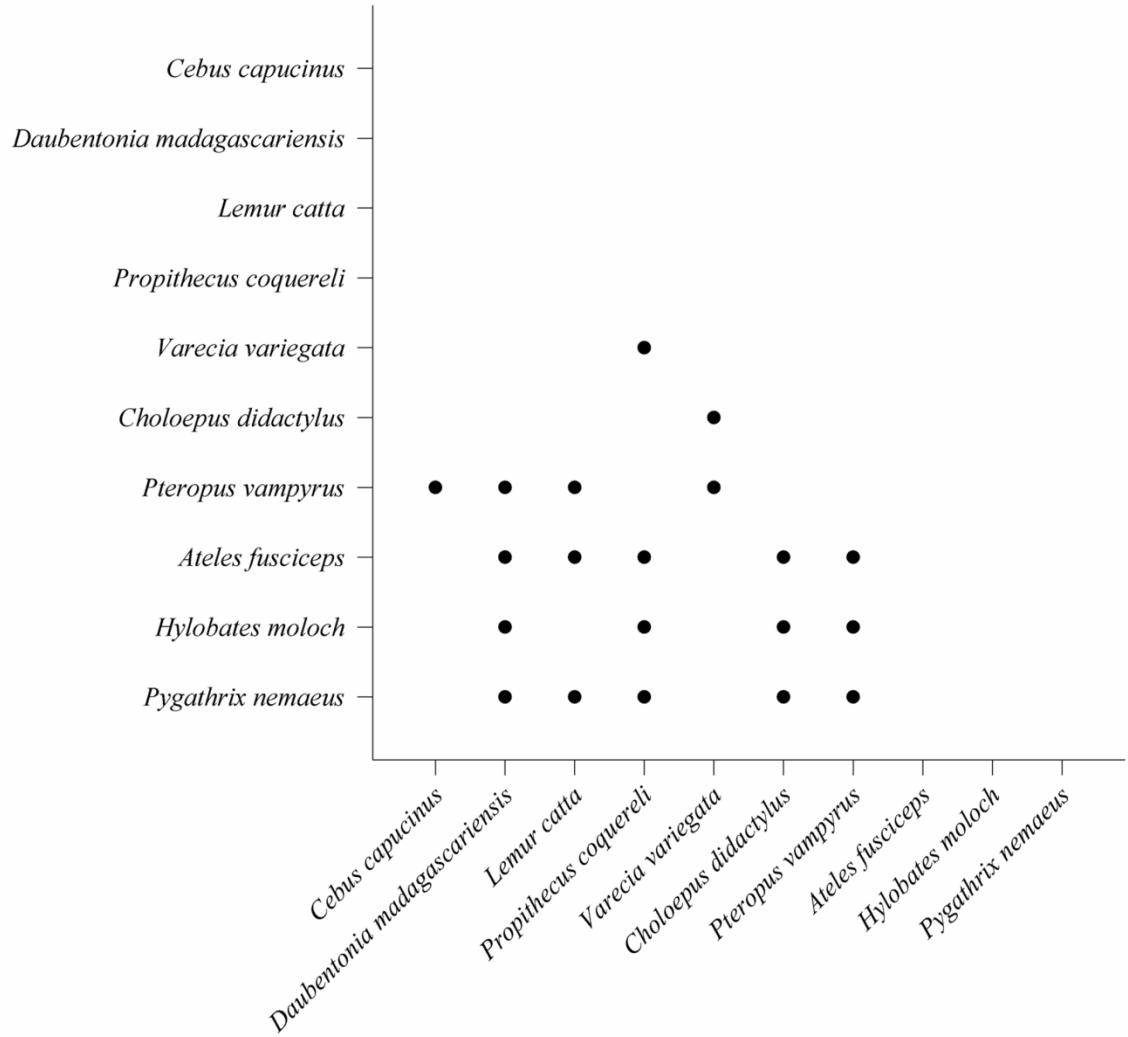

Figure 165: Multiple statistical comparisons between elbow angle at the end of support phase in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

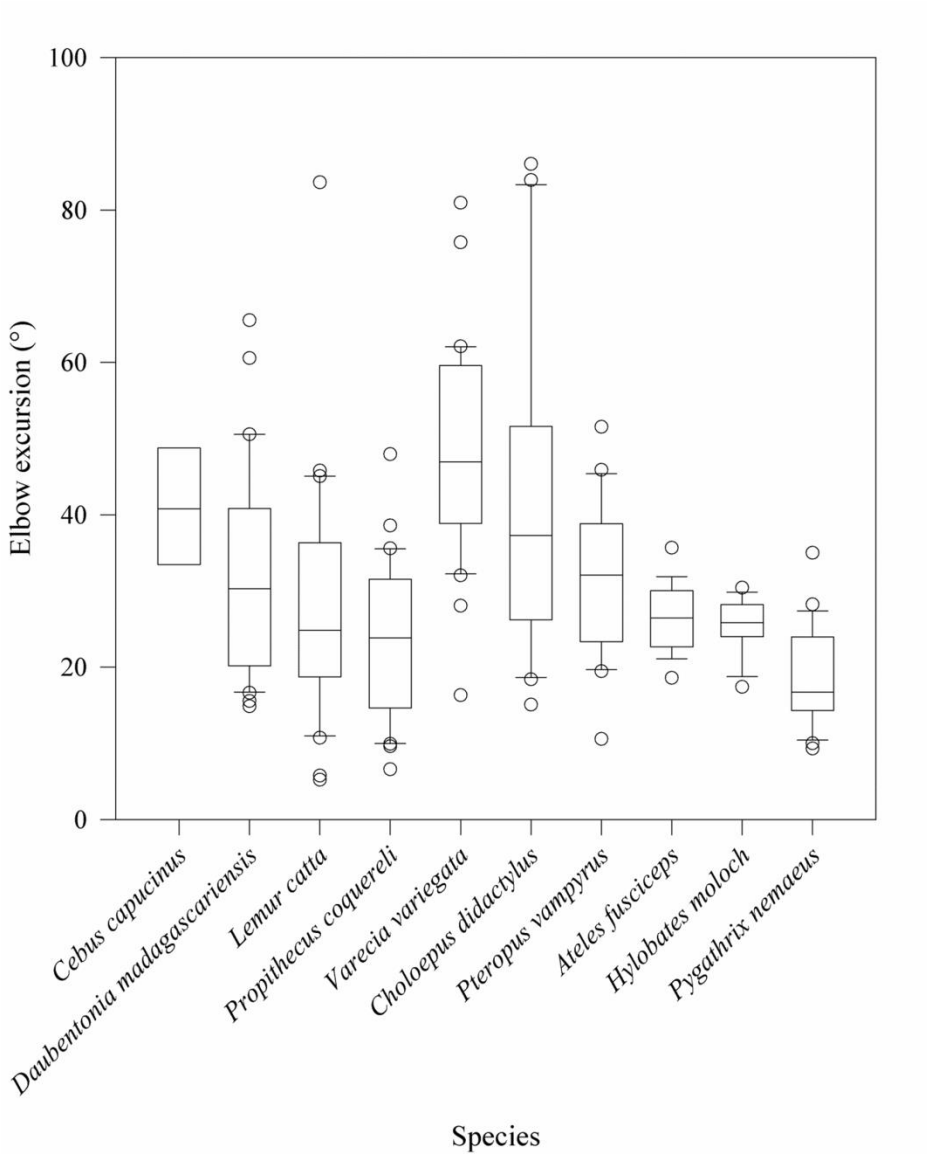

Figure 166: Mean and standard deviation values of elbow excursion (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species.

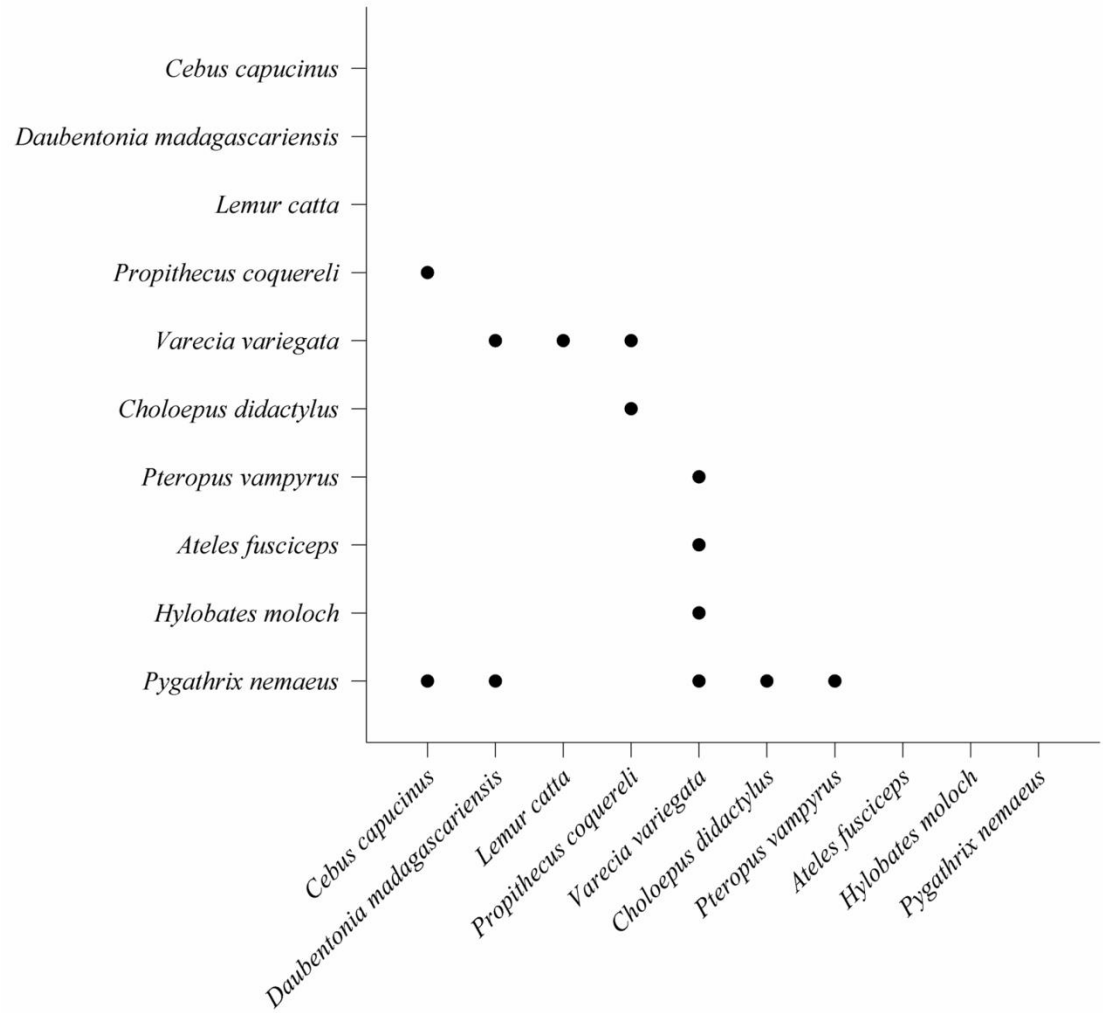

Figure 167: Multiple statistical comparisons between elbow excursion in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

During below branch quadrupedal locomotion all species used supinated hook grasps, but the movement of the wrist displayed a marked distinction between primate and non-primate mammals (Figures 168-171). During supinated hook grasps in primates, movements of the wrist are largely confined to ulnar and radial deviation. For animals that use this grasp type, the wrist is slightly ulnarly deviated during touchdown, and then subsequently radially deviates throughout the remainder of support phase. Just prior to lift-off, the wrist ulnarly deviates once again and enters a more neutral position. In *C. didactylus* and *P. vampyrus* the wrist is ulnarly deviated throughout support phase, and although there is a tendency for the wrist to reach a more neutral position near the end of support phase the overall joint excursion tends to be lower in these species than in the primates. During arm-swinging, *P. nemaeus* grabs the support with pronated hook grasps. This means that as *P. nemaeus* grabs onto the support the wrist is first ulnarly deviated, and subsequently radially deviated throughout the remainder of the stride. Both *H. moloch* and *A. fusciceps* use supinated hook grasps to grab onto the support, but positioning of the wrist varied substantially for both species. In *H. moloch* the wrist demonstrated very little movement, and maintained a position near neutral throughout support phase. In contrast, *A. fusciceps* used radially deviated wrist positions at touchdown, and subsequently ulnarly deviated its wrist throughout the remainder of support phase. Overall levels of wrist excursion tended to be higher in *A. fusciceps* and *P. nemaeus* than all other species (Figures 172 and 173).

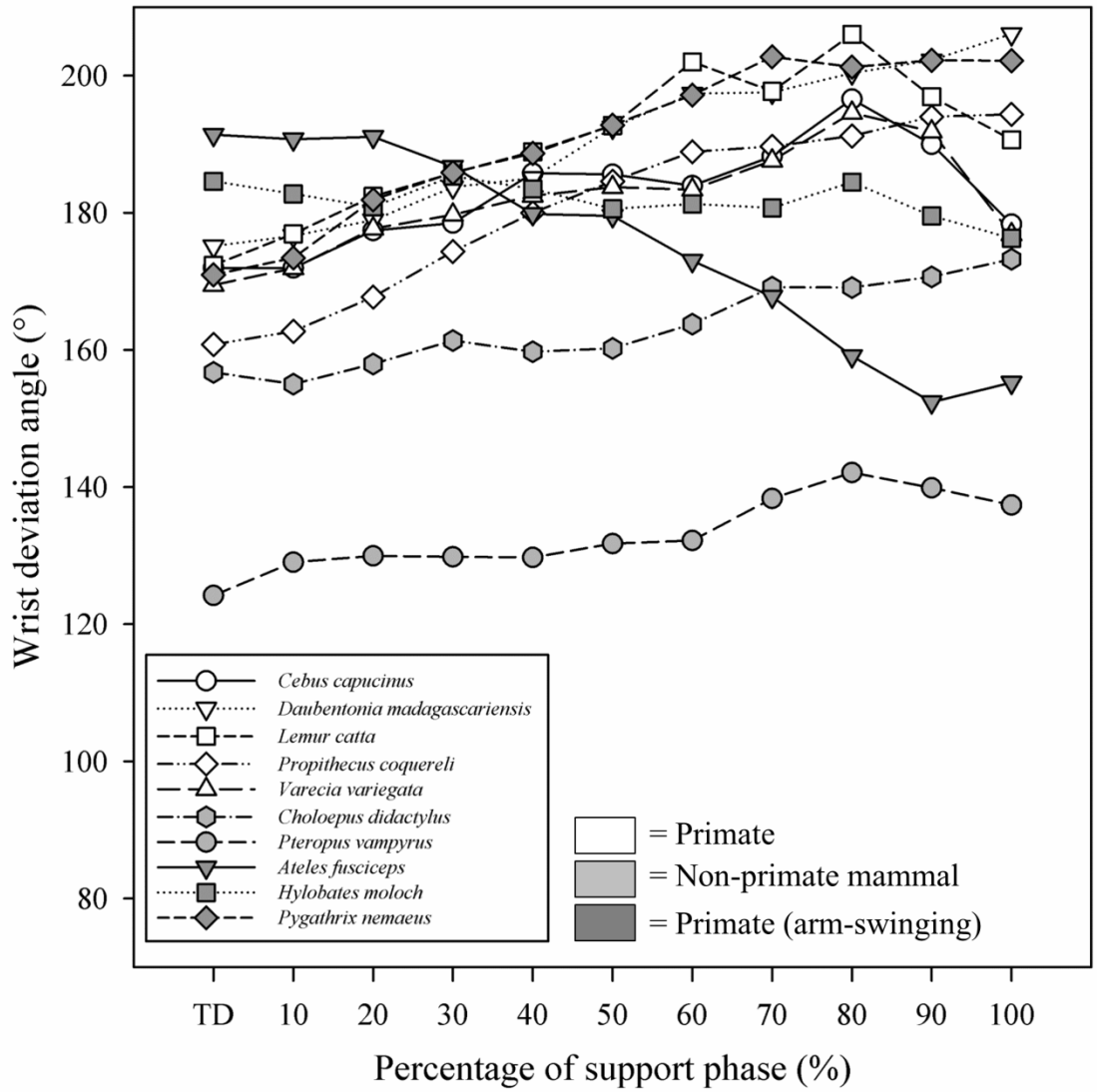

Figure 168: Patterns of mean wrist movement (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species.

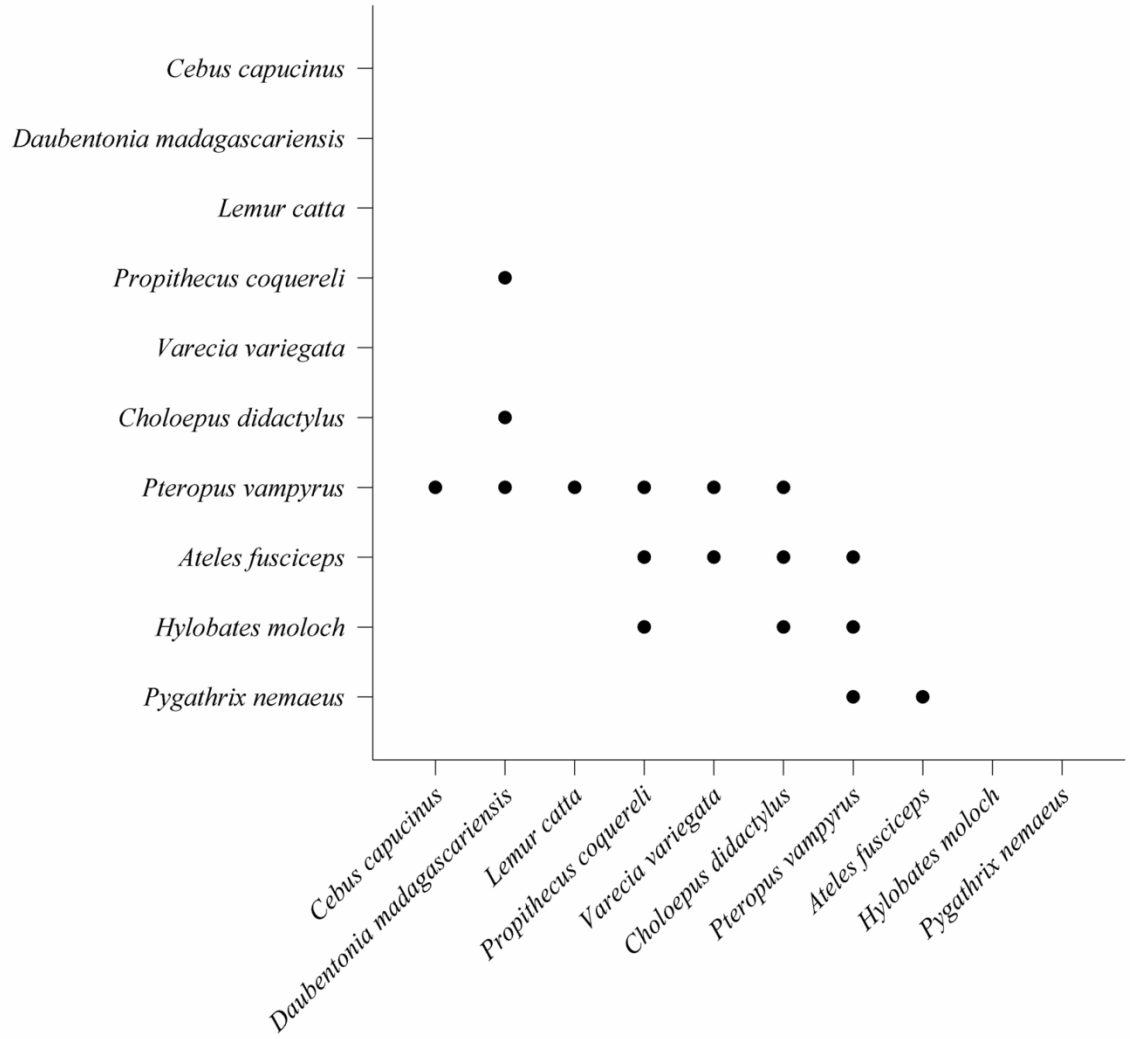

Figure 169: Multiple statistical comparisons between wrist angle at touchdown in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance (*P* ≤ 0.001) between the different species.

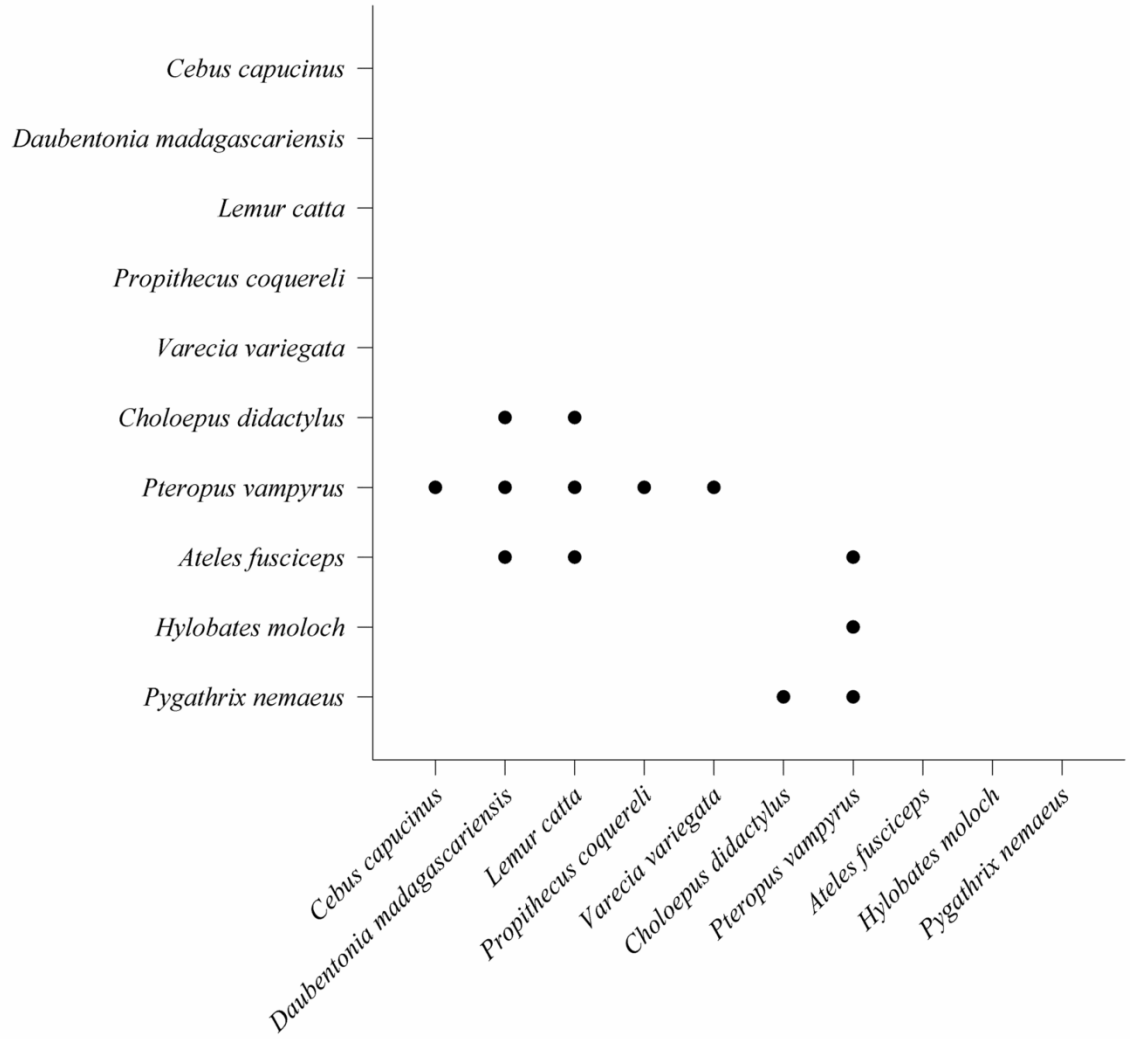

Figure 170: Multiple statistical comparisons between wrist angle at mid-support in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

