An Integrative Investigation of Convergent Bipedal Locomotion in Desert Rodents

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Abstract

Bipedalism is commonly assumed to be an adaptive convergence because it has evolved independently three times in small desert rodents. However, the functional benefits of bipedality in this ecosystem have long been unclear. In this thesis I integrate phylogenetics, functional morphology, biomechanics, information theory, and behavior to investigate whether and how bipedality increases fitness in desert ecosystems, and whether bipedal rodents convergently evolved to have the role in their respective ecosystems.

Based on the diversity of extant dipodid rodents, I begin by statistically reconstructing the pattern of morphological evolution in jerboas. I find that the strongest indicator of bipedality is metatarsal to humerus length, and that changes in this ratio are associated with increased rates of speciation, supporting a punctuated equilibrium pattern of evolution in this clade. Furthermore, the distinct patterns of morphological evolution suggest that a complex suite of genetic and developmental mechanisms governs the acquisition of bipedality in jerboas.

I then use an inverse dynamics approach to characterize the biomechanics of bipedal hopping in a derived jerboa. I find that the dynamics of jerboa hopping are generated predominantly by muscular contractions, rather than tendon–based elastic energy storage and return between strides. Therefore hopping in small rodents favors rapid production and absorption of forces, rather than sustained bouts of steady–state locomotion.

By reviewing predator–prey studies in biomechanics, ecology, and evolution I hypothesize that ricochetal locomotion enhances the ability of small rodents to evade predators that hunt via ballistic interception. I then develop Information Theoretic techniques to measure the unpredictability of escape trajectories in sympatric bipedal and quadrupedal rodents. As expected, bipedal rodents use significantly more unpredictable escape trajectories, likely enhancing predator evasion ability

and enabling foraging in exposed areas with higher predation risk. I then found that bipedal rodents exhibit a stronger preference for exploring open spaces, matching previously established foraging patterns. These findings suggest that the evolution of bipedality enables spatial resource partitioning to limit interspecific competition in desert rodents.

Based on the functional studies in my thesis, I evaluate ecological models to predict the occurrence of convergent bipedal rodents in Myomorpha. I show that diet specialization and aridity are insufficient to predict the locomotor morphology of these rodents and develop novel hypotheses for the convergent evolution of bipedalism in desert rodents.

My thesis investigates the functional consequences of morphological evolution in the context of evolutionary ecology. By considering the interconnectedness of ecology, behavior, and evolution, studies in biomechanics can be designed to inform each of these fields. This interdisciplinary approach is necessary to study the adaptive nature of behavioral traits that are governed by myriad genetic, developmental, and environmental factors.

Contents

Abstract . . . iii
Acknowledgments . . . viii

Introduction **1**

1 Multiple phylogenetically distinct events shaped the evolution of limb skeletal morphologies associated with bipedalism in the jerboas **4**
1.1 Summary . . . 4
1.2 Introduction . . . 5
1.3 Results . . . 6
1.3.1 Axial skeleton . . . 7
1.3.2 Appendicular skeleton . . . 8
1.3.3 Center of mass . . . 9
1.3.4 Identification of limb morphotypes . . . 9
1.3.5 Digit loss . . . 11
1.3.6 Skeletal fusion . . . 12
1.3.7 Hindlimb–Forelimb Allometry . . . 12
1.3.8 Within–Hindlimb Allometry . . . 15
1.4 Discussion . . . 17
1.5 Experimental Procedures . . . 21
1.6 Acknowledgements . . . 23

2 Inverse dynamics of the Lesser Egyptian Jerboa (*Jaculus jaculus*) vertical leaping **25**
2.1 Summary . . . 25
2.2 Introduction . . . 26
2.3 Materials and Methods . . . 27
2.3.1 Animals . . . 27
2.3.2 Experimental Setup . . . 27
2.3.3 Inverse Dynamics . . . 28
2.4 Results . . . 30
2.5 Discussion . . . 34
2.6 Acknowledgments . . . 38

3 Outrun or Outmaneuver: Predator Prey Interactions as a Model System for Integrating Biomechanical Studies in a Broader Ecological and Evolutionary Context 39
3.1 Synopsis . . . 39
3.2 Behavioral studies direct evolutionarily relevant inquiry into biomechanics . . . 40
3.3 Predation is a model system for the integrative study of locomotion, behavior, and evolution . . . 41
3.3.1 Ambush predation . . . 43
3.3.2 Ballistic interception . . . 44
3.3.3 Pursuit predation . . . 46
3.4 Insights from an integrative perspective . . . 47
3.4.1 Understanding how locomotor ecology affects predator–prey interactions aids experimental design . . . 47
3.4.2 Indirectly or directly limiting the predator's ability to predict the locomotion of prey discourages predation . . . 49
3.4.3 Mechanisms determining locomotor variability at multiple levels of biological complexity may confer anti–predator advantages . . . 51
3.5 Future directions . . . 53
3.6 Acknowledgements . . . 54
3.6.1 Funding . . . 54

4 Unpredictability of escape trajectory explains predator evasion ability and taxonomic diversity of desert rodents 55
4.1 Abstract . . . 55
4.2 Significance . . . 56
4.3 Introduction . . . 56
4.4 Results . . . 58
4.4.1 Gait Dynamics . . . 58
4.4.2 Trajectory Unpredictability . . . 60
4.4.3 Risk Aversive Behavior . . . 63
4.5 Discussion . . . 64
4.6 Methods . . . 66
4.6.1 Laboratory Gait Analysis . . . 66
4.6.2 Field Trajectory Unpredictability . . . 67
4.6.3 Entropy Calculation . . . 68
4.6.4 Entropy Significance Test . . . 69
4.6.5 Field–Based Open–Field Exploration Test . . . 70
4.6.6 Laboratory–Based Light–Dark Exploration Test . . . 70
4.7 Acknowledgements . . . 71

5 Modeling the ecological convergence of small bipedal rodents **72**
5.1 Abstract . . . 72
5.2 Introduction . . . 72
5.2.1 Climate . . . 73
5.2.2 Locomotion . . . 74
5.2.3 Dietary Ecology . . . 76
5.3 Methods . . . 77
5.3.1 Morphometrics . . . 77
5.3.2 Diet Data . . . 78
5.3.3 Substrate, Climate, and Occurrences . . . 78
5.3.4 Phylogeny . . . 79
5.3.5 Pilot Study . . . 79
5.3.6 Phylogenetic Comparative Analysis . . . 81
5.4 Results . . . 82
5.4.1 Substrate Analysis . . . 82
5.4.2 Climatic Niche Modeling . . . 83
5.4.3 Hindlimb Morphology . . . 85
5.4.4 Diet Specialization . . . 87
5.4.5 Model Results . . . 88
5.5 Discussion . . . 89
5.5.1 Alternative Hypotheses . . . 92
5.6 Acknowledgements . . . 93

Conclusion **94**

References **98**

Appendix A Appendix to Chapter 1 **113**
A.1 Supplemental Figures . . . 113
A.2 Supplemental Tables . . . 117
A.3 Supplemental Experimental Methods . . . 123

Appendix B Appendix to Chapter 2 **165**
B.1 Supplementary Tables . . . 165

Appendix C Appendix to Chapter 4 **167**
C.1 Supplementary Methods for Continuous Entropy Calculation . . . 167
C.2 Supplementary Results . . . 170
C.2.1 Detailed Light–Dark Box Results . . . 173

Appendix D Appendix to Chapter 5 **174**
D.1 Supplementary Tables . . . 174

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Introduction

Adaptation by natural selection is an important driver of diversity in the natural world. Despite a common familiarity with the concept of adaptation since Empedocles in 430 BC, there are very few cases in which we understand exactly how an adaptation has evolved. This is because selection on an adaptive trait is determined not only by genetic and developmental regulation of morphology, but how that morphology interacts with the environment through individual behavior (e.g. predator evasion, foraging).

Bipedal hopping has evolved multiple times in desert rodents that are crepuscular (twilight–active), burrowing, and granivorous. Due to similarities in climate, morphology, resource use, and predators, it was commonly assumed that bipedalism is adaptive in these animals, convergently evolving under similar selection pressures in similar ecosystems. In this thesis I undertake studies in morphology, biomechanics, locomotor ecology, and phylogenetic modeling to investigate whether bipedalism is an adaptive convergence.

In my first chapter I identify and trace the evolutionary history of morphological features that are associated with bipedalism. Bipedal rodents can be identified by their elongate hindlimbs and reduced forelimbs. In jerboas (Superfamily Dipodoidea), the largest and most ancient group of bipedal rodents, features associated with bipedalism are associated with increased rates of speciation, providing evidence for punctuated equilibrium in this clade. This pattern of evolution supports the idea that bipedalism is an adaptation, possibly shifting the ecological niche of the rodent and releasing it from competition.

To understand how bipedality determines the ecology of rodents, my second chapter uses controlled, laboratory–based settings to characterize the dynamics of bipedal hopping. By comparing jerboas to existing data on kangaroo rats (*Dipodomys sp.*) and red kangaroos (*Macropus*

rufus), I find that bipedal locomotion at small scales is vastly different to bipedal hopping at large scales. Bipedal hopping in small rodents favors the rapid production and absorption of high forces and quick changes in speed and direction, but decreases the ability to sustain locomotion.

The literature review in my third chapter provides an ecological context for understanding how this energetically costly locomotion can enhance fitness. I hypothesize that these short bouts of unpredictable locomotion by prey are especially effective for evading single–strike predators — those that hunt by predicting an animal's future location and committing to an intercept trajectory.

To test whether bipedal rodents are more unpredictable than sympatric quadrupedal rodents, my fourth chapter simulates predation events in semi–natural conditions, and uses Information Theory to quantitatively the escape trajectories of sympatric rodents. I find that all bipedal rodent escape trajectories are significantly more unpredictable than those of their sympatric quadrupeds. In addition, I show that bipedal rodents show a stronger preference for exploration of open environments when compared to sympatric quadrupedal rodents. Thus, bipedal rodents are equipped with both the biomechanical and the behavioral opportunity to successfully forage in open–field environments common to desert ecosystems.

The divergence in microhabitat preference corresponding to locomotor unpredictability suggests that desert rodents spatially partition resources. Bipedal rodents can be highly selective while foraging in exposed areas with greater predation risk. Conversely, quadrupedal rodents must be less selective as they are limited to areas protected from predators. My fifth chapter tests whether differences in diet specialization and climate can be used to predict the occurrence of bipedal rodents. By constructing an climatic niche model, I show that the presence and absence of each bipedal rodent is primarily predicted by different climatic variables, though aridity is an important factor in all bipedal niche models. I then compile data from primary and secondary literature to determine diet specialization across 127 taxa in the mouse–related clade of rodents that include all three acquisitions of desert bipedalism. Using Phylogenetically–Generalized Least–Squares methods I demonstrate that although the existing ecological literature suggests that these factors are important determinants of bipedal rodent ecology, they are not sufficient to predict the variation we see in the locomotor morphology of Myomorpha.

My results support previous studies suggesting that bipedal rodents do not currently fulfill the same ecological niche in each desert ecosystem. Yet, the functional advantages of bipedality

in response to predation remain similar. Although the climatic and foraging niches of bipedal rodents may not be exactly convergent, they may fulfill an equivalent functional role in each ecosystem. Field–based functional studies and observations of behavioral interactions within and between species are necessary to determine whether bipedality in desert rodents is indeed an adaptation to fill an equivalent ecological niche.

Chapter 1

Multiple phylogenetically distinct events shaped the evolution of limb skeletal morphologies associated with bipedalism in the jerboas [1]

1.1 Summary

Recent rapid advances in experimental biology have expanded the opportunity for interdisciplinary investigations of the evolution of form and function in non–traditional model species. However, historical divisions of philosophy and methodology between evolutionary/organismal biologists and developmental geneticists often preclude an effective merging of disciplines. In an effort to overcome these divisions, we take advantage of the extraordinary morphological diversity of the rodent superfamily Dipodoidea, including the bipedal jerboas, to experimentally study the developmental mechanisms and biomechanical performance of a remarkably divergent limb structure. Here, we place multiple limb character states in a locomotor and phylogenetic context. While obligate bipedalism arose once in the ancestor of extant jerboas, we find that

[1] Co–authored with Chris L. Organ, Scott V. Edwards, Andrew A. Biewener, Clifford J. Tabin, Farish A. Jenkins Jr., Kimberly L. Cooper. Originally published in Current Biology 2015. (Moore *et al.*, 2015a)

digit loss, metatarsal fusion, between limb proportions, and within hindlimb proportions all evolved independently of one another. Digit loss occurred three times through at least two distinct developmental mechanisms, and elongation of the hindlimb relative to the forelimb is not simply due to growth mechanisms that change proportions within the hindlimb. Furthermore, we find strong evidence for punctuated evolution of allometric scaling of hindlimb elements during the radiation of Dipodoidea. Our work demonstrates the value of leveraging the evolutionary history of a clade to establish criteria for identifying the developmental genetic mechanisms of morphological diversification.

1.2 Introduction

The vertebrate limb has long been of interest to evolutionary biologists due to the extraordinary diversity of forms, to biomechanists for the corresponding variety of locomotor functions, and to developmental biologists as a model of patterning and morphogenesis. We stand to gain a more complete understanding of the mechanisms that shape the development and evolution of form and function by integrating these traditionally distinct disciplines. We focus on the rodent superfamily, Dipodoidea, comprised of 51 extant species including the quadrupedal birch mice, facultative bipedal jumping mice, and 33 species of obligate bipedal jerboas (Lebedev *et al.*, 2013). Together, these species exhibit diverse limb morphologies with varying degrees of specialization. The most basal species exhibit an ancestral generalized quadrupedal rodent morphology while the most derived bipedal species have lost the pre– and postaxial hindlimb digits, greatly elongated the hindlimbs, and disproportionately elongated and fused the three central metatarsals.

Studies of jerboa anatomy have been largely limited to dissections of a few species and casual observations of captive individuals prior to the 1940s (Flower and Lydekker, 1891; Lull, 1904; Howell, 1932; Hatt, 1932). Even at that time, the morphological characters associated with bipedal saltation in the jerboas were noted as similar to those associated with cursorial locomotion in more familiar and better–studied quadrupedal ungulates. Elongated limbs increase range of motion while reduced distal elements decrease the energy required to swing the limb during sustained running (Lull, 1904; Biewener, 2005). However, the inaccurate and often contorted posture of jerboas in museum exhibits and texts dating to the late 19th and early 20th century (Jones, 1871)

highlights a general unfamiliarity in the West with the way these animals actually move.

The diverse morphologies of extant dipodoid rodents have long been a challenge to pre–molecular taxonomists. These trees are well–reviewed elsewhere (Lebedev *et al.*, 2013). Recently, DNA sequence phylogenetics has resolved the relationships of taxa within Dipodoidea, the monophyletic origin of bipedalism, and the subsequent radiation of species (Lebedev *et al.*, 2013; Zhang *et al.*, 2012; Wu *et al.*, 2014; Pisano *et al.*, 2015). Given that the genes included in these analyses are not under selection for bipedal locomotion, these broadly consistent molecular phylogenies likely represent the true taxonomic relationships. Therefore many of the morphological characters previously used to assign relationships are convergent. The consensus molecular tree thus provides an opportunity to understand evolutionary patterns of these complex morphologies. Here, we first generate posturally–accurate skeletal reconstructions to understand the locomotor advantage of derived skeletal characters of the obligate bipedal jerboa compared to a close quadrupedal relative. We next identify eight distinct hindlimb morphotypes represented within Dipodoidea based on digit number, the extent of metatarsal fusion, and limb element allometry. We then trace the evolutionary history of each character in the context of a multi–locus, time–calibrated molecular phylogeny. We show that the adaptation of limb structure for a specialized locomotor strategy occurred through a combination of temporally and therefore genetically distinct changes during the radiation of Dipodoidea. Our work demonstrates the value of phylogenetic analyses in evolution and development, particularly in species too distantly related for genetic hybridization, in which multiple intersecting lines of evidence are critical to strengthen hypotheses regarding developmental mechanism that are often initially correlative in nature.

1.3 Results

The acquisition of bipedality in jerboas coincides with multiple skeletal transformations (Howell, 1932), (Hatt, 1932) that are most informative in the context of a living animal in movement. Thus we generated to–scale postural reconstructions of the complete skeletons of the three–toed lesser Egyptian jerboa, *Jaculus jaculus* and one of the most closely related extant quadrupeds, the Northern birch mouse, *Sicista betulina* (Lebedev *et al.*, 2013). The illustration of *J. jaculus* is informed by X–ray fluoroscopy of a live jerboa (Figure A.3) and is represented in an aerial phase

just prior to landing. Since a living birch mouse was not available for imaging, we reconstructed the skeleton of *S. betulina* based on postural data of a morphologically similar semi–arboreal species (Horner, 1954) – the forest deer mouse, *Peromyscus maniculatus* (Figure A.4). While largely qualitative in nature due to specimen limitations, our observations provide context for the major postural and skeletal changes in the evolution of jerboa bipedalism.

1.3.1 Axial skeleton

The foreshortened skull and thorax of *J. jaculus* are suspended from the pelvis by a vertebral column that is highly modified when compared to quadrupedal rodents (Hatt, 1932) (Figure 1.1). The jerboa vertebral column appears to have a more extreme sigmoidal curvature: the lumbar column of *J. jaculus* aligns almost horizontally with respect to gravity, while the thoracic column dives vertically and curves again with the pronounced dorsiflexion of a shortened neck.

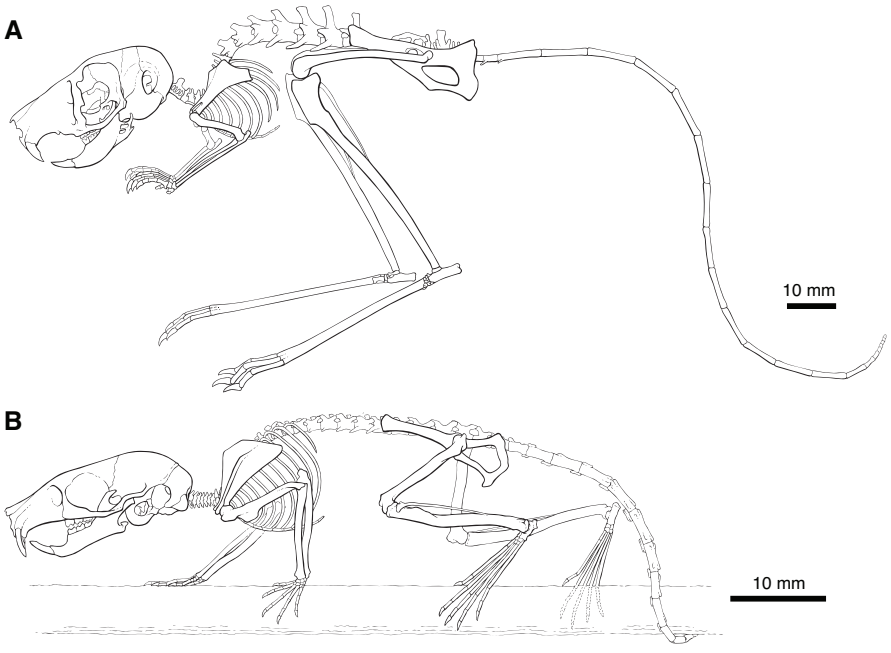


Figure 1.1: *Comparison of the bipedal lesser Egyptian jerboa (A,* Jaculus jaculus*) and the semi–arboreal quadrupedal Northern birch mouse (B,* Sicista betulina*) in the context of posture in movement.*

While the first cervical vertebra (C1, or atlas) is freely mobile in the jerboa, the central cervicals (C2–C6), including the axis, are fused ventrally into a single plate and dorsally into a single large spinous process with lateral openings for the egression of the cervical spinal nerves. The

posterior cervical vertebra, C7, is unfused. This is concordant with Howell (Howell, 1932) for the genus *Jaculus*, whereas Beddard (Beddard, 1902) and Lull (Lull, 1904) reported the posterior six to be fused in *Dipus*. Flower and Lydekker (Flower and Lydekker, 1891) reported all the cervical vertebrae in *Dipus*, *Alactaga* [sic], and *Platycercomys* (now *Pygeretmus*) to be "more or less ankylosed." Indeed our investigation of several available related taxa (Table A.1) indicates varying degrees of fusion with a subset of vertebrae fully fused, as in *J. jaculus*, or tightly articulated with thin fissures between vertebrae as in *Salpingotus thomasi* and *Allactaga tetradactyla*. In *Sicista* there are seven unfused cervical vertebrae, and only C2, the axis, has a prominent neural spine.

As with most rodents (Burke *et al.*, 1995), *S. betulina* has 13 thoracic vertebrae, and T10 is the anticlinal vertebra. In contrast, there are 12 thoracic vertebrae in *J. jaculus*, and T12 is the anticlinal vertebra. The presence of seven lumbar vertebrae in *J. jaculus* compared to six in *S. betulina* suggests a transformation of T13 into a lumbar vertebra with an additional posterior shift in the position of the anticlinal vertebra. Howell (Howell, 1932) suggested that by transforming the last thoracic vertebra into an additional lumbar vertebra, the jerboa shortens the thorax without decreasing the size of each individual thoracic vertebral element, which we confirmed (Table A.2).

Of the four sacral vertebrae in *J. jaculus*, only the first is fused to the ilium whereas the first two are fused in *S. betulina*. Decreased fusion may increase iliosacral mobility during jumping in *J. jaculus* as in frogs that have limited iliosacral contact (Shubin and Jenkins, 1995). The sacrum of *J. jaculus* is widened in comparison to *S. betulina*, and the spinous processes of the lumbar vertebrae are enlarged, which may support greater back musculature and also increase jumping ability (Hatt, 1932). Additionally, the spinous process of the 4th sacral vertebra is enlarged, indicating robust tail suspensory musculature. *J. jaculus* has 24 elongate caudal vertebrae, and the tail is approximately 1.47 times the naso–anal distance ($n = 3$; $s.d. = 0.12$). *S. betulina* has 34 caudal vertebrae, and the tail is 1.25–1.5 times the naso–anal distance varying by population (Shenbrot *et al.*, 2008), (Olsen, 2013).

1.3.2 Appendicular skeleton

The composite hindlimb length from the greater trochanter of the femur to the distal tip of the central metatarsal is approximately 3.2 times the length of the analogous forelimb elements for the

jerboa, compared to 1.4 times for the birch mouse (Table A.1). Within hindlimb proportions also differ between species. Whereas the femur of *S. betulina* comprises 34.6% and the third metatarsal is 20.5% of total limb length, the femur of *J. jaculus* is 28.6% and the third metatarsal is 30.6% of hindlimb length. The proportion of the tibia is more similar at 44.9% for *S. betulina* and 43.0% for *J. jaculus*. The small vestiges of the first and fifth metatarsals of the jerboa are tucked along the ventral–lateral edges of the fused central canon bone, which is comprised of metatarsals II–IV. The distal–most aspect of the canon bone remains unfused and articulates with each of the three toes. Lastly, the quadrupedal rodents are plantigrade (fore) and digitigrade (hind) (Figure A.4) while the bipedal *J. jaculus* is sub–unguligrade (Figure A.3). The nails and distal toe pads contact the ground while the digits are elevated atop a tuft of coarse bristles on the plantar surface of the toes.

1.3.3 Center of mass

The reduction of the thorax and expansion of the lumbar region together with the position of the body with respect to the limbs in our X–ray videos led us to hypothesize that the center of mass may be shifted in the bipedal jerboa relative to quadrupedal rodents. We found the center of mass of *P. maniculatus* is located approximately 54.5% ($n = 3$; $s.d. = 0.073\%$) of the naso–anal distance consistent with the quadrupedal Siberian chipmunk, *Tamias sibiricus* (Lammers and Zurcher, 2011). The center of mass of *J. jaculus* measures only slightly more posterior at 57.5% ($n = 4$; $s.d. = 0.025\%$) of the naso–anal distance. More striking, we found in our X–ray videos that the hindlimb base of support of *P. maniculatus* at mid–stance is positioned approximately 74% of the distance from head to tail base while the jerboa hindlimb base of support is approximately 47% of body length. This places the center of mass approximately 19% ahead of the hindlimb base of support of *P. maniculatus* and 11% behind the hindlimb base of support of *J. jaculus*.