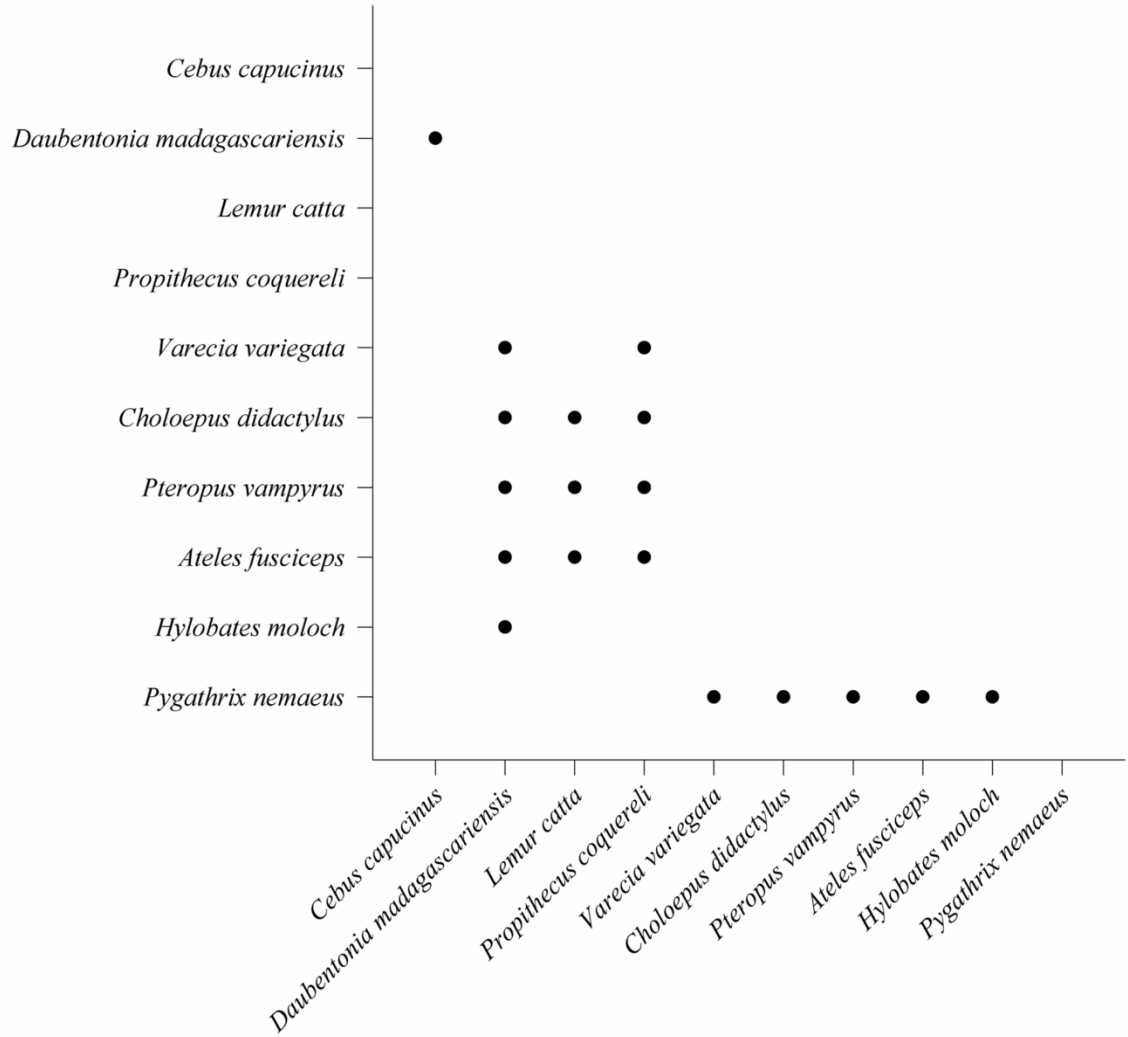

Figure 171: Multiple statistical comparisons between wrist angle at the end of support phase in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

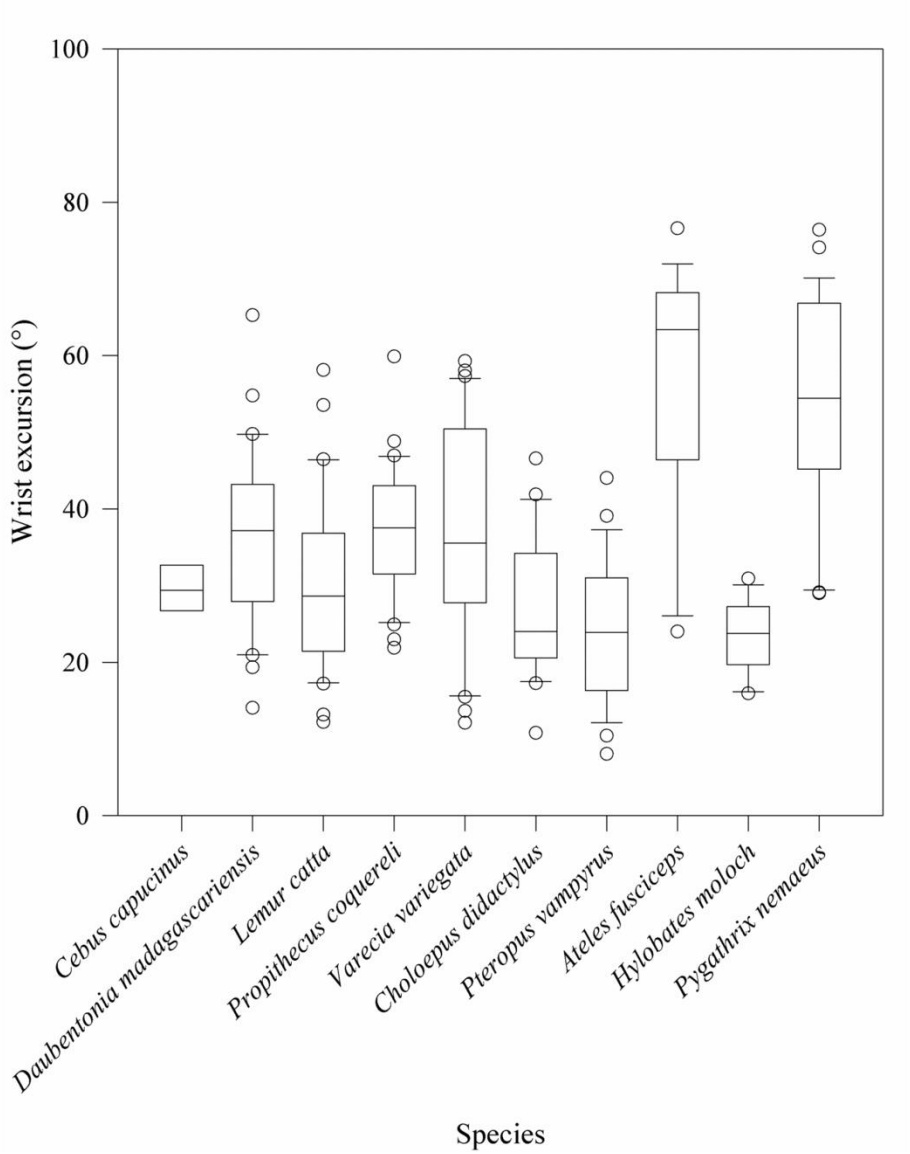

Figure 172: Mean and standard deviation values of wrist excursion (°) observed during below branch quadrupedal locomotion and arm-swinging in the study species.

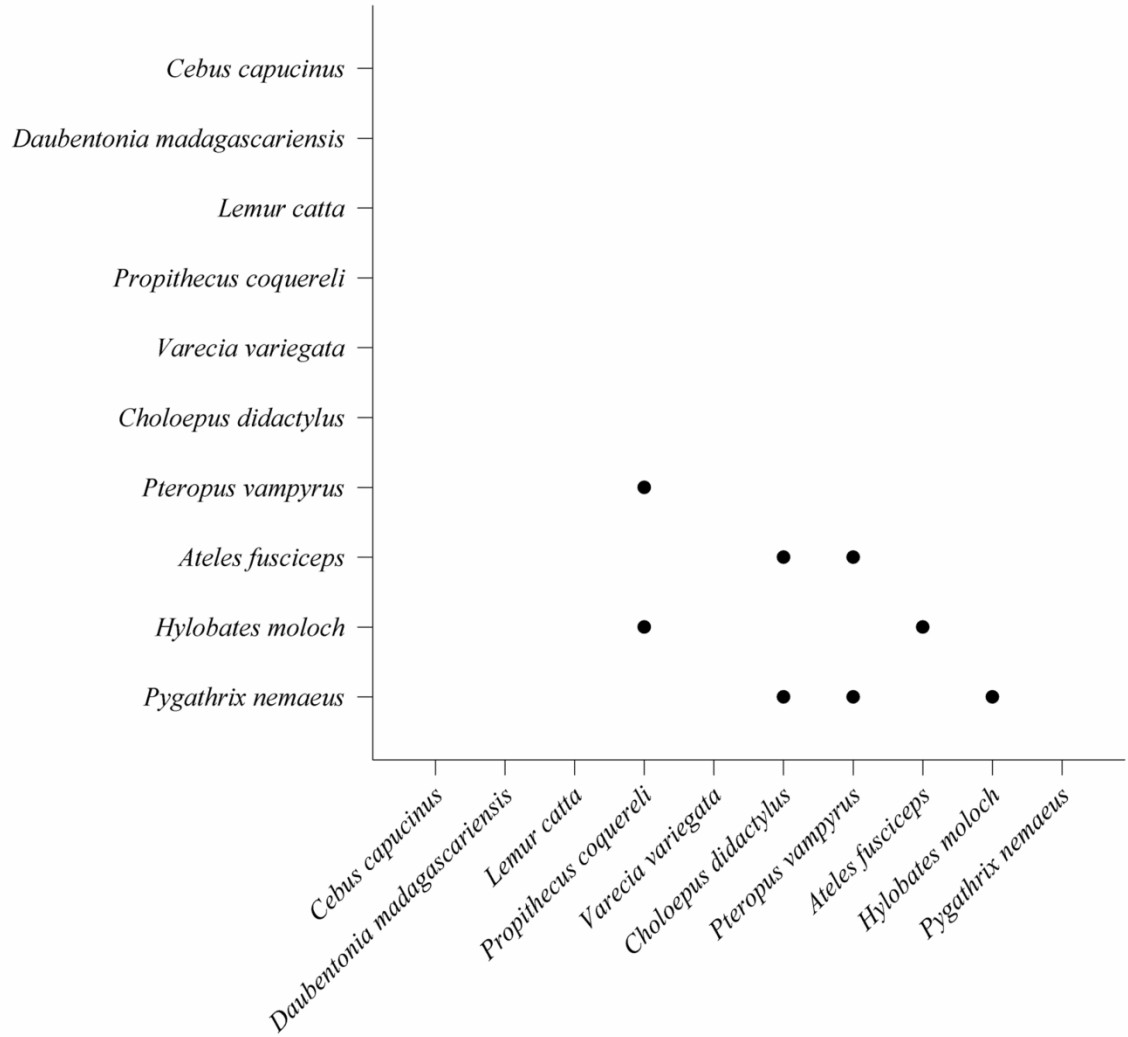

Figure 173: Multiple statistical comparisons between wrist excursion in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

3.2.3 Spatiotemporal gait variables

In total, 460 strides were used for spatiotemporal gait analysis. Table 14 summarizes the number of steps collected per limb for each species, and data, stride duration, stride length, and forelimb duty factor and relative swing proportion. All data displayed a non-normal distribution and unequal variances, therefore non-parametric statistics were used for all comparisons. A significant ($P \leq 0.001$) positive association was observed between stride duration and stride length. No significant relationship between normalized speed and the other spatiotemporal gait variables collected were observed.

Table 14. Mean and standard deviation values for spatiotemporal gait variables collected during below branch quadrupedal locomotion and arm-swinging in primate and non-primate mammals.

Species	Orientation	N	Velocity (m/s)	Relative forelimb swing	Forelimb duty factor	Stride distance (m)	Stride duration (sec)
Cebus capucinus	Below	6	0.59 ± 0.07	0.43 ± 0.07	0.57 ± 0.07	0.57 ± 0.05	0.83 ± 0.13
Daubentonia madagascariensis	Below	49	0.47 ± 0.15	0.45 ± 0.11	0.56 ± 0.14	0.53 ± 0.10	1.29 ± 0.43
Lemur catta	Below	76	0.54 ± 0.18	0.36 ± 0.10	0.65 ± 0.11	0.39 ± 0.11	0.75 ± 0.12
Propithecus coquereli	Below	84	0.51 ± 0.08	0.44 ± 0.12	0.56 ± 0.14	0.52 ± 0.09	1.05 ± 0.23
Varecia variegata	Below	52	0.60 ± 0.08	0.42 ± 0.02	0.59 ± 0.09	0.57 ± 0.07	0.97 ± 0.10
Choloepus didactylus	Below	51	0.11 ± 0.04	0.34 ± 0.11	0.72 ± 0.31	0.87 ± 0.32	1.25 ± 0.43
Pteropus vampyrus	Below	46	0.17 ± 0.05	0.38 ± 0.12	0.71 ± 0.26	0.34 ± 0.10	2.04 ± 0.34
Desmodus rotundus	Below	34	0.18 ± 0.06	0.44 ± 0.20	0.62 ± 0.18	0.23 ± 0.01	1.29 ± 0.68
Hylobates moloch	Arm-swinging	13	1.23 ± 0.20	0.44 ± 0.04	0.56 ± 0.04	1.52 ± 0.22	1.24 ± 0.15
Ateles fusciceps	Arm-swinging	25	1.27 ± 0.19	0.54 ± 0.07	0.46 ± 0.07	2.00 ± 0.26	1.60 ± 0.18
Pygathrix nemaeus	Arm-swinging	24	1.12 ± 0.24	0.54 ± 0.17	0.40 ± 0.14	1.42 ± 0.30	1.28 ± 0.16

In regards to stride duration and distance, significant differences were observed between species during below branch quadrupedal locomotion and arm-swing (Figures 174-177). Stride duration demonstrated a negative association with normalized speed, and although significant differences were observed between species no appreciable patterns were detected as a whole. For *C. capucinus* and *L. catta* stride duration was significantly shorter than observed in most other species. Stride duration tended to be longer in *P. vampyrus* and *A. fusciceps* after being corrected for normalized speed. Stride distance was positively correlated with normalized speed, and varied greatly between species. After accounting for variation in normalized speed between species, *C. didactylus* and the arm-swinging primates demonstrated significantly greater stride distance, and *D. rotundus* demonstrated significantly shorter stride distance than what was observed in other species.

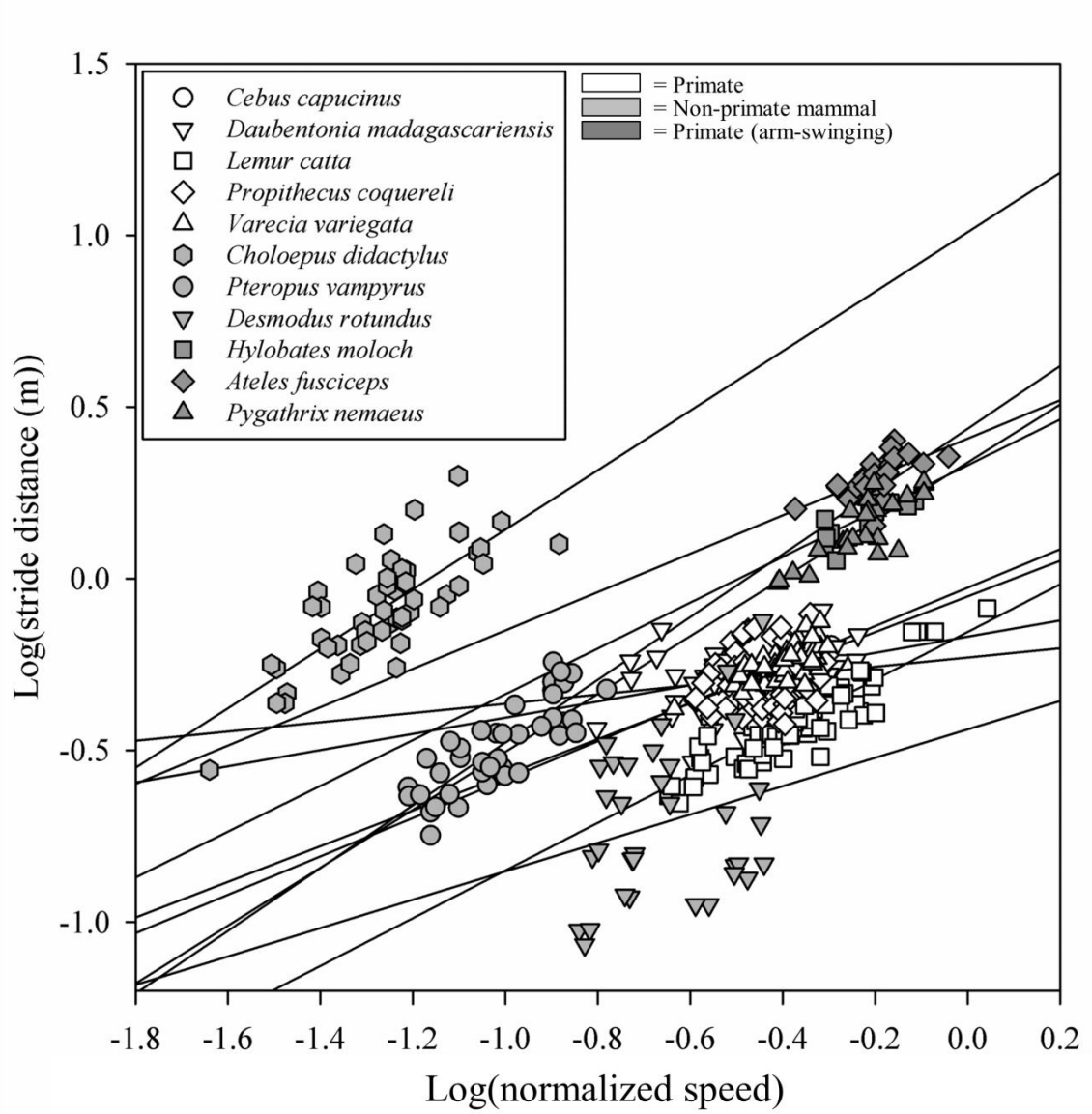

Figure 174: The relationship between log-transformed normalized speed and stride duration (sec) during below branch quadrupedal locomotion and arm-swinging in the study species.

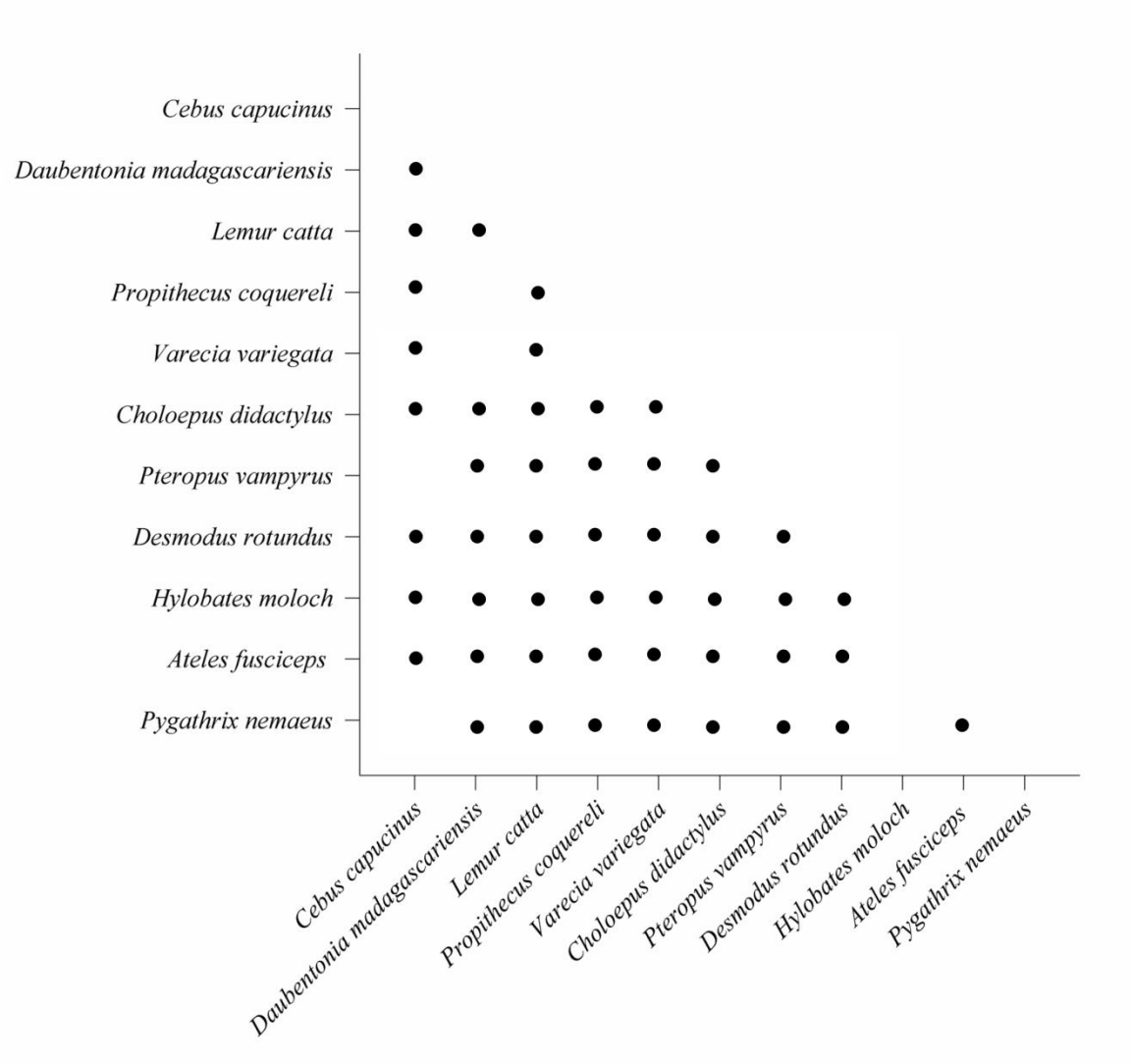

Figure 175: Multiple statistical comparisons between stride duration in the study species in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

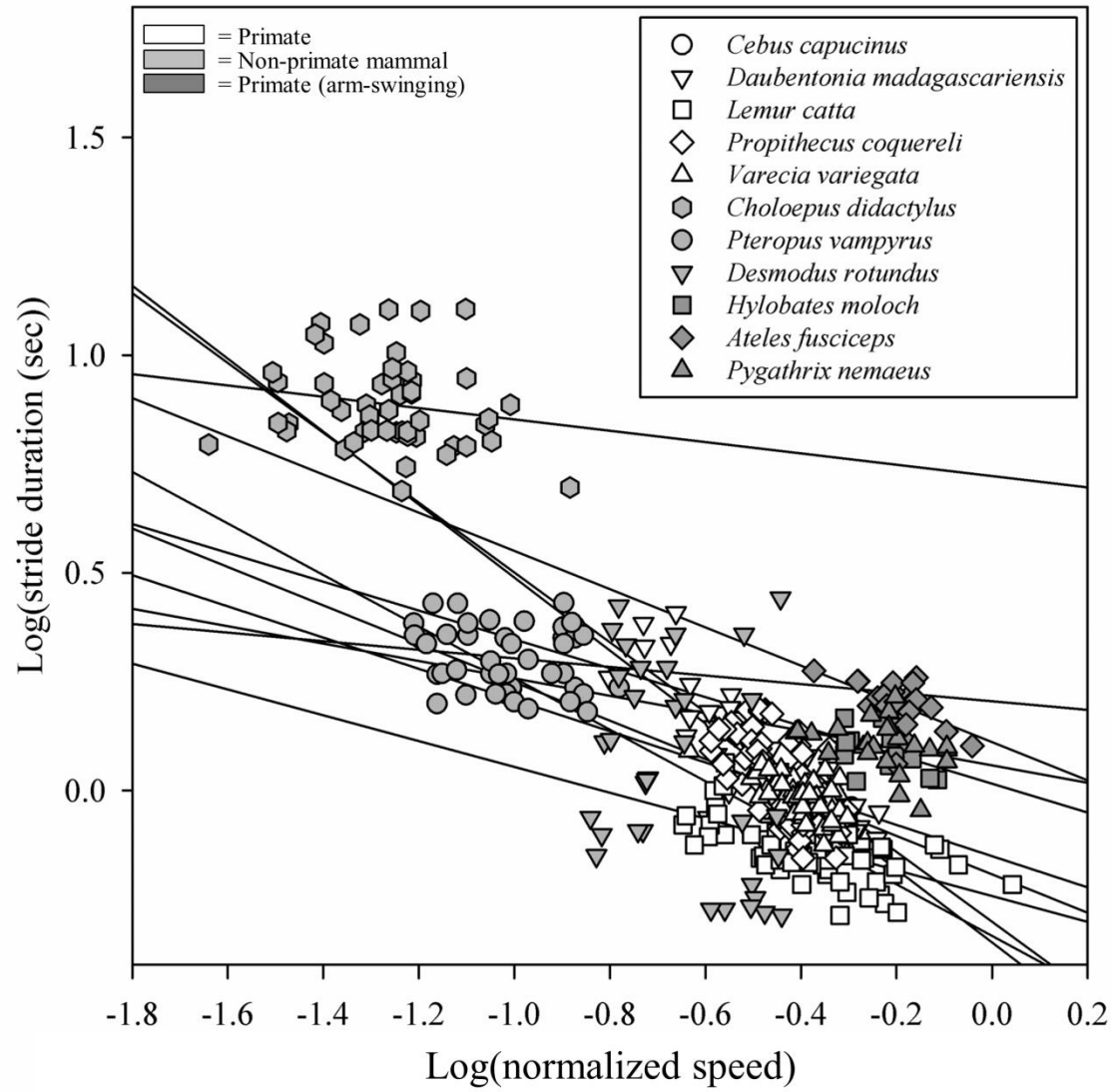

Figure 176: The relationship between log-transformed normalized speed and stride distance (m) during below branch quadrupedal locomotion and arm-swinging in the study species.

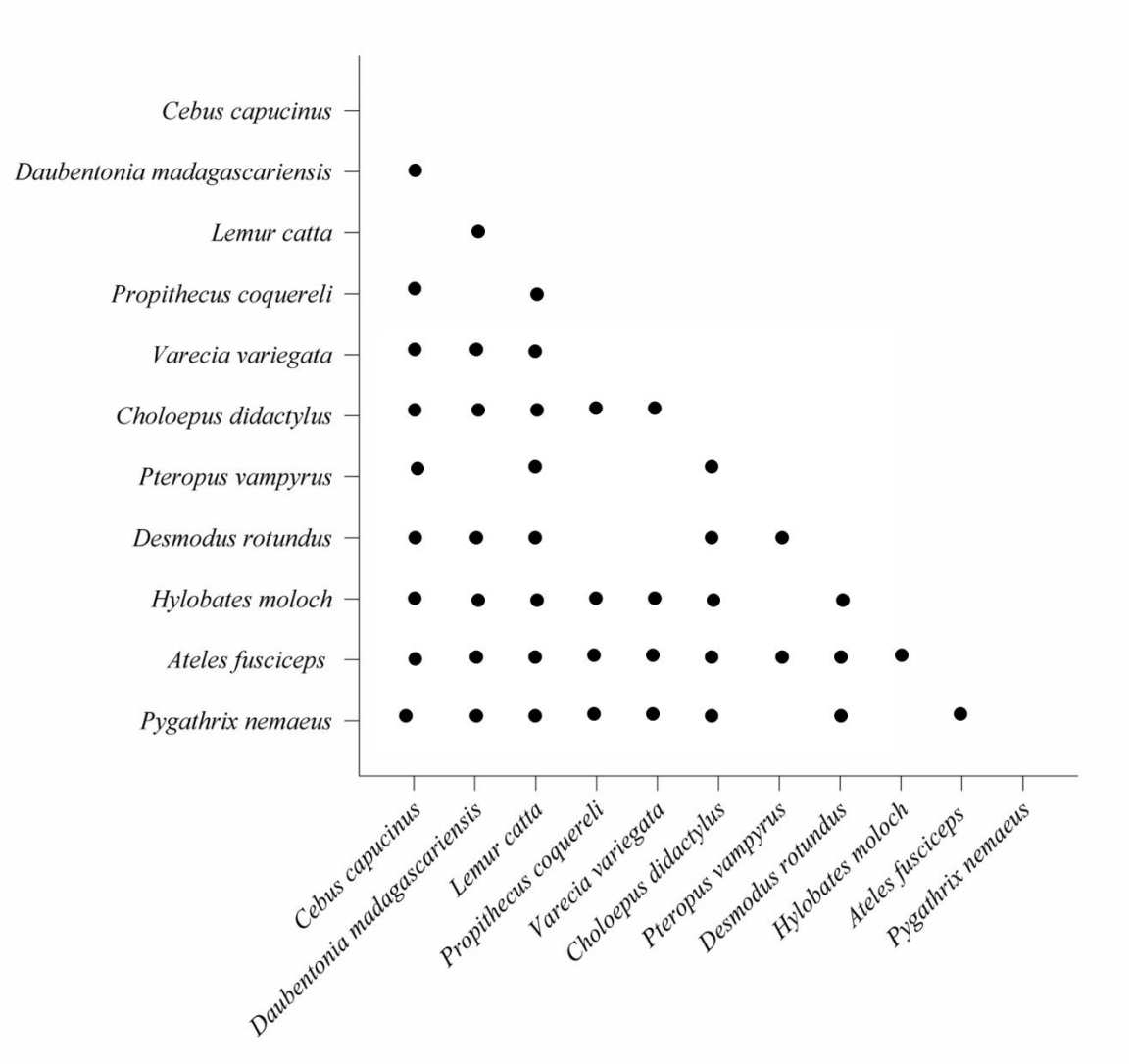

Figure 177: Multiple statistical comparisons between stride duration in primate and non-primate mammals during below branch quadrupedal locomotion. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

Patterns of forelimb and hindlimb duty factor and relative swing phase largely showed the same pattern across all species during below branch quadrupedal locomotion, although some exceptions were present. In general, forelimb duty factor tended to be slightly longer, and forelimb relative swing phase tended to be slightly shorter in the non-primates species, but clear taxonomic differences were not observed. During arm-swinging, relative swing phase tended to be relatively longer and forelimb duty factor tended to be relatively shorter than what was observed during below branch quadrupedal locomotion (Figures 178-181).

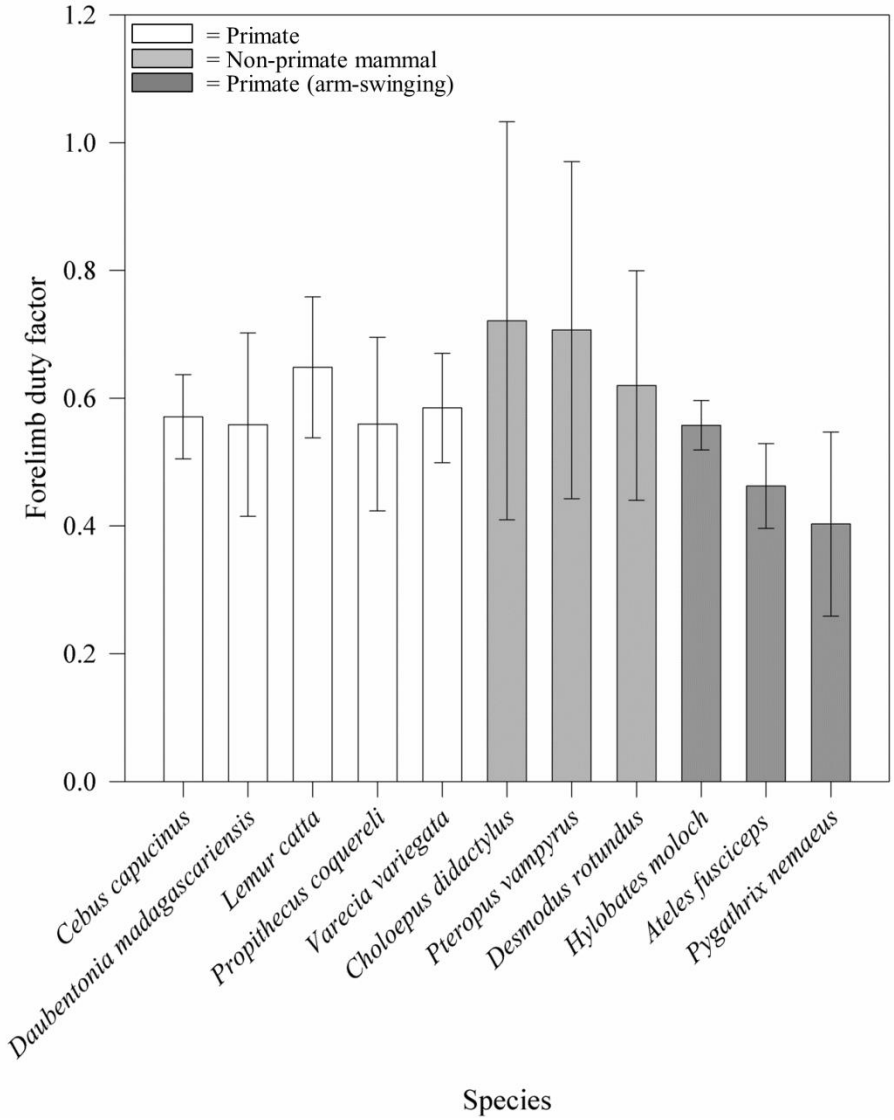

Figure 178: Forelimb duty factor (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals.

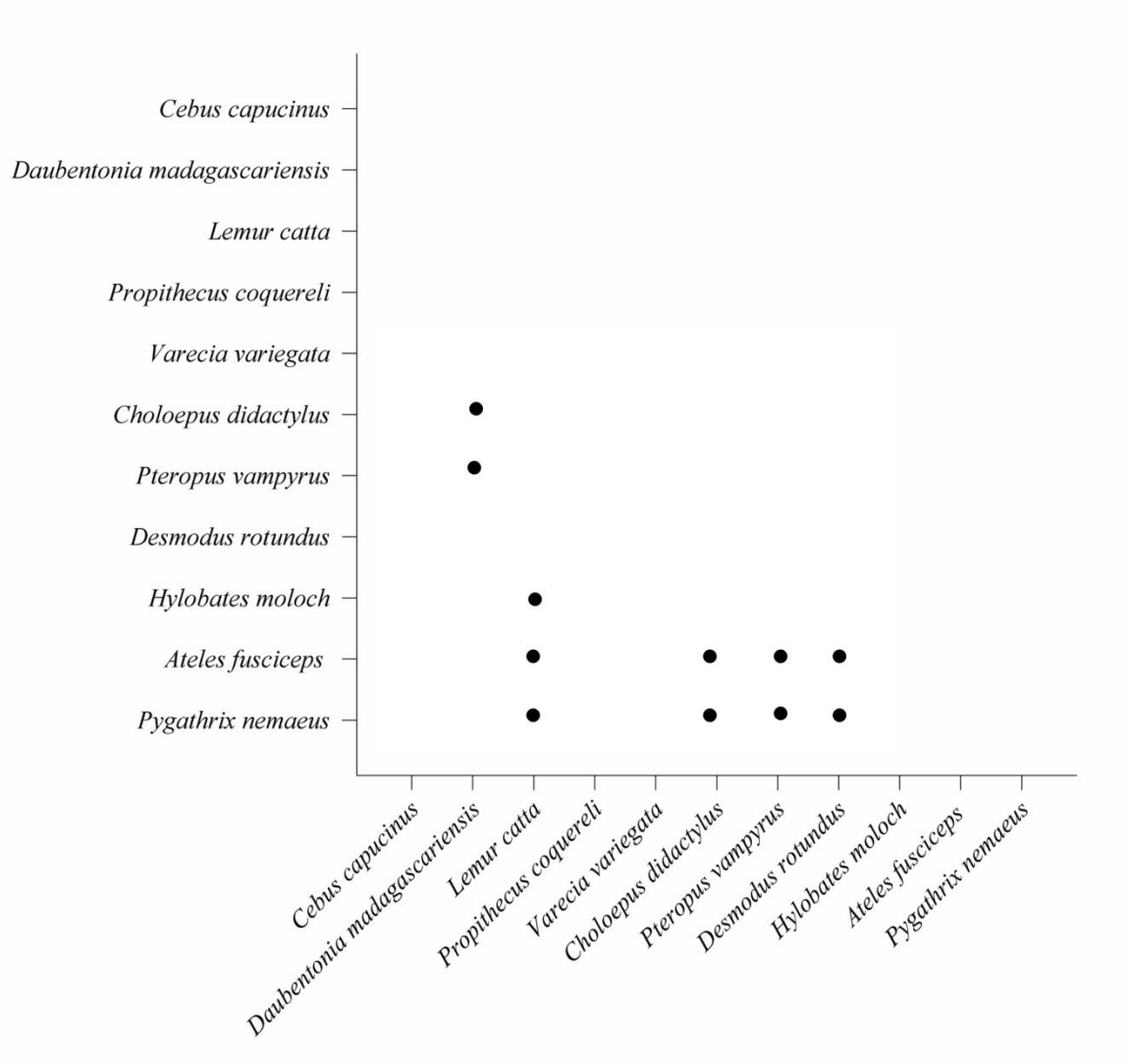

Figure 179: Multiple statistical comparisons between forelimb duty factor in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

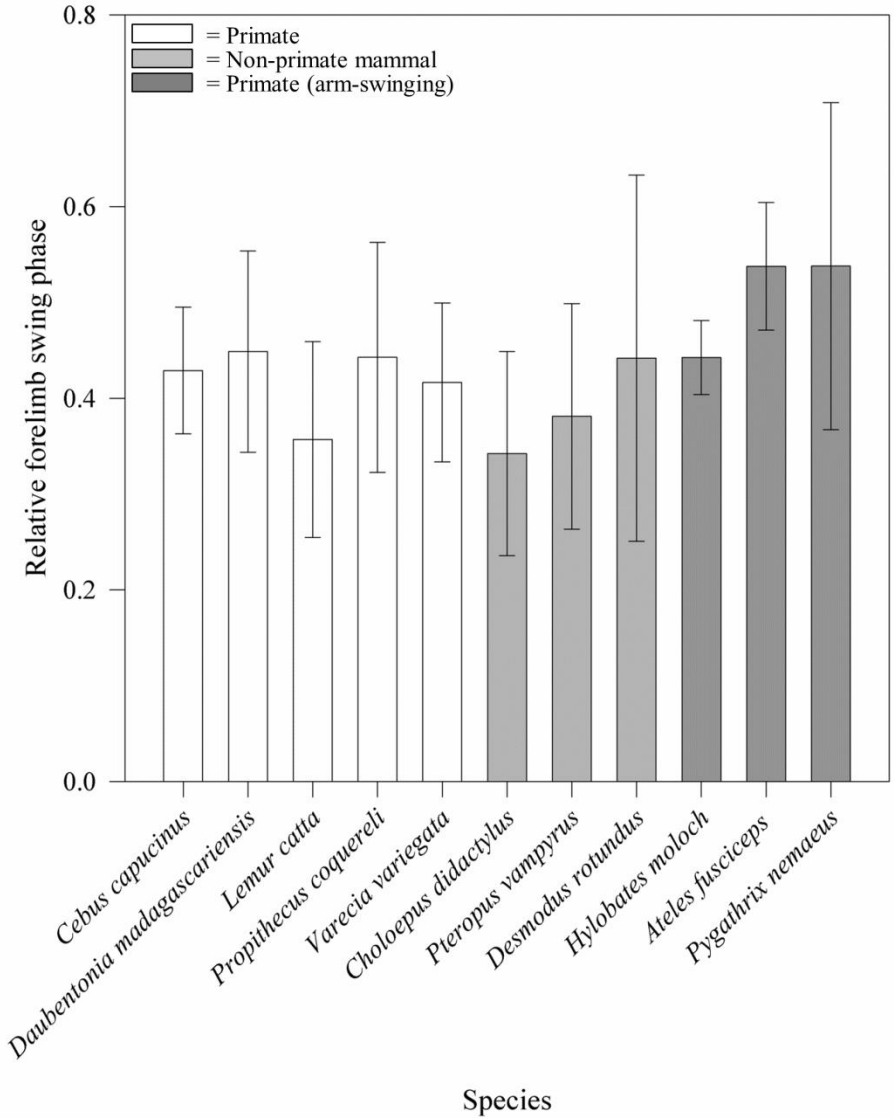

Figure 180: Relative forelimb swing phase (mean and standard deviation) during below branch quadrupedal locomotion in primate and non-primate mammals

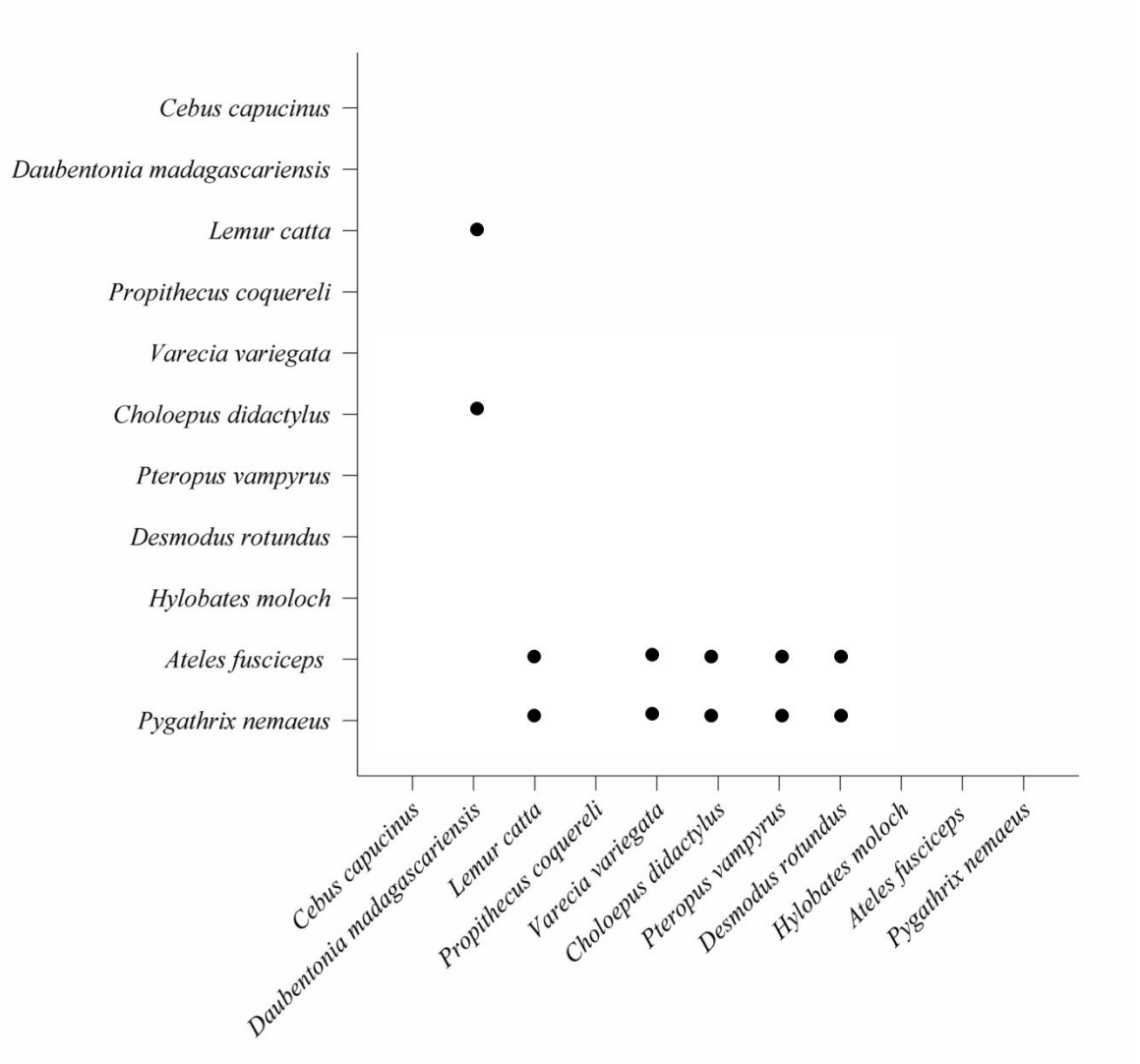

Figure 181: Multiple statistical comparisons between relative forelimb swing phase in the study species during below branch quadrupedal locomotion and arm-swinging. Kruskal-Wallis (non-parametric ANOVA) method with Bonferroni adjusted P-values used for statistical comparisons. Symbols indicate statistical significance ($P \leq 0.001$) between the different species.

4. Discussion

The goal of this study was to explore the mechanical behaviors used by primates and other mammals during below branch quadrupedal locomotion to determine how these behaviors relate across species, to above branch quadrupedal locomotion, and to arm-swinging. Specifically, this thesis sought to determine: (1) whether patterns of above branch locomotion are the same during below branch locomotion; (2) whether below branch movement involves new motor programs as evidenced by changes in kinematics, kinetics and spatiotemporal variables; (3) whether patterns of below branch behavior are uniform across species, and thus, represent shared mechanical requirements, or if species vary and can solve problems in different ways that reflect their individual evolutionary histories; and (4) whether the mechanics of below branch quadrupedal locomotion are similar to those of arm-swinging locomotion and whether the adoption of below branch quadrupedalism facilitates the evolution of arm-swinging.

Suspensory locomotion has been intimately linked to the evolutionary history of primates. All primates can, and do, adopt suspensory behaviors, but some groups emphasize these movements more effectively, or for longer periods of time than others. There exists no comprehensive theory about the acquisition of suspensory locomotion in primates, and no work has yet to explore this gap experimentally. This study provides experimental evidence to test theoretical models about the evolution of below branch quadrupedal locomotion in primates and other mammals and the evolution of arm-swinging in primates. From the data collected, it is clear that the patterns of below branch quadrupedal locomotion observed in primates are mechanically distinct from what is

observed in when walking above the support. Most notable, is that the features considered advantageous for maintaining balance above thin arboreal supports (i.e., diagonal-sequence footfall patterns, increased humeral protraction, and relatively lower forelimb peak vertical forces) disappear when shifting below branches. The presence in primates of more gait characteristics more similar to non-primate mammals during below branch quadrupedal locomotion likely indicates that primates experience some sort of reduced mechanical restraint (a form of "mechanical release") from the biomechanical requirements and difficulties (i.e., balance and maintaining limb joints relative to gravity) of above branch arboreal movement

This dissertation found that not all features of below branch quadrupedal locomotion are the same between primate and non-primate mammals. Limb loading patterns across taxa show reveal that all primate species demonstrate higher peak vertical forces on their forelimbs, while non-primate mammals show approximately equal (*D. rotundus* and *C. didactylus*) or hindlimb dominant (*P. vampyrus*) force distribution across their limbs. This difference is important and is likely the underlying reason for why arm-swinging evolved only in the order Primates. While there are many mechanical specializations observed in extant arm-swinging animals, at its most basic level arm-swinging is the release of the hindlimbs from their weight-bearing role. In this context, it seems likely that the transition from below branch quadrupedal locomotion to arm-swinging would have been relatively easy for primates; as their hindlimbs already experience a reduced proportion of weight support during suspensory locomotion. Based on the data of this study, the presence of below branch quadrupedal locomotion should be

considered as a transitionary locomotor mode prior to acquisition of arm-swinging in primates, and therefore should be considered as an important locomotor mode in the evolutionary history of primates.

4.1 A mechanical and evolutionary interpretation of below branch quadrupedal locomotion in primates and non-primate mammals

4.1.1 A mechanical synthesis of below branch quadrupedal locomotion in primates and non-primate mammals

Across the five species of quadrupedal primates (*C. capucinus, V. variegata, D. madagascariensis, L. catta,* and *P. coquereli*) sampled, the patterns of above branch quadrupedal locomotion closely matched what has been reported in other studies (Kimura et al., 1979; Franz et al., 2005; Wallace and Demes, 2008; Schmitt, 2010; Larson and Demes, 2011; Granatosky et al., 2016). Data from this study provide additional information to the growing body of literature on the gait mechanics of above branch quadrupedal locomotion in extant primates. Interestingly, even *P. coquereli,* an anatomically specialized vertical clinging and leaping (VCL) species, displays similar gait characteristics to more anatomically generalized primate species. The anatomy of VCL primates is characterized by relatively long hindlimbs relative to the forelimbs (Hall-Craggs, 1965; Oxnard et al., 1981a; b; Burr et al., 1982; Gebo and Dagosto, 1988; Ravosa et al., 1993; Demes et al., 1996; Connour et al., 2000; Schaefer and Nash, 2007). This anatomical pattern is thought to make quadrupedal locomotion ungainly and inefficient (Wunderlich et al., 2011, 2014), but despite this, arboreal quadrupedal locomotion has been witnessed in a number of VCL primates (Gebo, 1987). The finding that *P. coquereli* adopts the characteristic patterns of primate arboreal locomotion

provides evidence for the idea that these patterns may represent a functional suite that may be adaptive for arboreal locomotion and is potentially a basal primate gait condition (Schmitt and Lemelin, 2002). Further evidence to support the presence of a locomotor functional suite comes from experimental studies that suggest that many of the unusual features observed during primate quadrupedal locomotion are active processes, and are not simply by-products of some other anatomical or behavioral mechanism (Reynolds, 1985a; Vilensky, 1987; Vilensky and Larson, 1989; Schmitt, 1998, 1999; Larson et al., 2000; Larney and Larson, 2004; Larson and Stern, 2009).

From the data collected in this study, it is clear that, at least in primates, animals use differing mechanical strategies during above and below branch quadrupedal locomotion. Therefore, it is possible to reject the null hypothesis that above and below branch quadrupedal locomotion (at least in primates) are mechanical inverses of each other. With regard to limb loading, during above branch quadrupedal locomotion the animals in this study showed kinetic patterns consistent with those reported for other primates (Kimura et al., 1979; Reynolds, 1985a; Schmitt and Lemelin, 2002; Schmitt, 2010; Granatosky et al., 2016), including relatively higher hindlimb Vpk forces, forelimbs that were net braking and hindlimbs that were net propulsive, and generally low mediolateral forces that tended to be medially oriented when moving on arboreal substrates (Schmitt, 2003a; Carlson et al., 2005; Franz et al., 2005). The data collected in this study during below branch quadrupedal locomotion were consistent with that of Granatosky et al. (2016) and Ishida et al. (1990) (discounting the issues associated with lorisid limb loading patterns already outlined in section 1.5.2). The primary kinetic

changes that occur when the primates here investigated switch from above to below branch quadrupedal locomotion are: (1) during below branch quadrupedal locomotion, the forelimb becomes the primary propulsive element, while the hindlimb serves a braking role; (2) medially directed forces, although highly variable and inconsistent, were much higher during below branch quadrupedal than during above branch quadrupedal locomotion suggesting at some level a relatively high degree of side-to-side movement; and (3) the forelimb serves as the primary weight-bearing limb, while the hindlimb reduces its weight-bearing function. These patterns were similar for all five species of primates, and appear to not be affected by the relative amount of time each species utilizes suspensory locomotor behaviors in their natural locomotor repertoires.

The altered pattern of braking and propulsive forces of the limbs during below branch quadrupedal locomotion are not entirely unexpected, and may be explained in part by pendular mechanics. As described by Chang et al. (2000) in relation to brachiation in gibbons, any form of suspensory locomotion can be modeled as a typical simple pendulum at some level (Preuschoft and Demes, 1984; Swartz, 1989). As a typical pendulum swings downward from some initial height, it is accelerated by gravity until it reaches its lowest point, thereafter gravity acts to decelerate the pendulum. It is likely that during below branch quadrupedal walking animals are somewhat governed by this mechanism (but see Nyakatura and Andrada, 2012).

Perhaps one of the most radical changes to occur during the switch from above to below branch quadrupedal locomotion was the functional switch in the braking and propulsive roles of the forelimbs and hindlimbs. During above branch quadrupedal

locomotion, the forelimb tends to serve a net braking role, while the hindlimb is net propulsive. This pattern switches during below branch quadrupedal locomotion. It was originally predicted that these differences were due to the levels of protraction and retraction observed in the limb based on prediction observed in bipedal walking (Kimura et al., 1977; Inman et al., 1981) and Reynolds (1985a), but based on the data collected in this study there is no evidence to support the claim that the transition from limb protraction to retraction (i.e., mid-stance) is associated with the braking/propulsive (B/P) transition (or propulsive to braking transition during below branch quadrupedal locomotion). Additionally, there was no evident relationship between the degree of protraction and retraction and whether the limb served a propulsive or breaking function.

As an alternative, it is possible that the differences in the functional roles of the limbs can be understood by a consideration of limb placement throughout the stride relative to the COM, and the normal pattern of braking and propulsive forces. If one assumes the animal's COM is roughly between the shoulders and hips, the forelimb will be mostly in front of the COM throughout forelimb support phase, and the hindlimb will be mostly behind the COM throughout hindlimb support phase during below and above branch quadrupedal locomotion. As the animal contacts the substrate with the forelimb during below branch quadrupedal locomotion, it will begin the downward phase of pendular motion relying on gravity, and therefore, producing a propulsive force. The animal's COM will continue its downward swing to produce a propulsive force until the animal's COM passes beneath the point of contact. After that, the animal's COM will decelerate (indicating a braking force) due to the upswing phase of pendular motion until

forelimb lift-off. Because of the forelimb's position in front of the COM throughout most of forelimb support phase, it will have a long propulsive phase and a short braking phase. This will result in the forelimb being net propulsive. The same model is true for the hindlimb, but because the hindlimb will be mostly behind the COM throughout support phase, it will have a short propulsive phase and a long braking phase. This will result in the hindlimb being net braking (Figure 182).