1.3.4 Identification of limb morphotypes

We classified eight distinct hindlimb morphotypes among the 51 extant species of Dipodoidea based primarily on degree of metatarsal fusion and number of digits (Lebedev *et al.*, 2013), (Walker, 1964) (Table A.3) and broadly considering allometric scaling of the hindlimb and principal components clustering discussed in further detail below. These include the quadrupedal birch

mouse (Sicistinae), the facultative bipedal jumping mice (Zapodinae), and six morphotypes within the obligate bipedal jerboas (Figure 1.2).

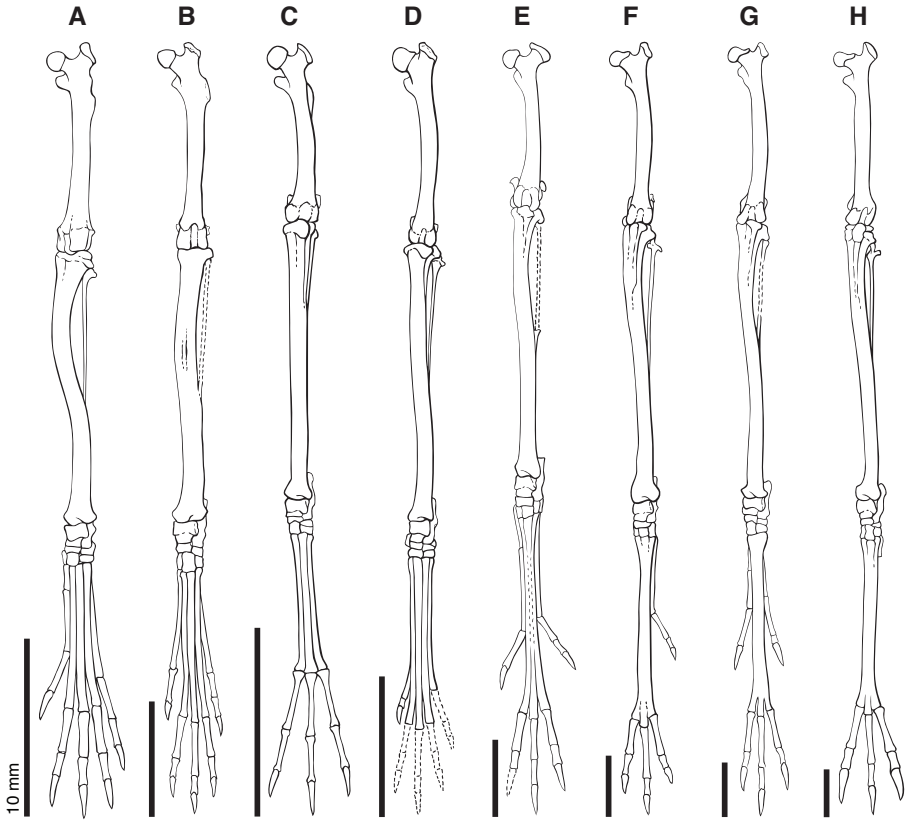


Figure 1.2: *Frontal illustrations of the hindlimbs of a representative of each morphotype scaled to the same length. (A)* Sicista betulina*. (B)* Napaeozapus insignis insignis*. (C)* Salpingotus thomasi*. (D)* Cardiocranius paradoxus*. (E)* Euchoreutes naso*. (F)* Allactaga tetradactyla*. (G)* Allactaga sibirica *[*mongolica*]. (H)* Jaculus orientalis*. Dashed outlines indicate missing elements.*

One distinctive feature of the *S. betulina* hindlimb relative to other dipodoid rodents is the lateral curvature of the tibia (Figure 1.2A). Curvature of long bones is indicative of predictable off–axis bending forces (Bertram and Biewener, 1988). In the case of *S. betulina*, tibial long–axis curvature may reflect laterally–directed loading forces during climbing as evidenced by the mediolateral orientation of the femur and undulation of the pelvis during locomotion in *P. maniculatus* (Figure A.6) (Biewener, 1989). In contrast, *J. jaculus* hindlimbs fall directly below the body during locomotion (Figure A.5), and the tibia is straighter in each of the obligate bipedal species (Figure 1.2C–H). The shape of the femoral head also transforms from a rounded knob in *S. betulina* (Figure 1.2A) to a saddle shape with a femoral neck oriented nearly perpendicular with

respect to the bone shaft in the most derived of the jerboas (Figure 1.2F–H).

Compared to quadrupedal *S. betulina*, the facultative bipedal jumping mice, including *Napaeozapus insignis*, have slightly elongated metatarsals comprising a larger proportion of the hindlimb length discussed in detail below (Figure 1.2B, 5B). Significant morphological diversity arises in the obligate bipedal jerboas. The three and five–toed pygmy jerboas (Cardiocraniinae – Figure 1.2C, *Salpingotus thomasi* and Figure 1.2D, *Cardiocranius paradoxus*, respectively) have individual metatarsals that do not fuse. The long–eared jerboa, *Euchoreutes naso* has five toes with elongated and partially fused metatarsals II–IV (Figure 1.2E, partial fusion indicated by dashed lines). The Allactaginae are represented by *Allactaga sibirica* (Fig 2G) with a fully fused canon bone comprised of metatarsals II–IV and five toes where the central three are much larger and longer than digits I and V. A single species, *A. tetradactyla* (Figure 1.2F) has lost the anterior–most digit and retains digits II–V. The Dipodinae, including *Jaculus orientalis* (Figure 1.2H), are characterized by the same elongate and fused central canon bone but have entirely lost the pre– and postaxial digits and have only digits II–IV remaining. Using the molecular reconstruction of Wu *et al.* (2014), with the addition of *Allactaga tetradactyla*, we mapped each of these osteological character states.

1.3.5 Digit loss

Early taxonomies placed the four–toed jerboa, *Allactaga tetradactyla*, within the five–toed jerboas of Allactaginae indicating an independent loss of the first digit within this clade (Wilson and Reeder, 2005). An alternative hypothesis is that the four–toed jerboa represents an ancestral state to the three–toed morphology and that cranial and dental morphologies are convergent. To test these hypotheses, we examined the position of *A. tetradactyla* and found that the species indeed groups within Allactaginae and most closely with *A. hotsoni*, suggesting a relatively recent and independent loss of the first digit (Figure 1.3A; Figure A.1). Additionally, the three–toed pygmy jerboa, *Salpingotus thomasi*, groups with the five–toed pygmy jerboa, *Cardiocranius paradoxus*, and ancestral to the divergence of Euchoreutinae, Allactaginae, and Dipodinae. This suggests the independent loss of digits occurred at least three times – in *Salpingotus* and in Dipodinae with loss of the pre– and postaxial digits and with loss of the pre–axial digit in *A. tetradactyla*. However, while pre– and postaxial digits are present in many jerboa species, they are effectively

non–functional for locomotion in Euchoreutinae and Allactaginae, as they flank the central canon bone and do not contact the substrate (pers. observation).

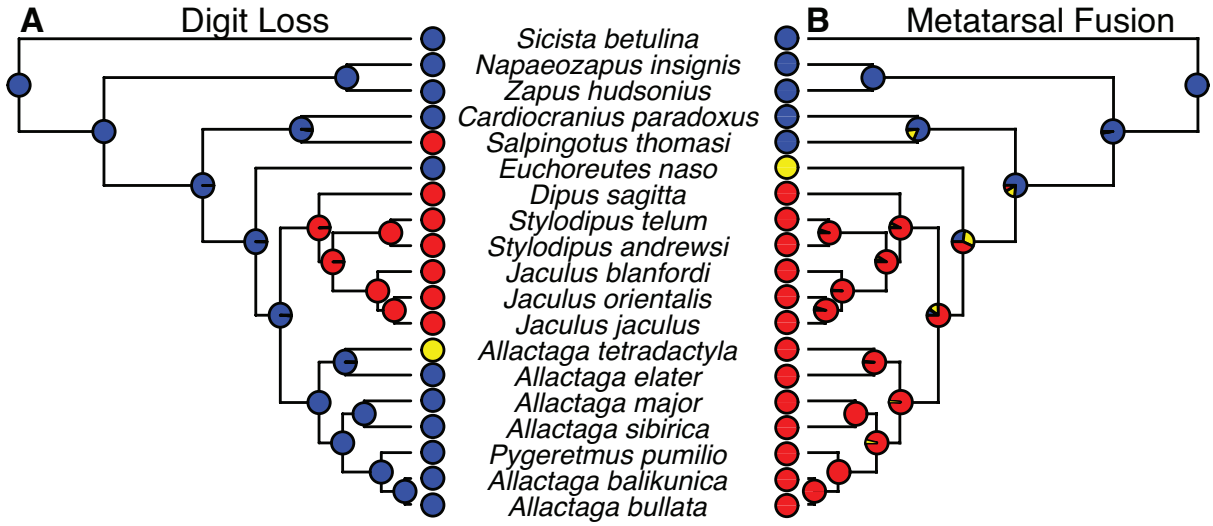


Figure 1.3: *Discrete characters, (A) digit loss and (B) metatarsal fusion, mapped on a molecular phylogeny of Dipodoidea. The ancestral state is blue, the intermediate derived state is yellow (four toes or partially fused), and the ultimate derived state is red. The probability of the ancestor at each node taking a specific state is denoted by a pie graph at that node.*

1.3.6 Skeletal fusion

The single species within Euchoreutinae, *Euchoreutes naso*, also represents the emergence of partial fusion of the three central metatarsals, and all species of Allactaginae and Dipodinae have completely fused central metatarsals (Figure 1.3B). Thus metatarsal fusion is monophyletic within the jerboas.

1.3.7 Hindlimb–Forelimb Allometry

Allometric scaling refers to a change in the size of an element relative to another or as a proportion of the whole body. Differences in cranial length and body proportions complicate the use of axial length for body size normalization. Additionally, because the taxa are not independent from one another, the variation in morphological measurements in closely related groups would be less than expected under a Brownian Motion model. Thus, we performed a phylogenetically–weighted Principal Components Analysis (pPCA) to remove the effect of relatedness and body size on our

morphological measurements (Revell, 2009). To better understand the scaling relationships and the dynamics of allometric scaling over evolutionary time, we expanded our analysis to a broad selection of rodents representing diverse forms of locomotion.

We used measurements of the femur, tibia, third metatarsus, and humerus in our analysis. Distal forelimb elements were often not available for measurement in many specimens, but the humerus and metacarpals do scale approximately isometrically for available specimens within Myomorpha (Figure A.2A). The first phylogenetically–weighted principal component (pPC1) accounts for 90.9% of the variation in the data, loads approximately equally with all of our morphological measurements (Table A.4), and therefore associates with changes due to body size. The remaining principal components (pPCs 2, 3, 4) all describe variation in limb proportions independent of body size. pPC2 loads strongly positively with the metatarsus and negatively with the humerus, and accounts for 86.1% of the remaining morphometric variation in limb proportions. This relationship is illustrated by the repeated appearance of rodents with

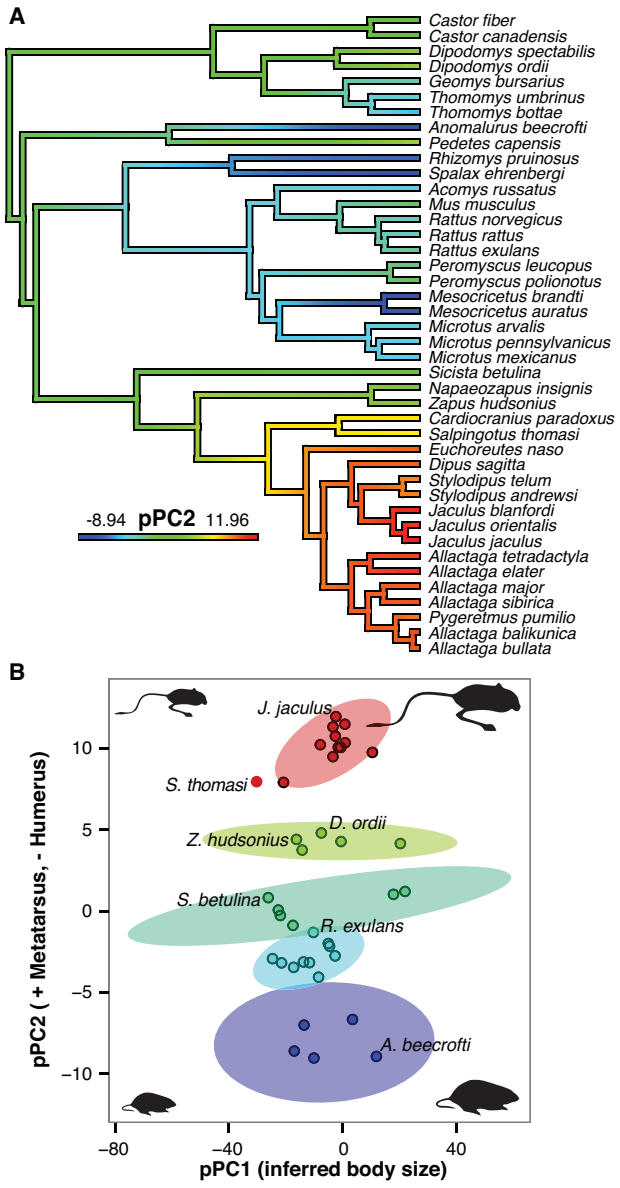


Figure 1.4: *Phylogenetically corrected principal components analysis illustrates major proportional differences across rodent limbs. (A) pPC2 is mapped as a continuous trait on the phylogeny of rodents with ancestral states reconstructed (graded color). (B) Clusters of similar ecomorphs plotted with respect to pPC1 (representing variation due to body size; 90.9% of the total variance) and pPC2 (representing degree and direction of limb specialization; 86.1% of remaining variance with pPC1 removed). Shaded ellipses demark the 95% confidence interval of each cluster.*

elongate metatarsals, shortened humerus, and large values of pPC2, and rodents with shorter metatarsals, elongate humerus, and small values of pPC2 (Figure 1.4A; Table A.5).

The hypothesis that limb skeletal structures in the body are predominantly shaped according to their functions predicts that grouping animals with similar limb proportions should also categorize species according to similar locomotor ecomorphs. Since pPCs 2, 3, and 4 each represent changes in limb element proportions independent of body size, we performed a clustering analysis on these principal components (Figure 1.4B; Figure A.2B). We identified up to five distinct clusters that are separated predominantly by values in pPC2 and correspond well to known locomotor ecomorphs from diggers and gliders (longer forelimb) to the most derived of obligate bipedal species (longer hindlimb) (Walker, 1964), (Samuels and Van Valkenburgh, 2008), (Feldhamer *et al.*, 2015).

Starting from the lowest values of pPC2, the first group includes the fossorial mole–rat (*Spalax*) and bamboo rat (*Rhizomys*), the semi–fossorial hamsters (*Mesocricetus*) (Larimer *et al.*, 2011), and the gliding spiny tailed squirrel (*Anomalurus*). The second group contains fossorial gophers (*Thomomys and Geomys*), and the generalist voles (*Microtus*), spiny mouse (*Acomys*), and rats (*Rattus*). *Rattus exulans* falls within the 95% confidence intervals of both this group and the third group, which contains the semi–aquatic beavers (*Castor*), the generalist house mouse (*Mus*), and the semi–arboreal/generalist deer mice (*Peromyscus*) (Hyams *et al.*, 2012) and semi–arboreal birch mouse (*Sicista*). The fourth group has no overlap with the previous and includes the facultatively bipedal jumping mice (*Napaeozapus* and *Zapus*) and kangaroo rat (*Dipodomys*) and the large obligate bipedal springhare (*Pedetes*). The fifth group exhibits the greatest separation from the previous groups and includes all of the obligate bipedal jerboas.

To quantify the allometric scaling relationships within Dipodoidea, we generated log–transformed[2] plots of the combined length of the hindlimb elements (femur, tibia, and third metatarsal) versus the forelimb elements (humerus, ulna, and third metacarpal) (Figure 1.5A, C). Log transformation of limb lengths allows us to compare the scaling relationships between groups of animals using a linear regression (Huxley, 1924). For comparison to bipedal species, we chose the "mouse–like" generalist/semi–arboreal quadrupedal rodents in the second and third ecomorph groups described

[2]Post–publication comment: Log base 10

above. These all fall along a line (blue) with a slope of 0.991 indicating that the smallest birch mouse (*S. betulina*) has the same hindlimb to forelimb proportions as the largest rat (*R. exulans*). All of the highly derived bipedal Allactaginae and Dipodinae together form a line (red) with very similar slope of 0.979 but with a positively shifted y–intercept from 0.160 to 0.521 indicating an increased length of the hindlimb relative to forelimb. A phylogenetically controlled ANCOVA test strongly supports two regression lines for different limb ratios between the quadrupedal and most–derived bipedal species (Table A.6; $p = 4E - 08$). The jumping mice (e.g. *Z. hudsonius*), three– and five–toed pygmy jerboas (*S. thomasi* and *C. paradoxus*) and the long–eared *E. naso* lay between and outside the 95% confidence intervals (grey shading) of the regression lines for quadrupedal and derived bipedal species and are designated as "basal bipeds" (orange).

1.3.8 Within–Hindlimb Allometry

We next sought to test the hypothesis that the allometric scaling between limbs is mechanistically attributed to the change in proportion of elements within the hindlimb. In a log–log plot of metatarsus versus femur, the group two and three ecomorphs, including *S. betulina*, fit a regression line (blue) with a slope of 0.729 (Figure 1.5B). Again, the most derived bipedal jerboas (Allactaginae and Dipodinae) form a line (red) with a y–intercept shifted upward to 0.151 from –0.002 in quadrupedal species and slope of 0.893 indicating a relative increase of metatarsus:femur ratio. Phylogenetically controlled ANCOVA strongly supports two regression lines (Table A.6; $p = 3E - 03$) compared with a single regression model. The jumping mice (e.g. *Z. hudsonius*) and pygmy jerboas, *S. thomasi* and *C. paradoxus*, fall between these lines. However, while the pygmy jerboas are between the confidence intervals for between limb proportions (Figure 1.5A), they lie within the 95% confidence interval (grey shading) of derived bipeds for within hindlimb allometry (Figure 1.5B). This may be in part due to the majority of more derived bipedal jerboas with larger values of metatarsal and femur lengths, resulting in a spread of the confidence interval at smaller values. This hypothesis is further supported by the observation that *S. thomasi* and *C. paradoxus* have smaller metatarsal:femur ratios than one would expect given their phylogenetic position among obligate bipeds (Figure 1.5D). A Bayesian phylogenetic outlier test (Organ *et al.*, 2011) demonstrates that 94% of the predictive distribution for the metatarsal:femur ratio of obligate

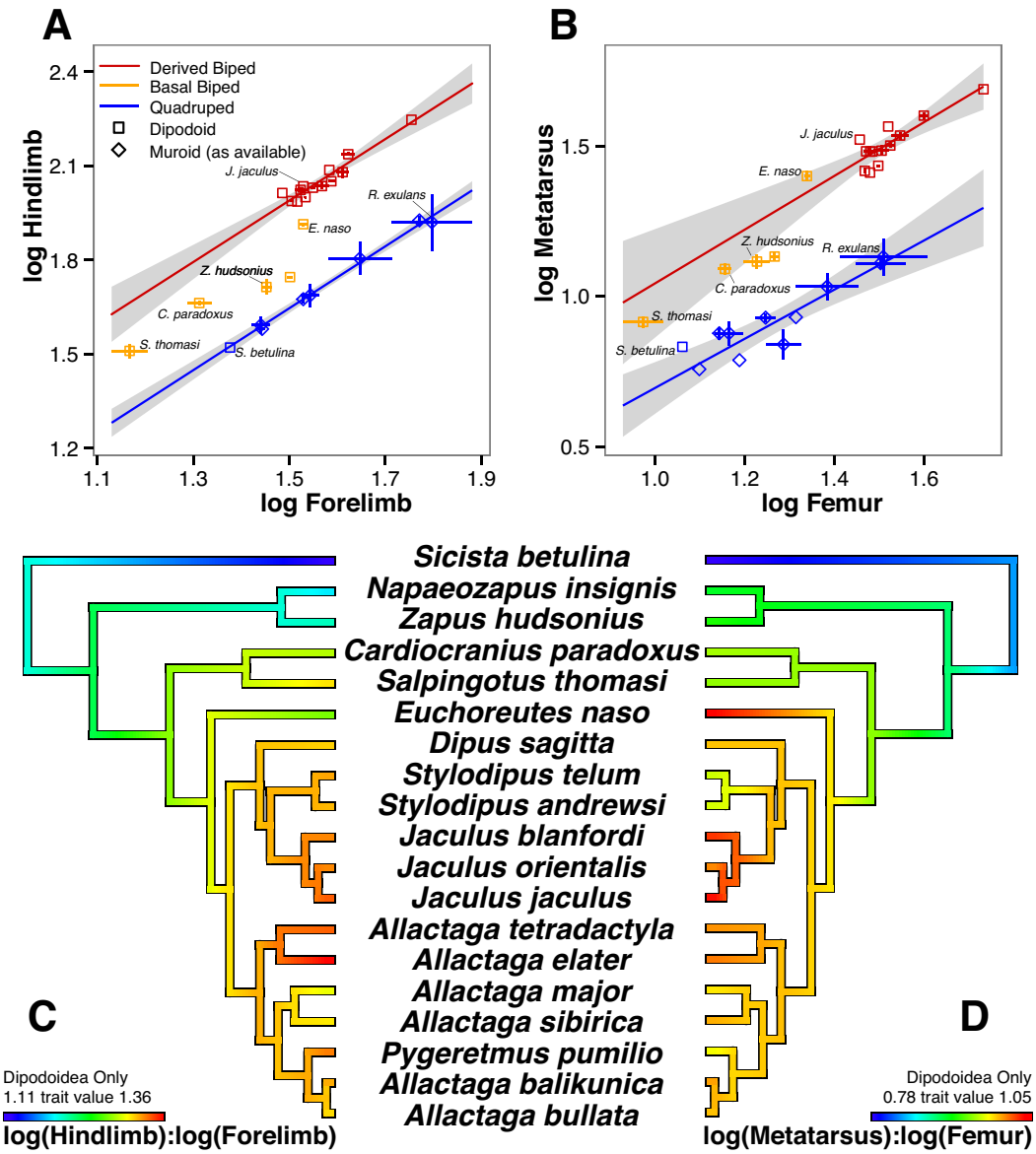


Figure 1.5: *Allometric scaling between limbs and within the hindlimb illustrates the complex evolution of proportion. Log–log plots illustrating scaling of (A) hindlimb versus forelimb and (B) metatarsus versus femur. Derived bipeds, Allagtaginae and Dipodinae, are designated red. Basal and intermediate bipeds, Zapodinae, Cardiocraniinae, and Euchoreutinae, are designated orange. Quadrupeds that cluster together in the second and third ecomorph groups are designated blue. Grey shading indicates 95% confidence intervals, and vertical and horizontal lines represent variation one standard deviation away from the mean. Phylogenies of Dipodidae, with (C) log_{10}(hindlimb):log_{10}(forelimb) or (D) log_{10}(metatarsal):log_{10}(femur) mapped as continuous traits with ancestral states reconstructed by maximum likelihood (graded color).*

bipeds lies above the measured ratios of these two species.

In stark contrast to its low hindlimb:forelimb ratio compared to the most derived bipedal jerboa taxa (Figure 1.5A), the long–eared jerboa, *Euchoreutes naso*, falls within the 95% confidence

interval of the regression for metatarsus:femur (Figure 1.5B). Indeed, while both ratios follow a trend toward increasing values in more derived species, they do not share the same distribution [Figure 1.5C, D; Wilcoxon signed–rank test: $n = 19$, sum of ranks $(V) = 190$, $p = 3.82E-6$]. Together these trees suggest the mechanisms that establish the proportion of hind relative to forelimb length are genetically separable from the mechanisms that determine proportions within the hindlimb.