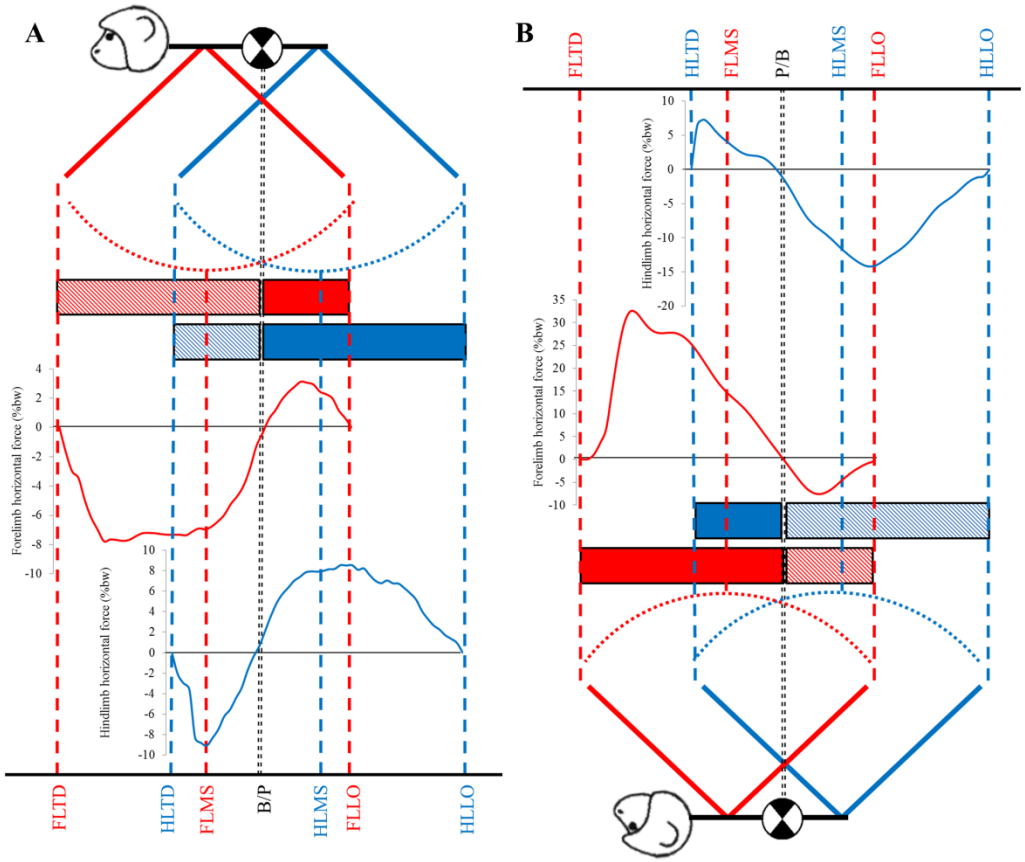

Figure 182: A model explaining the differentiation of the propulsive and braking roles of the forelimbs and hindlimbs during (A) above and (B) below branch quadrupedal locomotion. Red represents the forelimb (FL) and blue represents the hindlimb (HL). Total excursion is indicated by lines with short dashes. Specific footfall events are indicated by lines with medium-length dashes (TD = touchdown, MS = mid-stance, and LO = lift-off). Lines with double dashes indicate the proposed transition between braking and propulsive force application (B/P or P/B depending on orientation). The circle with an inlaid hourglass represents the center-of-mass (COM), and the rectangular bars represent the theoretical time during which a limb would be most effectively able to produce braking (dashed fill) or propulsive (solid fill) forces. As drawn, this model applies to an animal with equal forelimb and hindlimb length, a COM positioned equidistant between the shoulder and hip joint, and equal forelimb and hindlimb excursions. To test the model, a scaled representative force trace [data displayed as a proportion of body weight (%bw)] is presented for each limb collected during (A) above and (B) below branch quadrupedal locomotion.

During (A) above branch quadrupedal locomotion the limb (forelimb or hindlimb) first applies a braking force to the substrate as it touches down, that

decelerates the animal's COM, followed by a propulsive force prior to lift-off that accelerates the animal's COM. During the period when the limb is cranial to the COM it will most effectively produce a braking force. As the limb passes behind the body's COM, it is now in a position to accelerate the COM. As a result, during (A) above branch quadrupedal locomotion the forelimbs, which land far ahead of COM, have a relatively long period over which they can effectively generate a braking force compared to the hindlimb. In contrast, the hindlimbs spend on average more time caudal to the COM and thus have a longer period over which to effectively produce propulsive force. During (B) below branch quadrupedal locomotion instead of decelerating the COM at touchdown the limb pulls the body forward during the first part of stance and decelerates the body during the latter. Therefore, based on the relative position of the limb, the model predicts that the forelimb should serve as the primary propulsive limb, while the hindlimb is in a better position to serve as the braking limb. Representative force traces follow these predicted patterns.

This perspective also works to explain differing braking/propulsive roles of the forelimbs and hindlimbs observed during upright walking. While limb placement is very similar between above and below branch quadrupedal locomotion (i.e., the forelimb will be mostly in front of the COM throughout forelimb support phase and the hindlimb will be mostly behind the COM throughout hindlimb support phase), above branch quadrupedal locomotion can be better modeled as an inverted, rather than a conventional pendulum. In other words, as the animal places down the forelimb during above branch quadrupedal locomotion, it will start the upward deceleration phase of inverted pendular motion (indicating a braking force). The animal's COM will continue its upwards swing, and continue to produce a braking force until the animal's COM passes above the point of contact, after that the animal's COM will accelerate (indicating a propulsive force) due to the downward phase of inverted pendular motion until forelimb lift-off. Because of the forelimb's position in front of the COM throughout most of forelimb support phase, it will have a long braking phase and a short propulsive phase. This will result in the forelimb being net braking during above branch quadrupedal locomotion. The same model is true for the hindlimb, but because the hindlimb will be mostly behind the COM throughout support phase, it will have a short braking phase and a long propulsive phase. This will result in the hindlimb being net propulsive.

As described above, this system relies on a dynamic and pendular model, which may be the case in many animals. But, as in sloths (Nyakatura and Andrada, 2012) and potentially primates, the assumption of pendular movement may not be justified, and pendular movements alone may not be the only way to explain braking/propulsive

patterns observed here. It is also possible to think of this system as a hinged arch with the hands and feet as two points of contact each with a limb and the body as a span in the middle attaching with hinges to the limbs. As the system moves forward above or below the branch, the points of contact will switch from 'braking' to 'propulsion' depending on their position relative to the body COM, regardless of whether the system is a conventional or inverted pendulum, or even not moving as a pendulum at all. Thus, it is likely that pendular motion and/or the position of the contact points relative to the COM contribute to the pattern of net propulsive and braking on the limbs during above and below branch quadrupedal locomotion.

If this interpretation is correct, then during quadrupedal locomotion the B/P transition should deviate substantially from mid-stance, and instead be present at the point at which the limb passes under the COM. Specifically, the B/P transition for the forelimb should occur after mid-stance, and the B/P transition for the hindlimb before mid-stance. The data collected in this study support the validity of this model. Understanding the mechanical underpinnings as to why a limb serves a propulsive or braking role has important ramifications for our understanding of limb loading patterns during normal movement. Additionally, it serves as an important factor to consider when exploring the mechanical interplay between limb kinematics and COM movements, and how animals adjust themselves to maintain similar levels of braking and propulsive forces throughout a stride. Studies that explore limb loading patterns during periods of eccentric COM movements (Hanna et al., 2006), or during times when COM position shift (Golomer et al., 1990; Lemelin and Schmitt, 2004; Forczek and Staszkiewicz, 2012)

would be of incredible interest to test this model and adjustments animals make in order to maintain normal locomotion.

Mediolateral forces during both above and below branch quadrupedal locomotion tended to be primarily medially oriented, a pattern that has been observed in other studies (Ishida et al., 1990; Schmitt, 2003a; Carlson et al., 2005; Franz et al., 2005). For all primate species, these medially directed forces tended to be relatively higher when walking below branches than when walking above. Although not a direct measure, these relatively greater mediolateral forces suggest that side-to-side movements are likely higher during below branch movement than when animals are walking on top of branches. This assumption is supported by movements observed in some species of arm-swinging primates (Schmitt et al., 2005, 2009; Granatosky, 2015), and sloths (Nyakatura and Fischer, 2010b). It is likely that by moving below branches, animals are released from the mechanical constraints of limiting side-to-side movement that is observed during above branch quadrupedal locomotion. These side-to-side movements may simply be by-products of other aspects of gait, or could indicate a means of achieving lateral pendular motion as a means of energy recovery as reported in the waddling behavior of penguins (Griffin and Kram, 2000).

The altered role of the forelimb as the primary weight-bearing limb during below branch quadrupedal locomotion in primates significantly deviates from the normal limb loading pattern observed in primates during above branch quadrupedal locomotion (Kimura et al., 1979; Reynolds, 1985a; Schmitt and Lemelin, 2002; Franz et al., 2005; Granatosky et al., 2016). The standard limb loading pattern observed in primates is

thought to be an important mechanism to free the forelimbs from their normal weight-bearing role during locomotion, permitting the forelimbs to become highly manipulative and mobile grasping organs (Wood Jones, 1916; Reynolds, 1985a; Schmitt and Lemelin, 2002). As mentioned in section 1.5.2, The mechanism by which this is accomplished is still a matter of inquiry, and whether this altered limb loading pattern is an active process (Reynolds, 1985a; b, 1987; Schmitt, 1999), in which primates to shift weight away from the forelimbs, or a passive process, which is simply an unintentional by-product of other aspects of normal primate locomotor patterns (Raichlen et al., 2009) remains under discussion.

As a group, primates are characterized by a relatively greater degree of limb excursion during above branch quadrupedal locomotion (Larson et al., 2000) that tends to place relatively protracted hindlimbs underneath the COM for longer periods than relatively retracted forelimbs (Raichlen et al., 2009). It has been argued that this pattern is thought to result in relatively greater hindlimb Vpk forces simply because the hindlimb's position relative to the body's COM, though its importance was disputed by Larson and Demes (2011). It is unclear as to whether this mechanism, if active during above branch quadrupedal locomotion, is also at play during below branch quadrupedal locomotion because the incorporation of the kinematic data necessary to address this hypothesis is beyond the scope of this study. Patterns of braking and propulsive impulses do however allow us to address this issue. If one accepts the interpretation above regarding why the forelimbs assume the primary propulsive role during below branch quadrupedal locomotion, then any level of braking force exerted by the forelimb represents a time in

which the forelimb is positioned behind/beneath the COM. As evidenced by the data, during below branch quadrupedal walking, the forelimb exerts substantially greater breaking impulse that is comparable to what is observed in the hindlimb. In contrast, the hindlimb shows only limited propulsive impulse during below branch quadrupedal locomotion, a pattern suggesting only minimal time in which the hindlimb is positioned ahead of/beneath the COM. This pattern suggests that during below branch quadrupedal locomotion, primates are placing forelimbs underneath the COM for longer periods when compared to the hindlimbs, and this mechanism alone may account for the relatively greater Vpk forces observed in the forelimbs during below branch quadrupedal locomotion compared to the hindlimb.

In respect to the hypothesis that primates actively shift weight to the hindlimbs, two biomechanical models have been proposed to explain how primates maintain relatively higher Vpk forces on their hindlimbs. The first model, proposed by Reynolds (1985a,b, 1987) and supported by Larson and Stern (2009), suggests that primates actively shift weight caudally on their relatively protracted hindlimbs using powerful muscular retractors of the hindlimb. The second model, proposed by Schmitt (1998, 1999) and tested by Larney and Larson (2004), argues that primates change vertical stiffness of their limbs by increasing limb yield, contact time, and angular excursion. These models are not mutually exclusive and both provide important mechanisms by which locomotor forces on the limbs can be moderated (Schmitt and Hanna, 2004; Young, 2012).

It is unclear though, whether either of these active models would apply in the context of below branch quadrupedal locomotion. Schmitt's (1999) model of limb yield does not apply because rather than a passive system that acts to reduce joint reaction forces, additional muscular energy would need to be added into the system, which would only serve to increase joint reaction forces. Reynolds' (1985a) argument for the advantages of actively shifting weight caudally during above branch quadrupedalism would also not apply to below branch quadrupedal locomotion since activation of hindlimb retractors while the hindlimb was in a protracted position as a mechanism to reduce Vpk forces on the forelimbs would have the added effect of applying a braking force during the downward swing of the COM therefore pull the forequarters away from the support, thereby introducing unnecessary backwards pitch into the system. It is possible that the absence of this mechanism (i.e., primates not activating hindlimb retractors during protracted hip positions) during below branch quadrupedal locomotion is what allows the forelimbs to experience relatively higher Vpk forces. The argument for why primates reduce forelimb loading has largely centered on the idea that it is important for these animals to reduce high compressive loads on mobile and weak glenohumeral joints. During below branch quadrupedal locomotion, compressive loads are likely quite low (i.e., only from activation of flexor musculature), so perhaps primates have little need to actively shift weight off the forelimbs. It could also be argued that during below branch quadrupedal locomotion, there is a need to reduce tensile-loading stresses (Swartz et al., 1989) off the hindlimb bones and joints that rarely experience such loads during upright locomotion. It may be possible that during below branch quadrupedal locomotion

primates are activating forelimb or hindlimb protractors to pull the trunk toward the support. By applying the model described by Reynolds (1985a) into an inverted system, this would have the effect of increasing forelimb Vpk forces while both reducing hindlimb Vpk forces. Data from this study largely support this model, but only by following procedures advocated by Larson and Stern (2009) can this issue be addressed more fully.

Another possible mechanism to explain the disparity in the forelimb and hindlimb forces in primates may be found in kinematic movements during below branch quadrupedalism. As suggested by Granatosky et al. (2016), active forelimb flexion appears in many taxa during below branch quadrupedal locomotion (Turnquist, 1975; Ishida et al., 1990; Nyakatura et al., 2010; Fujiwara et al., 2011), and arm-swinging (Bertram, 2004; Michilsens et al., 2010). This forelimb flexion indicates that as the animals activate flexor musculature to "pull-up" the COM toward the support, the animals experience higher Vpk forces on the substrate. Data from this study, however, largely refute this explanation because levels of forelimb flexion are largely similar across both primates and non-primates. While primates show higher Vpk forces in the forelimbs, the same is not true for non-primate mammals sampled in this study.

Thus far, most of this discussion has focused on the kinetic differences between above and below branch quadrupedal locomotion in primates. Comparisons between the kinetic patterns of below branch quadrupedal locomotion between primates and non-primate mammals are largely similar to one another, but with one important exception. As mentioned above, all primates sampled display greater Vpk forces on the forelimbs

compared to the hindlimbs during below branch quadrupedal locomotion. This was not the case for the non-primate mammals. For *P. vampyrus*, Vpk forces were relatively greater in the hindlimb, and in *C. didactylus* and *D. rotundus* Vpk forces were not significantly different between the limbs. This finding indicates that while primates appear to reduce the weigh-bearing function of the hindlimb during below branch quadrupedal locomotion, non-primate mammals still rely quite heavily on support from the hindlimb. This distinction has likely important implications for the evolution of arm-swinging and will be discussed in greater detail below.

As with limb loading patterns, the movements of many the joints varied in primates between above and below branch quadrupedal locomotion, and between primates and non-primate mammals during below branch quadrupedal locomotion. The hip, however, showed relatively few intra- and/or interspecific differences beyond a relatively greater range of overall joint excursion during below branch quadrupedal locomotion. This difference makes sense in context of the anatomy observed in suspensory species (i.e., anatomical features that promote hip mobility), and it is possible that the necessity for this increased hip movement during below branch quadrupedal locomotion may have increased selection for more a more mobile hip joint in highly suspensory taxa.

In contrast to the relative similarities in the hip between orientations and species, differences in shoulder movements were substantial when comparing above and below branch quadrupedal locomotion. Consistent with what has been reported by other studies (Larson et al., 2000; Schmitt and Lemelin, 2002), all primates in this study positioned

their forelimb down onto the support with considerable degree of humeral protraction, and then showed a large amount of shoulder excursion by the end of support phase. During below branch quadrupedal locomotion (in primates and non-primate mammals), the level of humeral protraction was substantially reduced, but overall levels of shoulder excursion remained similar, or even exceeded what was observed when walking above branches.

The role of humeral protraction at touchdown during above branch quadrupedal locomotion has been debated by a number of studies, and multiple ideas have been outlined as to why primates show such high levels compared to non-arboreal mammals. As outlined by many studies, protracted humeral positions allow for an overall greater stride length (Reynolds, 1987; Schmitt, 1998, 1999; Larson et al., 2001). This in turn reduces the number of strides necessary to get from one point to another, thereby reducing the frequency a limb contacts the support. This reduced stride frequency is thought to be an important mechanism for limiting substrate oscillations on relatively thin arboreal supports. Alternatively, Larson et al. (2000) proposed that forelimb protraction can be thought of as part of the suite of mechanical features that help primates accomplish a compliant gait (Schmitt, 1994, 1998, 1999). According to Larson et al. (2000), humeral protraction lowers the body's COM at the beginning of support phase, and has the added effect of increasing step length and contact time. This lower body position, in combination with elbow yield associated with a compliant gait, works together to produce a crouching posture that is critical for maintaining balance and stability on a branch, as well as reducing the tendency to cause branch sway.

Additionally, by adopting compliant gaits, primates are able to modulate better the vertical position of the COM, thereby reducing the possibility of collisional losses (Ruina et al., 2005). Finally, there is the possibility that some kinetic effects can occur by altering the level of limb protraction at touchdown. McMahon et al. (1987) and Chi and Schmitt (2005) demonstrated that by increasing the level of limb protraction at touchdown, vertical landing speed and vertical stiffness of the body can be reduced. This in turn can reduce impact Vpk forces during touchdown.

It is difficult to determine which, if any, of these scenarios apply during below branch quadrupedal locomotion. From the data collected in this study, it is evident that stride length and overall contact time are not solely dependent on the amount of humeral protraction, but can also be modulated by increasing humeral retraction. Additionally, altering COM position to reduce collisional losses can also be accomplished through other mechanisms (i.e., increased elbow and knee flexion), and therefore increased humeral protraction is not required. It may also be possible that the mechanisms used by primates when walking above branches to reduce substrate oscillations just do not matter for animals walking below the support. The “mechanical release” of no longer having to worry about toppling off branches may negate the previously advantageous aspects of primate gait, and therefore allow primates re-establish more “primitive gait characteristics” (i.e., decreased forelimb protraction).

In a biomechanically optimal scenario, all animals should display stiff extended limbs during the support phase (Swartz, 1989) while adjusting accordingly for collisional losses (Ruina et al., 2005; O’Neill and Schmitt, 2012). This allows for the COM to be

vaulted over, or under, the stiff limb and optimize pendular movement (Swartz, 1989; Schmitt, 2003c; Lee et al., 2013). This type of movement results in generally high levels of energy recovery and longer stride length. Both of which are thought to increase the efficiency of locomotion (Ruina et al., 2005; O'Neill and Schmitt, 2012). For the most part, striding bipedalism in humans and arm-swinging in primates does approximate these movements, but for many animals such optimization is not possible (Schmitt, 1999; Usherwood, 2003; Schmitt and Hanna, 2004; Ruina et al., 2005; Bishop et al., 2008). During above branch quadrupedal locomotion, both elbow and knee angles demonstrated marked levels of yield throughout the stride. The adaptive scenarios of this yield are numerous, and include such mechanical consequences as lower joint reaction forces, increased contact time, and smoother COM movements (Schmitt, 1998, 1999; Larney and Larson, 2004). During below branch quadrupedal locomotion, elbow flexion was significantly higher than what was observed during above branch quadrupedal locomotion, and was substantial in both primates and non-primates mammals. As mentioned above, forelimb flexion during suspensory locomotion requires animals to activate flexor musculature to pull-up the COM closer to the support. The fact that this flexion is an active process, and appears to be ubiquitous among all species during below branch quadrupedal locomotion, suggests that there may be some incredibly important functional reasons for this behavior (Fujiwara et al., 2011).

Determining the causal mechanism underlying this behavior is challenging because there are number of potential benefits that may be driving this pattern of forelimb flexion. As during above branch quadrupedal locomotion, forelimb flexion can be used as

a mechanism to “smooth out” COM movements throughout a stride, thereby limiting collisional losses that may occur from more eccentric COM oscillations (Usherwood, 2003; Bertram, 2004; Ruina et al., 2005). Stiff limbed movement, often associated with extended limb bipedalism, quadrupedalism, and arm-swinging, has the benefit of being highly efficient (at least measured by energy recovery), but at the potential of being energetically costly due to collisional losses (Bertram et al., 1999; Ruina et al., 2005; Lee et al., 2011, 2013; see section 1.5.1 for a lengthier discussion of COM movements during locomotion). While many animals are able to adopt kinematic mechanisms to reduce collisional losses, COM oscillations remain high due to the COM vaulting over stiff extended limbs (Lee et al., 2011, 2013). This can in turn result in substrate oscillations when supports are compliant (Schmitt, 1995, 1999; Larson et al., 2000; O’Neill and Schmitt, 2012). Arboreal animals walking on thin branches need to limit these COM oscillations, and to do so, show a certain level of limb compliance throughout the stride that reduce vertical displacement of the COM (Schmitt, 1999; Larson et al., 2001; Larney and Larson, 2004; O’Neill and Schmitt, 2012). During below branch quadrupedal locomotion, animals actively flex their limbs throughout the stride, and as a result, pull the COM closer to the support. Although not tested specifically, the level of limb flexion appears to be so high during below branch quadrupedal locomotion that the vertical position of COM during mid-stance may be equal, or even above the COM position observed during touchdown or at the end of support phase (Figure 183). This finding likely indicates that for animals moving quadrupedally below branches, maintaining a smooth COM position throughout the stride is more important than the energy saving

effects (as measured by energetic recovery) of pendular motion. A similar conclusion was proposed by Ishida et al. (1990) and Nyakatura and Andrada (2012).

The reason as to why an animal walking below branches displays such a smooth pattern is still unknown and beyond the scope of this study, but according to Nyakatura and Andrada (2012) high substrate oscillations resulting from high COM oscillations can be very harmful for a deliberate moving quadrupedal animal moving below branches that is unable to quickly adjust if the substrate were to break. Interestingly, most primates demonstrate the speed and maneuverability within an arboreal context to make quick adjustments during times of substrate failure. It may be the case that primates moving quadrupedally below branches do not show the same level of COM "smoothing" as observed in non-primate mammals, and may perhaps take some benefits from pendular motion. It is possible that as primates spent a greater proportion of their locomotor repertoire walking quadrupedally below branches throughout their evolutionary history, their ability to deal with high COM oscillations would have increased and pendular mechanics during locomotion would have become more common. Eventually, this may have led to the adoption of extended limb arm-swinging to increase energetic recovery during suspensory locomotion. A study focused on quantifying COM movements between primates and non-primate mammals during below branch quadrupedal locomotion would provide the information needed to test this claim.

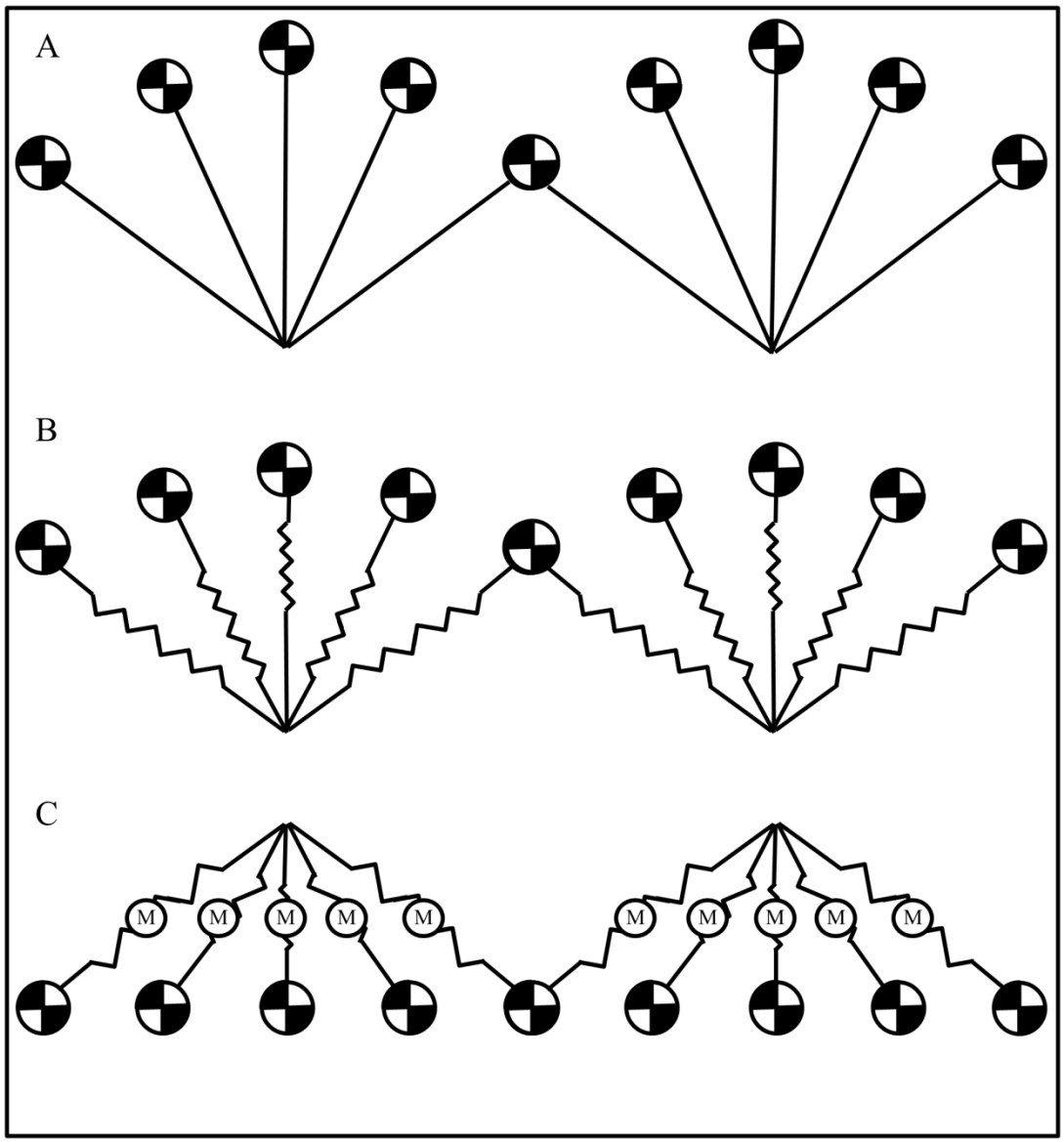

Figure 183: A model for understanding hypothetical center of mass (COM) movements during above and below branch quadrupedal locomotion. During stiff, extended limb quadrupedal gaits (A), the COM moves as an inverted pendulum and is vaulted over a stiff limb resulting in relatively large COM oscillations. In contrast, during compliant quadrupedal gaits (B) the COM still moves as an inverted pendulum, but the limbs demonstrate a level of compression throughout the stride that acts to lower COM oscillations. During below branch quadrupedal gaits (C), the COM moves like a conventional pendulum in which the COM is below the support. Muscular effort (M) is used to pull the COM closer to the support, and serves to "smooth out" COM movement throughout the stride.