Lastly, we analyzed rates of evolutionary allometric growth versus rates of net speciation (nodes along phylogenetic path lengths) as a test for punctuated evolution where the coefficient of determination ($R2$) denotes the percent of character variation explained by punctuated evolution, and the slope of the regression (β) represents the magnitude of the effect of punctuation (Pagel *et al.*, 2006). A correlation between trait values and net speciation suggests that the trait in question underwent punctuated, rather than gradual, evolution – though not necessarily punctuated equilibrium as originally defined by Eldredge and Gould Eldredge and Gould (1972) because of the inability to detect periods of stasis. Although the exact process producing such a pattern is difficult to determine (Pennell *et al.*, 2014), such a test does imply that bursts of morphological change were coupled with speciation (Pagel *et al.*, 2006; Mattila and Bokma, 2008; Venditti and Pagel, 2010; Rabosky *et al.*, 2013; Venditti and Pagel, 2014).

We find that the lengths (log) of hindlimb elements are all strongly correlated with net speciation along phylogenetic path lengths (Table A.7; metatarsal $R^2 = 0.293$, $\beta = 0.0519$, $p = 0.006$; tibia $R^2 = 0.762$, $\beta = 0.0669$, $p = 8.45E-9$; femur $R^2 = 0.657$, $\beta = 0.0575$, $p = 6.63E-7$) while the lengths (log) of forelimb elements are at most marginally significant (Table A.7; metacarpal $R^2 = 0.052$, $\beta = 0.0191$, $p = 0.12$; ulna $R^2 = 0.164$, $\beta = 0.0307$, $p = 0.05$; humerus $R^2 = 0.153$, $\beta = 0.0333$, $p = 0.04$). This suggests that hindlimb length underwent more evolutionary change during speciation rather than gradual Darwinian change over time in all branches.

1.4 Discussion

The evolution of bipedal locomotion is associated with dramatic changes in structure and posture. Indeed, Hatt (1932) accurately depicts the bipedal rodents, jerboas included, as “so compacted

as to be popularly described as looking like potatoes on toothpicks." *J. jaculus* has transformed to an elevated horizontal body posture, suspended from the pelvis, and has shifted the single position of support to lie ahead of the center of mass. This likely increases stability and may require less energy to prevent forward pitching during bipedal locomotion. Cervical fusion and neck shortening in saltatorial rodents may further stabilize the head during the quick maneuvers and high–acceleration jumps typical of jerboa escape behaviors (Hatt, 1932). With the neck stabilized, the elongate tail may serve as a more effective counterbalance with the potential to control body orientation during the aerial phase of locomotion as has been proposed for kangaroo rats (Bartholomew and Caswell, 1951) and lizards (Libby *et al.*, 2012a).

The appendicular skeletal changes are even more pronounced than those of the axial skeleton. The straightness of the tibia and the saddle–shaped femoral head suggest reduced variability in the direction of skeletal loading stresses (Bertram and Biewener, 1988) perhaps due to the restricted range of motion primarily limited to a sagittal plane in the strictly cursorial[3] *J. jaculus*. Also associated with the acquisition of bipedal locomotion, the hindlimbs of jerboas are elongate while the forelimbs, released from the constraints of quadrupedal locomotion, are slightly reduced in size. The strong correlation between degree of hindlimb allometric specialization and speciation events at nodes suggests that one may have driven the other. Therefore punctuated evolution likely represents the mode of radiation of Dipodoidea coincident with the climactic changes in the region at the time of the Himalayan uprising that led to ecological diversification (Pisano *et al.*, 2015).

Hindlimb elongation also coincides with fusion of the three central metatarsals into a single bone in all Allactaginae and Dipodinae, which according to beam theory (Gere and Timoshenko, 1999) likely increases metatarsal resistance to bending loads by increasing the second moment of area, thus providing more effective weight support. This may be an important structural adaptation since bipedal saltation increases hindlimb loading in two ways. First, the body weight is entirely supported by both or a single hindlimb, depending on gait. Second, saltatory locomotion necessitates an aerial phase, which increases forces associated with take off and landing (Hayes and Alexander, 1983).

[3]Post–publication comment: The term 'cursorial' here is meant to imply sagittal motion in contrast to lateral undulation. The dynamics of Jerboa locomotion in fact reflect ricochetal saltation (as described in Chapters 2 and 4)

While metatarsal fusion occurred once, digit loss has occurred repeatedly in the evolution of Dipodoidea. Hindlimb elongation increases stride length and is compensated for by digit reduction to decrease the limb moment of inertia (Lull, 1904), (Biewener, 2005). Whereas the Allactaginae retain five hindlimb digits, the axial and postaxial digits are smaller and do not make contact with the ground. It is possible therefore that both digit size reduction and loss provide an energetic advantage by decreasing the distal mass and energy required to propel and redirect the motion of the limb.

Our analysis of characters associated with bipedalism also provides an opportunity to approximate genetic complexity and to identify species, structures, and genetic pathways for further analysis. For example, Klippel–Feil Syndrome (Tassabehji *et al.*, 2008) and Apert Syndrome (Yu *et al.*, 2000) are human syndromes that include cervical vertebral fusion suggesting pathways (GDF6 and FGFR2 respectively) that may underlie the evolution of vertebral fusion. *J. jaculus* has also transformed a thoracic vertebra into a lumbar vertebra, a classic sign of a shift in the spatial domain of expression of Hox genes that establish segmental identity (Burke *et al.*, 1995). However, the additional shift in the position of the anticlinal vertebra from T10 to T12 in *J. jaculus* suggests the mechanism may be more complex than, for example, a simple anterior shift in register of one of the Hox group 10 paralogues (Carapuço *et al.*, 2005; Hostikka *et al.*, 2009). Continuing down the axial column and into the tail, the reduced number of caudal vertebrae in *J. jaculus* suggests an earlier termination of the somite segmentation clock, the developmental process that iteratively pinches off blocks of tissue that will later form the vertebrae (Pourquié, 2003). At the same time the total length of the *J. jaculus* tail is approximately the same proportion of body length as *S. betulina* indicating that at least a subset of the vertebrae elongate more rapidly or for a longer period of time in skeletal development or initiate as larger somites in the embryo.

Within the limb, the evolutionary history of jerboa phenotypes provides insight into mechanisms of digit formation and skeletal growth. We previously showed that axial and postaxial expansion of cell death carves away the tissue that would give rise to the first and fifth digits in *Dipus sagitta* (Cooper *et al.*, 2014). It is possible that the convergent loss of the first and fifth digits in the pygmy jerboa, *Salpingotus*, occurs by a similar mechanism of expanded cell death, perhaps even by convergence on the same molecular mechanisms. While the independent loss of the first digit in *Allactaga tetradactyla* suggests there are at least two distinct mechanisms, our character

analysis of extant species does not rule out a stepwise loss of digit I followed by V in either of the three–toed clades. Loss of the first digit occurs in a variety of human birth defects (Basson *et al.*, 1994; Gold *et al.*, 2011), mouse mutants (Mortlock *et al.*, 1996; Bruneau *et al.*, 2001), and throughout evolutionary history, often as a prelude to the subsequent loss of additional digits (Shapiro, 2002; Prothero and Foss, 2007).

In contrast to the discrete nature of digit loss and metatarsal fusion, skeletal allometry manifests as a continuum of values. Close examination of these allometries in the context of phylogenetic relationships demonstrates that the genetic mechanisms determining inter– and intra–limb proportions are uncoupled in Dipodoidea. Most notably, the obligate bipedal *Euchoreutes naso* exhibits a smaller hindlimb:forelimb length ratio than any other jerboa, yet also has one of the largest metatarsus:femur length ratios. Human congenital skeletal dwarfisms and loss–of–function mutations in mice have identified genes that are required for all long bone growth (Deng *et al.*, 1996; Chusho *et al.*, 2001; Minina *et al.*, 2002), but the mechanisms that deploy these genes at the precise time and levels to generate correct individual bone sizes and proportions largely remain a mystery. The genetic uncoupling we observe here indicates that these mechanisms are complex and may act at the level of global control of size in the anterior versus posterior regions of the body as well as at the level of individual limb skeletal elements.

Not only do we highlight the genetic and regional complexity of skeletal growth control, our finding that hindlimb elements have undergone punctuated evolution also provides an opportunity to apply the same punctuation tests to gene sequences of candidates for growth regulation. Since the genes underlying differences in growth have undergone the same selection as the adult morphologies that result from these developmental differences, we expect the degree of sequence divergence of causative loci to similarly associate with the number of nodes along a path. This finding provides strong justification for the generation of draft genome sequences of species at the tips of a variety of path lengths. Together, this work illustrates the extraordinary value of leveraging a priori analyses of evolutionary history to inform subsequent analyses of developmental and genetic mechanisms of evolution.

1.5 Experimental Procedures

All work with live *Jaculus jaculus* and *Peromyscus maniculatus* were in accordance with Harvard FAS IACUC protocols. All museum specimens that were included in our character analysis are listed in Table A.1.

X–ray fluoroscopy recordings were taken at 1000 frames per second using high speed cameras (Photron 1024) mounted into Siemens Tridoros 150 G–3 C–arms and sampled every other frame. Radiation was set at 5 mA and 60 KVP. Jerboas were restricted to a linear path using a cardboard track. The postural reconstruction of *J. jaculus* is represented in an aerial phase just prior to landing (Figure A.3). The size and shape of each bone was based on the skeleton of a female *J. jaculus* in the private collection of K.C. (JJ 0001). The postural reconstruction of *Sicista betulina* was derived from a live semi–arboreal forest deer mouse, *P. maniculatus* walking along a thin wooden rod and is represented in mid–stance (Figure A.4). The movie also shows loose PVC tubing that was used to induce locomotor instability for a separate project. The skeletal size and shape reconstruction of *S. betulina* is derived from μCT images of a female *S. betulina* alcohol specimen (MVZ 176617) and a male skeleton (AMNH 206585). Hindlimb morphotype reconstructions are based on specimens listed in Table A.1.

Center of mass was measured by placing the euthanized animal on a rigid ruler supported by a scale at each end (Lammers and Zurcher, 2011). The animal was arranged into a physiologically relevant position on the ruler and moved anteriorly or posteriorly until the mass recorded on each scale was equal. The anatomical location of the center point between the two scales corresponded to the location of the center of mass as a percentage of naso–anal distance.

We produced a time–calibrated tree with MrBayes (Figure A.1). Sequences of 28 species (23 Dipodoidea, 5 outgroups) were used including the Dipodoid species from the work of Wu *et al.* (2014) plus the following sequences obtained from Genbank: *Jaculus orientalis* (JN214562.1), *Pygeretmus pumilio* (JF938718.1, JQ347916.1, JQ347936.1, JQ347894.1, JF938696.1, JF938896.1), and *Stylodipus telum* (JF938723.1, JF938802.1, JQ347920.1, JQ347940.1, JQ347898.1, JF938701.1, JF938901.1). DNA sequences for *A. tetradactyla* were obtained by PCR from leg muscle genomic DNA using previously published (Wu *et al.*, 2014) primers for A2AB, CNR1, GHR, IRBP, LCAT, BRCA1, vWF, ATP7a, CREM, RAG2, and DMP1 (Accession numbers KT164755, KT164756,

KT164757, KT164758, KT164759, KT164760, KT164761, KT164762, KT164763, KT164764). We calibrated nodes using divergence times from Date–a–Clade and Wu *et al.* (2012): the root, Dipodidae, mouse/rat split, Cardiocraniinae, and the Dipodinae/Allactaginae split (Supplemental Text). The MCMC procedure ran for 10,000,000 iterations in four chains over two runs, and sampled every 1,000th iteration. The genus *Jaculus* was poorly resolved (*J. blanfordi* and *J. orientalis* were grouped with a posterior probability of 59%) but was used for the comparative analysis as this level of phylogenetic uncertainty has little impact on our results. After the tree was inferred *Allactaga balikunica* was placed manually (Smith and Xie, 2008) because no sequences were available.

The resulting tree was embedded into a Rodentia phylogeny (Fabre *et al.*, 2012). We then trimmed away all taxa except for those associated with morphological data. This tree was used for pPCA and contains 42 taxa: 19 Dipodoidea, 14 Muroidea, and 9 other rodents. Genetic information was available for *Salpingotus koslovi*, but specimens were only available for *S. thomasi*. *S. thomasi* is therefore listed on the figures at the phylogenetic position of *S. koslovi* since this clade is well–resolved at the genus level. Similarly, *Sicista betulina* morphological data is presented in place of *S. tianshanica* on the phylogeny.

Categorical data representing the number of toes on the hindfeet and the degree of metatarsal fusion (none, partial, full) were collected for each taxon. The length of each long bone segment of the forelimb (humerus, ulna, third metacarpal) and hindlimb (femur, tibia, third metatarsal) was measured by digital microcaliper. Humerus, femur, tibia, and third metatarsal data were included in a phylogenetically–weighted Principal Components Analysis using the phyl.pca function in the Phytools package for R. Clustering analysis was performed on these latter components using the kmeans function in the Stats package for R and is represented as the within groups sum of squares by number of clusters extracted (Figure A.2B) (Hothorn and Everitt, 2014).

We reconstructed ancestral states for digit loss using the function make.simmap in the Phytools package for R and set five digits as the prior state. The directional pattern of metatarsal fusion without reversion in Dipodoidea suggests that fusion evolves as an ordered state. We therefore used the function ancThresh in the Phytools package for R, which assumes that the discrete character is determined by underlying, ordered, and unobservable continuous traits. We constructed the ancestral states of continuous variables (Forelimb:Hindlimb, Femur:Metatarsus, pPC2) using the function contMap in the Phytools package for R. For each character, we ran the

function on all taxa in the rodent clade for which we had data but focus our analyses of discrete characters within Dipodoidea as these have not occurred more broadly within rodents.

For the ANCOVA tests, we used dummy variables (and their interactions with the independent variable) to separate different groups from one another. Likelihood ratio tests for the ANCOVA models compare the dummy–variable (two line) model against a simpler single line model (LRT is 2 x the log–likelihood ratio assuming a chi squared distribution and degrees of freedom equal to the difference in parameters of the models). We assessed significance for the regression lines (including the punctuated evolution regression models) with t–scores ($t = \beta 1/SE$) where $\beta 1$ is the slope of the regression line and SE is the standard error of the slope with the degrees of freedom equal to n–2. To account for multiple hypothesis testing we adjusted p–values using the Bonferroni–Holm step–down procedure (Holm, 1979).

We used the maximum likelihood method in BayesTraits v2 (http://www.evolution.rdg.ac.uk) to test for punctuated evolution and perform the ANCOVA tests using the chronogram above. Phylogenetic signal (λ) was estimated during these analyses. To test for punctuated evolution, root–to–tip path lengths are regressed onto the number of nodes (net speciation events) along that path (Pagel *et al.*, 2006). Here we use log–transformed measurements of limb elements instead of path lengths. A positive relationship between path length and the number of nodes suggests punctuated evolution.

1.6 Acknowledgements

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Chapter 2

Inverse dynamics of the Lesser Egyptian Jerboa (*Jaculus jaculus*) vertical leaping [1]

2.1 Summary

Numerous historical descriptions of the Lesser Egyptian jerboa, *Jaculus jaculus*, a small bipedal mammal with elongate hindlimbs, make special note of their extraordinary leaping ability. We observed jerboa locomotion in a laboratory setting and performed inverse dynamics analysis to understand how this small rodent generates such impressive leaps. We combined kinematic data from video, dynamic data from a force platform, and morphometric data from dissections to calculate the relative contributions of each hindlimb muscle and tendon to the total movement. Notably, we found that the mean energy stored in the primary hindlimb tendons comprised 5% of the energy of the associated leap. The limited use of tendon elastic energy storage in the jerboa parallels the morphologically similar kangaroo rat, *Dipodomys spectabilis*. When compared to larger saltatory kangaroos that sustain hopping over long periods of time, these small saltatory rodents store and recover less elastic strain energy in their tendons, resulting in rapid accelerations and decreased locomotor economy.

[1] Co–authored with Alberto Rivera and Andrew A. Biewener

2.2 Introduction

Jerboas are small rodents native to the deserts of northern Africa and Eurasia that use erratic hopping locomotion, often called ricochetal saltation, to navigate their arid habitat, forage for scarce resources, and escape from predators. They constantly switch between hopping, running, turning, and leaping vertically as they move on the shifting sand (Schropfer *et al.*, 1985) (Ch. 4). The inconsistency of the inherently variable locomotion renders detailed studies of each gait both statistically and biologically irrelevant (Moore *et al.*, 2012) (also see Ch. 4). Fortunately, the jerboa's pronounced vertical escape leap is a sterotyped behavior necessary for survival that can be consistently elicited in a laboratory setting.

Understanding how animals recruit their muscloskeletal system to generate locomotion informs our understanding of their locomotor performance. Since muscles require energy to actively contract, whereas tendons are passively elastic, determining the relative energy contributions of the muscles and tendons can predict locomotor endurance. Cursorial animals adapted for sustained and repetitive locomotion tend to have greater elastic energy storage in tendons; energy recovered from tendons stretched in the previous stride limits the amount of muscle input required for the current stride, significantly lowering cost of transport. For example, the cursorial bipedal red kangaroo (*Macropus rufus*) provides 40%–70% of its total mechanical energy elastically during sustained hopping (Alexander and Vernon, 1975) and cursorial horses (*Equus ferus caballus*) elastically recover 36% of mechanical energy during galloping (Biewener, 1998). Both of these animals are able to sustain high speed locomotion over long periods of time because the passive energy storage in tendons decreases the need for muscle contribution to each step.

Although tendon energy storage is more economical, the time required for tendon lengthening can delay the transmission of force from a muscle to the limb. Therefore, small prey animals requiring quick accelerations to escape tend to use less tendon energy storage in their locomotion. For example the kangaroo rat, *Dipodomys spectabilis*, which reflexively leaps in response to the vibrations emitted by their predators (Webster, 1962), elastically recovers only 14% of the mechanical energy in tendons during these vertical leaps (Biewener *et al.*, 1981). Despite the great phylogenetic distance between the kangaroo rat and jerboa (Blanga-Kanfi *et al.*, 2009), the morphological and behavioral similarity between the species lead us to hypothesize that the

jerboa, like the kangaroo rat, will store only a small amount of elastic energy in its tendons during vertical jumping.

In this study we used inverse dynamics to calculate the relative contributions of jerboa hindlimb muscle and tendon to the vertical jump. We chose this non–invasive method to prevent injury to their fragile hindlimbs, especially since jerboa availability in North America is extremely limited. We followed the inverse dynamics procedures used to study red kangaroos (Alexander and Vernon, 1975). Jerboa hindlimb morphology has been previously described in comparison to kangaroo rats (Howell, 1932), and in the context of hindlimb elongation in the family Dipodidae (Moore *et al.*, 2015a). In this study we build upon these descriptions with detailed dissections of hindlimb muscle and tendon, and determine the precise role of each hindlimb element in the execution of a vertical jump.

2.3 Materials and Methods

2.3.1 Animals

We tested three *J. jaculus* (2 males, 1 female) from the colony at the Concord Field Station. Their masses ranged from 53g to 74g, and they were originally captured from the wild in Egypt. To estimate the morphological measurements of each subject, we dissected three other jerboas and assumed geometric scaling between individuals. Before experimentation, we shaved the jerboas' legs and used a non–toxic marker to indicate joint positions.

2.3.2 Experimental Setup

At the start of each trial we placed the animal in a wood and plexiglas structure (103 x 15 x 15 cm) on a 2–axis (vertical and fore–aft) custom–made (6 x 12cm) strain gauge force platform (Biewener and Full, 1992), which fed into a data acquisition system (BioPac MP150). A meter stick attached to back of the enclosure indicated the maximum height of each jump. We used quick bursts of compressed air to motivate the animals to jump.

To film each trial, we lit the area with a 500W light (Omni Lowell) and placed two high speed cameras in front of the enclosure where the animals jumped. A camera (Casio ZR100) with a

wide angle lens was placed close to the vertical track. This camera filmed the entirety of each jump at 240fps and provided maximum jump height of each trial. The camera equipped with the zoom lens (IDT NR5) at the far side of the room provided a smaller field of view including joint positions during contact with the force platform. This camera filmed at 250fps while the jerboa's feet contacted the ground. For this analysis, we selected only jumps in which both feet were in contact with the force platform. We assumed that the animal jumped with equal force on both legs, and divided total ground reaction force in half to compute single limb forces. Positions of the joints (Metatarsal–Phalangeal, Ankle, Knee, and Hip), eye, and base of tail indicated with marks on the skin were tracked using custom tracking software (DLTdv5 Matlab program) (Hedrick, 2008).

2.3.3 Inverse Dynamics

We used an inverse dynamics approach to calculate the muscle force required at each joint (from distal to proximal) to resist the moment produced by the ground reaction force (GRF) in each frame of video. The GRF moment is the cross product of the GRF measured by the force platform and the moment arm from the center of pressure (COP) to the joint (Alexander and Vernon, 1975). The forces measured had negligible horizontal components, so we estimated each GRF moment arm to be a horizontal distance between the joint and center of pressure.

The ringing error due to resonance of the two vertical force sensors made estimating COP by calculating percent contribution to total vertical force unreliable (Biewener and Full, 1992). Therefore, we assumed that the COP began at 25% of the distance from MTP (Metatarsal–Phalangeal Joint) to the Toe, then exponentially moved towards the toe over the course of jump takeoff. The maximum distance to the MTP was constrained so that the maximum muscle stress in either the digital flexor or plantaris muscle would not exceed 400kPa.

We assumed that the GRF moments at each joint are resisted by the contraction of muscles at that joint, creating a joint moment. At each joint, we assumed that each agonist muscle exerts a force proportional to its physiological cross–sectional area (PCSA). We calculated PCSA using the equation

$$PCSA = \frac{mass * cos(\phi)}{\rho_m * fiberlength} \tag{2.1}$$

where ϕ is pennation angle, and ρ_m is the density of muscle ($1060 kg/m^3$ according to (Mendez and Keyes, 1960)). Additionally, we assumed no co–contraction of antagonistic muscle pairs, except in the cases of biarticulate muscles spanning two joints.

The muscles in opposition to the GRF moment at the most distal joint, the MTP, are the digital flexors and plantaris. At the ankle, plantar flexor muscles — the plantaris, soleus, and gastrocnemius — resist the joint moment. Since the plantaris muscle exerts a moment at both the MTP and ankle joint, plantaris force was calculated at the MTP joint, then subtracted from the total ankle moment ($M_A - F_{plant} \times r_{plant}$), leaving the remainder of the force to be generated by the gastrocnemius and the soleus. At the knee joint, rectus femoris, vastus lateralis, vastus medialis, and vastus intermedius all resist the GRF knee flexor moment, in addition to flexor moments produced by the gastrocnemius and plantaris that have origins from the femoral epicondyles. Thus the knee extensors balance the sum of the GRF moment at the knee and the opposing flexor moments from the gastrocnemius and plantaris: ($M_K + F_{gast} \times r_{gast} + F_{plant} \times r_{plant}$). Similarly, the rectus femoris applies an opposing flexor moment at the hip. The hip extensors we considered to resist GRF hip flexor moments were the biceps femoris, gluteus muscles (medius, medialis, and minimus), adductor magnus, and semitendinosus, which resist the GRF moment at the hip in addition to that produced by rectus femoris at the knee ($M_H + F_{recF} \times r_{recF}$). For further simplificaton, we ignored segmental moments in our muscle force calculations, as well as changes in COM location due to relative motion of limb segments relative to the body.