An alternative mechanism proposed by Fujiwara et al. (2011) suggests that forelimb flexion during below branch quadrupedal locomotion may act to maximize the moments arms between the elbow joint and the flexor musculature of the forelimb (Figure 184). By maintaining levels of flexion during below branch quadrupedal locomotion, animals maximize the effectiveness of antigravity and locomotor functions of the forelimb flexors during below branch quadrupedal locomotion (Fujiwara et al., 2011). Data from their study show that all species use levels of forelimb flexion comparable to what would be expected based on the position and attachment sites of the forelimb flexors. Future studies should be undertaken to test more rigorously this assertion. Finally, bone and joints are generally weaker under tensile loading (Crowninshield and Pope, 1974; Carter and Hayes, 1976; Wright and Hayes, 1976; Fung, 1993, 2013). While some species have overcome tensile weakness by altering bone mineral density (Carlson and Patel, 2006; Patel and Carlson, 2008) and material properties (Skedros et al., 1994), it is relatively uncommon. In turn, any effort by animals to reduce these tensile loads through behavioral means would be beneficial in assuring maintenance of the material properties and overall structural integrity of the bones and joints. Active forelimb flexion during below branch quadrupedal locomotion may be an important mechanism for assuring that compressive loading will occur along the bones and joints (Beck, 2009; Judex and Carlson, 2009).

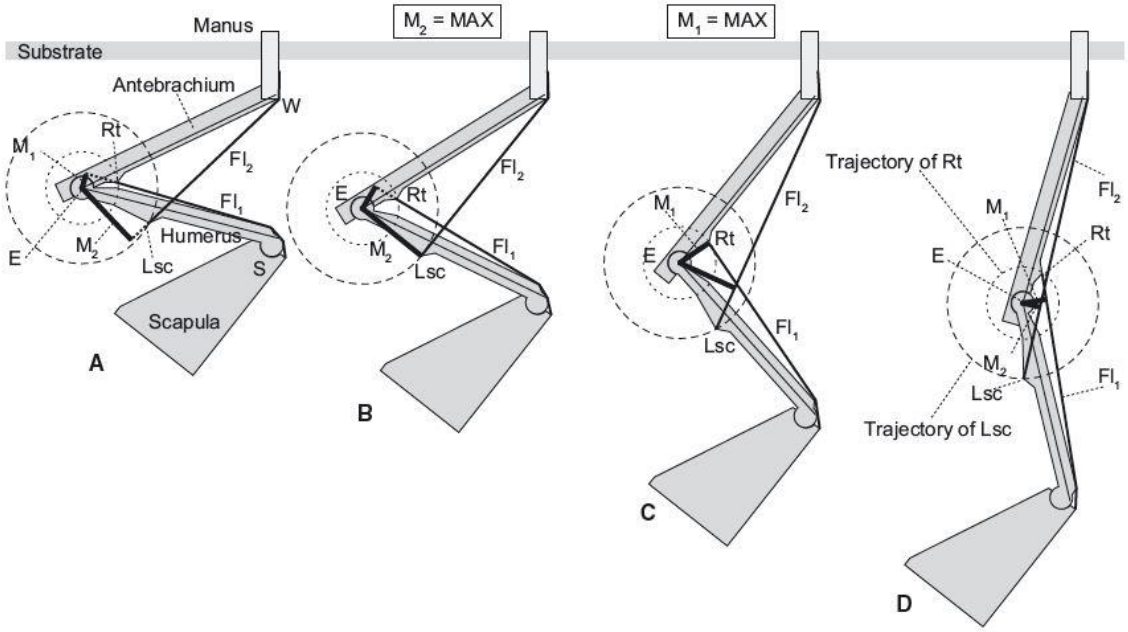

Figure 184: Model of forelimb mechanics during below branch quadrupedal locomotion in various elbow joint angles from (A) flexed to (D) extended. The elbow is subject to an extensor torque induced by body weight and resisted by counteracting muscle forces times moment arms (M_n). M_2 and M_1 are maximized at the specific elbow joint angle shown in (B) and (C), where the lines E-Lsc and E-Rt are perpendicular to $Fl_2$and Fl_1, respectively. E = center of elbow joint rotation; $Fl_1$and Fl_2 = flexor muscle groups along the brachium and antebrachium, respectively; $M_1$and M_2 = moment arms of Fl_1 and Fl_2, respectively; Lsc = lateral supracondylar crest; Rt = radial tuberosity; S and W = shoulder and wrist joints, respectively. Figure from Fujiwara et al. (2011).

Theoretically, the same principles observed in the elbow should also apply to the knee, but surprisingly, while this appears to be true for primates, this is not the case for non-primate mammals. The reason for this observation may be because of highly specialized anatomy observed in the hindlimbs of *P. vampyrus* (Schutt, 1993; Simmons and Quinn, 1994) and *C. didactylus* (Mendel, 1981) that utilize unique passive mechanisms to reduce the effort required by the flexor musculature to maintain its antigravity function. If one were to observe below branch quadrupedal locomotion in an anatomically-generalized non-primate mammal (e.g., the kinkajou), it is then possible that the same patterns of active flexion observed at the elbow may be be present at the knee.

Patterns of wrist and ankle movement were highly variable and difficult to interpret in a functional context. For all primates, wrist movements were primarily radially deviated, both during above and below branch quadrupedal locomotion, although wrist angles tended to be closer to neutral and species showed a greater deal of excursion throughout support phase during below branch quadrupedal locomotion. In contrast, wrist movements in *C. didactylus* and *P. vampyrus* were kept in an ulnarly deviated position and showed relatively little excursion throughout support phase. With respects to the ankle, substantial differences in the orientation (i.e., all primates were characterized with cranially oriented ankle angles, while all non-primate mammals tended to keep their ankles closer to a neutral position) were observed between primates and non-primate mammals, although overall excursion at this joint tended to be relatively lower for all species.

The interspecific differences in the overall movements of both of these joints is most likely a result of the specialized wrist and ankle anatomy observed in obligate suspensory species such as *C. didactylus* and *P. vampyrus* (see section 1.3.2 and 1.3.3). In these animals, the wrist and ankle have become modified for high mobility and to maintain a neutral position during locomotor behavior (Miller, 1935; Mendel, 1979). This anatomical reorganization likely allows these species to maintain a relatively more neutral wrist and ankle position throughout support phase. Interestingly, although these joints are highly mobile [as determined by cadaveric studies (Mendel, 1979, 1981)], they show relatively little movement during locomotion. This result has also been observed by Nyakatura et al. (2010) in sloths and led these authors to claim that most of the forward progression observed during below branch quadrupedal locomotion is accomplished primarily by the proximal limb elements rather than the wrist or ankle. These findings support the hypothesis of Cartmill and Milton (1977) and Mendel (1979) suggesting that wrist mobility may not be a direct result of suspensory locomotion, but instead an adaptation for careful limb placement on thin arboreal supports often experienced by cautious arboreal quadrupeds (i.e., the lorisids) and suspensory taxa. It may be the case that primates and other arboreal mammals occasionally adopting suspensory locomotion, but still maintain upright locomotion as their primary locomotor mode, are unable to compensate the movements of the proximal limb elements to make up for the loss of movement at the wrist and ankle joint. It is possible that as species reduce their reliance on upright locomotion, wrist and ankle movements are decreased (at least with regard to radial and ulnar deviation in the wrist and cranial and caudal deviation in the ankle), and

the more proximal limb elements to make up for this loss of movement. This idea is somewhat supported in arm-swinging species such as *Ateles* (Turnquist, 1975) and *Hylobates* (this study; Jenkins, 1981).

As discussed in section 1.5.2, interlimb coordination and general timing of support and swing phase can have important effects on balance, security, velocity, and stride distance. In general, velocity is lower (as reflected by lower normalized speed) during below branch quadrupedal locomotion and variables like security appear to be very important for animals moving quadrupedally below branches. Data indicate that across all species of primates, relative swing phase and duty factor for both limbs appear to be timed to minimize the portion of a stride in which a limb is off the support. These observations concur with Demes et al. (1990) and Nyakatura et al. (2010) noting that the lorisids and sloths alter intrinsic gait characteristics in order to maximize support phase. This may be related to careful and deliberate locomotor behavior and the avoidance of aerial phases in lorises (Demes et al., 1990; Jouffroy and Petter, 1990) and sloths (Nyakatura et al., 2010).

Changes in interlimb coordination were drastic between above and below branch quadrupedal locomotion. As predicted, primates displayed an almost exclusive use of DSDC gaits during above branch quadrupedal locomotion, but during below branch quadrupedal locomotion gait patterns were much more variable, and there was an increase in laterality (i.e., use of LS gaits) across all species. This increase in LS gait frequency (with DS gaits still present) coupled with high variability in gait choice was also observed in all the non-primate mammals. Nyakatura et al. (2010) posited that this

high variability was a result of speed (i.e., diagonality increased with speed), but testing this hypothesis was beyond the scope of this study. Mechanically, the adoption of LSDC gaits makes sense in an inverted context. This footfall sequence is inherently more stable than LSLC or DSDC gaits due to the lower likelihood of limb interference and the generally low proportion of the stride spent as a unilateral bipod (~22%), and the relatively high proportion of the stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support) (see section 1.5.4; Hildebrand, 1967; Cartmill et al., 2002). In general, foot positions arranged as diagonal bipods and large tripods are thought to be highly stable because a quadruped with a nearly centered COM is more nearly balanced over a line passing through diagonally opposite feet than over one passing through two ipsilateral feet (Hildebrand, 1967; Cartmill et al., 2002, 2007; Shapiro and Raichlen, 2005).

The use of DSDC gaits during above branch quadrupedal locomotion has been considered advantageous for balancing and walking on thin arboreal supports. This gait pattern maximizes the proportion of the stride in which the limbs are arranged as a widely splayed diagonal bipod (though not as high as LSDC gaits) and ensures that one of the grasping hindfeet, which bears a majority of the animals weight, is placed in a protracted position (and thus lies roughly underneath the animal's COM) on a tested support at the moment when the contralateral forefoot strikes down on an untested support during arboreal locomotion (Cartmill et al., 2002, 2007; Lemelin and Cartmill, 2010). It seems unlikely though, based on the findings of this study, that DSDC gaits would be

particularly advantageous during below branch quadrupedal locomotion, especially because the hindlimb does not bear a majority of the animal's body weight (at least in primates). The high variability in gait selection may indicate that during branch quadrupedal locomotion primates and other non-primate mammals are able to move more freely between gait types because the mechanical constraints of resisting toppling over support are mitigated, and the only possible risk may arise from interlimb interference (Hildebrand, 1967; Cartmill et al., 2002). Data from this study support this interpretation as the occurrence of LSLC gaits is relatively less common than both LSDC and DSDC gaits during below branch quadrupedal locomotion.

4.1.2 An evolutionary perspective of below branch quadrupedal locomotion in primates and non-primate mammals

This study takes an experimental approach to explore the evolution of below branch quadrupedal locomotion in primates and other mammals, and specifically tests the assertion by Demes et al. (1990) and Nyakatura (2011) that below branch quadrupedal locomotion is a neuromuscular mirror of above branch quadrupedal locomotion. From the data collected in this study, it is possible to reject the idea that above and below branch quadrupedal locomotion (at least in primates) are mechanical mirrors of each other. The basic characteristics of below branch quadrupedal locomotion can be summarized as: (1) the forelimb becomes the primary propulsive element, while the hindlimb serves a braking role; (2) in primates the forelimb serves as the primary weight-bearing limb, while the hindlimb reduces its weight-bearing function; (3) in non-primate mammals the forelimbs and hindlimbs serve a similar weight-bearing function; (4) mediolateral forces

are medially oriented and higher than what is observed during above branch quadrupedal locomotion; (5) humeral protraction is relatively low; (6) elbow flexion is higher than what is observed during above branch quadrupedal locomotion; (7) contact with the support throughout support phase is maximized; and (8) interlimb coordination is highly variable and demonstrates decreased diagonality.

It is interesting to note, that while the characteristics described above are vastly different when compared to the quadrupedal locomotor characteristics of primates, they are not that distinct from what is observed during quadrupedal locomotion in non-primate mammals. The unusual gait characteristics observed in primates during above branch quadrupedal locomotion are thought to be important mechanism for moving and maintaining balance on thin arboreal supports, but when an animal moves below branches the benefits of these gait characteristics appear to be nullified. Instead of viewing the characteristics of below branch quadrupedal locomotion as some set of features that aim to achieve a mechanical optimum, it may be more appropriate to view these features as a “release” from the biomechanical demands of moving above thin arboreal supports. While certain characteristics during below branch quadrupedal locomotion such as increased forelimb Vpk forces in primates, the reversed propulsive and braking role of the limbs, and the increased level elbow flexion deserve special attention, and will be discussed below, most of the characteristics appear to very similar to what is observed during normal walking in non-primate mammals. Perhaps the assertion of Demes et al. (1990) and Nyakatura (2011) that below branch quadrupedal locomotion is a neuromuscular mirror of above branch quadrupedal locomotion should be

modified to say that below branch quadrupedal locomotion has many features in common with what is observed during normal quadrupedal locomotion in non-primate mammals.

4.2 A mechanical and evolutionary interpretation of arm-swinging in primates

4.2.1 A mechanical synthesis of arm-swinging in primates

Thus far, the entire discussion has focused on the transition from above to below branch quadrupedal locomotion in primates and other mammals. In this next section, the role of below branch quadrupedal locomotion will be discussed in terms of its relevance to evolution of arm-swinging. Before I begin, however, it is important to discuss how the mechanical characteristics of arm-swinging compare across distantly-related species that use this highly specialized form of suspensory locomotion.

Kinetic patterns during arm-swinging largely reflect what is expected for an animal moving similarly to a simple pendulum. The force traces collected from *H. moloch* and *P. nemaeus* in this study are characterized by single vertical peak occurring approximately at mid-support, a propulsive force occurring within the first half of the support phase, and a braking force occurring during the latter half of support. In *P. nemaeus,* mediolateral forces were higher than expected for a simple pendulum, which should be relatively low. This finding supports earlier findings by Byron and Covert (2004) and Granatosky (2015) that demonstrate that *P. nemaeus* uses some side-to-side movement during arm-swinging. A similar pattern has also been reported during arm-swinging in *Lagothrix* (Schmitt et al., 2005).

The average Vpk forces observed in *H. moloch* (1.67% of body weight) and *P. nemaeus* (1.3% of body weight) in this study are slightly lower than what has been observed in other kinetic studies of arm-swinging in other studies (Chang et al., 2000; Michilsens et al., 2012). The reason for this may simply be a result of higher speed strides collected by Chang et al. (2000) and Michilsens et al. (2011), which could have significant effects on the magnitude of substrate reaction forces (Demes et al., 1994). It is also possible that active forelimb flexion or leg-pumping commonly observed during arm-swinging in gibbons (Fleagle, 1974; Michilsens et al., 2011), but not observed in this study, could have resulted in the higher Vpk forces reported by Chang et al. (2000) and Michilsens et al. (2011).

The general patterns of shoulder movements collected during arm-swinging in this study closely match what has been observed in other studies on the movements of arm-swinging primates (Turnquist et al., 1999; Michilsens et al., 2011; Tripp et al., 2015). At touchdown, the shoulder is protracted beyond the neutral position and is subsequently retracted throughout the remainder of the stride. In all three species, the levels of protraction and retraction are approximately equidistant from the neutral position and demonstrate substantial angular excursion throughout support phase. The consistency of this kinematic pattern across arm-swinging primates likely represents a mechanical necessity that is required to swing the body effectively below branches. This idea of mechanical necessity is further supported by the anatomical convergence observed in scapular morphology between these distantly related arm-swinging primates (Erikson, 1963; Su and Jablonski, 2009; Bailey and Pampush, 2015a; b).

The patterns of elbow movements also closely match what has been reported for other arm-swinging primates (i.e., the elbow remains extended throughout the stride, and some flexion occurs at the beginning and end of support phase) (Turnquist, 1975; Turnquist et al., 1999; Michilsens et al., 2011; Tripp et al., 2015). This finding is not surprising because longer pendulum lengths (i.e., extended elbows) are thought to result in more efficient arm-swinging overall [but see Usherwood (2003)]. The ability to extend the elbow joint is largely determined by the length of the olecranon process of the ulna. A shorter olecranon process allows for a greater range of extension at the elbow joint, but at the cost of muscular mechanical advantage (a trait necessary for terrestrial and arboreal quadrupeds). This morphology is well known in the atelids and hylobatids; even *P. nemaeus* has a relatively short olecranon process compared to other closely-related colobines, with a morphology more similar to that of other suspensory species (Su and Jablonski, 2009). The short olecranon process, and the functional consequence of greater elbow extension, may represent a feature selected for in all arm-swinging primates.

Overall, patterns of wrist movements during arm-swinging were highly variable for all species. As mentioned above, radial and ulnar wrist movements in *Hylobates* are minimal, and it may be the case that highly anatomically-specialized suspensory taxa achieve forward progression primarily through movement at the proximal limb elements (Nyakatura et al., 2010). The data collected from this study provide some support for this idea; even though ranges of shoulder and elbow movement appear to be largely similar across species during arm-swinging, *H. moloch* shows the lowest stride distance. This means that without the contribution of radial and ulnar wrist movements, overall forward

movement in *H. moloch* is limited compared to other species. It is unclear, and beyond the scope of this study, what effect, if any, rotary wrist movements (Jenkins, 1981) have on overall forward progression. In *P. nemaeus* wrist movements were consistent across strides and individuals, although angular values were variable. As first reported by Byron and Covert (2004), and confirmed in this study, *P. nemaeus* grabs the support with pronated handholds. This means that as *P. nemaeus* grabs onto the support the wrist is first ulnarly deviated, and subsequently radially deviated throughout the remainder of the stride. In contrast, *A. fusciceps* grasps the support with supinated handholds. This means that as *A. fusciceps* grabs onto the support, the wrist is first radially deviated, and subsequently becomes ulnarly deviated throughout the remainder of the support phase.

Based on the experimental data collected in this study, there appears to be no consistent pattern of wrist movement observed during arm-swinging. This high level of mechanical flexibility likely indicates that selection is not driving wrist movements to reach some sort biomechanical optimum, but instead there are many solutions as to how to move the wrist during arm-swinging. This finding is in line with Lewis' (1971) and Larson's (1998) findings that demonstrated a greater range in wrist morphology in arm-swinging primates. According to Lewis (1971), the finding that hominoids display shared wrist morphology separate from other arm-swinging primates (i.e., *Lagothrix* and *Ateles*) demonstrates that these non-hominoid arm-swinging species have failed to reach the optimal functional wrist morphology necessary for arm-swinging. Data from this study, and others (Turnquist, 1975; Turnquist et al., 1999; Granatosky, 2015), demonstrate that this is not the case as arm-swinging appears to equally proficient among distantly-related

taxa. Rather than Lewis' (1971) assertion of the hominoid wrist as some sort "arm-swinging optimal", it is likely that Larson's (1998) interpretation of this wrist morphology as a synapomorphy that evolved early in hominoid evolution to promote hand mobility may be more appropriate (Napier and Davis, 1959; Rose, 1983; Beard et al., 1986). Additionally, it is interesting to note that while Larson (1998) observed high levels of convergence across the postcranial skeleton of primates that use arm-swinging locomotion, the wrist showed relatively few examples of convergence. This finding, in combination with the kinematic movements of the wrist observed in this study, could indicate that selection is not driving wrist movements and morphology to reach some sort biomechanical convergence like other joints of the forelimb. It may be more important for arm-swinging taxa to maintain a level of joint mobility and neuromuscular flexibility in order to deal with the challenges associated with suspensory locomotion. A phylogenetic and comparative assessment exploring the strength of selection across the postcranial skeleton would provide a quantitative means of testing this claim.

While variation in wrist movements were high, all other variables collected during arm-swinging in this study appear to be fairly consistent across taxa. This finding might indicate that there are limited functional solutions to the challenges associated with arm-swinging, and selection may drive species to reach a level of mechanical convergence similar to a simple pendulum (Swartz, 1989; Turnquist et al., 1999; Michilsens et al., 2012; Granatosky, 2015). This interpretation is also supported through analyses of postcranial morphology (Larson, 1998), and has profound implications for the evolution suspensory locomotion.

While it well accepted that arm-swinging has evolved independently between the hominoids, Asian colobines, and atelids, there is still considerable debate concerning evolution of suspensory locomotion among the hominoids. Originally, the presence of suspensory locomotion and/or the anatomical features associated with it in all extant apes led to assumption that suspensory locomotion must have originated in the last common ancestor of hominoids (Larson, 1998; Almécija et al., 2007; Alba et al., 2012, 2015). This assumption was rattled however by the discovery of the postcranial skeleton of *Sivapithecus*, a Miocene hominoid with close taxonomic ties to *Pongo*, that displayed locomotor adaptations not consistent with suspensory locomotion (Andrews, 1983; Rose, 1986; Madar et al., 2002; Begun and Kivell, 2011). This led to a revision in our thinking about the evolution of suspensory locomotion, and whether this behavior in fact evolved in parallel within the hominoids (Larson, 1998; Begun and Kivell, 2011). A consensus on this debate has not been reached, and the discovery of new crown hominoids (*Hispanopithecus* and *Pliobates*) with anatomical features associated with suspensory locomotion (Almécija et al., 2007; Alba et al., 2012, 2015) further complicates the issue. Trying to determine which one of these scenarios is more plausible is beyond the scope of this study, but based on the finding of this study that three species of distantly related arm-swinging primates all converge on a similar mechanical pattern it seems at least possible that arm-swinging can evolve any number of times and result in similar mechanical behaviors and anatomical features. Future analyses aiming to address the evolution of suspensory locomotion in hominoids should consider this high level of

mechanical convergence as a potentially confounding variable in locomotor trait evolution.

4.2.2 An evolutionary perspective of arm-swinging in primates

In section 1.4, this study advocated for a view that considers the evolution of below branch quadrupedal locomotion and the evolution of arm-swinging as two distinct entities. As discussed above, the acquisition of below branch quadrupedal locomotion was probably due to relatively large-bodied animals having trouble maintaining balance on thin arboreal supports. To solve this problem, heavier animals shifted their COM below the support, thereby adopting suspensory positional behaviors. Once below the support, these animals likely adjusted quickly, as the locomotor mechanics of below branch quadrupedal locomotion share many features in common with those observed during normal quadrupedal locomotion in non-primate mammals. The question remains however: how did arm-swinging arise in the first place, and why is it only observed in primates?

Based on the data collected in this study, it is possible to argue that the origins of arm-swinging arose from the modified pattern of below branch quadrupedal locomotion observed in primates compared to non-primate mammals. Most notable is the observation that during below branch quadrupedal locomotion, primates support a majority of body mass on the forelimbs and reduce the weight-bearing role of the hindlimb. This finding is not observed in non-primate mammals. As discussed above, the reason for this pattern is likely a consequence of the other mechanical specializations that have occurred due to the long evolutionary association between primates and thin arboreal supports. During above

branch quadrupedal locomotion, primates shift weight away from more mobile and weaker forelimb joints to those of the hindlimb (Reynolds, 1985a; b; Demes et al., 1994; Schmitt and Lemelin, 2002). This results in relatively larger compressive loading in the hindlimbs, which occurs because of the increased muscular activity and the added proportion of body weight that is shifted away from the forelimbs (Demes et al., 2001; Carlson and Patel, 2006; Patel and Carlson, 2008; Beck, 2009; Judex and Carlson, 2009). As a result, the primate hindlimb has adapted to this increased compressive loading with a number of anatomical features (Schaffler and Burr, 1984; Ruff, 1988; Swartz, 1989; Berg et al., 1991; Rafferty and Ruff, 1994; Ryan and Walker, 2010).

When shifting below branches, gravity is acting to pull the COM away from the support, and thereby subjecting the limbs to relatively greater tensile forces than during above substrate locomotion (Swartz et al., 1989). While muscular flexion can act to prevent excessive tension (Beck, 2009; Judex and Carlson, 2009), it is evident that certain bones and joints are subjected to net tensile loading (Swartz et al., 1989) during suspensory locomotion. In this orientation, a bone or joint that has been modified to resist compressive loading is ill-fitted to deal with any sort of tensile loads (Boyette and London, 1948; Hamilton et al., 1973; Crowninshield and Pope, 1974; Carter and Hayes, 1976; Wright and Hayes, 1976; Newman, 1985; Michaels, 1989; Sacchetti et al., 1990; Schunk, 1990; Fung, 1993; Choung and Heinrich, 1995; Macias et al., 1998; O'Driscoll et al., 2000). Therefore, it would be advantageous for primates to shift (either actively or passively) weight away from the compressively adapted hindlimb towards the forelimb, a finding that is supported by the data in this study. It is possible that arm-swinging could

have evolved from an anatomically-generalized arboreal primate foraging and moving below branches more often. During these suspensory bouts, weight would have been shifted away from the hindlimbs towards the forelimbs. As the frequency of these bouts increased, the reliance of the forelimbs as the sole providers of weight support would have also increased. This form of functional decoupling may have released the hindlimbs from their weight-bearing role during suspensory locomotion, and eventually arm-swinging would have replaced below branch quadrupedal locomotion as the primary mode of suspensory locomotion observed in some primate species.

This idea is supported by data here and broader observations in living taxa. Among all the species sampled in this study, *P. coquereli* displays the greatest disparity between forelimb and hindlimb Vpk forces. This indicates that during below branch quadrupedal locomotion this species shows the greatest reliance on the forelimb for weight support. Interestingly, this species is the only taxa of strepsirrhine whose locomotor repertoire includes a substantial proportion of arm-swinging (Gebo, 1987; Pichon and Simmen, 2015) (Figure 185). While it is unlikely that a sifaka-like ancestor gave rise to arm-swinging in anthropoid primates, this example does provide intriguing evidence supporting the claim that the mechanical patterns of below branch quadrupedal locomotion observed in primates could provide a link to the origins of arm-swinging.

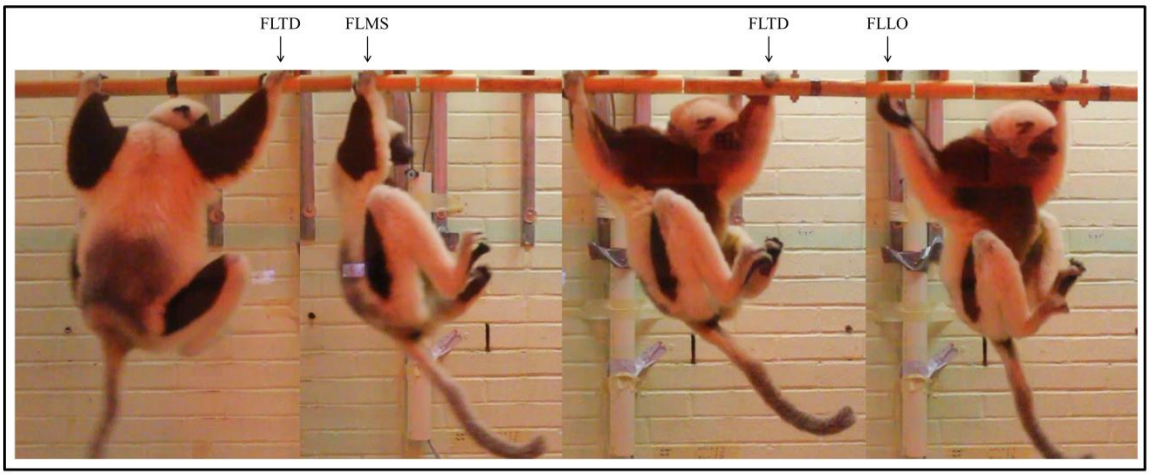

Figure 185: Arm-swinging in *Propithecus coquereli*. Note the high level of elbow flexion observed during forelimb support phase. FLTD = forelimb touchdown; FLMS = forelimb mid-stance; and FLLO = forelimb lift-off.

One concern in proposing a link between below branch quadrupedal locomotion and arm-swinging comes from comparisons in elbow flexion between the two forms of suspensory locomotion. During arm-swinging, all species sampled show almost complete elbow extension throughout support phase. In contrast, the elbow remains flexed during below branch quadrupedal locomotion. The role of elbow extension is thought to be incredibly important during suspensory locomotion, and the anatomical features associated with this extension (e.g., shortening of the olecranon process) have been used by many to identify suspensory taxa in the primate fossil record (Fleagle, 1977, 1983; Rose, 1983, 1997; Larson, 1998; Drapeau, 2004; Rein et al., 2015). It may be the case that the ability to fully extend the elbow throughout the support phase may represent a derived characteristic of arm-swinging that only evolved in taxa that have made the full transition to this locomotor mode. It is possible that for primates only using suspensory locomotion occasionally, the evolution of anatomical modifications and neuromuscular control necessary for extended elbow movements is unnecessary. On the other hand, shifting to elbow extension is likely relatively easy and an effective aspect of arm-swinging. If primates were to add elbow extension to the suite of characters already developed as part of below branch quadrupedal locomotion (i.e., greater weight support by the forelimb, a propulsive role for the forelimb, and broad shoulder motions), it seems plausible that arm-swinging could have evolved from primates walking quadrupedally below branches.

Support for this claim comes from two pieces of evidence. Firstly, when observing the kinematics of arm-swinging in species that habitually do not use this

behavior, significant levels of elbow flexion can be observed (Figure 185). This may be a mechanism to resist tensile loads on bones and joints and/or a means to optimize the effectiveness of the forelimb flexors for weight-support and forward movement (Fujiwara et al., 2011). Secondly, the role of forelimb flexors appears to be drastically different between below branch quadrupedal locomotion and arm-swinging (Jungers and Stern, 1981; Jouffroy and Stern, 1990). In below branch quadrupedal locomotion, the forelimb flexors are assumed to both serve an antigravity function and a propulsive means to pull the body during forward progression (Jouffroy and Stern, 1990). During arm-swinging however, forelimb flexors are thought to control and resist rapid elbow extension throughout support phase, whereas the shoulder musculature, is thought to provide the primary propulsive force necessary to keep the body in motion (in addition to pendular motion) (Stern et al., 1980b; Jungers and Stern, 1981). While electromyography studies have been conducted during below branch quadrupedal locomotion and arm-swinging, the data on specific muscle groups have been limited, especially during below branch quadrupedal locomotion (Stern et al., 1980a; b; Jungers and Stern, 1981; Jouffroy and Stern, 1990). A study focused on separating the propulsive and antigravity functions of the shoulder muscles and forelimb flexors during below branch quadrupedal locomotion and arm-swinging in anatomically generalized primates (e.g., *Lagothrix*, *Alouatta*, *Cebus*, and *Propithecus*) could provide additional experimental support for the claim that there is a hypothetical link between below branch quadrupedal locomotion and arm-swinging in primates, and insight into how this transition may have occurred from a neuromuscular perspective.

With regard to the debate as to whether suspensory locomotion, and more specifically arm-swinging, evolved only once or multiple times in hominoids, the data from this study provide evidence that multiple parallel origins of suspensory locomotion would have been possible within Hominoidea. As articulated by Larson (1998), hominoids as group are characterized by relatively large body size, and, as mentioned many times throughout this thesis, balance on thin flexible branches is difficult for large-bodied animals. In this situation, anatomically-generalized hominoid ancestors would have moved below branches and most likely foraged and locomoted by means of below branch quadrupedal locomotion. These animals would have likely shown a marked forelimb/hindlimb weight support disparity, and from there, forelimb-dominated locomotion would have become more common. Obviously, the data collected in this study cannot provide evidence in favor of either of these scenarios, but considering the mechanical tendency for forelimb-dominated locomotion during all forms of suspensory locomotion should be considered during future reconstructions of hominoid locomotor evolution.

Ever since Wood Jones (1916), arm-swinging and its relevance to the evolutionary history of primates has fascinated biologists. As a potential link to the evolution of bipedalism, arm-swinging has deserved also a special place in the study of the evolution of our species. Despite its importance and the interest associated with it, relatively few studies have addressed the mechanical origins of arm-swinging and why it is not observed in any other mammal species. This study provides the first experimental evidence supporting the hypothetical link between below branch quadrupedal locomotion

and arm-swinging in primates. These data should be taken into account during future investigations of suspensory locomotion, and the experimental methodology used to collect these data should be considered as a solid framework to investigate the evolution of locomotor transitions in cases where morphology or paleontology are lacking or uninformative. It is the goal of this study to provide future investigators with a number of questions and testable predications that can support or falsify the claims that have been proposed throughout this work. Hopefully, additional research focused on this fascinating transition will occur, and from these it will be possible to concretely support or reject the hypothetical link between below branch quadrupedal locomotion and arm-swinging in primates.

Literature Cited

Alba DM, Almécija S, Casanovas-Vilar I, Méndez JM, Moyà-Solà S. 2012. A partial skeleton of the fossil great ape *Hispanopithecus laietanus* from Can Feu and the mosaic evolution of crown-hominoid positional behaviors. PloS One 7:e39617–e39617.

Alba DM, Almécija S, DeMiguel D, Fortuny J, Ríos MP de los, Pina M, Robles JM, Moyà-Solà S. 2015. Miocene small-bodied ape from Eurasia sheds light on hominoid evolution. Science 350:aab2625.

Alexander RM. 1984. The gaits of bipedal and quadrupedal animals. Int J Robot Res 3:49–59.

Alexander RM. 1991. Elastic mechanisms in primate locomotion. Z Morphol Anthropol 78:315–320.

Alexander RM, Jayes AS. 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. J Zool 201:135–152.

Almécija S, Alba DM, Moyà-Solà S, Köhler M. 2007. Orang-like manual adaptations in the fossil hominoid *Hispanopithecus laietanus*: first steps towards great ape suspensory behaviours. Proc Biol Sci 274:2375–84.

Ancrenaz M, Lackmanancrenaz I, Mundy N. 1994. Field observations of aye-ayes (*Daubentonia madagascariensis*) in Madagascar. Folia Primatol 62:22–36.

Andrews P, Groves C. 1976. Gibbons and brachiation. In: Gibbon and Siamang, Vol 4: Basel: Karger, p 167–218.

Andrews PJ. 1983. The natural history of *Sivapithecus*. New York: Springer.

Ankel-Simons F. 2000. Primate anatomy: an introduction. New York: Academic Press.

Argot C. 2001. Functional-adaptive anatomy of the forelimb in the didelphidae, and the paleobiology of the paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 247:51–79.

Ashton EH, Oxnard CE. 1964. Functional adaptations in the primate shoulder girdle. Proc Zool Soc Lond 142:49–66.

Avis V. 1962. Brachiation: the crucial issue for man's ancestry. Southwest J Anthropol:119–148.

Bailey K, Pampush JD. 2015a. Preliminary analysis of the functional morphology of the douc langur scapulae. Am J Phys Anthropol S60:75 (abstract).

Bailey K, Pampush JD. 2015b. Intrageneric shape variation of the douc langur scapula (Genus *Pygathrix*). Vietnam J Primatol 2:25–32.

Beard KC. 1989. Postcranial anatomy, locomotor adaptations, and paleoecology of early Cenozoic Plesiadapidae, Paromomyidae, and Micromomyidae (Eutheria, Dermoptera). PhD. dissertation. Baltimore: The Johns Hopkins University.

Beard KC. 1990. Gliding behaviour and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). Nature 345:340–341.

Beard KC, Teaford MF, Walker A. 1986. New wrist bones of *Proconsul africanus* and *P. nyanzae* from Rusinga Island, Kenya. Folia Primatol 47:97–118.

Beck BR. 2009. Muscle forces or gravity–what predominates mechanical loading on bone? Introduction. Med Sci Sports Exerc 41:2033–6.

Begun DR, Kivell TL. 2011. Knuckle-walking in Sivapithecus? The combined effects of homology and homoplasy with possible implications for pongine dispersals. J Hum Evol 60:158–170.

Bergeson D. 1996. The positional behavior and prehensile tail use of *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus*. PhD. dissertation. Seattle: Washington University

Bergeson DJ. 1998. Patterns of Suspensory Feeding in *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus*. In: Strasser E, Fleagle J, Rosenberger A, McHenry H, editors. Primate Locomotion. New York: Plenum Press. p 45–60.

Berg HE, Dudley GA, Haggmark T, Ohlsen H, Tesch PA. 1991. Effects of lower limb unloading on skeletal muscle mass and function in humans. J Appl Physiol 70:1882–1885.

Bertram J, Chang YH. 2001. Mechanical energy oscillations of two brachiation gaits: measurement and simulation. Am J Phys Anthropol 113:201–216.

Bertram JE a. 2004. New perspectives on brachiation mechanics. Am J Phys Anthropol Suppl 39:100–17.

Bertram JE, Ruina A, Cannon CE, Chang YH, Coleman MJ. 1999. A point-mass model of gibbon locomotion. J Exp Biol 202:2609–2617.

Bezanson M. 2009. Life history and locomotion in *Cebus capucinus* and *Alouatta palliata*. Am J Phys Anthropol 140:508–517.

Billet G, Hautier L, Asher RJ, Schwarz C, Crumpton N, Martin T, Ruf I. 2012. High morphological variation of vestibular system accompanies slow and infrequent locomotion in three-toed sloths. Proc Biol Sci 279:3932–3939.

Bishop KL, Pai AK, Schmitt D. 2008. Whole body mechanics of stealthy walking in cats. PloS One 3:e3808–e3808.

Blanchard ML, Crompton RH. 2011. Field study methods for primate locomotor ecology and biomechanics. In: D'Août K, Vereecke EE, editors. Primate locomotion: linking field and laboratory research. New York: Springer. p 183–199.

Bokkers EA, Koene P. 2002. Sex and type of feed effects on motivation and ability to walk for a food reward in fast growing broilers. Appl Anim Behav Sci 79:247–261.

Bonnet X, Ineich I, Shine R. 2005. Terrestrial locomotion in sea snakes: the effects of sex and species on cliff-climbing ability in sea kraits (Serpentes, Elapidae, Laticauda). Biol J Linn Soc 85:433–441.

Boyer DM, Bloch JI. 2008. Evaluating the mitten-gliding hypothesis for Paromomyidae and Micromomyidae (Mammalia,"Plesiadapiformes") using comparative functional morphology of new Paleogene skeletons. In: In: Dagosto MJ, Sargis EJ. (Eds.), Mammalian Evolutionary Morphology. New York: Springer. p 233–284.

Boyette DP, London AH. 1948. Subluxation of the head of the radius "nursemaid's elbow." J Pediatr 32:278–281.

Budsberg SC, Verstraete MC, Soutas-Little RW. 1987. Force plate analysis of the walking gait in healthy dogs. Am J Vet Res 48:915–918.

Burr DB, Piotrowski G, Martin RB, Cook PN. 1982. Femoral mechanics in the lesser bushbaby (*Galago senegalensis*): structural adaptations to leaping in primates. Anat Rec 202:419–29.

Byrnes G, Libby T, Lim NT-L, Spence AJ. 2011a. Gliding saves time but not energy in Malayan colugos. J Exp Biol 214:2690–6.

Byrnes G, Lim NT-L, Spence AJ. 2008. Take-off and landing kinetics of a free-ranging gliding mammal, the Malayan colugo (*Galeopterus variegatus*). Proc R Soc Lond B Biol Sci 275:1007–1013.

Byrnes G, Lim NT-L, Yeong C, Spence AJ. 2011b. Sex differences in the locomotor ecology of a gliding mammal, the Malayan colugo (*Galeopterus variegatus*). J Mammal 92:444–451.

Byron CD, Covert HH. 2004. Unexpected locomotor behaviour: brachiation by an Old World monkey (*Pygathrix nemaeus*) from Vietnam. J Zool 263:101–106.

Cannon CH, Leighton M. 1994. Comparative locomotor ecology of gibbons and macaques: Selection of canopy elements for crossing gaps. Am J Phys Anthropol 93:505–524.

Cant JGH. 1986. Locomotion and feeding postures of spider and howling monkeys: field study and evolutionary interpretation. Folia Primatol 46:1–14.

Cant JG. 1987a. Effects of sexual dimorphism in body size on feeding postural behavior of Sumatran orangutans (*Pongo pygmaeus*). Am J Phys Anthropol 74:143–148.

Cant JGH. 1987b. Positional behavior of female bornean orangutans (*Pongo pygmaeus*). Am J Primatol 12:71–90.

Cant JG, Youlatos D, Rose MD. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuní National Park, Ecuador: general patterns and nonsuspensory modes. J Hum Evol 41:141–166.

Cant JG., Youlatos D, Rose MD. 2003. Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuní National Park, Ecuador. J Hum Evol 44:685–699.

Carlson KJ, Demes B, Franz TM. 2005. Mediolateral forces associated with quadrupedal gaits of lemurids. J Zool 266:261–273.

Carlson KJ, Patel BA. 2006. Habitual use of the primate forelimb is reflected in the material properties of subchondral bone in the distal radius. J Anat 208:659–670.

Carter DR, Hayes WC. 1976. Bone compressive strength: the influence of density and strain rate. Science 194:1174–1176.

Cartmill M. 1985. Climbing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. Functional vertebrate morphology. Cambridge, MA: Belknap. p 73–88.

Cartmill M. 1992. New views on primate origins. Evol Anthropol Issues News Rev 1:105–111.

Cartmill M, Lemelin P, Schmitt D. 2002. Support polygons and symmetricalgaits in mammals. Zool J Linn Soc 136:401–420.

Cartmill M, Lemelin P, Schmitt D. 2007. Understanding the adaptive value of diagonal-sequence gaits in primates: a comment on Shapiro and Raichlen, 2005. Am J Phys Anthropol 133:822–827.

Cartmill M, Milton K. 1977. The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. Am J Phys Anthropol 47:249–272.

Cavagna GA, Heglund NC, Taylor CR. 1977. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am J Physiol 233:R243–R261.

Chang Y, Bertram J, Lee D. 2000. External forces and torques generated by the brachiating white-handed gibbon (Hylobates lar). Am J Phys Anthropol 113:201–216.

Cheyne SM. 2011. Gibbon locomotion research in the field: problems, possibilities, and benefits for conservation. In: D'Août K, editor. Primate locomotion: linking field and laboratory research. New York: Springer. p 201–213.

Chi K-J, Schmitt D. 2005. Mechanical energy and effective foot mass during impact loading of walking and running. J Biomech 38:1387–1395.

Chivers DJ. 1972. The siamang and the gibbon in the Malay Peninsula. In: Gibbon and siamang. Rumbaugh DM. (Ed.). Basel: Karger: 103–135.

Choung W, Heinrich SD. 1995. Acute annular ligament interposition into the radiocapitellar joint in children (nursemaid's elbow). J Pediatr Orthop 15:454–456.

Churchill SE, Holliday TW, Carlson KJ, Jashashvili T, Macias ME, Mathews S, Sparling TL, Schmid P, de Ruiter DJ, Berger LR. 2013. The upper limb of *Australopithecus sediba*. Science 340:1233477–1233477.

Clark WE. 1926. On the anatomy of the pen-tailed tree-shrew (*Ptilocercus lowii*.). In: Proc Zool Soc Lond 96, 1179–1309.

Cliffe RN, Avey-Arroyo JA, Arroyo FJ, Holton MD, Wilson RP. 2014. Mitigating the squash effect: sloths breathe easily upside down. Biol Lett 10:20140172.

Congdon K. 2014. Grasping pressures and phalangeal curvature in primates: an experimental in vivo approach. PhD. dissertation. Columbia: University of Missouri.

Congdon KA. 2012. Interspecific and ontogenetic variation in proximal pedal phalangeal curvature of great apes (*Gorilla gorilla*, *Pan troglodytes*, and *Pongo pygmaeus*). Int J Primatol 33:418–427.

Connour JR, Glander K, Vincent F. 2000. Postcranial adaptations for leaping in primates. J Zool 251:79–103.

Crowninshield RD, Pope MH. 1974. The response of compact bone in tension at various strain rates. Ann Biomed Eng 2:217–225.

Cullum AJ. 1998. Sexual dimorphism in physiological performance of whiptail lizards (genus *Cnemidophorus*). Physiol Biochem Zool 71:541–552.

Curtis DJ, Feistner ATC. 1994. Positional behaviour in captive aye-ayes (*Daubentonia madagascariensis*). Folia Primatol (Basel) 62:155–159.

Dagosto M. 1995. Seasonal variation in positional behavior of malagasy lemurs. Int J Primatol 16:807–833.

Dagosto M, Yamashita N. 1998. Effect of habitat structure on positional behavior and support use in three species of lemur. Primates 39:459–472.

Dalloz MF, Loretto D, Papi B, Cobra P, Vieira MV. 2012. Positional behaviour and tail use by the bare-tailed woolly opossum *Caluromys philander* (Didelphimorphia, Didelphidae). Mamm Biol - Z Für Säugetierkd 77:307–313.

Demes B, Jungers WL, Fleagle JG, Wunderlich RE, Richmond BG, Lemelin P. 1996. Body size and leaping kinematics in Malagasy vertical clingers and leapers. J Hum Evol 31:367–388.

Demes B, Jungers WL, Gross TS, Fleagle JG. 1995. Kinetics of leaping primates: influence of substrate orientation and compliance. Am J Phys Anthropol 96:419–29.

Demes B, Jungers WL, Nieschalk U. 1990. Size-and speed-related aspects of quadrupedal walking in slender and slow lorises. In: Jouffroy, F., Stack, M., Niemitz, C. (Eds.), Gravity, Posture and Locomotion in Primates. Firenze, Il Sedicesimo. p 175–197.

Demes B, Larson SG, Stern JT, Jungers WL, Biknevicius AR, Schmitt D. 1994. The kinetics of primate quadrupedalism: “hindlimb drive” reconsidered. J Hum Evol 26:353–374.

Demes B, Qin Y-X, Stern JT, Larson SG, Rubin CT. 2001. Patterns of strain in the macaque tibia during functional activity. Am J Phys Anthropol 116:257–265.

Dietz V. 2002. Do human bipeds use quadrupedal coordination? Trends Neurosci 25:462–467.

Dietz V. 2003. Spinal cord pattern generators for locomotion. Clin Neurophysiol 114:1379–1389.

Diogo R. 2009. The head and neck muscles of the Philippine colugo (Dermoptera: *Cynocephalus volans*), with a comparison to tree-shrews, primates, and other mammals. J Morphol 270:14–51.

Doran DM. 1992. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: a case study of paedomorphism and its behavioral correlates. J Hum Evol 23:139–157.

Doran DM. 1993. Sex differences in adult chimpanzee positional behavior: the influence of body size on locomotion and posture. Am J Phys Anthropol 91:99–115.

Doran DM. 1996. Comparative positional behavior of the African apes. In: Great Ape Societies. Cambridge, MA: Cambridge University Press. p 213–224.

Doran DM. 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. J Hum Evol 32:323–344.

Doran DM, Hunt KD. 1996. Comparative Locomotor Behavior of Chimpanzees and Bonobos. In: Chimpanzee Cultures. Cambridge, MA: Harvard University Press. p 93–108.

Drapeau MS. 2004. Functional anatomy of the olecranon process in hominoids and plio-pleistocene hominins. Am J Phys Anthropol 124:297–314.

Drew T, Prentice S, Schepens B. 2004. Cortical and brainstem control of locomotion. Prog Brain Res 143:251–61.

Dzulhelmi MN, Abdullah MT. 2009. An ethogram construction for the Malayan flying lemur (*Galeopterus variegatus*) in Bako National Park, Sarawak, Malaysia. J Trop Biol Conserv 5:31–42.

Eberhart HD, Inman VT. 1951. An evaluation of experimental procedures used in a fundamental study of human locomotion. Ann N Y Acad Sci 51:1213–1228.

Emmons LH. 2000. Tupai: a field study of Bornean treeshrews. University of California Press.

Erikson GE. 1963. Brachiation in New World monkeys and in anthropoid apes. Symp Zool Soc Lond 10:135–164.

Essner RL. 2007. Morphology, locomotor behaviour and microhabitat use in North American squirrels. J Zool 272:101–109.

Fan P, Scott MB, Fei H, Ma C. 2013. Locomotion behavior of cao vit gibbon (*Nomascus nasutus*) living in karst forest in Bangliang Nature Reserve, Guangxi, China. Integr Zool 8:356–364.

Fleagle JG. 1974. Dynamics of a brachiating siamang [*Hylobates* (*Symphalangus*) *syndactylus*]. Nature 248:259–260.

Fleagle JG. 1976. Locomotion, posture, and comparative anatomy of Malaysian forest primates.

Fleagle JG. 1977. Locomotor behavior and muscular anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Am J Phys Anthropol 46:297–307.

Fleagle JG. 1978. Locomotion, posture, and habitat utilization in two sympatric, Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Ecol Arboreal Folivores: 243–251.

Fleagle JG. 1980. Locomotion and posture. In: Malayan forest primates. Springer. p 191–208.

Fleagle JG. 1983. Locomotor adaptations of Oligocene and Miocene hominoids and their phyletic implications. In: New interpretations of ape and human ancestry. Springer. p 301–324.

Fleagle JG. 2013. Primate Adaptation and Evolution. 3rd ed. San Diego: Academic Press.

Fleagle J, Mittermeier R. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. Am J Phys Anthropol 52:301–314.

Fleagle J, Stern J, Jungers W. 1981. Climbing: a biomechanical link with brachiation and with bipedalism. Symp Zool Soc Lond 48:359–375.

Fontaine R. 1990. Positional behavior in *Saimiri boliviensis* and *Ateles geoffroyi*. Am J Phys Anthropol 82:485–508.

Forczek W, Staszkiewicz R. 2012. Changes of kinematic gait parameters due to pregnancy. Acta Bioeng Biomech 14:113–119.

Franz TM, Demes B, Carlson KJ. 2005. Gait mechanics of lemurid primates on terrestrial and arboreal substrates. J Hum Evol 48:199–217.

Fujiwara S, Endo H, Hutchinson JR. 2011. Topsy-turvy locomotion: biomechanical specializations of the elbow in suspended quadrupeds reflect inverted gravitational constraints. J Anat 219:176–191.

Fung Y. 2013. Biomechanics: mechanical properties of living tissues. Springer Science & Business Media.

Fung Y-C. 1993. Bone and Cartilage. In: Biomechanics. Springer New York. p 500–544.