We then calculated the energy storage in the digital flexor, plantaris, and Achilles tendons. Each muscle and its corresponding tendon experience the same force, so we calculated tendon stress by dividing the force by the cross–sectional area of the tendon. Tendon cross–sectional area was calculated using the following equation:

$$CSA = \frac{mass}{\rho_t * length} \tag{2.2}$$

where the density of tendon (ρ_t) is $1120 kg/m^3$ (Ker, 1981). Strain is stress divided by the tendon elastic modulus (1 GPa according to Bennett *et al.* (1986), Pollock and Shadwick (1994), and Maganaris and Paul (1999)), and change in tendon length is strain multiplied by resting tendon length. Tendons act as elastic energy–storing springs and total energy is approximated by assuming tendon is a linear elastic spring: $W = \frac{1}{2} F \Delta L$. This simple equation overestimates

tendon energy recovery and ignores the "toe" region of the J–shaped tendon elasticity curve. The resilience of tendon is ≈ 93%, and does not vary greatly between species, so we multiplied our tendon energy by 0.93 to account for resilience (Matson *et al.*, 2012; Summers and Koob, 2002). We compared the total tendon energy from each trial to the total energy of the jump, as determined by potential energy at maximum jump height, to compute relative tendon energy contributions for each trial. To account for error in the estimation of the COM location, we recorded the lowest point on the jerboa trunk at maximum jump height to calculate potential energy.

2.4 Results

We analyzed 28 trials from three jerboas (5-14 jumps per animal). 12 of these trials involved no contact with the sides of the enclosure, and were thus used to determine maximum jump height and total energy of the jump.

Jerboas jumped to a mean height of 0.33 m, with a maximum jump height exceeding 0.60 m (not analyzed, as these trials involved escape from the enclosure). The highest jumps were approximately 10 times hip height at mid–stance (6.4 cm). The mean GRF was 1.84 N (4.31 Body Weights) with a maximum of 4.9 N (7.39 Body Weights). There is a weak positive correlation between the peak height at the apex of the jump and the maximum instantaneous force the jerboa applied to the ground (Figure 2.1). This matches our intuition that the animal must apply more force to jump higher.

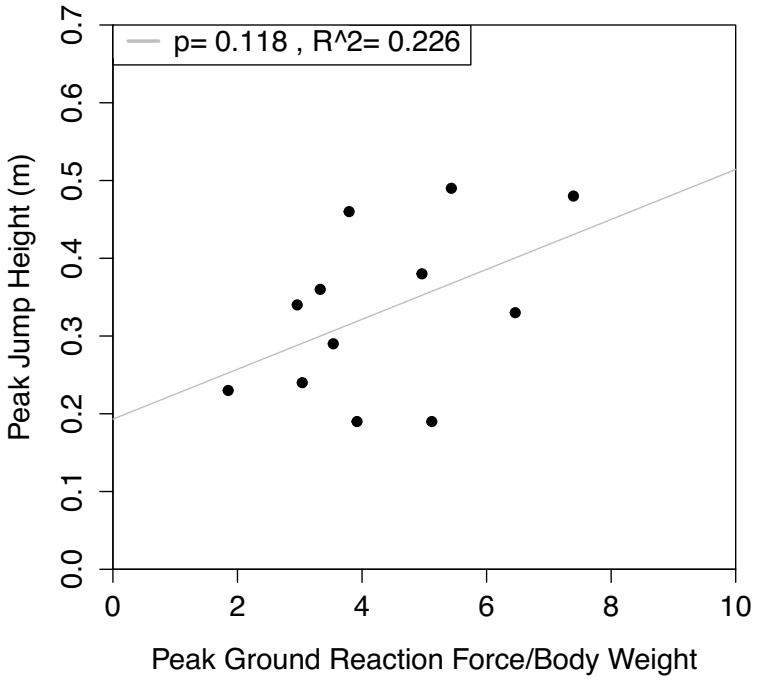


Figure 2.1: *Height versus normalized force for each trial. The x–axis represents the maximum force recorded during each jump divided by body weight. The y–axis is a conservative measurement of peak jump height.*

The muscle and tendon measurements are shown in Tables B.2 and B.1. MTP (plantar) flexors

accounted for 5.39% of the total hindlimb muscle mass (categorizing the mass of muscles acting at multiple joints at their more distal joint), ankle extensors 14.05%, knee extensors 24.14%, and hip extensors made up 56.50%. As expected for fast–moving limbs, the mass of the muscles decreases in the more distal limb segments, decreasing the moment of inertia of the limb. In contrast, the cross–sectional area of the MTP flexors, ankle, knee, and hip extensors accounted for 9.00%, 33.94%, 25.81%, and 31.24% of the total hindlimb muscle cross–sectional area, respectively. Since force generation is proportional to muscle cross–sectional area, this led us to predict that the ankle and MTP extensors contribute more force with respect to their mass. We assumed geometric scaling of physical dimensions to estimate the morphometric features of our experimental subjects from the dissected animals.

We first calculated the GRF moments of each joint (Figure 2.2) to check that the COP location is reasonable. The MTP joint contributed the most to vertical jumps, with an average of 40% of the total joint forces (Figure 2.3). The force generated by the plantaris was the highest for any single muscle (though less than the two heads of the gastrocnemius combined) (Figure 2.4 a,b). Given that a 64g jerboa weighs approximately 0.63N, maximum forces generated by the Plantaris were nearly 5 times the animal's weight (Figure 2.4 a). The MTP muscles, digital flexor and plantaris, experienced mean stresses of 91.67 kPa (Figure 2.5 a). The maximum stress we recorded (267.60 kPa) is less than the peak isometric stresses recorded in the kangaroo rat ankle extensors during vertical jumping (350 kPa) (Biewener and Blickhan, 1988; Biewener *et al.*, 1988). However, greater muscle stresses were likely achieved in the higher jumps not analyzed.

The ankle joint contributed an average of 33% of the total joint forces (Figure 2.3). We found that the similarity in physiological cross–sectional area (PCSA) in lateral and medial heads of the gastrocnemius resulted in nearly identical muscle forces (Figure 2.4 b). The maximum gastrocnemius force for a single head was 3.71 times average jerboa weight. Each head of the gastrocnemius experienced stresses with a mean of 22 kPa, and a maximum of 68.21 kPa (Figure 2.5 b). Due to a much smaller PCSA, the soleus contributed very little to the moment at the ankle, with a maximum force of 0.15 N.

Muscles acting at the knee contributed an average of 16% of the total moments resisting the GRF moment, which is considerably less than expected from relative cross–sectional areas (Figure 2.3). The vastus lateralis generated the greatest force at this joint (mean 0.38 N, max 1.64 N, Fig.

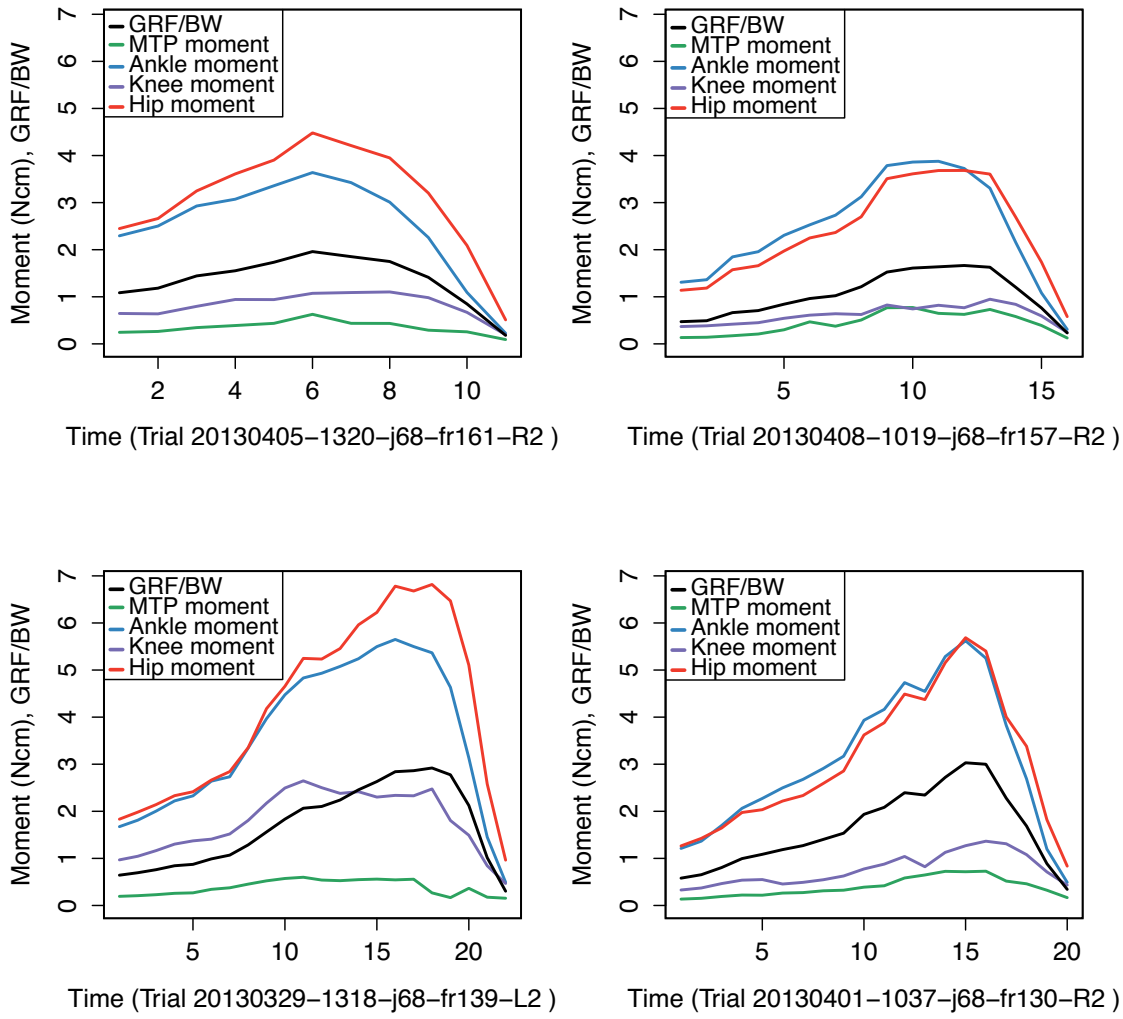


Figure 2.2: *Four sample trials show how the moments of each joint increase and decrease throughout a trial, along with ground reaction force normalized to body weight (GRF/BW).*

2.4 c) , and experienced the greatest stresses (mean 10.07 kPa, max 43.85 kPa, Fig. 2.5 c). The vastus intermedius contributed the least at this joint.

The muscles at the hip contributed an average of 10% of the total moments resisting the GRF moment (Figure 2.3 d). The biceps femoris generated the greatest forces at the hip (mean 0.15 N, 0.58 N, Fig. 2.4 d) and experienced the greatest stresses (mean 5.00 kPa, max 18.71 N, Fig. 2.5 d). Although the hip extensors have a greater total cross–sectional area, and a greater number of muscles acting at this joint in comparison to agonist muscle extensor groups at more distal joints,

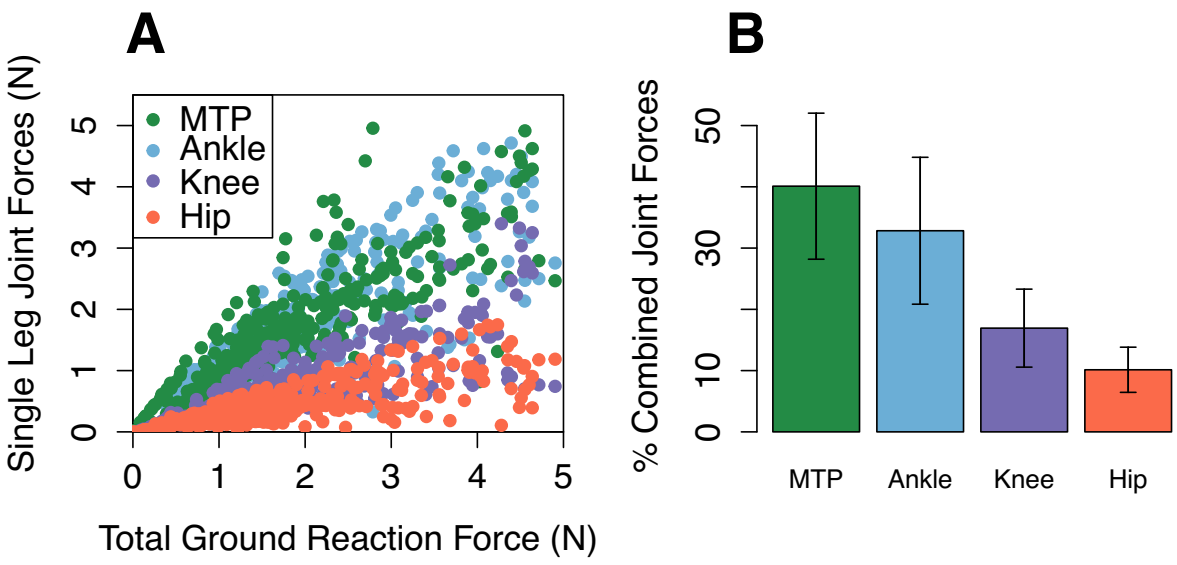


Figure 2.3: *a) The total force exerted by the muscles at each joint to balance the ground reaction force moment. b) The force at each joint as a percentage of the combined muscle–tendon forces produced to resist the GRF moment at each joint.*

the hip extensors contributed less energy toward the vertical leap than the other muscle group.

We analyzed the plantaris, digital flexor, and achilles tendons (assuming that both heads of the gastrocnemius contribute equally to the achilles tendon stress) for tendon strain energy storage, as these are the largest tendons in the hindlimbs and are attached to muscles producing the greatest force. The plantaris experienced the greatest stresses, and the gastrocnemius experienced the least (Figure 2.6 a). All tendon stresses were well within the established tensile strength of vertebrate tendon, 100 MPa (Bennett *et al.*, 1986), and had a minimum safety factor of 4.

The low tendon stresses reflect the meager amounts of energy stored by the tendons. The contribution of a single tendon was below 2 mJ, and the maximum total energy stored in the tendons for a single trial was 2.57 mJ (Figure 2.6 c). This amount is quite small when considering the maximum jump energy recorded was 307.33 mJ. The tendon contribution to total jump energy averaged 3.00% and showed no significant relationship with peak jump height (Figure 2.6 b).

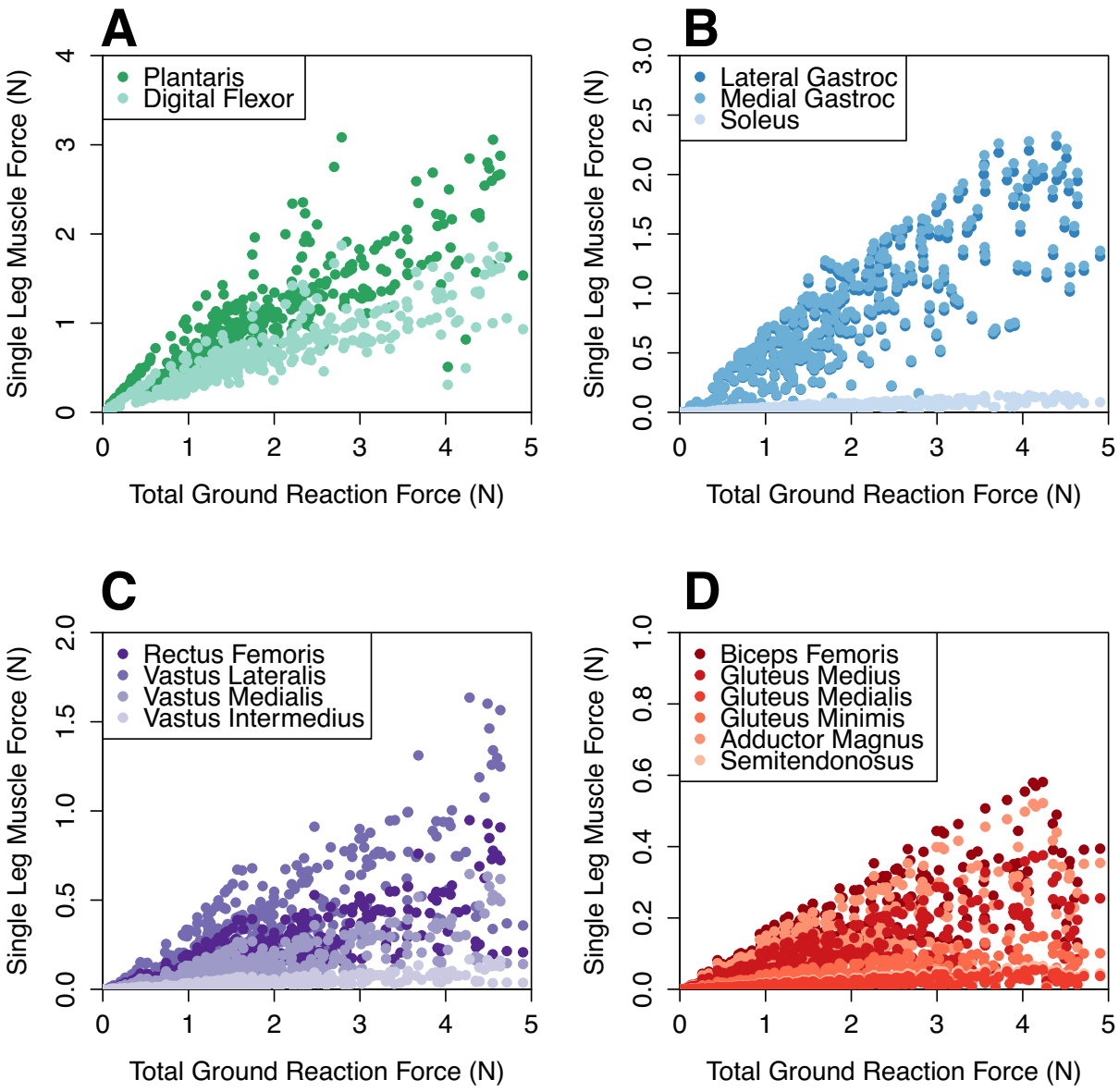


Figure 2.4: *Forces generated by each muscle, sorted by joint. a) Metatarsal–phalangeal flexors. b) Ankle extensors; synergistic plantaris forces not pictured. c) Knee extensors; antagonistic gastrocnemius force not pictured. d) Hip extensors; antagonistic rectus femoris not pictured.*

2.5 Discussion

This study of jerboa jumping in controlled laboratory conditions is an important first step in understanding how and why these small mammals generate disporportionately large jumps. Although we observed jumps in excess of 10 times hip height in the laboratory, observations of

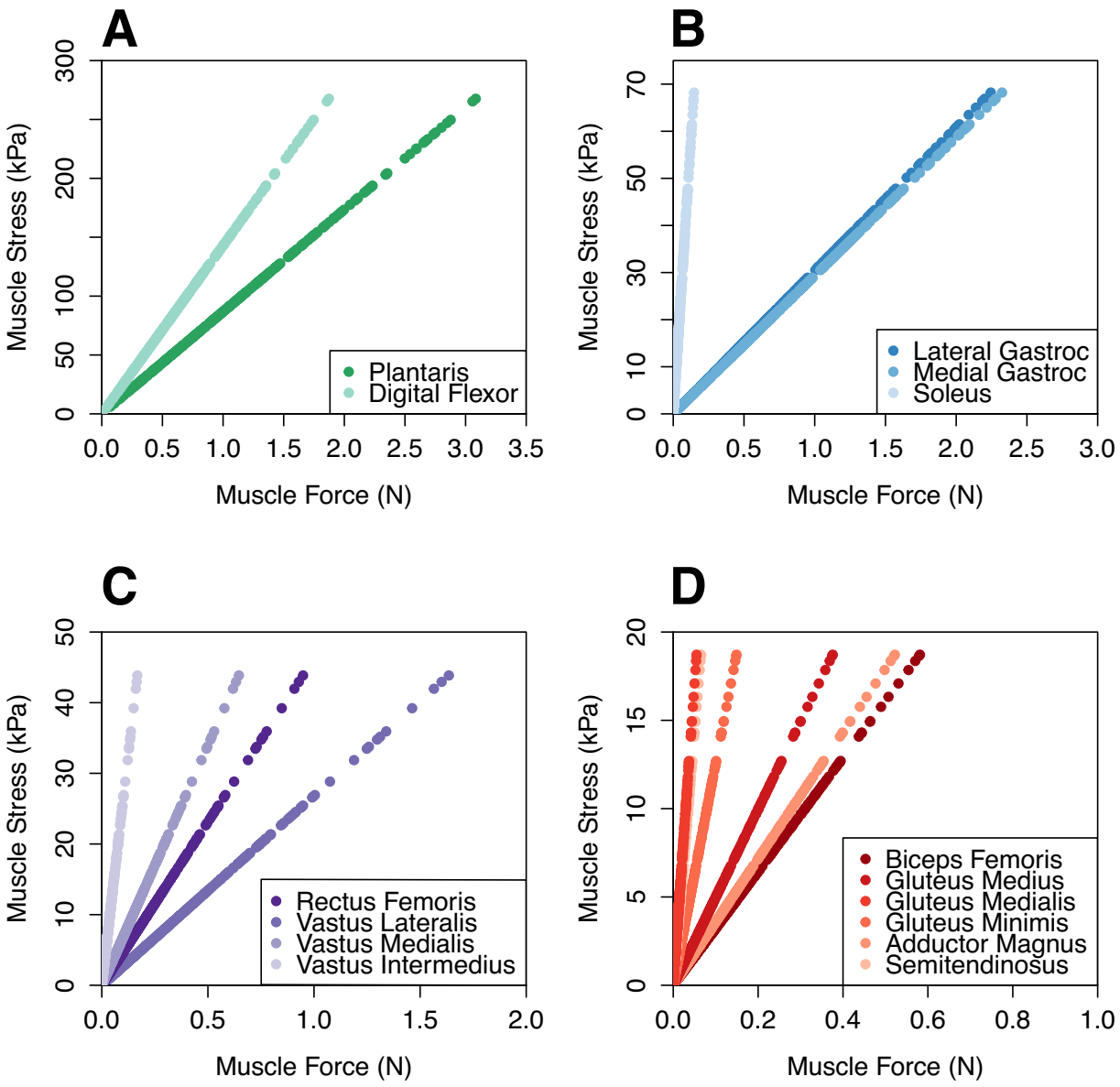


Figure 2.5: *The stresses of each muscle versus the force of each muscle.*

jerboas in the wild suggest that jerboas are capable of more extreme jumping maneuvers (Berman, 1985). Indeed, the low muscle and tendon stresses we calculated here suggest a greater capacity for jumping and accelerative maneuvering than we observed in the laboratory. Although jerboa behavior is somewhat subdued in a laboratory setting, the mechanistic understanding gained from this approach helps predict the limits of their performance and the selective pressures favoring

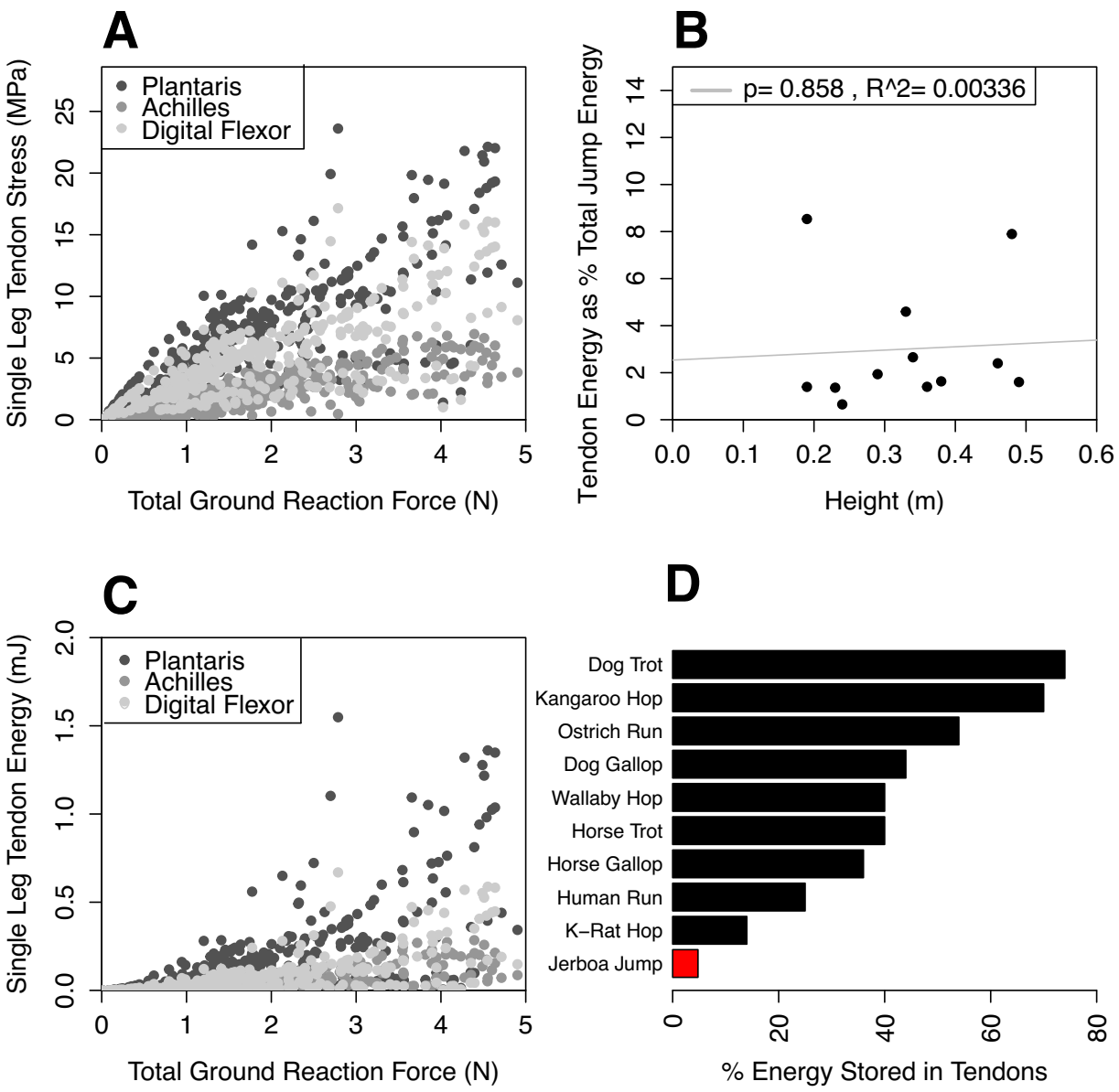


Figure 2.6: *a) Tendon stress as a function of ground reaction forces. b) Tendon energy contribution to the total energy of the jump, calculated from the potential energy at peak jump height. c) Tendon energy contributions as a function of ground reaction force. d) Jerboa tendon energy contribution to total limb mechanical work (forward locomotion in all cited studies) or COM work (vertical jumping in jerboas) compared to other species. Dog data from Gregersen et al. (1998), kangaroo and wallaby data from Alexander and Vernon (1975), ostrich and human data from Rubenson et al. (2011), horse data from Biewener (1998), k[angaroo] rat data from Biewener et al. (1981).*

the evolution of their locomotion.

The jerboa tendon contribution to COM work is surprisingly low, even when compared to tendon elastic energy recovery in kangaroo rat forward hopping, despite these animals being

morphologically and behaviorally convergent (Biewener *et al.*, 1981). The unusually low tendon energy savings in jerboas and kangaroo rats suggests that smaller bipedal rodents do not encounter the same selective pressures on their locomotion as bipedal and quadrupedal cursorial animals that perform sustained bouts of high–speed stereotyped locomotion. For cursorial animals, even small stride–to–stride energy savings can add up to substantial energy savings over time, which may mean the difference between outrunning a predator and becoming dinner. Dogs, horses, kangaroos, and ostriches can recycle 36–74% of their total limb mechanical work by storing energy elastically in tendons (Gregersen *et al.*, 1998; Biewener, 1998; Alexander and Vernon, 1975; Rubenson *et al.*, 2011). Because these animals are all larger than 1kg, it is difficult to discern whether the small size of jerboas and kangaroo rats is somehow constraining the capacity for tendons to store and recovery energy. Unfortunately, few dynamic analyses have been performed on the terrestrial locomotion of quadrupedal mammals less than 1kg. Elephant shrews (*Elephantulus spp.*, Macroscelidae) would provide the most informative comparison, as they are the only known micro–cursorial mammals (Lovegrove and Mowoe, 2014). Most other small mammals (including the quadrupedal ancestors of jerboas) are ambulatory generalists (Polly, 2007). Because these rodents have few obvious biomechanical specializations, the dynamics of their locomotion is rarely the subject of comparative biomechanical inquiry (Bonnan *et al.*, 2016).

While energetically costly, locomotion that is predominantly powered by muscular contraction has the benefit of producing force more rapidly. More compliant tendons result in greater stretch for a given amount of force, so it requires a muscle to shorten a greater distance (and for a given shortening rate, a longer time) to produce a movement at the joint. Therefore, minimal tendon stretching and energy storage can be advantageous, especially for prey animals that must produce rapid joint movements to change speed or direction to evade predators (Moore and Biewener, 2015). Because of the high energetic cost, this strategy would be most appropriate for evading predators that are committed to a single strike, rather than being pursued over long distances.

An important difference between the laboratory and the natural habitat of the jerboa is a loose granular substrate. This flowing substrate almost certainly influences jerboa locomotion, since the displacement of sand particles limits the ability of the substrate to provide a rapid rise in GRF due to the displacement of substrate particles as force rises. However, upon rapid impact, granular media are known to exhibit "effective solidification," in which the granules interlock and

resist forces as a solid. Small, sand–adapted vertebrates, such as lizards and baby sea turtles, have been shown to take advantage of this property of their granular substrate during locomotion (Li *et al.*, 2012; Mazouchova *et al.*, 2010). Small bipedal rodents are only found in desert ecosystems with eolian sand Mares (1993). This restriction to granular substrate and morphology specialized for rapid accelerations suggest that jerboas may be capable of solidifying granular media, and encourage future studies of jerboa locomotion on their native substrate.

In conclusion, the hindlimb morphology of jerboas, much like kangaroo rats, favors the rapid production and absorption of large forces during jumping. Such short bouts of rapid jumping would be particularly well suited to evading single–strike predators, especially in desert ecosystems where sympatric quadrupedal rodents may not be capable of producing effective solidification and thus not capable of producing large ground reaction forces. Studies of biomechanical performance in a field setting will provide important insight into the evolutionary and ecological context of this spectacular jumping rodent.

2.6 Acknowledgments

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Chapter 3

Outrun or Outmaneuver: Predator Prey Interactions as a Model System for Integrating Biomechanical Studies in a Broader Ecological and Evolutionary Context [1]

3.1 Synopsis

Behavioral studies performed in natural habitats provide a context for the development of hypotheses and the design of experiments relevant both to biomechanics and to evolution. In particular, predator–prey interactions are a model system for integrative study because success or failure of predation has a direct effect on fitness and drives the evolution of specialized performance in both predator and prey. Although all predators share the goal of capturing prey, and all prey share the goal of survival, the behavior of predators and prey are diverse in nature. This article presents studies of some predator–prey interactions sharing common predation

[1] Co–authored with Andrew A. Biewener. Originally published in Integrative and Comparative Biology 2015 (Moore *et al.*, 2015b)

strategies that reveal general principles governing the behaviors of predator and prey, even in distantly related taxa. Studies of predator–prey interactions also reveal that maximal performance observed in a laboratory setting is not necessarily the performance that determines fitness. Thus, considering locomotion in the context of predation ecology can aid in evolutionarily relevant experimental design. Classification by strategy reveals that displaying unpredictable trajectories is a relevant anti–predator behavior in response to multiple predation strategies. A predator's perception and pursuit of prey can be affected indirectly by divergent locomotion of similar animals that share an ecosystem. Variation in speed and direction of locomotion that directly increases the unpredictability of a prey's trajectory can be increased through genetic mutation that affects locomotor patterns, musculoskeletal changes that affect maneuverability, and physical interactions between an animal and the environment. By considering the interconnectedness of ecology, physical constraints, and the evolutionary history of behavior, studies in biomechanics can be designed to inform each of these fields.

3.2 Behavioral studies direct evolutionarily relevant inquiry into biomechanics

Behavioral studies of animals in their natural habitat provide a context for the integration of biomechanical and evolutionary analysis. Laboratory experiments often focus on determining maximal performance, such as peak velocity, which is important for understanding the capabilities derived from a certain morphology. However, maximal performance is only one of several determinants of fitness for an animal in its natural context. For example, cryptic stick–insects avoid predation by "rocking" their body in ways that closely resemble the gentle swaying of twigs in the wind, which is far from the maximal performance capabilities of stick–insect morphology observed in a laboratory environment (Robinson, 1969).

Many biomechanical studies are performed in laboratory settings, where the sensory and physical landscape can differ greatly from the natural habitat. In an outdoor carnival contest[2], frogs (*Lithobates catesbeianus*) jumped up to twice the maximum distance recorded in the laboratory

[2]Post–publication note: The study was performed at the 4–day Calaveras County Jumping Frog Jubilee, which is where *The Guinness Book of World Records* reports the longest distance bullfrog jumps have occurred.

(Astley *et al.*, 2013). Similarly, flights by fruit flies in an outdoor setting reach significantly higher peak velocities than those occurring within a laboratory (Combes *et al.*, 2012). These studies suggest that experimentation in a laboratory may underestimate, and therefore limit, the understanding of both the biomechanics and the relevant ecological context of an animal operating in a model experimental system.

Behavioral studies can thus direct evolutionarily relevant inquiry into biomechanics. For these types of integrative studies, it is important to focus on a behavior in which physical performance determines fitness. Specialized herbivorous feeding, sexual selection on male–male competition, and predator–prey interactions are examples of behaviors in which biomechanical function determines fitness and drives the evolution of associated morphological features. Each of these behaviors can therefore serve as a model system for integrative studies (Emlen *et al.*, 2007; Lopez-Darias *et al.*, 2012; Grant and Grant, 2014). Predator–prey interactions are especially interesting and potentially illuminating because they involve co–evolution between different species.

3.3 Predation is a model system for the integrative study of locomotion, behavior, and evolution

Predator–prey interactions strongly influence the evolutionary fitness underlying the locomotor performance both of predator and of prey. Successful predation events sustain the predator's life and prevent the prey from further reproduction, making success or failure reliable proxies for fitness. Since successful hunting and escape often require specialized morphology, understanding the variation in relevant structures over time is critical for the study of adaptive evolution. Predator–prey interactions represent an opportunity to connect biomechanical and evolutionary studies, given the underlying selective drive for highly co–adapted locomotion and morphology.

Behavioral studies of predator–prey interactions in the natural habitat are often analyzed in isolation or classified taxonomically (Domenici *et al.*, 2011b). While these investigations further the understanding of a particular species–pair in its ecosystem, it is difficult to determine whether the conclusions drawn from a particular study are applicable to other species. Alternatively, theoretical models of predator–prey interaction often are generalized with respect to a predator's strategy

Table 3.1: *Studies in various fields, and in various model systems, that share common predation strategy. See References for full citation information.*

	Ambush	**Ballistic Interception**	**Pursuit**
Theory	Caraco 1986, *Spider*	Rossel 2002, *Archer fish*	Howland 1974, *Falcon* Broom 2005, *Theoretical*
Biomechanics	deVries 2012, *Stomatopod*	Peters 1996, *Leopard Frog* Anderson 2010, *Chameleon* Mischiati 2014, *Dragonfly*	Ghose 2009, *Brown Bat*
Behavioral Ecology	Fouts 1999, *Angel Shark* Bradley 1996, *Trapdoor Spider*	Combes 2010, 2012, 2013, *Dragonfly* Nishiumi 2014, *Snake*	Wilson 2013, *Cheetah*
Application	Ewert 2001, *Frog*	Scott–Samuel 2011, *Torpedo*	Yuan1948, *Target–Seeking Devices*

(Broom and Ruxton, 2005; Yuan, 1948). Sorting diverse predator–prey interactions by studying predation strategy can reveal patterns of form–function principles shared by even distantly related taxa. This integrative approach makes it possible to test general hypotheses regarding the effect of differing strategies on the evolution of morphology and performance.

The behavioral and ecological factors that drive predator–prey interactions are essentially straightforward: in the presence of an acceptable prey item, the predator benefits by expending as little energy as possible to capture the prey, while successful escape by the prey enhances its survival and potential to reproduce (Lima and Dill, 1990). Relatively simple models can predict the ideal escape behavior in simple cases of predator–prey interaction, in which the predator and prey move in the same geometric plane and the prey must avoid capture by the predator (Broom and Ruxton, 2005; Ellard and Eller, 2009; Cooper and Frederick, 2010). However, such simple models fail to explain the diversity and complexity of escape behaviors observed in the natural world (Domenici *et al.*, 2011a,b). Additionally, most animals act as predator or as prey in different biotic interactions throughout their lives. While creating a model for combined predator and prey strategies would inform an estimation of overall fitness throughout an animal's lifetime, an overarching model of this sort would be extremely complex and is beyond the scope of our paper.

This review classifies the existing diversity in predator–prey behavior with respect to predation strategy to reveal common principles underlying predator–prey interactions in each classification (Table 3.1). Ambush predation (Figure 3.1, A) involves a stereotyped behavior triggered by the presence of prey. No prediction of the prey's behavior or feedback is involved. Ballistic interception (Figure 3.1, B) involves the predator adjusting an attack trajectory to observed movements by the prey, and commitment to that trajectory without the use of feedback. Pursuit predation (Figure

3.1, C) involves the predator adjusting their intercept–trajectories according to updated sensory feedback on the prey's movements. Many forms of predation, such as stalking by Anolis sp. or persistence–hunting by hominins, do not fit into the strategies presented here (Moermond, 1981; Liebenberg, 2006). Similarly, the effects of sociality and feeding–pressure are reviewed elsewhere (Lima and Dill, 1990). Rather than providing a comprehensive list of all predator–prey interactions, we focus on three strategies, ambush predation, ballistic interception, and pursuit predation, which serve as preliminary examples of the integration of biomechanics, behavior, and evolution in determining some general principles underlying the evolution of locomotion.

3.3.1 Ambush predation

The simplest predation strategy to model is that of a predator ambushing its prey using one stereotypic motion, which is triggered by a key stimulus (namely, prey entering the predator's proximity). Ambush predators typically have heightened visual, chemical, or tactile senses that they use in detecting prey. Examples of ambush predators include angel sharks, trapdoor spiders, and frogs (Fouts and Nelson, 1999; Bradley, 1996; Ewert *et al.*, 2001). As "sit–and–wait" predators, ambush predators often create a burrow in which they hide, which constrains the target range of their stereotyped attack (Caraco and Gillespie, 1986). Rapid movement is key to a successful strike, as the predator does not need to predict the prey's movement if it can move quickly enough to prevent the prey from sensing and reacting to the oncoming attack (DeVries *et al.*, 2012). These circumstances have favored the evolution of ambush behavior as a fixed action pattern with little or no feedback in response to the prey's behavior. The simplicity of this system makes ambush predation an attractive model for studying pattern recognition and motor reflexes (Ewert *et al.*, 2001).

Ambush predation is most effective when there is a high density of suitable prey near the hiding predator (Bradley, 1996). In systems with a lower density of prey, ambush predators create lures that attract prey to the predator's proximity (Hagman *et al.*, 2008). The prey can only avoid predation if it has evolved either acute sensory organs that can detect the hidden predator, or quick reflexes that permit escape once the predator has revealed itself (Martin and Hammerschlag, 2012). Since predation is highly stereotypic and does not rely on feedback in

response to movement by the prey, the prey can move away from the predator via a variety of headings, so long as it can move quickly enough. However, both predator and prey face a lower boundary to their co–evolutionary arms race; reaction time is limited by the sensory–motor neural processing required before adjustments in the trajectory of movement can be initiated (Jindrich and Full, 2002).

3.3.2 Ballistic interception

Ballistic interception consists of an initial observation of movement by the prey, prediction of the prey's future location, computation of an intercept course, feed–forward neuromuscular control and commitment to that course, and a subsequent discrete success or failure at the time and location of predicted interception. The delay between the commitment to the course and the discrete endpoint of success or failure is the window of opportunity for the prey to escape. Ambush predation and ballistic interception exist on the same continuum of predation strategy, but it is useful to distinguish between the two when addressing predators' aiming. Ballistic interception at close distances still requires adjustment of the predator's attack

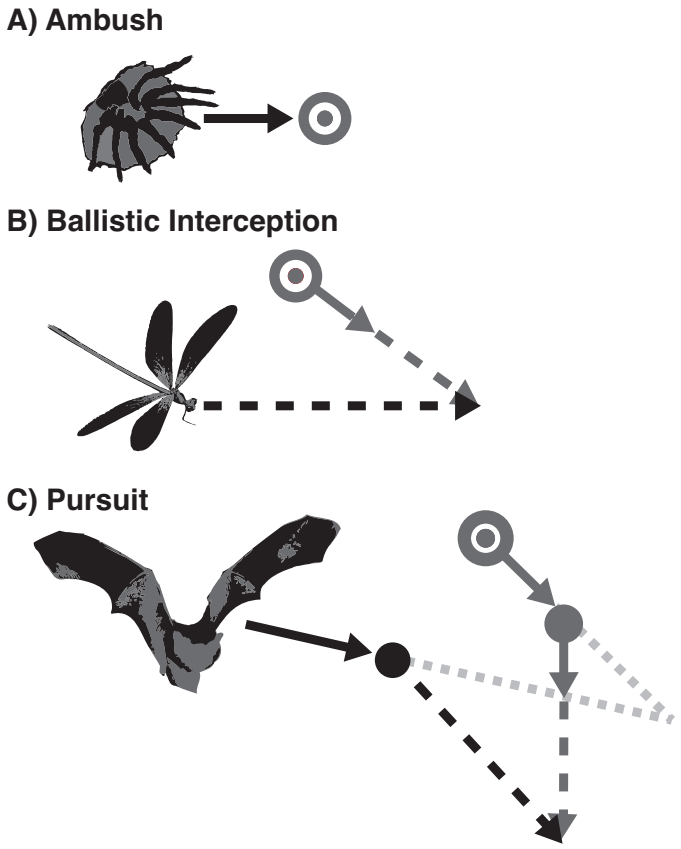


Figure 3.1: *Schematic showing the predation strategies discussed in this article. Black arrows indicate predator movement, gray arrows indicate movements of prey. Solid lines indicate instantaneous velocity*[3]*, dashed lines indicate future trajectories predicted by the predators. A) Ambush predation is represented by the trapdoor spider,* Misgolas rapax *(Bradley, 1996). B) Ballistic interception is represented by the dragonfly,* Plathemis lydia *(Mischiati et al., 2014). C) Pursuit predation is represented by the big brown bat,* Eptesicus fuscus *(Ghose et al., 2009).*

[2]Mistake in publication corrected here

behavior in response to the behavior of the prey, while ambush predators use a stereotyped motion to attack at the same target area with respect to their own location. Predation of unmoving prey is a variant of ballistic interception because the predator must aim and predict the future location of the prey, even though the predator may strike when the prey is not moving. The predator is predicting the future state of the prey as unmoving, and fails when the prey moves during an attack. On the other hand, ambush predation as defined above does not require any aiming or prediction of future locations of prey, and is simply a fixed strike pattern triggered by the presence of prey in the target range. Examples of ballistic predators include dragonflies, chameleons, the colubrid snake Elaphe quadrivirgata, archerfish, and submarines launching torpedoes at boats during the First World War (Mischiati *et al.*, 2014; Anderson and Deban, 2010; Nishiumi and Mori, 2014; Rossel *et al.*, 2002; Scott-Samuel *et al.*, 2011).

To determine whether dragonflies use ballistic interception to capture prey, head and body orientation of the dragonfly and heading and location of the prey were tracked during attempts at predation (Mischiati *et al.*, 2014)[4]. Tracking dragonflies' eyes with respect to the location of the prey revealed that the eyes track the predicted path of the prey. Purely reactive tracking, such as Parallel Navigation (Yuan, 1948), were inconsistent with dragonflies' tracking behavior, indicating that the predation strategy is predominantly predictive. In light of these findings, studies of the ability of dragonflies to track prey during flight, or of the mechanics of initiating sharp turns, may not be very informative for evaluating evolutionary or ecological hypotheses since these metrics are not necessary for successful predation. Instead, it is more generally useful to study how natural behavior of the prey and environmental variation affect dragonflies' ability to predict the future location of prey. This can be assessed indirectly by recording the factors associated with the initiation of predation, or lack thereof (Combes *et al.*, 2012). Recent work has shown that dragonflies do not initiate predation when the speed, size, or distance of the prey limits reliable prediction of its trajectory. Indeed, failure of initiated attempts at predation is correlated with highly variable flight trajectories of the prey, thereby limiting the relevance of predictive interception (Combes *et al.*, 2013).

Escape by prey depends on multiple factors, including the prey's intrinsic ability to move,

[4]Mistake in publication corrected here.

conspecific behavior linked to the predator–prey interaction, and features of the local habitat. The frog *Pelophylax nigromaculatus* escaping from a ballistic strike from the snake *E. quadrivirgata* presents an escape strategy contingent on these factors. In response to the presence of a snake, the frog adopts the behavioral strategy of waiting and letting the snake approach slowly (Nishiumi and Mori, 2014). By freezing while the snake approaches, the frog allows for the possibility that another prey item will distract the snake during the approach. Next, the "Close–Quarters Effect" works to the frog's advantage: if the frog jumps while the snake is far away, the angular adjustment in the direction of the snake's attack is relatively minor. Since biomechanical studies show that terrestrial frogs are not capable of repeated jumps (Peters *et al.*, 1996), it is unlikely that the frog would be able to immediately perform another maneuver to escape the re–adjusted strike. The closer the snake is to the frog before the frog jumps, the greater is the angular adjustment the snake must make, thereby decreasing the likelihood of a successful strike. Finally, the frog often waits until after the snake initiates a strike to begin its jump. Since the snake is committed to a specific trajectory (N. Nishiumi, *pers. comm.*), it cannot adjust to strike at the frog's new position. Thus, even prey that are only capable of intermittent locomotion may successfully escape due to the feed–forward sensory–motor planning of the ballistic interception strategy.

3.3.3 Pursuit predation

Pursuit predation involves high–speed locomotion both of the predator and the prey. In the absence of the prey turning or exploiting features of the landscape inaccessible to predators, the predator must simply maintain a speed greater than the prey for a sufficient time to successfully catch the prey. In this simplest case of a linear rundown, sensory–motor and musculoskeletal adaptations for faster speed and acceleration can improve the fitness both of the predator and the prey. Visual and auditory camouflage is favored, potentially allowing predators to get as close as possible to the prey before the pursuit begins, and permitting prey to avoid the pursuit altogether (Lima and Dill, 1990).

When prey turn during an attempted escape, the pursuit strategy must become reactive for successful predation, involving ongoing sensory–motor feedback to execute new intercept–trajectories during the pursuit. A simple model for the neural control of predators adopting the

pursuit strategy in a two–dimensional plane is the Parallel Navigation Principle, the strategy used by bats hunting mantises (Ghose *et al.*, 2009). According to this model, the predating bat holds the mantis at a fixed angle to its own heading while reducing the distance to the mantis. A fixed angle of approach minimizes the mantis's relative perception of the bat's movement. If the mantis changes heading, the bat compensates by establishing a new intercept course, again keeping the mantis at a fixed angle while decreasing the distance between the two. The Parallel Navigation Principle strategy of pursuit naturally evolved in bats and goshawks (Kane *et al.*, 2015), and humans convergently derived the strategy to control target–seeking devices (Yuan, 1948). Pursuit predation is a useful model system for determining effective morphologies and strategies for tracking while the tracker is moving. Animals acting as predator or prey in pursuit predation are well suited to biomechanical examination because their locomotor structures often exhibit morphologies that confer high maneuverability.

A well–known strategy for evasion of a predator by prey in the context of pursuit predation is the Turning Gambit (Howland, 1974), in which predator and prey are assumed to be moving in the same two–dimensional plane. As described above, the predator maintains a higher speed than the prey. However, there is a tradeoff between speed and maneuverability for most forms of locomotion (Biewener, 2003; Jindrich and Qiao, 2012). Because predators are typically larger than their prey, most predators are unable to make turns as sharply or as quickly as the prey, so the prey can escape even if they move more slowly. Studies of encounters can reveal whether predator and prey are successful by outrunning or outmaneuvering each other. A recent study integrating structural ecology, behavioral interactions, and biomechanical performance showed that in response to prey that take many sharp turns, cheetahs run at sub–maximal speeds, thereby improving their ability to turn and successfully capture prey (Wilson *et al.*, 2013).