Gaudin TJ. 2004. Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. Zool J Linn Soc 140:255–305.

Gebo D. 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. Am J Phys Anthropol 101:55–92.

Gebo D. 2014. Primate comparative anatomy. Baltimore: Johns Hopkins University Press.

Gebo DL. 1987. Locomotor diversity in prosimian primates. Am J Primatol 13:271–281.

Gebo DL. 1989. Postcranial adaptation and evolution in lorisidae. Primates 30:347–367.

Gebo DL. 1992. Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. Am J Primatol 26:277–290.

Gebo DL, Beard KC, Teaford MF, Walker A, Larson SG, Jungers WL, Fleagle JG. 1988. A hominoid proximal humerus from the Early Miocene of Rusinga Island, Kenya. J Hum Evol 17:393–401.

Gebo DL, Chapman CA. 1995. Positional behavior in five sympatric Old World monkeys. Am J Phys Anthropol 97:49–76.

Gebo DL, Dagosto M. 1988. Foot anatomy, climbing, and the origin of the Indriidae. J Hum Evol 17:135–154.

Gittins SP. 1983. Use of the forest canopy by the agile gibbon. Folia Primatol (Basel) 40:134–144.

Glassman D, Wells J. 1984. Positional and activity behavior in a captive slow loris: a quantitative assessment. Am J Primatol 7:121–132.

Godfrey LR, Jungers WL. 2003. The extinct sloth lemurs of Madagascar. Evol Anthropol Issues News Rev 12:252–263.

Golomer E, Ducher D, Arfi GS, Sud R. 1990. Simple locomotion and during load carrying in pregnant women. J Gynecol Obstet Biol Reprod (Paris) 20:406–412.

Golubitsky M, Stewart I, Pietro-Luciano B, Collins JJ. 1999. Symmetry in locomotor central pattern generators and animal gaits. Nature 401:731–731.

Goodenberger KE, Boyer DM, Orr CM, Jacobs RL, Femiani JC, Patel BA. 2015. Functional morphology of the hallucal metatarsal with implications for inferring grasping ability in extinct primates. Am J Phys Anthropol 156:327–348.

Granatosky MC. 2015. Kinetic and kinematic patterns of arm-swinging in the red-shanked douc langur (*Pygathrix nemaeus*). J Vietnam Primatol 2:33–40.

Granatosky MC, Lemelin P, Chester SGB, Pampush JD, Schmitt D. 2014a. Functional and evolutionary aspects of axial stability in euarchontans and other mammals. J Morphol 275:313–27.

Granatosky MC, Miller CE, Boyer DM, Schmitt D. 2014b. Lumbar vertebral morphology of flying, gliding, and suspensory mammals: implications for the locomotor behavior of the subfossil lemurs *Palaeopropithecus* and *Babakotia*. J Hum Evol 75:40–52.

Granatosky MC, Tripp CH, Schmitt D. 2016. Gait kinetics of above and below branch quadrupedal locomotion in lemurid primates. J Exp Biol 219:53–63.

Grand TI. 1967. The functional anatomy of the ankle and foot of the slow loris (*Nycticebus coucang*). Am J Phys Anthropol 26:207–218.

Grand TI. 1972. A Mechanical Interpretation of Terminal Branch Feeding. J Mammal 53:198–198.

Grand TI, Barboza PS. 2001. Anatomy and development of the koala, *Phascolarctos cinereus*: an evolutionary perspective on the superfamily Vombatoidea. Anat Embryol (Berl) 203:211–223.

Grass A. 2014. Inferring lifestyle and locomotor habits of extinct sloths through scapula morphology and implications for convergent evolution in extant sloths. PhD. dissertation. Iowa City: The University of Iowa.

Green DJ, Alemseged Z. 2012. *Australopithecus afarensis* scapular ontogeny, function, and the role of climbing in human evolution. Science 338:514–7.

Greenwood AD, Castresana J, Feldmaier-Fuchs G, Pääbo S. 2001. A molecular phylogeny of two extinct sloths. Mol Phylogenet Evol 18:94–103.

Griffin TM, Kram R. 2000. Biomechanics: penguin waddling is not wasteful. Nature 408:929–929.

Griffin TM, Main RP, Farley CT. 2004. Biomechanics of quadrupedal walking: how do four-legged animals achieve inverted pendulum-like movements? J Exp Biol 207:3545–3558.

Guillot D. 2011. Forelimb suspensory gait characteristics of wild *Lagothrix poeppigii* and *Ateles belzebuth*: developing video-based methodologies in free-ranging primates. In: D'Août K, Vereecke EE, editors. Primate locomotion: linking field and laboratory research. Springer New York. p 247–269.

Hall-Craggs EC. 1965. An osteometric study of the hind limb of the Galagidae. J Anat 99:119–26.

Hamilton W, Parkes JC, others. 1973. Isolated dislocation of the radial head without fracture of the ulna. Clin Orthop 97:94–96.

Hammond AS. 2014. *In vivo* baseline measurements of hip joint range of motion in suspensory and nonsuspensory anthropoids. Am J Phys Anthropol 153:417–434.

Hamrick MW. 1996. Functional morphology of the lemuriform wrist joints and the relationship between wrist morphology and positional behavior in arboreal primates. Am J Phys Anthropol 99:319–344.

Hamrick MW, Rosenman BA, Brush JA. 1999. Phalangeal morphology of the Paromomyidae (?Primates, Plesiadapiformes): the evidence for gliding behavior reconsidered. Am J Phys Anthropol 109:397–413.

Hamrick MW, Simons EL, Jungers WL. 2000. New wrist bones of the Malagasy giant subfossil lemurs. J Hum Evol 38:635–650.

Hanna JB, Polk JD, Schmitt D. 2006. Forelimb and hindlimb forces in walking and galloping primates. Am J Phys Anthropol 130:529–35.

Harrison T. 1989. New postcranial remains of *Victoriapithecus* from the middle Miocene of Kenya. J Hum Evol 18:3–54.

Hedrick TL. 2008. Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. Bioinspir Biomim 3:034001.

Hildebrand M. 1967. Symmetrical gaits of primates. Am J Phys Anthropol 26:119–130.

Hirasaki E, Kumakura H, Matano S. 2000. Biomechanical analysis of vertical climbing in the spider monkey and the Japanese macaque. Am J Phys Anthropol 113:455–472.

Howell DJ, Pylka J. 1977. Why bats hang upside down: a biomechanical hypothesis. J Theor Biol 69:625–631.

Hunt K. 1991. Positional behavior in the Hominoidea. Int J Primatol 12:95–118.

Hunt KD. 1992. Positional behavior of *Pan troglodytes* in the Mahale mountains and Gombe stream national parks, Tanzania. Am J Phys Anthropol 87:83–105.

Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardized descriptions of primate locomotor and postural modes. Primates 37:363–387.

Ijspeert AJ. 2008. Central pattern generators for locomotion control in animals and robots: a review. Neural Netw Off J Int Neural Netw Soc 21:642–53.

Inman VT, Ralston HJ, Todd F. 1981. Human walking. Williams & Wilkins.

Iriarte-Diaz J, Riskin DK, Breuer KS, Swartz SM. 2012. Kinematic plasticity during flight in fruit bats: individual variability in response to loading. PloS One 7:e36665–e36665.

Ishida H, Jouffroy F, Nakano Y. 1990. Comparative dynamics of pronograde and upside down horizontal quadrupedalism in the slow loris (*Nycticebus coucang*). In: Gravity, posture and locomotion in primates. In: Jouffroy, F., Stack, M., Niemitz, C. (Eds.), Gravity, Posture and Locomotion in Primates. Firenze, Il Sedicesimo. p 209–220.

Jenkins FA Jr. 1970. Anatomy and function of expanded ribs in certain edentates and primates. J Mammal 51:288–301.

Jenkins FA Jr. 1981. Wrist rotation in primates: a critical adaptation for brachiators. Symp Zool Soc Lond 48:429–451.

Jenkins FA Jr, Dombrowski PJ, Gordon EP. 1978. Analysis of the shoulder in brachiating spider monkeys. Am J Phys Anthropol 48:65–76.

Johnson LE. 2012. Biomechanics of vertical clinging and grasping in primates. PhD Dissertation. Durham: Duke University

Johnson SE, Shapiro LJ. 1998. Positional behavior and vertebral morphology in atelines and cebines. Am J Phys Anthropol 105:333–354.

Johnston Rob'yn. 2014. Capitular morphology in primates and fossils: 3-D measurements of the capitulum and possible implications for reconstructing locomotor adaptations in fossil primates.

Jones FW. 1916. Arboreal man. Longmans.

Jouffroy FK, Petter A. 1990. Gravity-related kinematic changes in lorisine horizontal locomotion in relation to position of the body. In: Gravity, Posture and Locomotion in Primates. In: Gravity, posture and locomotion in primates. In: Jouffroy, F., Stack, M., Niemitz, C. (Eds.), Gravity, Posture and Locomotion in Primates. Firenze, Il Sedicesimo. p 199–208.

Jouffroy F, Stern J. 1990. Telemetered EMG study of the antigravity versus propulsive actions of knee and elbow muscles in the slow loris (*Nycticebus coucang*). In: Gravity, posture and locomotion in primates. In: Gravity, posture and locomotion in primates. In: Jouffroy, F., Stack, M., Niemitz, C. (Eds.), Gravity, Posture and Locomotion in Primates. Firenze, Il Sedicesimo. p 221–236.

Judex S, Carlson KJ. 2009. Is bone's response to mechanical signals dominated by gravitational loading. Med Sci Sports Exerc 41:2037–43.

Jungers WL, Godfrey LR, Simons EL, Chatrath PS. 1997. Phalangeal curvature and positional behavior in extinct sloth lemurs (Primates, Palaeopropithecidae). Proc Natl Acad Sci U.S.A 94:11998–2001.

Jungers WL, Stern JT. 1981. Preliminary electromyographical analysis of brachiation in gibbon and spider monkey. Int J Primatol 2:19–33.

Kagaya M, Ogihara N, Nakatsukasa M. 2010. Is the clavicle of apes long? An investigation of clavicular length in relation to body mass and upper thoracic width. Int J Primatol 31:209–217.

Karantanis N-E, Youlatos D, Rychlik L. 2015. Diagonal gaits in the feathertail glider *Acrobates pygmaeus* (Acrobatidae, Diprotodontia): insights for the evolution of primate quadrupedalism. J Hum Evol 86:43–54.

Karanth KP, Delefosse T, Rakotosamimanana B, Parsons TJ, Yoder AD. 2005. Ancient DNA from giant extinct lemurs confirms single origin of Malagasy primates. Proc Natl Acad Sci U.S.A 102:5090–5.

Kaufmann JH. 1962. Ecology and the social behavior of the coati, *Nasua nanca*, on Barro Colorado Island, Panama. Univ Calif Publ Zool 60:95–222.

Kimura T, Okada M, Ishida H. 1977. Dynamics of primate bipedal walking as viewed from the force of foot. Primates 18:137–147.

Kimura T, Okada M, Ishida H. 1979. Kinesiological characteristics of primate walking: its significance in human walking. In: Morbeck M, Preuschoft H, Gomberg N, editors. Environment, behavior, morphology: dynamic interactions in primates. New York: Gustav Fischer. p 297–311.

Kirk EC, Lemelin P, Hamrick MW, Boyer DM, Bloch JI. 2008. Intrinsic hand proportions of euarchontans and other mammals: implications for the locomotor behavior of plesiadapiforms. J Hum Evol 55:278–299.

Kivell TL, Barros AP, Smaers JB. 2013. Different evolutionary pathways underlie the morphology of wrist bones in hominoids. BMC Evol Biol 13:229.

LaFleur M, Sauther ML. 2015. Seasonal feeding ecology of ring-tailed lemurs: a comparison of spiny and gallery forest habitats. Folia Primatol 86:25–34.

Lambert JE, Fellner V, McKenney E, Hartstone-Rose A. 2014. Binturong (*Arctictis binturong*) and kinkajou (*Potos flavus*) digestive strategy: implications for interpreting frugivory in Carnivora and Primates. PLoS ONE 9:e105415.

Lammers AR, Gauntner T. 2008. Mechanics of torque generation during quadrupedal arboreal locomotion. J Biomech 41:2388–2395.

Larney E, Larson SG. 2004. Compliant walking in primates: elbow and knee yield in primates compared to other mammals. Am J Phys Anthropol 125:42–50.

Larson A, Losos JB. 1996. Phylogenetic systematics of adaptation. San Diego: Academic Press, p 187–220.

Larson SG. 1988. Subscapularis function in gibbons and chimpanzees: implications for interpretation of humeral head torsion in hominoids. Am J Phys Anthropol 76:449–462.

Larson SG. 1995. New characters for the functional interpretation of primate scapulae and proximal humeri. Am J Phys Anthropol 98:13–35.

Larson SG. 1996. Estimating humeral torsion on incomplete fossil anthropoid humeri. J Hum Evol 31:239–257.

Larson SG. 1998. Parallel evolution in the hominoid trunk and forelimb. Evol Anthropol Issues News Rev 6:87–99.

Larson SG, Demes B. 2011. Weight support distribution during quadrupedal walking in *Ateles* and *Cebus*. Am J Phys Anthropol 144:633–642.

Larson SG, Schmitt D, Lemelin P, Hamrick M. 2000. Uniqueness of primate forelimb posture during quadrupedal locomotion. Am J Phys Anthropol 112:87–101.

Larson SG, Schmitt D, Lemelin P, Hamrick M. 2001. Limb excursion during quadrupedal walking: how do primates compare to other mammals? J Zool 255:353–365.

Larson SG, Stern JT. 1986. EMG of scapulohumeral muscles in the chimpanzee during reaching and "arboreal" locomotion. Am J Anat 176:171–190.

Larson SG, Stern JT. 2009. Hip extensor EMG and forelimb/hind limb weight support asymmetry in primate quadrupeds. Am J Phys Anthropol 138:343–55.

Laska M. 1998. Laterality in the use of the prehensile tail in the spider monkey (*Ateles geoffroyi*). Cortex J Devoted Study Nerv Syst Behav 34:123–130.

Lawrence MJ. 1969. Some observations on non-volant locomotion in vespertilionid bats. J Zool 157:309–317.

Lee DV, Bertram JEA, Anttonen JT, Ros IG, Harris SL, Biewener AA. 2011. A collisional perspective on quadrupedal gait dynamics. J R Soc Interface 8:1480–1486.

Lee DV, Comanescu TN, Butcher MT, Bertram JEA. 2013. A comparative collision-based analysis of human gait. Proc R Soc Lond B Biol Sci 280:20131779.

Lemelin P. 1995. Comparative and functional myology of the prehensile tail in New World monkeys. J Morphol 224:351–368.

Lemelin P, Cartmill M. 2010. The effect of substrate size on the locomotion and gait patterns of the kinkajou (*Potos flavus*). J Exp Zool Part Ecol Genet Physiol 313:157–168.

Lemelin P, Schmitt D. 1998. The relation between hand morphology and quadrupedalism in primates. Am J Phys Anthropol 105:185–197.

Lemelin P, Schmitt D. 2004. Seasonal variation in body mass and locomotor kinetics of the fat-tailed dwarf lemur (*Cheirogaleus medius*). J Morphol 260:65–71.

Lemelin P, Schmitt D, Cartmill M. 2003. Footfall patterns and interlimb co-ordination in opossums (Family Didelphidae): evidence for the evolution of diagonal-sequence walking gaits in primates. J Zool 260:423–429.

Lewis OJ. 1971. Brachiation and the early evolution of the Hominoidea. Nature 230:577–579.

Lewis OJ. 1985a. Derived morphology of the wrist articulations and theories of hominoid evolution. Part I. The lorisine joints. J Anat 140:447–460.

Lewis OJ. 1985b. Derived morphology of the wrist articulations and theories of hominoid evolution. Part II. The midcarpal joints of higher primates. J Anat 142:151–172.

Losos JB, Miles DB. 1994. Adaptation, constraint, and the comparative method: phylogenetic issues and methods. In: Ecological morphology: integrative organismal biology. p 60–98.

Lovejoy CO. 2009. Reexamining human origins in light of *Ardipithecus ramidus*. Science 326:74- 74e8.

Lovejoy CO, Suwa G, Simpson SW, Matternes JH, White TD. 2009a. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. Science 326:73–73, 100–106.

Lovejoy CO, Suwa G, Spurlock L, Asfaw B, White TD. 2009b. The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. Science 326:71–71e6.

Macias CG, Bothner J, Wiebe R. 1998. A comparison of supination/flexion to hyperpronation in the reduction of radial head subluxations. Pediatrics 102:e10–e10.

Macias ME. 2015. Functional integration of the hominin forelimb. PhD Dissertation. Durham: Duke University.

MacKay-Lyons M. 2002. Central pattern generation of locomotion: a review of the evidence. Phys Ther 82:69–83.

MacLatchy L, Gebo D, Kityo R, Pilbeam D. 2000. Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. J Hum Evol 39:159–83.

Madar SI, Rose MD, Kelley J, MacLatchy L, Pilbeam D. 2002. New *Sivapithecus* postcranial specimens from the Siwaliks of Pakistan. J Hum Evol 42:705–752.

Magne de la Croix P. 1936. The evolution of locomotion in mammals. J Mammal 17:51–54.

Manduell KL, Morrogh-Bernard HC, Thorpe SKS. 2011. Locomotor behavior of wild orangutans (*Pongo pygmaeus wurmbii*) in disturbed peat swamp forest, Sabangau, Central Kalimantan, Indonesia. Am J Phys Anthropol 145:348–359.

McClearn D. 1990. Limb proportions of raccoons (*Procyon*) and coatis (*Nasua*). American Zoologist 30: 8a.

McClearn D. 1992. Locomotion, posture, and feeding behavior of kinkajous, coatis, and raccoons. J Mammal 73:245–261.

McClure NK, Phillips AC, Vogel ER, Tocheri MW. 2012. Unexpected pollex and hallux use in wild *Pongo pygmaeus wurmbii*. Am J Phys Anthropol S147:208.

McDonald HG, De Iuliis G. 2008. Fossil history of sloths. Biol Xenarthra:39–55.

McGraw W. 1998. Comparative locomotion and habitat use of six monkeys in the Tai forest, Ivory Coast. Am J Phys Anthropol 105:493–510.

McMahon TA, Valiant G, Frederick EC. 1987. Groucho running. J Appl Physiol 62:2326–2337.

Meldrum DJ. 1991. Kinematics of the cercopithecine foot on arboreal and terrestrial substrates with implications for the interpretation of hominid terrestrial adaptations. Am J Phys Anthropol 84:273–89.

Meldrum DJ. 1998. Tail-assisted hind limb suspension as a transitional behavior in the evolution of the platyrrhine prehensile tail. In: Primate locomotion: recent advances. New York: Plenum Press, p 145–156.

Meldrum DJ, Dagosto M, White J. 1997. Hindlimb suspension and hind foot reversal in Varecia variegata and other arboreal mammals. Am J Phys Anthropol 103:85–102.

Mendel FC. 1979. The wrist joint of two-toed sloths and its relevance to brachiating adaptations in the hominoidea. J Morphol 162:413–424.

Mendel FC. 1981. Foot of two-toed sloths: its anatomy and potential uses relative to size of support. J Morphol 170:357–372.

Michaels MG. 1989. A case of bilateral nursemaid's elbow. Pediatr Emerg Care 5:226–227.

Michilsens F, D'Août K, Aerts P. 2011. How pendulum-like are siamangs? Energy exchange during brachiation. Am J Phys Anthropol 145:581–91.

Michilsens F, D'Août K, Vereecke EE, Aerts P. 2012. One step beyond: different step-to-step transitions exist during continuous contact brachiation in siamangs. Biol Open 1:411–421.

Michilsens F, Vereecke EE, D'Août K, Aerts P. 2009. Functional anatomy of the gibbon forelimb: adaptations to a brachiating lifestyle. J Anat 215:335–54.

Michilsens F, Vereecke EE, D'Août K, Aerts P. 2010. Muscle moment arms and function of the siamang forelimb during brachiation. J Anat 217:521–35.

Miller RA. 1935. Functional adaptations in the forelimb of the sloths. J Mammal 16:38–51.

Mittermeier RA. 1978. Locomotion and Posture in *Ateles geoffroyi* and *Ateles paniscus*. Folia Primatol 30:161–193.

Morbeck ME. 1972. A re-examination of the forelimb of the Miocene Hominoidea.

Mori S. 1987. Integration of posture and locomotion in acute decerebrate cats and in awake, freely moving cats. Prog Neurobiol 28:161–195.

Mori S, Matsuyama K, Miyashita E, Nakajima K, Asanome M. 1996. Basic neurophysiology of primate locomotion. Folia Primatol 66:192–203.

Muybridge E. 1887. Animals in motion. Courier Corporation.

Nagy KA, Montgomery GG. 1980. Field metabolic rate, water flux, and food consumption in three-toed sloths (*Bradypus variegatus*). J Mammal 61:465–472.

Napier JR. 1967. Evolutionary aspects of primate locomotion. Am J Phys Anthropol 27:333–341.

Napier JR, Davis PR. 1959. The fore-limb skeleton and associated remains of *Proconsul africanus*. British Museum.

Newman J. 1985. "Nursemaid's elbow" in infants six months and under. J Emerg Med 2:403–404.

Nowak RM. 1999. Walker's mammals of the world. Johns Hopkins University Press.

Nyakatura JA. 2011. The convergent evolution of suspensory posture and locomotion in tree sloths. J Mamm Evol 19:225–234.

Nyakatura JA, Andrada E. 2012. A mechanical link model of two-toed sloths: no pendular mechanics during suspensory locomotion. Acta Theriol (Warsz) 58:83–93.

Nyakatura JA, Fischer MS. 2010a. Research three-dimensional kinematic analysis of the pectoral girdle during upside-down locomotion of two-toed sloths (Choloepus didactylus, Linné 1758). Front Zool 7:21.

Nyakatura JA, Fischer MS. 2010b. Functional morphology and three-dimensional kinematics of the thoraco-lumbar region of the spine of the two-toed sloth. J Exp Biol 213:4278–90.

Nyakatura JA, Fischer MS, Schmidt M. 2008. Gait parameter adjustments of cotton-top tamarins (*Saguinus oedipus*, Callitrichidae) to locomotion on inclined arboreal substrates. Am J Phys Anthropol 135:13–26.

Nyakatura JA, Petrovitch A, Fischer MS. 2010. Limb kinematics during locomotion in the two-toed sloth (*Choloepus didactylus*, Xenarthra) and its implications for the evolution of the sloth locomotor apparatus. Zool Jena Ger 113:221–34.

O'Driscoll SW, Jupiter JB, King GJW, Hotchkiss RN, Morrey BF. 2000. The unstable elbow. J Bone Jt Surg Am 82:724–724.

Olejnik SF, Algina J. 1984. Parametric ANCOVA and the rank transform ANCOVA when the data are conditionally non-normal and heteroscedastic. J Educ Behav Stat 9:129–149.

O'Neill MC, Schmitt D. 2012. The gaits of primates: center of mass mechanics in walking, cantering and galloping ring-tailed lemurs, *Lemur catta*. J Exp Biol 215:1728–39.

Organ JM. 2008. The functional anatomy of prehensile and nonprehensile tails of the Platyrrhini (Primates) and Procyonidae (Carnivora). PhD Dissertation. Baltimore: The Johns Hopkins University.

Orlando L, Calvignac S, Schnebelen C, Douady CJ, Godfrey LR, Hänni C. 2008. DNA from extinct giant lemurs links archaeolemurids to extant indriids. BMC Evol Biol 8:121.

Oxnard CE. 1967. The functional morphology of the primate shoulder as revealed by comparative anatomical, osteometric and discriminant function techniques. Am J Phys Anthropol 26:219–240.

Oxnard CE, Crompton RH, Lieberman SS. 1990. Animal lifestyles and anatomies: The case of the prosimian primates. University of Washington Press.

Oxnard CE, German R, Jouffroy F-K, Lessertisseur J. 1981a. A morphometric study of limb proportions in leaping prosimians. Am J Phys Anthropol 54:421–430.

Oxnard CE, German R, McArdle JE. 1981b. The functional morphometrics of the hip and thigh in leaping prosimians. Am J Phys Anthropol 54:481–498.

Parsons P, Taylor C. 1977. Energetics of brachiation versus walking: a comparison of a suspended and an inverted pendulum mechanism. Physiol Zool:182–188.

Patel BA, Carlson KJ. 2008. Apparent density patterns in subchondral bone of the sloth and anteater forelimb. Biol Lett 4:486–9.

Patel BA, Wallace IJ, Boyer DM, Granatosky MC, Larson SG, Stern JT Jr. 2015. Distinct functional roles of primate grasping hands and feet during arboreal quadrupedal locomotion. J Hum Evol 88:79–84.

Pereira ME, Seeligson ML, Macedonia JM. 1988. The behavioral repertoire of the black-and-white ruffed lemur, *Varecia variegata variegata* (Primates: Lemuridae). Folia Primatol 51:1–32.

Pichon C, Simmen B. 2015. Energy management in crowned sifakas (*Propithecus coronatus*) and the timing of reproduction in a seasonal environment. Am J Phys Anthropol 158:269–278.

Prates HM, Bicca-Marques JC. 2008. Age-sex analysis of activity budget, diet, and positional behavior in *Alouatta caraya* in an orchard forest. Int J Primatol 29:703–715.

Preuschoft H, Demes B. 1984. Biomechanics of brachiation. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes: evolutionary and behavioral biology. Edinburgh: Edinburgh Press Publishing. p 96–118.

Preuschoft H, Demes B. 1985. Biomechanic determinants of arm length and body mass in brachiators. Fortschr Zool 30:39–43.

Prost JH. 1965. A definitional system for the classification of primate locomotion. Am Anthropol 67:1198–1214.

Rafferty KL, Ruff CB. 1994. Articular structure and function in *Hylobates*, *Colobus*, and *Papio*. Am J Phys Anthropol 94:395–408.

Raichlen DA, Pontzer H, Shapiro LJ, Sockol MD. 2009. Understanding hind limb weight support in chimpanzees with implications for the evolution of primate locomotion. Am J Phys Anthropol 138:395–402.

Rasmussen DT. 1990. Primate origins: lessons from a neotropical marsupial. Am J Primatol 22:263–277.

Ravosa MJ, Meyers DM, Glander KE. 1993. Relative growth of the limbs and trunk in sifakas: heterochronic, ecological, and functional considerations. Am J Phys Anthropol 92:499–520.

Read CS. 2001. A comparative analysis of the wrist and ankle morphology of hominoids and lorisids, with implications for the evolution of hominoid locomotion. Ms Thesis. Durham: Durham University.

Rein TR, Harvati K, Harrison T. 2015. Inferring the use of forelimb suspensory locomotion by extinct primate species via shape exploration of the ulna. J Hum Evol 78:70–79.

Remis MJ. 1999. Tree structure and sex differences in arboreality among western lowland gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. Primates 40:383–396.

Reynolds T. 1985a. Stresses on the limbs of quadrupedal primates. Am J Phys Anthropol 67:351–362.

Reynolds T. 1985b. Mechanics of increased support weight by the hindlimbs in primates. Am J Phys Anthropol 67:335–349.

Reynolds T. 1987. Stride length and its determinants in humans, early hominoids, primates, and mammals. Am J Phys Anthropol 72:101–115.

Richmond BG. 2007. Biomechanics of phalangeal curvature. J Hum Evol 53:678–690.

Riskin DK, Bertram JE, Hermanson JW. 2005. Testing the hindlimb-strength hypothesis: non-aerial locomotion by Chiroptera is not constrained by the dimensions of the femur or tibia. J Exp Biol 208:1309–1319.

Riskin DK, Hermanson JW. 2005. Biomechanics: independent evolution of running in vampire bats. Nature 434:292–292.

Riskin DK, Parsons S, Schutt WA, Carter GG, Hermanson JW. 2006. Terrestrial locomotion of the New Zealand short-tailed bat *Mystacina tuberculata* and the common vampire bat *Desmodus rotundus*. J Exp Biol 209:1725–1736.

Roberts D. 1974. Structure and function of the primate scapula. Primate Locomotion: 171–200.

Robinson JG, Redford KH. 1986. Intrinsic rate of natural increase in Neotropical forest mammals: relationship to phylogeny and diet. Oecologia 68:516–520.

Rollinson J, Martin R. 1981. Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. Symp Zool Soc Lond 48:377–427.

Rose MD. 1978. Feeding and associated positional behavior of black and white colobus monkeys (*Colobus guereza*). Ecol Arboreal Folivores:253–262.

Rose MD. 1983. Miocene hominoid postcranial morphology. In: Ciochon RL, Corruccini RS, editors. New Interpretations of Ape and Human Ancestry. New York: Plenum Press, p 405–417.

Rose MD. 1986. Further hominoid postcranial specimens from the Late Miocene Nagri Formation of Pakistan. J Hum Evol 15:333–367.

Rose MD. 1988. Another look at the anthropoid elbow. J Hum Evol 17:193–224.

Rose MD. 1997. Functional and phylogenetic features of the forelimb in Miocene hominoids. In: Function, Phylogeny, and Fossils. New York: Plenum Press, p 79–100.

Rosenberger AL, Halenar L, Cooke SB, Hartwig WC. 2008. Morphology and evolution of the spider monkey, genus *Ateles*. Spider Monkeys Behav Ecol Evol Genus Ateles:19–49.

Rosenberger AL, Stafford BJ. 1994. Locomotion in captive *Leontopithecus* and *Callimico*: a multimedia study. Am J Phys Anthropol 94:379–394.

Ruff C. 1988. Hindlimb articular surface allometry in hominoidea and *Macaca*, with comparisons to diaphyseal scaling. J Hum Evol 17:687–714.

Ruina A, Bertram JE, Srinivasan M. 2005. A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. J Theor Biol 237:170–192.

Russell E. 1986. Observations on the behaviour of the honey possum, *Tarsipes rostratus* (Marsupialia : Tarsipedidae) in captivity. Aust J Zool Suppl Ser 34:1–63.

Ryan TM, Walker A. 2010. Trabecular bone structure in the humeral and femoral heads of anthropoid primates. Anat Rec Adv Integr Anat Evol Biol 293:719–729.

Sacchetti A, Ramoska EE, Glascow C. 1990. Nonclassic history in children with radial head subluxations. J Emerg Med 8:151–153.

Sargis EJ. 2001a. A preliminary qualitative analysis of the axial skeleton of tupaiids (Mammalia, Scandentia): functional morphology and phylogenetic implications. J Zool 253:473–483.

Sargis EJ. 2001b. The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). J Zool 253:485–490.

Sargis EJ. 2004. New views on tree shrews: the role of tupaiids in primate supraordinal relationships. Evol Anthropol 13:56–66.

Sargis EJ. 2007. The postcranial morphology of *Ptilocercus lowii* (Scandentia, Tupaiidae) and its implications for primate supraordinal relationships. In: Primate Origins: Adaptations and Evolution. New York: Springer, p 51–82.

Sarringhaus LA, Maclatchy LM, Mitani JC. 2014. Locomotor and postural development of wild chimpanzees. J Hum Evol 66:29–38.

Schaefer MS, Nash LT. 2007. Limb growth in captive *Galago senegalensis*: getting in shape to be an adult. Am J Primatol 69:103–11.

Schaffler MB, Burr DB. 1984. Primate cortical bone microstructure: relationship to locomotion. Am J Phys Anthropol 65:191–197.

Schmidt A, Fischer MS. 2010. Arboreal locomotion in rats - the challenge of maintaining stability. J Exp Biol 213:3615–3624.

Schmidt M. 2005. Quadrupedal locomotion in squirrel monkeys (Cebidae: *Saimiri sciureus*): a cineradiographic study of limb kinematics and related substrate reaction forces. Am J Phys Anthropol 128:359–370.

Schmitt D. 1994. Forelimb mechanics as a function of substrate type during quadrupedalism in two anthropoid primates. J Hum Evol 26:441–457.

Schmitt D. 1995. A kinematic and kinetic analysis of forelimb use during arboreal and terrestrial quadrupedalism in Old World monkeys. PhD Dissertation. New York: Stony Brook University.

Schmitt D. 1998. Forelimb mechanics during arboreal and terrestrial quadrupedalism in Old World monkeys. In: Strasser E, Fleagle JG, Rosenberger AL, McHenry HM, editors. Primate locomotion. New York: Springer, p 175–200.

Schmitt D. 1999. Compliant walking in primates. J Zool 248:149–160.

Schmitt D. 2003a. Mediolateral reaction forces and forelimb anatomy in quadrupedal primates: implications for interpreting locomotor behavior in fossil primates. J Hum Evol 44:47–58.

Schmitt D. 2003b. Evolutionary implications of the unusual walking mechanics of the common marmoset (*C. jacchus*). Am J Phys Anthropol 122:28–37.

Schmitt D. 2003c. Insights into the evolution of human bipedalism from experimental studies of humans and other primates. J Exp Biol 206:1437–1448.

Schmitt D. 2010. Primate locomotor evolution: biomechanical studies of primate locomotion and their implications for understanding primate neuroethology. In: Platt ML, Ghazanfar AA, editors. Primate Neuroethology. Oxford University Press. p 10–30.

Schmitt D. 2011. Translating primate locomotor biomechanical variables from the laboratory to the field. In: D'Août K, Vereecke EE, editors. Primate locomotion: linking field and laboratory research. New York: Springer, p 7–27.

Schmitt D, Hanna JB. 2004. Substrate alters forelimb to hindlimb peak force ratios in primates. J Hum Evol 46:239–54.

Schmitt D, Lemelin P. 2002. Origins of primate locomotion: gait mechanics of the woolly opossum. Am J Phys Anthropol 118:231–238.

Schmitt D, Lemelin P. 2004. Locomotor mechanics of the slender loris (*Loris tardigradus*). J Hum Evol 47:85–94.

Schmitt D, Rose MD, Turnquist JE, Lemelin P. 2005. Role of the prehensile tail during ateline locomotion: experimental and osteological evidence. Am J Phys Anthropol 126:435–46.

Schmitt D, Turnquist JE, Rose MD. 2009. The relationship between arm-swinging behavior and postcranial morphology in *Ateles* and *Lagothrix*. Am J Phys Anthropol S48:328.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675.

Schunk JF. 1990. Radial head subluxation: epidemiology and treatment of 87 episodes. Ann Emerg Med 19:1019–1023.

Schutt WA. 1993. Digital morphology in the Chiroptera: the passive digital lock. Cells Tissues Organs 148:219–227.

Shapiro L. 1995. Functional morphology of indrid lumbar vertebrae. Am J Phys Anthropol 98:323–342.

Shapiro LJ. 2007. Morphological and functional differentiation in the lumbar spine of lorisids and galagids. Am J Primatol 69:86–102.

Shapiro LJ, Raichlen DA. 2005. Lateral sequence walking in infant *Papio cynocephalus*: implications for the evolution of diagonal sequence walking in primates. Am J Phys Anthropol 126:205–13.

Shapiro LJ, Raichlen DA. 2007. A response to Cartmill et al.: primate gaits and arboreal stability. Am J Phys Anthropol 133:825–827.

Shapiro LJ, Seiffert CVM, Godfrey LR, Jungers WL, Simons EL, Randria GFN. 2005. Morphometric analysis of lumbar vertebrae in extinct Malagasy strepsirrhines. Am J Phys Anthropol 128:823–839.

Shapiro LJ, Simons CV. 2002. Functional aspects of strepsirrhine lumbar vertebral bodies and spinous processes. J Hum Evol 42:753–783.

Shapiro LJ, Young JW. 2010. Is primate-like quadrupedalism necessary for fine-branch locomotion? A test using sugar gliders (*Petaurus breviceps*). J Hum Evol 58:309–19.

Shine CL, Penberthy S, Robbins CT, Nelson OL, McGowan CP. 2015. Grizzly bear (*Ursus arctos horribilis*) locomotion: gaits and ground reaction forces. J Exp Biol 218: 3012-3019.

Simmons NB, Quinn TH. 1994. Evolution of the digital tendon locking mechanism in bats and dermopterans: a phylogenetic perspective. J Mamm Evol 2:231–254.

Simons EL, Godfrey LR, Jungers WL, Chatrath PS, Rakotosamimanana B. 1992. A new giant subfossil lemur, *Babakotia*, and the evolution of the sloth lemurs. Folia Primatol 58:197–203.

Skedros JG, Hunt KJ, Bloebaum RD. 2004. Relationships of loading history and structural and material characteristics of bone: development of the mule deer calcaneus. J Morphol 259:281–307.

Skedros JG, Mason MW, Bloebaum RD. 1994. Differences in osteonal micromorphology between tensile and compressive cortices of a bending skeletal system: indications of potential strain-specific differences in bone microstructure. Anat Rec 239:405–413.

Skedros JG., Mason MW., Nelson MC., Bloebaum RD. 1996. Evidence of structural and material adaptation to specific strain features in cortical bone. Anat Rec 246:47–63.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523–559.

Sokal RR, Rohlf FJ. 2012. Biometry : the principles and practice of statistics in biological research. New York: W.H. Freeman and Company.

Soligo C. 2005. Anatomy of the hand and arm in *Daubentonia madagascariensis*: a functional and phylogenetic outlook. Folia Primatol 76:262–300.

Springer MS, Stanhope MJ, Madsen O, de Jong WW. 2004. Molecules consolidate the placental mammal tree. Trends Ecol Evol 19:430–438.

Squyres N, DeLeon VB. 2015. Clavicular curvature and locomotion in anthropoid primates: a 3D geometric morphometric analysis. Am J Phys Anthropol 158:257–268.

Srikosamatara S. 1984. Ecology of pileated gibbons in south-east Thailand. Lesser Apes Evol Behav Biol H Preuschoft DJ Chivers WY Brockelman N Creel Eds:242–257.

Stafford BJ, Thorington RW, Kawamichi T. 2003. Positional Behavior of Japanese Giant Flying Squirrels (*Petaurista leucogenys*). J Mammal 84:263–271.

Stern JT Jr. 1975. Before bipedality. Yearb Phys Anthropol 19:59–68.

Stern JT Jr. 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. Evol Anthropol Issues News Rev 9:113–133.

Stern JT Jr, Jungers WL, Susman RL. 1995. Quantifying phalangeal curvature: an empirical comparison of alternative methods. Am J Phys Anthropol 97:1–10.

Stern JT Jr, Oxnard C. 1973. Primate locomotion: some links with evolution and morphology. Primatologia 4:1–93.

Stern JT Jr, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. Am J Phys Anthropol 60:279–317.

Stern JT Jr, Wells JP, Jungers WL, Vangor AK. 1980a. An electromyographic study of serratus anterior in atelines and *Alouatta*: implications for hominoid evolution. Am J Phys Anthropol 52:323–334.

Stern JT Jr, Wells JP, Jungers WL, Vangor AK, Fleagle JG. 1980b. An electromyographic study of the pectoralis major in Atelines and *Hylobates*, with special reference to the Evolution of a pars clavicularis. Am J Phys Anthropol 52:13–25.

Su DF, Jablonski NG. 2009. Locomotor Behavior and Skeletal Morphology of the Odd-Nosed Monkeys. Folia Primatol (Basel) 80:189–219.

Sugardjito J. 1982. Locomotor behavior of the Sumatran orang-utan, *Pongo pygmaeus abelii* at Ketambe, Gunung Leuser National Park. Malay Nat J 35:57–64.

Sugardjito J, van Hooff JARAM. 1986. Age-Sex Class Differences in the Positional Behaviour of the Sumatran Orang-Utan (*Pongo pygmaeus abelii*) in the Gunung Leuser National Park, Indonesia. Folia Primatol (Basel) 47:14–25.

Susman RL. 1984. The locomotor behavior of *Pan paniscus* in the Lomako forest. Springer.

Susman RL, Badrian NL, Badrian AJ. 1980. Locomotor behavior of *Pan paniscus* in Zaire. Am J Phys Anthropol 53:69–80.

Sussman RW. 1991. Primate origins and the evolution of angiosperms. Am J Primatol 23:209–223.

Swartz S. 1989. Pendular mechanics and the kinematics and energetics of brachiating locomotion. Int J Primatol 10:387–418.

Swartz SM. 1990. Curvature of the forelimb bones of anthropoid primates: Overall allometric patterns and specializations in suspensory species. Am J Phys Anthropol 83:477–498.

Swartz SM, Bertram JE, Biewener AA. 1989. Telemetered in vivo strain analysis of locomotor mechanics of brachiating gibbons. Nature 342:270–2.

Sylvester AD. 2006. Locomotor decoupling and the origin of hominin bipedalism. J Theor Biol 242:581–590.

Taylor AB. 1997. Scapula form and biomechanics in gorillas. J Hum Evol 33:529–553.

Taylor BK. 1978. The anatomy of the forelimb in the anteater (*Tamandua*) and its functional implications. J Morphol 157:347–367.

Taylor BK. 1985. Functional anatomy of the forelimb in vermilinguas (anteaters). In: The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas. Washinton, DC: Smithsonian Institution Press. p 151–162.

Taylor ME. 1989. Locomotor Adaptations by Carnivores. In: Gittleman JL, editor. Carnivore Behavior, Ecology, and Evolution. Springer US. p 382–409.

Temerin LA, Cant JGH. 1983. The Evolutionary Divergence of Old World Monkeys and Apes. Am Nat 122:335–351.

Thorpe SKS, Crompton RH. 2006. Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. Am J Phys Anthropol 131:384–401.

Thorpe SKS, Crompton RH, Alexander RM. 2007a. Orangutans use compliant branches to lower the energetic cost of locomotion. Biol Lett 3:253–256.

Thorpe SKS, Holder R, Crompton RH. 2009. Orangutans employ unique strategies to control branch flexibility. Proc Natl Acad Sci U S A 106:12646–51.

Thorpe SKS, Holder RL, Crompton RH. 2007b. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science 316:1328–31.

Tilden CD. 1990. A study of locomotor behavior in a captive colony of red-bellied lemurs (*Eulemur rubriventer*). Am J Primatol 22:87–100.

Toledo N, Bargo MS, Cassini GH, Vizcaíno SF. 2012. The Forelimb of Early Miocene Sloths (Mammalia, Xenarthra, Folivora): Morphometrics and Functional Implications for Substrate Preferences. J Mamm Evol 19:185–198.

Tomita M. 1967. A study on the movement pattern of four limbs in walking (1). Observation and discussion on the two types of the movement order of four limbs seen in mammals while walking. J Anthropol Soc Nippon 75:126–146.

Tripp CH, Granatosky MC, Schmitt D. 2015. Forelimb mechanics during below-branch quadrupedalism in primates: A comparison to above-branch quadrupedalism and bimanual locomotion. Am J Phys Anthropol S60:307.

Turnquist JE. 1975. The elbow and forearm of Ateles: an anatomical and behavioral study of locomotion. PhD. dissertation. Philadelphia: University of Pennsylvania.

Turnquist JE, Schmitt D, Rose MD, Cant JG. 1999. Pendular motion in the brachiation of captive Lagothrix and Ateles. Am J Primatol 48:263–81.

Tuttle RH. 1972. Functional and evolutionary biology of hylobatid hands and feet. Gibbon Siamang 1:136–206.

Urbani B, Youlatos D. 2013. Positional behavior and substrate use of *Micromys minutus* (Rodentia: Muridae): insights for understanding primate origins. J Hum Evol 64:130–136.

Usherwood JR. 2003. Understanding brachiation: insight from a collisional perspective. J Exp Biol 206:1631–1642.

Vandoros JD, Dumont ER. 2004. Use of the wings in manipulative and suspensory behaviors during feeding by frugivorous bats. J Exp Zoolog A Comp Exp Biol 301A:361–366.

Van Valkenburgh B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. J Vertebr Paleontol 7:162–182.

Vickers AJ. 2005. Parametric versus non-parametric statistics in the analysis of randomized trials with non-normally distributed data. BMC Med Res Methodol 5:35.

Vilensky JA. 1987. Locomotor behavior and control in human and non-human primates: Comparisons with cats and dogs. Neurosci Biobehav Rev 11:263–274.

Vilensky JA, Larson SG. 1989. Primate Locomotion: Utilization and Control of Symmetrical Gaits. Annu Rev Anthropol 18:17–35.

Vilensky JA, Moore AM, Eidelberg E, Walden JG. 1992. Recovery of Locomotion in Monkeys With Spinal Cord Lesions. J Mot Behav 24:288–296.

Vilensky JA, Moore AM, Libii JN. 1994. Squirrel monkey locomotion on an inclined treadmill: Implications for the evolution of gaits. J Hum Evol 26:375–386.

Voisin J-L. 2006. Clavicle, a neglected bone: Morphology and relation to arm movements and shoulder architecture in primates. Anat Rec A Discov Mol Cell Evol Biol 288A:944–953.

Wainwright PC, Mehta RS, Higham TE. 2008. Stereotypy, flexibility and coordination: key concepts in behavioral functional morphology. J Exp Biol 211:3523–8.

Walker AC. 1974. Locomotor adaptations in past and present prosimian primates. In: Jenkins FAJ, editor. Primate Locomotion. New York: Academic Press Inc. p 341–381.

Wallace IJ, Demes B. 2008. Symmetrical gaits of *Cebus apella*: implications for the functional significance of diagonal sequence gait in primates. J Hum Evol 54:783–94.

Walton DW, Walton GM. 1970. Post-cranial osteology of bats. In: About Bats. A Chiropteran Symposium. Southern Methodist University Press: Dallas. . p 93–126.

Ward CV. 1993. Torso morphology and locomotion in *Proconsul nyanzae*. Am J Phys Anthropol 92:291–328.

White JL. 1993. Indicators of locomotor habits in xenarthrans: Evidence for locomotor heterogeneity among fossil sloths. J Vertebr Paleontol 13:230–242.

White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, WoldeGabriel G. 2009. *Ardipithecus ramidus* and the Paleobiology of Early Hominids. Science 326:64–64, 75–86.

Workman C, Covert HH. 2005. Learning the ropes: The ontogeny of locomotion in red-shanked douc (*Pygathrix nemaeus*), Delacour's (*Trachypithecus delacouri*), and Hatinh langurs (*Trachypithecus hatinhensis*) I. positional behavior. Am J Phys Anthropol 128:371–380.

Wright K, Stevens N, Covert H. 2008. Comparisons of suspensory behaviors among *Pygathrix cinerea*, *P. nemaeus*, and Nomascus leucogenys in Cuc Phuong National Park, Vietnam. Int J Primatol 29:1467–1480.

Wright TM, Hayes WC. 1976. Tensile testing of bone over a wide range of strain rates: effects of strain rate, microstructure and density. Med Biol Eng 14:671–680.

Wunderlich RE, Lawler RR, Williams AE. 2011. Field and Experimental Approaches to the Study of Locomotor Ontogeny in *Propithecus verreauxi*. In: D'Août K, Vereecke EE, editors. Primate Locomotion: Linking Field and Laboratory Research. New York, NY: Springer New York. p 135–154.

Wunderlich RE, Tongen A, Gardiner J, Miller CE, Schmitt D. 2014. Dynamics of locomotor transitions from arboreal to terrestrial substrates in verreaux's sifaka (*Propithecus verreauxi*). Integr Comp Biol 54:1148–58.

Xiong J, Gong S, Qiu C, Li Z. 2009. Comparison of locomotor behaviour between white-headed langurs *Trachypithecus leucocephalus* and François' langurs *T. françoisi* in Fusui, China. Curr Zool 55:9–19.

Yamanaka A, Gunji H, Ishida H. 2005. Curvature, length, and cross-sectional geometry of the femur and humerus in anthropoid primates. Am J Phys Anthropol 127:46–57.

Yoder AD, Rakotosamimanana B, Parsons TJ. 1999. Ancient DNA in Subfossil Lemurs. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM, editors. New Directions in Lemur Studies. Springer US. p 1–17.

Youlatos D. 1998. Seasonal variation in the positional behavior of red howling monkeys (*Alouatta seniculus*). Primates 39:449–457.

Youlatos D. 1999. Locomotor and postural behavior of *Sciurus igniventris* and *Microsciurus flaviventer* (Rodentia, Sciuridae) in eastern Ecuador. Mammalia 63:405–416.

Youlatos D. 2002. Positional behavior of black spider monkeys (*Ateles paniscus*) in French Guiana. Int J Primatol 23:1071–1093.

Young JW. 2012. Ontogeny of limb force distribution in squirrel monkeys (*Saimiri boliviensis*): insights into the mechanical bases of primate hind limb dominance. J Hum Evol 62:473–85.

Youlatos D, Karantanis NE, Byron CD, Panyutina A. 2015. Pedal grasping in an arboreal rodent relates to above-branch behavior on slender substrates. J Zool 296:239–248.

Youlatos D, Michael DE, Tokalaki K. 2007. Positional behavior of Siberian chipmunks (*Tamias sibiricus*) in captivity. J Ethol 26:51–60.

Youlatos D, Samaras A. 2010. Arboreal locomotor and postural behaviour of European red squirrels (*Sciurus vulgaris*) in northern Greece. J Ethol 29:235–242.

Biography

Michael C. Granatosky was born in Grosse Pointe, MI on August 15th, 1989, to Michael and Maria Granatosky. Michael graduated from the University of Florida in 2011, with a B.A. in Anthropology and a B.S. in Wildlife Ecology and Conservation. In 2011, Michael entered the Ph.D. program in the Department of Evolutionary Anthropology at Duke University. Michael has received funding and/ awards from the American Association of Physical Anthropologists, the Leakey Foundation, the Force and Motion Foundation, the National Science Foundation's Graduate Research Fellowship Program, the Duke Lemur Center's Molly Glander Award, the University of Florida, and Duke University. Michael has authored or co-authored 24 peer-reviewed publications entitled: Gait kinetics of above and below branch quadrupedal locomotion in lemurid primates; Kinematic and kinetic analysis of arm-swinging in the red-shanked douc langur (*Pygathrix nemaeus*); Distinct functional roles of primate grasping hands and feet during arboreal quadrupedal locomotion; Spatial patterning of bone stiffness in the anterior mandibular corpus of *Macaca fascicularis*: Implications for models of bone adaptation; Morphological Variation in the Mediterranean House Gecko (Gekkonidae: *Hemidactylus turcicus*) Along Geographical Gradients in the Southeastern United States; Lumbar vertebral morphology of flying, gliding, and suspensory mammals: Implications for the locomotor behavior of the subfossil lemurs *Palaeopropithecus* and *Babakotia;* Taxonomic assessment of Alligator Snapping Turtles (Chelydridae: *Macrochelys*), with the description of two new species from the southeastern United States; A New State Record of the Cuban Treefrog, *Osteopilus septentrionalis* (Duméril and Bibron 1841)

(Hylidae), in North Carolina; Functional and evolutionary aspects of axial stability in euarchontans and other mammals; Ontogeny of material stiffness heterogeneity in the macaque mandibular corpus; The Brown Anole, *Anolis sagrei* Duméril and Bibron 1837 (Dactyloidae), State Record and Introduction Pathway; *Nerodia fasciata* (Southern Watersnake): Ectoparasites; *Nerodia fasciata* (Southern Watersnake): Foraging Behavior; Ontogenetic Behavioral Shifts in Habitat Utilization of Treefrogs (Hylidae) in North-central Florida; *Terrapene carolina carolina* (Eastern Box Turtle). Range; Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: Outlining the invasion process and identifying invasion pathways and stages; *Osteopilus septentrionalis* (Cuban Treefrog). Diet; Reduced Stiffness of Alveolar Bone in the Colobine Mandible. *American Journal of Physical Anthropology*; Spatial patterning of bone stiffness variation in the colobine alveolar process; *Anolis sagrei* (Brown Anole). Geographic Distribution; *Caiman crocodilus* (Spectacled Caiman). Diet; *Leiocephalus carinatus* (Northern Curly-tailed Lizard). Geographic Distribution; and The Knight Anole (*Anolis equestris*) in Florida.