3.4 Insights from an integrative perspective

3.4.1 Understanding how locomotor ecology affects predator–prey interactions aids experimental design

Careful consideration of the locomotor ecology of predator–prey interactions, including the sensory and physical landscape, enables studies of animals in similar motivational states, as well

as co–option of natural triggers of locomotion for optimal experimental design. Sensory cues affect locomotion by allowing predators to detect prey or by alerting prey to pending predation (see Stevens and Merilaita (2009) for a comprehensive review). For instance, comparing the activity of burrowing rodents between sites without considering the phases of the moon may introduce error into an experiment, since as prey animals, nocturnal rodents decrease their activity owing to their increased visibility to predators during full moon (Diete *et al.*, 2015; Clarke, 1983; Griffin *et al.*, 2005; Daly *et al.*, 1992a). In addition to inhibiting locomotion, sensory cues can also elicit locomotion. Heteromyid rodents with inflated auditory bullae have evolved a stereotypical vertical jump in response to vibrations at the frequency produced by predators' locomotion (Webster and Webster, 1971). Similarly, a change in the flow of fluid produced by movement in water or air can trigger an escape response in prey (Stewart *et al.*, 2013; Domenici *et al.*, 2008). Experimenters can vary the natural sensory cues for predation or evasion in their study system to reliably elicit a desired behavior.

In certain cases there is selection for maximal performance, but other behaviors also contribute to fitness. For example, some prey modify behavior in ways that hide them from potential predators. Mice have few locomotor specializations and exhibit high anxiety in open fields, preferring the safety of cover (Bourin and Hascoe, 2003). Similarly, aquatic prey may choose to "hide" in areas of low flow, thereby reducing the likelihood that a predator will pick up their chemical cues (Hay, 2009). Many biomechanical experiments requiring locomotion in exposed areas may be confounded by an animal's open field anxiety, but the natural preferences of prey can also aid in experimental design. Lizards preferring shelter can be motivated to locomote by providing shelter at the opposite end of a racetrack (Libby *et al.*, 2012a). By affecting the prey's ability to avoid predation, the physical environment can thus have an effect on an animal's motivation to locomote.

Importantly, the locomotor matrix (i.e., water, substrate, air, or perches) spatially constrains the locomotion both of predator and prey. Transformation of forest into agricultural fields has caused documented vicariance in the native range of animals dependent on suitable perches for locomotion (Essner, 2007; Mattingly and Jayne, 2004; Anderson *et al.*, 2007). Predators attuned to the spatial limitations of their prey can hunt accordingly, such as the dolphins that cooperate to beach fish on the shore, where the fish lie immobile and unable to escape the elongate jaws

of these predators (Sargeant *et al.*, 2005). Studies of terrestrial locomotion often assume that movement in the horizontal plane is most relevant, but examination of trajectories measured in two dimensions can present misleading results when the experimental subjects are capable of significant excursions outside of that plane. In a study comparing the escape behavior of sympatric quadrupedal and bipedal rodents, analysis of locomotion limited to the horizontal plane did not show significantly different performance between the quadrupedal versus bipedal species (Djawdan and Garland, 1988), despite significant evidence that bipedal rodents evade predators more frequently (Longland and Price, 1991). Incorporating the considerable excursions of the bipedal *Dipodomys sp.* in the vertical plane of motion would likely reveal differences in escape behavior important for successful escape and for maintaining fitness. Indeed the escape behavior of kangaroo rats (*Dipodomys spectabilis*) in response to the sound of an approaching predator is to jump vertically and to hop erratically away (Webster and Webster, 1971), consistent with studies of maximal performance of jumping in this species (Biewener and Blickhan, 1988). Although the locomotor matrix often predisposes animals to move in a specific plane, animals capable of significant out–of–plane excursions demand consideration in three dimensions for ecologically and evolutionarily relevant analysis.

3.4.2 Indirectly or directly limiting the predator's ability to predict the locomotion of prey discourages predation

For successful pursuit predation and especially ballistic interception strategies, the predator must predict the future location of the prey. To decrease the predator's ability to build a reliable model of the prey's trajectories, and thus plot a successful interception, prey can produce unpredictable trajectories, also called "Protean Behavior" (Chance and Russell, 1959). Studies show that prey adopting a trajectory that is difficult for the predator to predict or perceive decreases the likelihood that predation will be attempted (Combes *et al.*, 2013). Unpredictability of trajectories can be increased indirectly, by comparison to the locomotion of other prey species, or by directly modifying trajectories.

To increase the perceived unpredictability of trajectories, prey can inhabit an ecosystem with similar organisms performing an alternative form of locomotion. A predator observing an

uncommon animal's trajectory would likely predict its future position incorrectly based on the trajectories of the more common species. This effect is enhanced if the species with differing trajectories exhibit similar cues to the predator. Human fighters illustrate this effect with the hypothesis for maintenance of lefthandedness at low frequency in human populations. Since left–handed humans are less common, it is less likely that a given fighter will have experience fighting a left–handed opponent, giving the left–handed opponent an advantage over the more common (and thus, predictable) right–handed opponents. Studies of cave paintings indicate that the frequency of left–handedness has been relatively constant over time, but slight increases have been noted in indigenous societies with higher rates of violence (Faurie and Raymond, 2005). If patterns of movement have equal intrinsic predictability, the fitness of the less common animal is highly frequency–dependent, and is therefore maintained at low frequency.

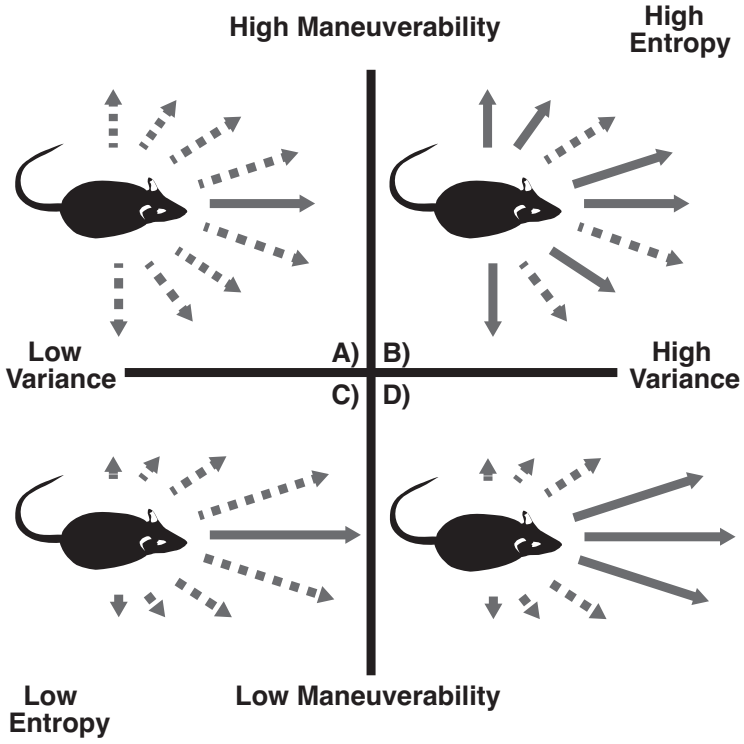


Figure 3.2: *Schematic showing how increases in maneuverability and variability contribute to greater entropy, or unpredictability. Dashed lines indicate directions in which the animal is capable of moving, and the length of the dashed line indicates the speed with which the animal is capable of moving in that direction. Solid lines indicate theoretically observed trajectories. Entropy, or unpredictability, is maximized when the number of possible trajectories increases and each of the possible trajectories are used with equal probability (quadrant B).*

Directly decreasing predictability of locomotion requires maneuverability: the physical ability to change the speed or direction of motion. Maneuverability can be quantified by determining how quickly and sharply an animal can perform a turn (Webb, 1983; Norberg, 1994). However, the ability to move in many directions does not, on its own, affect unpredictability. By choosing to move with more equal probability in multiple directions, prey increase the unpredictability of their movements (Figure 3.2). The majority of studies of escape trajectories concerned with Protean Behavior have quantified variance as a proxy for unpredictability (see Domenici *et al.* (2011a,b) for

comprehensive reviews). However, although unpredictability requires variability (made possible by maneuverability), not all variability contributes equally to unpredictability (Shannon, 1948). Indeed, natural systems of predator and prey show a difference in fitness between variability and unpredictability in escape behavior. For example, tentacled snakes can successfully catch fish that suddenly change in speed and direction, called a C–start. The escape behavior results in trajectories with variable direction, but the initiation of the behavior is so stereotyped that it is predictable (Catania, 2009).

Diversity in behavior has been classically cataloged by ethograms—histograms of how often distinct behaviors are exhibited. Ethograms are used in the analysis of different escape strategies of prey, e.g., to determine whether the prey uses only the optimal escape trajectory or a variety of sub–optimal escape trajectories (Domenici *et al.*, 2011a). Currently ethograms are rarely used because they depend strongly on the coordinate system used and the method for distinguishing behaviors (MacNulty *et al.*, 2007). Some behaviors even exhibit continuous variation and are impossible to discretize. Building on the history of ethogram analysis to determine the fitness of different escape behaviors, novel methods are currently being developed to characterize continuous variation in the locomotion of prey explicitly in the context of unpredictability, using information theory (Moore *et al.*, 2014). These methods enable characterization of non–steady–state locomotion in ways that relate more directly to the prey's fitness in the context of ballistic interception and pursuit predation.

3.4.3 Mechanisms determining locomotor variability at multiple levels of biological complexity may confer anti–predator advantages

The fitness advantage conferred by musculoskeletal sources of variability in locomotion is demonstrated in certain cases by biomechanical studies of ecologically relevant behaviors. However, the sources of variability have been identified at other levels of complexity, ranging from whole–body shape to single mutations of genes. Integrative approaches used to study the musculoskeletal system can lead to insights into the adaptive significance of these additional sources of variability.

At the musculoskeletal level, the relatively stiff tendons of kangaroo rats, *D. spectabilis*, transmit large forces and changes in length with little mechanical delay for rapid and powerful movements,

as in jumping (Biewener and Blickhan, 1988). Such a design favors successful escape in response to sound emitted by approaching predatory owls and rattlesnakes at frequencies to which the animal's auditory system is highly sensitive (Webster and Webster, 1971). Since these animals are natural predators of kangaroo rats, the rats' jumping, and the associated morphologies, are considered adaptations that enable them to evade predators.

The shape or general body plan of an animal also affects how it interacts with its physical environment during locomotion. For example, the location of sea lions' flippers dampen roll rotation and translational motion, but cannot significantly dampen rotations in the yaw and pitch axes, thereby enhancing turning performance in these axes during swimming (Fish *et al.*, 2003). While animals with bilateral symmetry favor locomotion in one direction, animals with radial symmetry, like brittle stars, can quickly change direction without turning by choosing to lead with a different limb (Astley, 2012). It is difficult to test the selective advantage these body shapes have on the locomotion of either predator or prey because they do not vary greatly in nature. However, it is possible to vary shape by modifying robot models (Briod *et al.*, 2014; Peterson *et al.*, 2011). If the variation in locomotion associated with each shape is correlated with a predator's preference (see the experimental design of Ioannou *et al.* (2012)), it may be possible to determine whether body shape can be adapted in ways that enhance evasive locomotion.

Genetic mutations may also affect motor control and thereby generate variability in gait and in patterns of the activation of muscles. For example, a premature stop–codon mutation in the DMRT3 gene is associated with the ability to perform pace and tölt gaits in horses, in addition to walks, trots, canters, and gallops (Andersson *et al.*, 2012). Knockouts of the same DMRT3 gene correspond to uncoordinated locomotion in a mouse model, demonstrating a causal effect between this gene and variability in locomotion. The locomotor effect of mutations in many genes has recently been studied in *Caenorhabditis elegans*. Each unique mutant displays distinct utilization of locomotor motifs, or "eigenworms" (Brown *et al.*, 2013). By comparing locomotion in mutant and wild–type *C. elegans*, it is possible to determine the effect of individual mutations on locomotor variability. If the behavioral consequences of mutations are understood, population–wide variability can be estimated by measuring the frequency of certain alleles in that population. Although these studies do not specifically address predator–prey interactions, investigation of genetic sources of variation in locomotion in a natural context would enable the use of population

genetics to make predictions regarding how the locomotion both of predator and of prey may evolve through time.

3.5 Future directions

The field of biomechanics currently benefits from an integrative approach that incorporates biology, physics, and engineering concepts. Similarly, applying an integrative approach that unites the fields of biomechanics, behavior, and evolution has the potential to contribute form–function insights into the evolution of biomechanical performance through time. Predator–prey interactions, in particular, can serve as a model system for integrative inquiry due to their strong effect on fitness and their dependence on locomotor performance.

Uniting diverse studies of predator–prey interactions from distinct fields is possible when classified by the strategies of predators and prey. Each of the strategies presented above have characteristic behavioral and sensory–motor patterns that favor distinct forms of locomotion both for predation and escape. Identifying underlying mechanisms that mediate such interactions enables comparison of even taxonomically distant animals that share a common strategy to reveal common co–evolutionary patterns between predator and prey. Thus, predator–prey interactions represent a model experimental study system for incorporating locomotor ecology into biomechanical inquiry, which increases the applicability of biomechanical results to evolutionary hypotheses.

Indeed, by espousing this integrative approach, it may be possible to determine whether predation strategies favor certain evolutionary patterns. For example escape from predation is often cited as a potential driver of the expansion or contraction of niches (Colwell and Fuentes, 1975; Sexton *et al.*, 2009). The evolutionary transitions from water to land [5] and from land to air involve expansion of the locomotor niche, and it has been suggested that evasion of predators drives the expansion of niches in these cases (Davenport, 1994; Dudley, 2000; Dial, 2003). Certain strategies, such as those that are reliant on discontinuity of locomotor matrix (Baylis, 1982), may be associated with niche expansion in prey. If there is an association between certain strategies for predator evasion and the expansion of prey niches, biomechanical and behavioral studies have the

[5] Mistake in publication corrected here

potential to make even more informative contributions towards the understanding of evolutionary patterns, such as adaptive radiations following invasion of a novel locomotor matrix.

3.6 Acknowledgements

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Chapter 4

Unpredictability of escape trajectory explains predator evasion ability and taxonomic diversity of desert rodents[1]

4.1 Abstract

Evolutionary change in limb morphology contributes to a cascade of changes in locomotion, behavior, and interspecies interactions. Mechanistically linking morphology to behavior and ecology is key to understanding the adaptive nature of locomotor evolution. Bipedality has long been considered an adaptation to increase the speed and economy of rodent locomotion in desert ecosystems, similar to cursorial animals. Here, we question these assumptions by quantifying biomechanical and behavioral performance associated with bipedality in jerboas (superfamily Dipodoidea). We find that jerboas do not follow predictions based on cursorial locomotion. Rather than enhancing locomotor economy, jerboas instead transition between three distinct gaits to enhance maneuverability and reduce the predictability of their movement trajectories. Highly unpredictable movement trajectories make it difficult for predators that use ballistic interception strategies to calculate intercept trajectories. Thus, bipedality in jerboas likely increases predator evasion ability. Consistent with this hypothesis, we also find jerboas have

[1]Co–authored with Kimberly L. Cooper, Andrew A. Biewener, and Ramanarayan Vasudevan

decreased anxiety–related behaviors in open fields relative to a sympatric quadrupedal species. The concomitant evolution of increased evasiveness and decreased open–field anxiety provides both the biomechanical and behavioral opportunity to forage in exposed microhabitats common to sparsely vegetated deserts. Locomotor innovation may therefore limit competition and maintain rodent diversity in resource–poor ecosystems.

4.2 Significance

Locomotion has the potential to determine many aspects of animal fitness, including foraging, finding mates, and evading predators. To understand how non–steady–state locomotion is particularly suited to evading interception–based predation, we present novel and integrative methods to characterize the kinematics, dynamics, and unpredictability of prey behavior in the context of community ecology. We show that bipedal hopping rodents use escape trajectories that are more unpredictable than those of sympatric quadrupedal rodents hunted by the same predators. Remarkably, enhanced predator evasion ability is accompanied by a quantifiable reduction in open–field anxiety in bipedal rodents. The behavioral divergence in microhabitat preference according to locomotor strategy likely decreases interspecific competition for limited resources, facilitating a greater diversity of rodents in desert ecosystems.

4.3 Introduction

Locomotion is an essential tool in the evolutionary 'arms race' between predator and prey, and the success of a particular evasive maneuver can be measured by directly observing predator–prey interactions (Domenici *et al.*, 2011a). But is it possible to predict predator evasion effectiveness as prey evolve novel forms of locomotion?

Convergent locomotor behavior in prey species can indicate a broadly successful evasion strategy. For example, bipedality is common in terrestrial prey animals. Lizards and cockroaches use transient bipedal locomotion at their highest running speeds, and some rodents are obligately bipedal (Alexander, 2004). Although this shift from quadrupedality to bipedality is commonly associated with prey species, it is unclear how this change in locomotion affects predator evasion

ability.

The evasive success of prey locomotion can only be understood in the context of the predation strategy encountered by the prey (Moore and Biewener, 2015). For example, predators such as owls or snakes hunt using a ballistic interception predation strategy, in which a predator uses observed prey movement to calculate an intercept course. When faced with this predation strategy, the ability to quickly deviate from a given trajectory enhances prey survival (Edut and Eilam, 2004). If the ballistic interception strategy is identified, predator evasion ability can be estimated by evaluating the ability of prey to produce rapid changes in trajectory (Mischiati *et al.*, 2014; Combes *et al.*, 2012). Thus, a mechanistic understanding of predator–prey interactions provides a basis for predicting predator evasion ability, even without direct observation of predation events.

Here we investigate whether and how the evolution of obligate bipedality in jerboas has enhanced their predator evasion ability. We compare jerboas to sympatric quadrupedal rodents, which exhibit the ancestral form of locomotion. Small desert rodents are targeted by owls and snakes that hunt via ballistic interception. We find that jerboas show significant deviation from the gait usage patterns stereotypic of quadrupedal steady–state cursorial locomotion. This led us to develop new quantitative methods to test the hypothesis that jerboas increase trajectory unpredictability in three–dimensional space. Indeed, the unusual gait usage is associated with an increase in trajectory unpredictability. Frequent transitions between gaits with distinct dynamic functions likely contribute to increased maneuverability, thus enhancing predator evasion ability.

Because of a tradeoff between foraging opportunity and predation risk associated with exposed microhabitats, biomechanical evasion ability is inversely correlated with risk–averse behavior (Lima and Dill, 1990; Kotler, 1984b; Hendrie *et al.*, 1998). We therefore used standard assays of rodent thigmotaxis — the behavioral affinity to shelter — to determine that bipedality is associated with a decrease in risk–averse behavior, further supporting our hypothesis that bipedality increases predator evasion ability. Our study, which integrates laboratory and field–based studies of biomechanics and behavior, demonstrates that the evolution of locomotor novelty is an important factor shaping interspecies interactions and taxonomic diversity within a community.

4.4 Results

4.4.1 Gait Dynamics

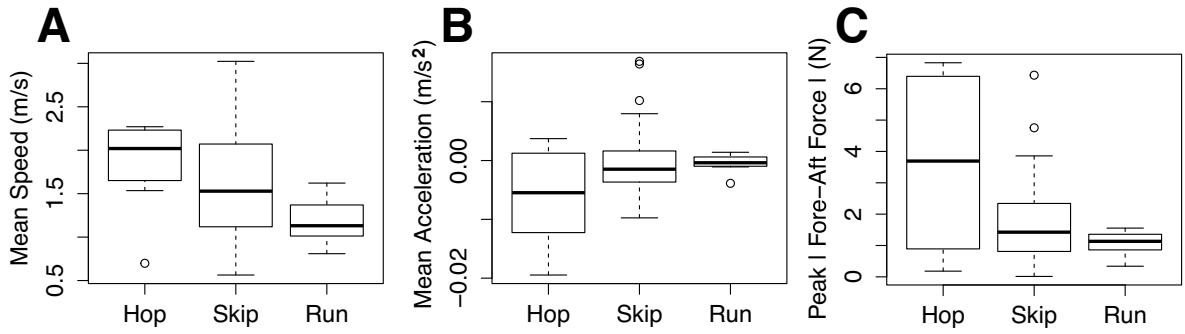


Figure 4.1: *Boxplots showing A) mean speed (magnitude of total x– and z–direction velocity), B) mean acceleration (derivative of speed in A), and C) the peak absolute value of fore–aft force recorded by the force platform. Mean speed is not as strong a predictor of gait ($p = 0.07$) in J.jaculus as mean acceleration ($p = 0.02$). The boxes span the interquartile range, the bold line represents the median, the whiskers extend to 1.5 times the interquartile range, and the open circles show outlier values outside of the whiskers.*

Although bipedalism has evolved multiple times in rodents, jerboas are the only group of rodents to employ three bipedal gaits (Schropfer *et al.*, 1985; Hayes and Alexander, 1983; Marlow, 1969). Other animals with multiple gaits are cursorial and have adapted to maximize speed, locomotor economy, and reduce the loading impact on the musculoskeletal system at high speeds (Lee *et al.*, 2011; Farley, 1997). Cursorial animals transition between gaits to increase endurance during migration, while outrunning predators, or while chasing down prey (Lull, 1904). The speeds at which cursorial animals transition between gaits can be estimated by the ratio of centripetal force to gravitational force (as an animal moves over its supporting limb), or the Froude number (Alexander and Jayes, 1983). Therefore, we first examined whether jerboa gait transitions are consistent with patterns associated with cursorial locomotion.

Table 4.1: *ANOVA table showing p–values for gait as a predictor of locomotor forces. Asterisks indicate statistical significance ($\alpha = 0.05$). |Peak| is the maximum of the absolute value of force values throughout a trial*

	Vertical Force				**Fore–Aft Force**			
	Peak	**|Peak|**	**Mean**	**Minimum**	**Peak**	**|Peak|**	**Mean**	**Minimum**
Gait	0.088	0.088	0.997	0.246	0.801	$2.37e-4$ *	0.135	0.015 *

Previous observations suggest that jerboas hop at the lowest speeds, skip at intermediate speeds, and run at the highest speeds (Happold, 1967; Schropfer *et al.*, 1985). The jerboa's hopping gait is similar to kangaroo hopping — stance phases in both hindlimbs are simultaneous and separated by extended aerial phases between each contact event. Skipping involves staggered but overlapping stance phases between hind limbs interposed between aerial phases. Finally, jerboa running is similar to human running, with an aerial phase separating the stance phases of each limb. Given a leg length of 0.064 m (mean hip height at mid stance), dynamic similarity based on equivalent Froude numbers predicts that the transition from hopping to skipping should occur at 0.56 ms^{-1}, and the transition from skipping to running should occur at 1.25 ms^{-1}. Surprisingly, we found no significant difference between the mean speed of each gait ($p = 0.07$, ANOVA, Figure 4.1 A), though the highest speeds were observed during hopping and the lowest speeds during running. Skipping exhibited the greatest range of speeds, and was used most often (64 of 80 single–gait trials). This pattern of using a single gait across the entire range of observed speeds contradicts the expectation based on cursorial locomotion that speed regulates gait usage in jerboas.

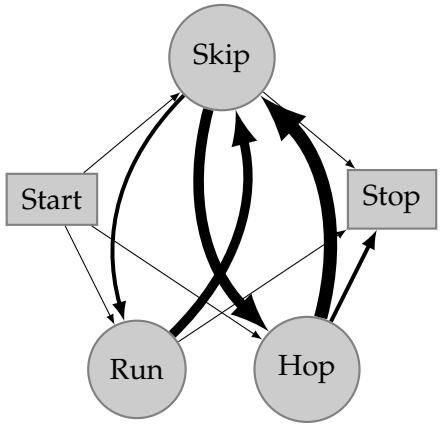


Figure 4.2: *Path diagram of transitions between gaits, starting, and stopping. The path thickness represents the probability of transitioning from one node to another. The camera field of view included the center of the track, not the ends, resulting in a bias towards capturing more stopping, rather than starting, events.*

We next quantified acceleration and ground–reaction forces to examine the dynamics underlying each gait. We found significant differences in mean acceleration among the gaits ($p = 0.02$, ANOVA, Figure 4.1 B). Hopping was associated with the greatest values of acceleration and deceleration. Indeed, a path analysis of transitions between gaits showed that hopping was preferentially used to decelerate (Figure 4.2). Skipping exhibited the most symmetrical variation in mean acceleration across the broadest range of speeds, and was the gait to which animals transitioned most frequently (Figure 4.2). Running showed the least variation in mean acceleration, and was likely used at lower speeds. Ground–reaction force data confirmed and explained these trends by revealing that gait is a strong predictor of both minimum fore–aft (or decelerative) and the absolute value (or magnitude) of fore–aft force (Table 4.1, Figure 4.1 C). Furthermore,

patterns of ground–reaction forces did not follow a characteristic pattern for each gait, as would be expected for a cursorial animal using steady–state locomotion. These results suggest that jerboas transition frequently between gaits that exhibit distinct functional dynamics, thus increasing their capacity for maneuverability.

4.4.2 Trajectory Unpredictability

While morphology determines the capacity to generate complex behaviors, or maneuverability, this is a measure of theoretical performance (Webb, 1983; Norberg, 1994). Predator–prey interactions are determined by the actual performance of locomotor trajectories that result from path planning behavior, given the animal's potential maneuverability (Moore and Biewener, 2015). This distinction is explicitly defined in the calculation of unpredictability, or Entropy (H):

$$H(p) = -\sum_{i \in X} p(i) \log p(i) \tag{4.1}$$

where H represents entropy, X is the set of possible outcomes, and $p(i)$ is the probability distribution of performing the outcomes in X (Shannon, 1948). Morphological traits that enable bipedal rodents to move extensively in the vertical plane increase the number of locomotor possibilities (increasing X) available to the animal, but the animal must *decide* to use these specialized morphological traits to generate more unpredictable locomotor trajectories (higher H).

The variance of observed escape trajectories has been used in previous studies to estimate predator evasion ability (reviewed in (Domenici *et al.*, 2011b)), but unpredictability more accurately estimates a predator's inability to compute a successful intercept course (Humphries and Driver, 1970). To illustrate, consider a prey animal with a sinusoidal trajectory (Figure 4.3). The animal can increase its variability by increasing the amplitude of the lateral displacements, yet the overall pattern, and thus the

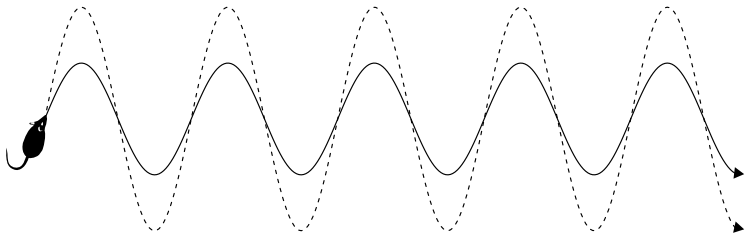


Figure 4.3: *Diagram showing two sinusoidal trajectories from a bird's eye view, traveling from left to right. The dashed path has twice the amplitude of the solid path. Consequently, the solid path has twice the variance of the dashed path, though both paths have the same unpredictability (H).*

unpredictability, of the locomotion remains the same. To quantify the effect of bipedal locomotion on trajectory unpredictability, we therefore developed methods to directly measure the unpredictability of rodent locomotion by generalizing the Shannon Entropy equation above (Equation 4.1) from discrete to continuous time and space.

In the laboratory, it was necessary to restrict jerboa movement within a narrow trackway to measure linear speed, gait, and forces. Consequently, the range of speeds used by jerboas in the laboratory was much lower compared to those reported in the field for the same species (Happold, 1967). Therefore, in an effort to quantify the effect of bipedality on trajectory unpredictability, we observed the locomotion of freely moving wild–caught sympatric rodents in response to simulated predation in their natural habitat.

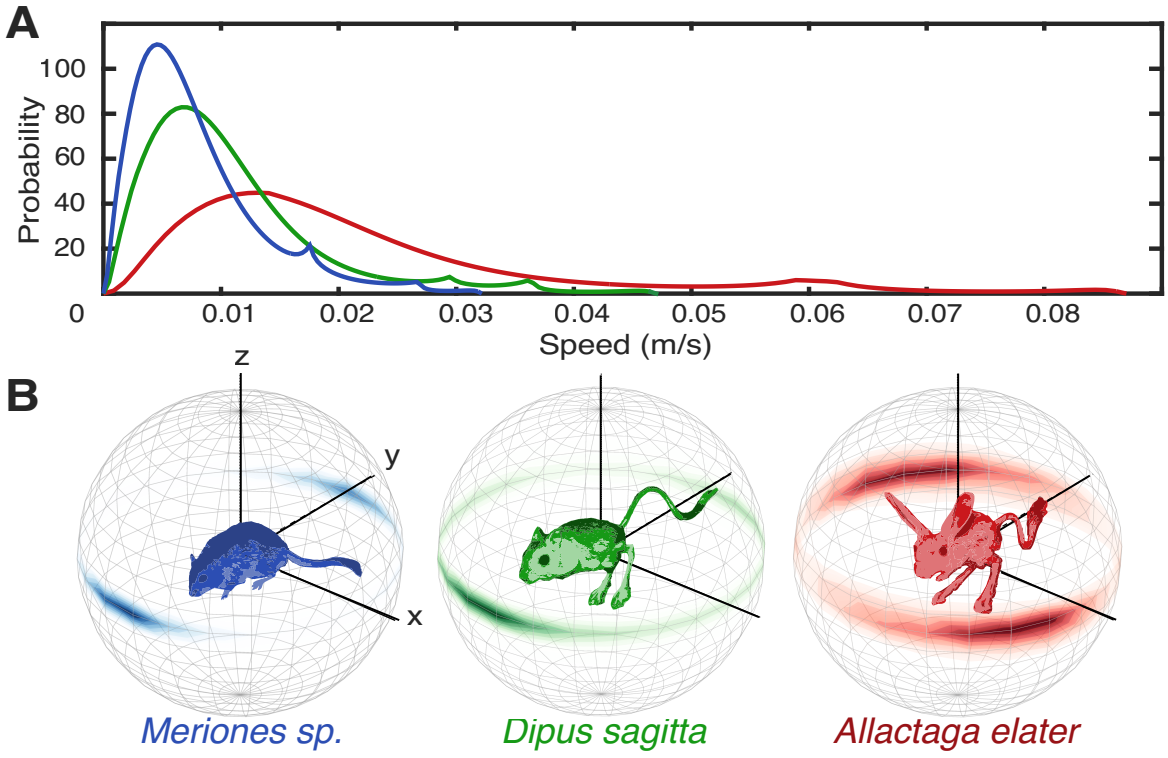


Figure 4.4: *Continuous probability distributions of A) speed and B) angle of locomotion for field animals. In A), the integral of each probability distribution is equal to one. In B), the color opacity at a given angle on the sphere corresponds to the probability of moving at that angle, with respect to the animal location in the previous frame (the center of the sphere).*

We captured and observed two species of bipedal jerboa (*Allactaga elater* and *Dipus sagitta*) and one species of quadrupedal jird (genus *Meriones*). *D. sagitta* is a three–toed jerboa closely

related, and of the same morphotype, as the *J. jaculus* jerboas in our laboratory experiments, and *A. elater* is a bipedal five-toed species where only the three central digits make contact with the substrate (Moore *et al.*, 2015a). As expected, bipedal jerboa trajectories were more unpredictable (higher entropy) than quadrupedal jird trajectories ($H(A.\ elater) = -9.936 > H(D.\ sagitta) = -12.60 > H(Meriones\ sp.) = -13.91$). When each is compared to a null-hypothesis generated from a mixed dataset selected from each pair of species (See Section 4.6.4), significant differences were found between the entropy (and therefore unpredictability) of bipedal *A. elater* and quadrupedal *Meriones* (Figure C.3 A, *A. e.* $p = 0$, *M. sp.* $p = 0.0002$). However, we were surprised to find that the difference in trajectory entropy between the bipedal jerboa *D. sagitta* and quadrupedal jird *Meriones sp.* was only trending towards significant (Figure C.3 C, *D. s.* $p = 0.0561$, *M. sp.* $p = 0.0605$). We also found that the two bipedal jerboa distributions differed significantly (Figure C.3 B, *A. e.* $p = 0$, *D. s* $p = 0.0002$). Thus, each sympatric species moved with a distinct pattern of trajectory unpredictability, measured in terms of its movement entropy over time.

To identify the locomotor behaviors that contribute to unpredictability in each species, we projected the multidimensional probability distribution into two marginal distributions: one illustrating the distribution of speeds (Figure 4.4 A) and another illustrating the distribution of angles (Figure 4.4 B). Quadrupedal jirds (*Meriones sp.*) used lower speeds most frequently, and the bipedal jerboa *A. elater* exhibited the most even distribution of speeds, reflecting a greater probability of acceleration and deceleration from step to step. The distributions of angles of motion reveal spatial preferences for each species. Quadrupedal jirds showed the greatest preference for forward locomotion with few turns. In contrast, both jerboa species showed an increased preference for vertical motion, suggesting that the evolution of bipedality likely facilitated the divergence in trajectory unpredictability between jerboas and jirds. However, *D. sagitta* exhibited a strong preference for forward locomotion, whereas *A. elater* showed a much stronger preference for turning. The asymmetry in movement preference about the forward direction was likely in response to asymmetry in the human–generated stimulus (Sorge *et al.*, 2014). The difference in preference of horizontal movement direction explains how two bipedal jerboas can exhibit such significant differences in locomotor unpredictability.

4.4.3 Risk Aversive Behavior

During the simulated–predation trials we observed considerable differences in the degree of thigmotaxis of each species, in that bipedal species explored the entire arena while quadrupedal jirds had an apparent affinity for the walled periphery. We therefore retrospectively analyzed the same locomotor trajectories using the Open–Field Exploration Test, frequently used to assess anxiety–related behavior in rodents (Bailey and Crawley, 2009). This test interprets a decrease in exploration and general locomotor activity in a brightly lit and exposed environment as a stress response to being without refuge from predators. Despite the stress being provided by simulated–predation rather than the more conventional bright lights, we found a significant increase in the percentage of time bipedal species spent in exposed areas (Figure 4.5 A).

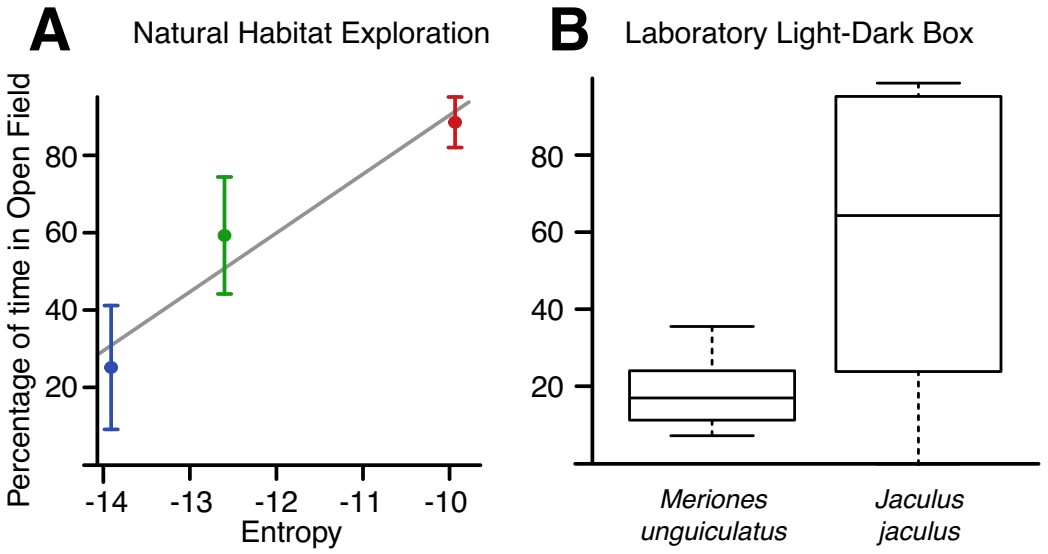


Figure 4.5: *A) Percentage of observed time spent in open field by species, as a function of the entropy of each species' trajectories during simulated predation trials in the natural habitat enclosures. Colors indicate species as in Figure 4.4, and error bars indicate 95% confidence intervals. The grey line represents a linear regression that is trending towards significant, despite a low sample size ($y = 15.23x - 242.66$, $p = 0.15$, adjusted $r^2 = 0.89$). B) Percentage of time spent in open field by species in laboratory Light–Dark Box trials. The boxes span the interquartile range, the bold line represents the median, the whiskers extend to 1.5 times the interquartile range, and the open circles show outlier values outside of the whiskers.*

To determine whether the divergence in microhabitat preference could be replicated under more controlled conditions, we performed the Light–Dark Exploration test, a standard assay of anxiety–related behavior with unambiguous categories of behavior and minimal restriction on locomotion (Bailey and Crawley, 2009). We recorded the amount of time each animal spent in

either the protection of a dark box or in exposed and brightly–lit open areas. Lab–reared bipedal jerboas (*J. jaculus*) spent significantly more time exploring the open area than the lab–reared quadrupedal jirds (*Meriones unguiculatus*) (Fig 4.5 B, $p = 0.00016$). These results corroborate the pattern we found in the natural habitat and suggest bipedality is associated with reduced anxiety in open microhabitats.

4.5 Discussion

Muybridge qualitatively categorized the locomotion of all bipedal hopping mammals as "ricochetal saltation" in 1899 (Muybridge, 1899), yet we have since learned that all bipedality is not dynamically equivalent. Kangaroos store elastic energy in their tendons, have a low cost of transport, and have force signatures during sustained locomotion consistent with cursoriality (Dawson and Taylor, 1973; Alexander and Vernon, 1975). On the other hand, the much smaller kangaroo rat is predominantly powered by muscle (Biewener and Blickhan, 1988), and exhibits short bouts of locomotion and rapid changes in speed and direction that truly evoke the adjective "ricochetal" (Bartholomew and Caswell, 1951). Like the kangaroo rat, the dynamics and kinematics of jerboa locomotion do not follow the patterns associated with cursorial saltation. Our approach identified quantitative biomechanical characteristics that distinguish ricochetal saltation, an unpredictable and non–steady–state form of locomotion, from cursorial saltation.

Highly variable animal behavior is often characterized with ethograms to record the frequency and variety of behavioral components (Grant, 1963; Kolmes, 1985). Unfortunately, these methods require discretization of continuously varying behavior, which introduces bias into the identification of behavioral components (MacNulty *et al.*, 2007). As we have shown, jerboas move with step–to–step changes in stride length, direction, gait, and speed, making it difficult to determine an appropriate discretization method. Sorting jerboa locomotion by each of these unique factors would require an ethogram with an infinite number of states or a binning that is so coarse that it obscures underlying patterns of behavior.

Instead, to quantify the unpredictability of locomotion that is continuously varying in both space and time, we developed a method to measure the continuous entropy of locomotor trajectories. Because only observed motion is used to calculate trajectory entropy, this method is agnostic

to the theoretical capabilities of an animal's morphology. This is beneficial because the relationship between morphology and biomechanical performance established in the laboratory can greatly differ from performance in the wild (Astley *et al.*, 2013; Combes *et al.*, 2012). Additionally, we are able to characterize motion comprised of different mean stride lengths and different planes of locomotion. Therefore, this method has broad applications for characterizing the behavioral expression of non–steady–state locomotion in a variety of species.

Non–steady–state locomotion enables prey to evade predators that hunt using a pre–calculated intercept course (Moore and Biewener, 2015; Edut and Eilam, 2004; Nishiumi and Mori, 2014). Although it has been shown that kangaroo rats produce evasive maneuvers in response to predator cues (Webster, 1962; Longland and Price, 1991), these studies lack metrics for quantifying the evasiveness of a maneuver. The novel method we present here to measure the unpredictability of locomotor trajectories enables quantitative studies of prey behavior, relevant comparison between diverse prey, and the estimation of evasiveness against interception–based predation. This method provides a framework for characterizing locomotion in a way that is relevant to biomechanical, ecological, and evolutionary inquiry.

For example, the increased trajectory unpredictability in bipedal jerboas enhances predator evasion and therefore decreases the risk associated with foraging in the exposed microhabitats common to sparsely vegetated deserts. However, the resultant increase in jerboa fitness would be minimal if bipedal rodents continue to forage near bushes in direct competition with quadrupedal rodents. Small quadrupedal rodents that follow more linear trajectories and are less able to evade predators exhibit high thigmotaxis — an affinity for darkness and shelter (Clarke, 1983; Kotler, 1984a; Griffin *et al.*, 2005; Ellard and Eller, 2009). We therefore expect an increase in predator evasion ability to evolve concomitantly with a reduction in thigmotaxis. This behavioral aversion to exposure is so ingrained in mice that it is a standard experimental system for understanding the genetics of anxiety and for measuring the effectiveness of therapeutic pharmaceuticals (Bailey and Crawley, 2009). Using established methods for evaluating rodent behavior, we found an inverse relationship between trajectory unpredictability and thigmotaxis in the field (Figure 4.5 A). Furthermore, the differences in thigmotaxis between bipedal and quadrupedal rodents were maintained even in lab–reared animals that had never encountered their natural predators (Figure 4.5 B). These results support our hypothesis that bipedal rodents have evolved both the predator

evasion ability and the behavioral predisposition necessary for foraging in exposed microhabitats.

Based on the relationship we found between trajectory unpredictability and microhabitat preference, bipedality likely influences desert community ecology. It is clear that divergence in microhabitat preference can enable resource partitioning to decrease competition in resource–poor ecosystems (Kotler *et al.*, 1994; Schropfer and Klenner-Fringes, 1991). The significant differences we have recorded in trajectory unpredictability and open–field anxiety between sympatric jerboas and jirds (Figure 4.5) suggests that bipedality limits interspecific competition, thereby maintaining diversity, among desert rodents (Rogovin, 1999). Indeed, many communities of desert rodents in Africa (Schropfer *et al.*, 1985; Petter, 1961), North America, (Harris, 1986; Kotler, 1984b), and Australia (Marlow, 1969; Dickman *et al.*, 2010) exhibit similar patterns of locomotor, behavioral, and ecological stratification that include the evolution of bipedality. Thus, since diversity in predator evasion ability and foraging strategy can enable resource partitioning and species coexistence (Schoener, 1974; Chesson, 2000), we propose that locomotor innovation is an important driver of taxonomic diversity.

4.6 Methods

All animal care and use protocols were approved by the Harvard Faculty of Arts and Sciences Institutional Animal Care and Use Committee (IACUC) and the United States Department of Agriculture.

4.6.1 Laboratory Gait Analysis

We collected 139 trials from 5 male jerboas (*J. jaculus*) from a breeding colony at the Harvard Concord Field Station. Each animal was encouraged to travel along a narrow trackway (2 x 0.15 x 0.4m) over a two–axis force platform (0.06 x .12m) and past a high–speed video camera recording at 500 fps. The camera field of view captured one to three strides, depending on speed.

We visually categorized the gait of each stride by footfall pattern following terminology specific to bipedal animals (Alexander, 2004), rather than terminology traditionally used to describe quadrupedal gaits (Schropfer *et al.*, 1985). 59 trials were excluded from speed and force analysis: 28 involved transitions between gaits, 8 included a stop or start from standstill (these

36 trials were used to generate Fig. 4.2), 2 involved changes between the leading foot between strides, and the gait in 20 trials was ambiguous. The remaining dataset included 80 trials, with 7 to 29 from a single individual.

We calculated the speed of each jerboa by tracking its eye using DLTdv5 tracking software for Matlab. The eye was used to estimate the location of the center of mass, as the *J. jaculus* have fused cervical vertebrae (Moore *et al.*, 2015a; Hatt, 1932), limiting head motion with respect to the body.

Gait transition predictions were made assuming that the transition from slow to medium gaits occurs at Fr=0.5, and the transition from medium to fast gaits occurs at Fr=2.5, and using the equation

$$Fr = \frac{u^2}{gl} \tag{4.2}$$

where l is the leg length, g is gravity, and speed is u (Alexander and Jayes, 1983).

4.6.2 Field Trajectory Unpredictability

We captured rodents from their native habitat in the desert north of Fukang, in Xinjiang Province, People's Republic of China. Bipedal jerboas (*A. elater* and *D. sagitta*) and quadrupedal jirds (*Meriones sp.*) were captured at night, then observed and released the following night. Animals were recorded moving within a 5 x 5m fenced area in the native habitat during their naturally active hours (21:00–1:00 CST, 19:00–23:00 Xinjiang Local Time). We illuminated the enclosure using infrared flood lights and recorded animal movements using cameras from which the infrared filter was removed. Each animal was filmed responding to stimuli (e.g. looming, loud noises) for fifteen minutes or until it presented signs of fatigue. The position of the rodent was tracked in three–dimensional space using DLTdv5 tracking software. In each video, continuous segments of tracked data less than 20 frames were excluded, and each remaining segment of continuously tracked data is hereafter referred to as a "trial." To reduce the effect of outliers, we retained only the most similar 97% of the data for each species. This dataset included 25397 frames for 5 *A. elater*, 11185 frames for 3 individuals of *D. sagitta*, and 20609 frames for 3 individuals of *Meriones sp.*

4.6.3 Entropy Calculation

To measure the locomotor unpredictability of each species, we developed methods to measure the entropy of each species in continuous three–dimensional space. The entropy analysis required 4.09 s for *A. elater*, 3.80 s for *D. sagitta*, and 3.47 s for *Meriones sp.* on a computer with 202.6 GHz processor cores and 128 GB ram.

Measuring the entropy of a species requires constructing a continuous probability distribution that best explains the observed locomotion of that species. This continuous probability distribution assigned a probability to each potential subsequent location given the current position. Unfortunately an infinite number of continuous probability distributions can explain any finite amount of data. According to the Principle of Maximum Entropy (Uffink, 1995), choosing the Maximum Entropy probability distribution from among the set of probable explanations for the given data allows one to make the fewest assumptions about the type of distribution producing the observed data ("epistemic modesty"). As a result, given data, the best continuous probability distribution is identified as the one that maximizes the entropy amongst all distributions that are able to fit the data.

To find the maximum entropy probability distribution, we first defined how to calculate the entropy of continuous probability distributions, which is called "Differential Entropy." Given a continuous probability density function, distribution f, the differential entropy is defined as:

$$\boldsymbol{H}[f] = -\int_{[-1,1]^3} f(x)\ln f(x)dx. \tag{4.3}$$

where the limits of the integral are defined by the maximum and minimum distance that the animal can move in any direction in an instance of time. Note, in this case we have chosen -1 and 1 for convenience without loss of generality. Because our data are in three–dimensional space, x and the limits of x are three–dimensional objects (i.e. $[-1,1]^3$ is a three–dimensional unit box).

We utilize the notion of moments to formalize the quality of fit. The m^α moment for a probability density function, f is defined as:

$$m_\alpha = \int_{[-1,1]^n} x^\alpha f(x)dx, \tag{4.4}$$

where α is an element in $\alpha = (\alpha_1, \alpha_2, \alpha_3) \in \mathbb{N}^3$ and $\mathbb{N}$ denotes the nonnegative integers. Also note

that for $x = (x_1, x_2, x_3)$ $x^\alpha = x_1^{\alpha_1}, x_2^{\alpha_2}, x_3^{\alpha_3}$. To define the moments of empirical dataset, suppose we are given individual data points $d_1, \ldots, d_N$ where $d_i \in \mathbb{R}^3$ for all $i \in \{1, \ldots, N\}$. Then the empirical moments, $\hat{m}_\alpha$, of the data are defined as:

$$\widehat{m}_\alpha = \frac{1}{N} \sum_{i=1}^{N} (d_i)^\alpha. \tag{4.5}$$

As the moments of the empirical data and the moments of the continuous probability distribution become more similar, the continuous probability distribution better fits the empirical data.

We can therefore restate the equation as this optimization problem:

$$\max_f \left\{ \boldsymbol{H}[f] \Big| \int_{[-1,1]^3} x^\alpha f(x) dx = \widehat{m}_\alpha, \ \forall \alpha \in \mathbb{N}_{2k}^3 \right\}, \tag{4.6}$$

where $\mathbb{N}_k^3$ refer to those $\alpha \in \mathbb{N}^3$ with $|\alpha| = \sum_{i=1}^3 [\alpha]_i \leq k$. That is, we seek to find a continuous probability density function f that simultaneously maximizes the differential entropy while having its first $2k$ moments equal to the given empirical moments.

See Supplemental Information to solve this optimization problem.

4.6.4 Entropy Significance Test

To determine whether there are significant differences in entropy between species pairs, we compared the entropy computed for each species to the entropy of a null hypothesis dataset containing data from an equal number of trials from both species.

For each unique pair of species, we computed the entropy of a dataset consisting of 50 trials randomly sampled from the continuous probability distribution of each species (100 trials sampled total). We repeated this process 10,000 times to generate a probability distribution. For each distribution we determined the proportion of the combined entropy values that are either greater than or less than the true entropy value of each species in the comparison. This outlying proportion divided by the total number of values (10,000) represents the p–value, or how significantly the data reject the null hypothesis (that there is no difference between the trajectory entropy of the two species) (Figure C.3).

4.6.5 Field–Based Open–Field Exploration Test

The same videos used to capture field trajectory unpredictability were visually analyzed for field usage following the "Open Field Exploration Test" as described in (Bailey and Crawley, 2009). Animals within two body–lengths of the enclosure walls were categorized as being in the "edge" state, including climbing on the walls of the enclosure. All other times the animals were visible were categorized as being in the "open" state.

4.6.6 Laboratory–Based Light–Dark Exploration Test

We performed this anxiety test following the procedures in (Bailey and Crawley, 2009). We used 4 adult male *J. jaculus* jerboas born (in March 2013) and raised in the laboratory colony at the Concord Field Station mentioned above. 6 adult jirds (*Meriones unguiculatus*, also commonly called 'gerbils') were obtained from Charles River, acclimated for three weeks, and were 70–72 days old at the time of experimentation. All rodents were housed individually, and animal housing, care, and experimental protocols were approved by Harvard IACUC and USDA.

Animals were transported from their home cages in an opaque plastic transportation case that was sanitized between trials. Video was recorded from above with the same camera as in the simulated predation (Casio ZR100) in HD (1920 x 1080 pixels) at 30 fps. Recording began before the animal was brought into the experimental area in a sterilized plastic box, and ended after the animal was removed from the experimental arena. The experimental arena (1 x 1 x 0.35 m) was made from clear plexiglas to aid in sterilization, with a yoga mat lining the bottom to provide grip. The shelter was an opaque plastic box (0.5 x 0.4 x 0.35 m) with a 5 cm radius semicircular opening. The experimental arena was lit from above by a combination of fluorescent and incandescent lights, at 9000 lx across the exposed area. Animals were placed inside the experimental arena in the exposed area facing away from the shelter. The experimenter left the room for five minutes, retrieved the animal, and returned it to its cage. The experimental area, shelter, and transport box were sterilized with a disinfectant (Quatricide) between trials to limit the possibility of scent signals from a previous animal affecting the behavior of other animals. We visually recorded the amount of time each animal spent within the shelter versus outside of the shelter, time spent in risk–assessment (face and forelegs outside of the shelter, with rest of the body within the shelter),

and number of transitions between light, dark, and risk–assessment.

4.7 Acknowledgements

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Chapter 5

Modeling the ecological convergence of small bipedal rodents

5.1 Abstract

There is a striking degree of morphological convergence between the small bipedal desert rodents of North America, Australia, and Afro–Eurasia. Although the morphology and ecology of these rodents is not completely convergent, they may occupy and perform an equivalent role in their respective ecosystems. If small bipedal rodents have converged on the same ecological niche, a similar set of ecological factors would predict the current occurrence of bipedal rodents. In this chapter I use climatic niche modeling, functional morphology, and comparative methods to determine the relationship between ecology, behavior, and morphology in the mouse–related group of rodents. This modeling will provide a deeper understanding of the role bipedal rodents play in their natural habitats. More generally, this provides a basis for incorporating the physical properties of the natural habitat as factors in ecological niche models.

5.2 Introduction

The evolution of novel forms of locomotion is often an adaptation to a drastic shift in ecology, such as water to land(Shubin *et al.*, 2006), land to water (Spoor *et al.*, 2002), or land to air (Dudley and Yanoviak, 2011). However, locomotor novelty does not have to be accompanied by major

changes in habitat. For instance, bipedality in small rodents has independently evolved three times in desert ecosystems, and is maintained in the presence of sympatric quadrupedal rodents (Mares, 1993). Although the repeated evolution of bipedality in association with desert ecosystems implies an adaptive convergence, the ecological factors favoring the evolution of bipedality are not immediately obvious.

The acquisition of bipedal locomotion in distantly–related desert rodents has captivated scientists for over a hundred years (Swainson, 1835; Lull, 1904), and represents a classic example of morphological convergence. Despite the history of interest in this system, there is still much debate regarding the adaptive benefit of bipedalism and whether these rodents play an equivalent role in their respective ecosystems (Mares, 1993; Ben-Moshe *et al.*, 2001; Howell, 1932; Berman, 1985). The convergent animals include: jerboas (superfamily Dipodoidea) native to North Africa and central Eurasia, kangaroo rats (family Heteromyidae) native to North America, and hopping mice (genus *Notomys*) native to Australia. Due to the great distance between each of these systems, a researchers rarely study more than one member of the convergence with the same methods. Furthermore, previous studies of bipedal taxa often focus on a single aspect of rodent biology (e.g. reproductive biology, respiration, or social dynamics), limiting their potential to reveal evolutionary tradeoffs, correlation between traits, or constraints. In this chapter I compare the climate, locomotion, and dietary ecology of all three groups to test whether the current distribution of bipedal rodents can be explained by a single model of evolution.

5.2.1 Climate

Although quadrupedal rodents can be found in virtually every climate (Walker, 1964), small bipedal rodents are only found in desert ecosystems with sparse and irregular rainfall. In the habitat of each bipedal rodent, substrates range from the shifting sand dunes to packed crusty earth sprinkled with hardy bushes.

The absence of bipedal rodents from all substrates other than desert sands suggests that the physical properties of granular media may be necessary for bipedal locomotion. Previous studies have found that animals specialized for living in sandy ecosystems are able to exploit the physical properties unique to granular media to enhance their locomotor performance (Maladen *et al.*, 2009;

Herreid and Full, 1986).

5.2.2 Locomotion

The erratic bouts of locomotion exhibited by small bipedal rodents is difficult to characterize using the biomechanical approaches developed for steady–state locomotion. Here I summarize the various biomechanical approaches that have been used to characterize the ricochetal locomotion of bipedal rodents.

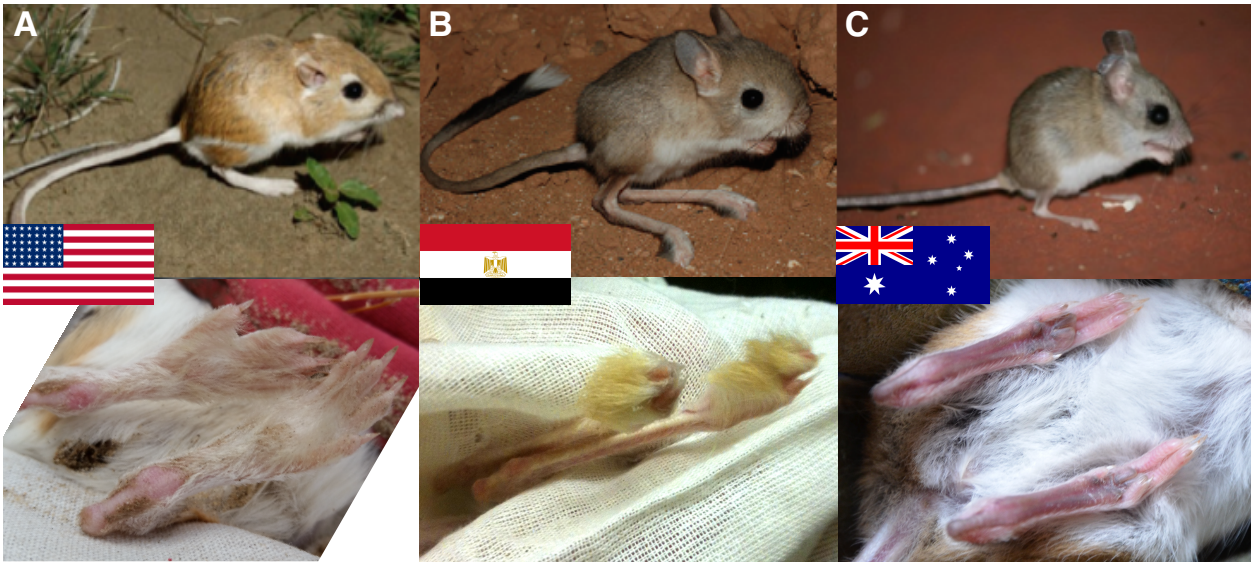


Figure 5.1: *The convergent bipedal desert rodents (top row), and the plantar surfaces of their feet. A)* Dipodomys spp. *and* Microdipodops spp. *in the family Heteromyidae are native to western North America, and have four or five toes. (Top photograph by Skyler Maynes, bottom photograph by Talia Yuki Moore) B) Jerboas in the family Dipodidae are native to northern Africa, the Arabian Peninsula, and central Eurasia, and have three to five toes. (Top photograph by Flickr user Gabri Mtnez, bottom photograph by Talia Yuki Moore) C)* Notomys spp. *in the family Muridae are native to Australia and retain all five toes. (Top photograph by Flickr user Michael J Barritt, bottom photograph by Christofer Clemente).*

Prior to the research that comprises this dissertation, the biomechanics of North American Kangaroo Rat locomotion were well characterized (Howell, 1932; Eisenberg, 1963; Bartholomew and Caswell, 1951). Kangaroo rats hop bipedally, but occasionally walk using all four legs. In response to the vibrations at the frequency produced by their predators, kangaroo rats reflexively leap vertically (Webster, 1962). These erratic and explosive leaps enable kangaroo rats to evade predators with greater success than sympatric quadrupedal rodents (Longland and Price, 1991). These leaps are generated primarily by muscular energy, rather than energy elastically stored

in tendons from the previous stride (Biewener and Blickhan, 1988). This increases their cost of transport over long distances, limiting their movements to a few explosive hops at a time (Heglund *et al.*, 1982).

Australian hopping mice (genus *Notomys*) are facultatively bipedal, and use quadrupedal motion for everything below 11 km hr^{-1} (Baudinette *et al.*, 1976). During quadrupedal locomotion, *Notomys alexis* exhibit patterns of speed–dependent gait transition and oxygen consumption similar to other cursorial mammals. Unfortunately, the only characterization of their bipedal locomotion is a footfall pattern analysis (Marlow, 1969), showing that *Notomys cervinus* hop with both hind feet simultaneously. Like kangaroo rats, Australian hopping mice use their bipedal locomotion to evade predators by quickly running to a burrow (Marlow, 1969).



Figure 5.2: *Radiograph of the pes of an adult* Jaculus jaculus *(by Talia Yuki Moore), with the red arrow indicating the sesamoid bone embedded within the achilles tendon.*

Jerboas are more morphologically and kinematically derived than kangaroo rats and hopping mice. Previous chapters of this dissertation have reconstructed the morphological evolution of the jerboa hindlimb (Ch. 1), computed the dynamics of jerboa hopping (Ch. 2), and characterized the unpredictability and behavior of jerboas in natural habitats (Ch. 4). Jerboa morphology is quite distinct: the metatarsus to femur ratio is the highest in Rodentia (in fact, at 1.2, it is higher than most Artiodactyls (Lovegrove and Mowoe, 2014), the three central metatarsals are completely fused into a canon bone, peripheral digits I and V are often lost (Ch. 1), there is an ossified sesamoid embedded within their achilles tendon (Figure 5.2), and jerboas exhibit the most dense patches of fur on the plantar surface of their phalanges (Figure 5.1). As adults they move

exclusively bipedally (Berman, 1985), use even less elastic energy storage and return between strides than kangaroo rats (Ch. 2), and perform three distinct gaits (Ch. 4). It is no surprise to find that jerboas are the oldest group of bipedal rodents, having evolved bipedality between 23 and 35 mya (Ch. 1) (as opposed to ~15 mya in Heteromyidae (Hafner *et al.*, 2007) and less than 7 mya in *Notomys spp.* (Nilsson *et al.*, 2010)).

5.2.3 Dietary Ecology

Each bipedal rodent shares its desert habitat with many other animals, including various quadrupedal rodents. North American and Afro–asian quadrupedal desert rodents are omnivores that forage in sheltered areas (Kotler, 1984b; Brown *et al.*, 1994) [1]. Although *Notomys spp.* are also omnivorous, kangaroo rats and jerboas are strictly herbivores that forage in exposed areas to find soft roots and seeds (Mares, 1993). Researchers who have trapped rodents in the deserts of Asia, Australia, and California have described a marked lack of aggression and reduced bite force of bipedal rodents when compared to sympatric quadrupedal rodents (*pers. observ.*, *pers. comm.* K. Cooper, C. Clemente, A. Horner). This divergence in diet and foraging behavior has led many researchers to propose that the evolution of bipedality enables species coexistence despite the limited resources in desert ecosystems (Rosenzweig and Winakur, 1969; Price, 1978; Schropfer and Klenner-Fringes, 1991; Brown *et al.*, 1994; Rogovin, 1999).

There is a striking congruence in the patterns of locomotor and foraging morphology specialization in desert rodents. Researchers have proposed that specialization between distinct aspects of an animal's ecology can be correlated, and can be used to explain the geographic ranges of animals (Brown, 1984). A previous study declared that the bipedal rodents do not occupy an equivalent niche on the basis of differences in diets (Mares, 1993), but this study did not consider locomotion and diet specialization as a continuum, or as a transitional form of a trait evolving towards an optimum. Although there is currently no straightforward way to measure degree of bipedality, in Chapter 4 I showed that the evolution of bipedality is not a discrete state, as different species of bipedal jerboa differ in their predator evasion ability and preference for open microhabitats. Therefore, I hypothesize that there is a relationship between locomotor and

[1] Equivalent studies have not been performed on Australian quadrupedal rodents

foraging ecology in desert ecosystems. In this chapter I use phylogenetic comparative methods to determine whether the variation in climate and foraging morphology across rodents is sufficient to predict the variation in locomotor specialization present in the mouse–related clade of rodents.

5.3 Methods

5.3.1 Morphometrics

Linear measurements were taken on skeletal preparations in museum collections using digital calipers by TYM (See appendix for specimen and museum information). Long bone elements were measured because variation in long bones is associated with variation in locomotion, as shown in (Moore *et al.*, 2015a) (humerus, ulna, femur, tibia, third metatarsal). Both male and female specimens were measured, to justify inclusion of specimens with unspecified sex. Specimens identified as juveniles were excluded from the study. Specimens that did not have the complete set of long bone measurements were excluded from this study.

All measurements were $\log_{10}$ transformed. The limb measurements underwent a phylogenetic Principal Components Analysis using the "phylopc" function in the phytools package for R, with the 'lambda' optimization method and a covariance matrix. The first principal component (pPC1) loaded similarly on all measurements and in the same direction. I attributed changes in this axis as resulting primarily from changes in body size. The remaining principal components were interpreted as representing changes due to locomotor specialization, and served as the dependent variable in the least squares models.

An evolutionary model for the pattern of rodent hindlimb evolution is necessary to perform the comparative methods. To determine the most appropriate model for the pattern of hindlimb evolution in bipedal rodents, I chose a random subset of 15 species in the mostly bipedal family Dipodidae and 23 species in the mostly quadrupedal Muridae. Using the OUwie package for R, I fit seven different models of evolution to the hindlimb data. The Dipodidae family was selected because it has the greatest number of extant bipedal rodents, which enhances the ability to statistically reconstruct the pattern of evolution in the clade. Brownian Motion (BM) models assume that random changes in traits are symmetric with a standard deviation (σ^2). Ornstein–Uhlenbeck (OU) models assume traits evolve with an affinity (strength α) towards an optimum

(θ), with a standard variation (σ^2). I fit seven distinct models of evolution to the hindlimb data: Brownian Motion with a constant rate of evolution (bm1), different rate parameters for each state on the tree (bms), and Ornstein–Uhlenbeck models with a single optimum for all species (ou1), different state means with a single α and σ^2 on all states (oum), different state means with multiple σ^2 (oumv), different state means with multiple α (ouma), and multiple α and σ^2 for each regime (oumva). Akaike Information Content analysis was used to select the most appropriate model for the data.

5.3.2 Diet Data

Diet data were derived from primary (Pizzimenti, 1980; Pinotti *et al.*, 2011; Balete *et al.*, 2012; Miljutin and Lehtonen, 2008) secondary literature (Nowak and Wilson, 1999; Sokolov *et al.*, 1996; Shenbrot *et al.*, 2008), and from online biodiversity databases (www.eol.org, www.iucnredlist.org, animaldiversity.org). Dietary descriptions were transformed into a presence–absence matrix for 18 distinct food sources (see Appendix D for data matrix). Two food sources used by only one taxon were removed (tree gum and mummified human flesh). Diet specialization was measured by dividing the number of food source categories a species ate by the total number of food source categories in the dataset.

5.3.3 Substrate, Climate, and Occurrences

Soil was sampled from the native ranges of each group of bipedal rodents. At each location, the surface strength of the soil was measured four times using a penetrometer with a wide foot for low–strength soils (Humboldt). Two trials measured the surface strength of a hard crust (if present), and two trials measured the surface strength of loose sand. Samples were dried and passed through a vibratory sieve shaker (Retsch) for a minimum of 12 hours to determine particle size distribution.

Occurrence data for all measured taxa were downloaded from The Global Biodiversity Information Facility (www.gbif.org), Vertnet (www.vertnet.org), and the Atlas of Living Australia (www.ala.org/au) databases. Outliers and records in bodies of water were excluded. The total dataset comprised 34029 occurrences for 127 taxa, with 63 to 4345 (mean 340.3, median 317.5)

occurrences per species. *Apodemus ponticus* had no georeferenced occurrences in the GBIF or VertNet databases, so the centroid of the range presented in the IUCN database was used as the only occurrence for this species.

Global climate was quantified using the Annual Global Aridity Index CGIAR–Consortium for Spatial Information (Zomer *et al.*, 2008) and the 19 Bioclimatic variables from the Global Climate Database (Hijmans *et al.*, 2005). Niche models were constructed using the Maxent package for R. Niche models based on each group of bipedal rodents separately, and all bipedal rodents together, were used to determine the climatic variable that is the best indicator of bipedal rodent occurrence.

Table 5.1: *The number of genera and species sampled from each family for the current analysis. All families within the mouse–related clade Myomorpha, according to Fabre et al. (2012).*

Family	Genera	Species
Anomaluridae	1	1
Calomyscidae	1	1
Castoridae	1	2
Cricetidae	46	52
Dipodidae	12	20
Geomyidae	2	2
Heteromyidae	5	7
Muridae	29	34
Nesomyidae	4	4
Pedetidae	1	1
Spalacidae	3	3

5.3.4 Phylogeny

I combined a Rodentia phylogeny with broad species representation (Fabre *et al.*, 2012) and a recently published molecular phylogeny for greater resolution within Dipodoidea (Moore *et al.*, 2015a). Pruning away taxa unrepresented in this analysis resulted in a tree with 127 taxa in 11 families and 105 genera (Table 5.1).

5.3.5 Pilot Study

An unsuccessful pilot study motivated the collection of a larger, broader, and more precise dataset. The pilot study was performed on a subset of taxa (39 specimens in 14 genera, with values averaged by genus) with morphological measurements that partially overlap the final dataset. The morphological measurements included: the distance from pelvis from the acetabulum to the distal tip of the ischium, the distance from the pubic symphysis to the iliac crest; the length, mediolateral and anteroposterior width of the humerus, femur, tibia, third metatarsal, and third proximal phalanx; the length, width, and thickness of the calcaneus. Only the linear measurements of

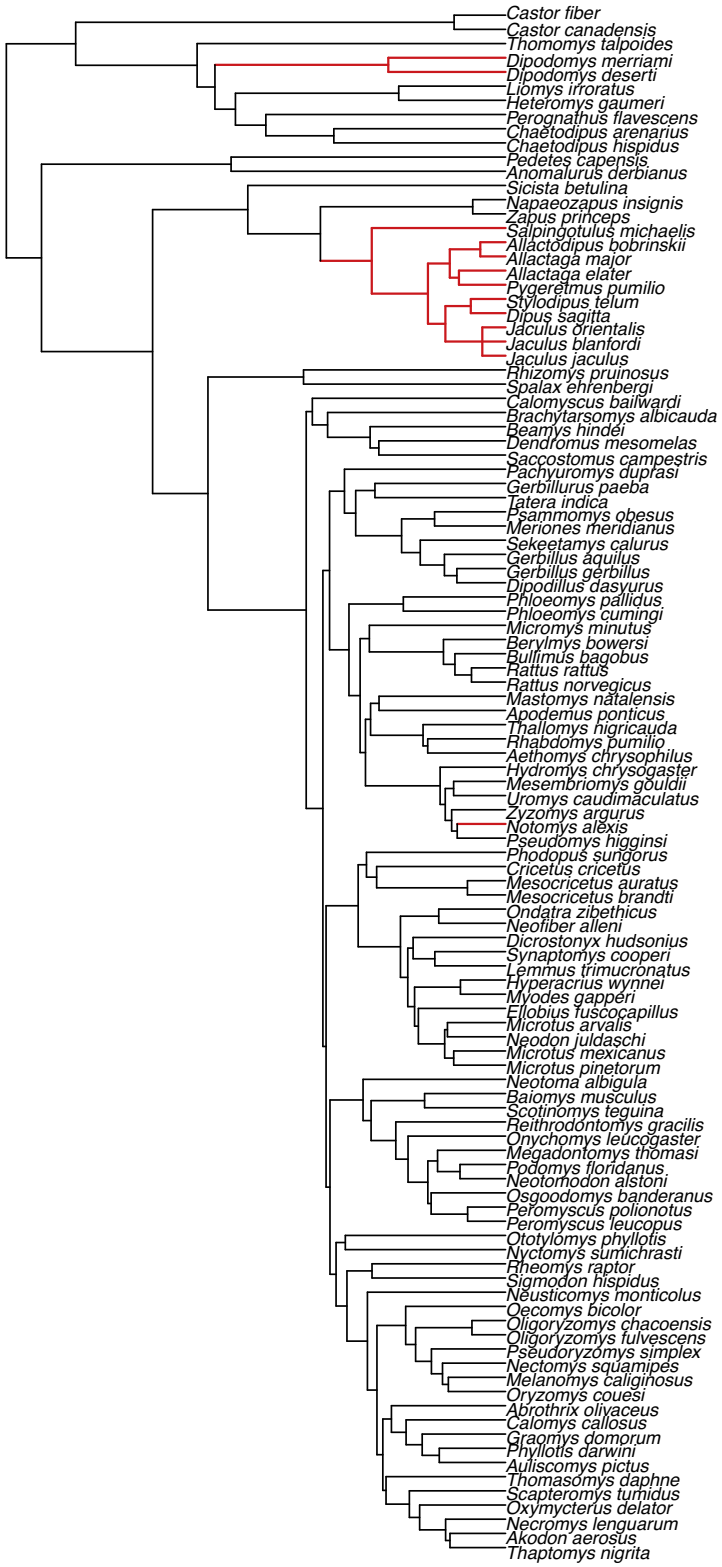


Figure 5.3: *Phylogeny of rodents included in this study. Small bipedal rodents are indicated with red branches.*

the humerus, femur, tibia, and third metatarsal were used in the final analysis. The genus–level phylogeny used (Blanga-Kanfi *et al.*, 2009) and the absence of climate data in the pilot study represent significant differences from the final analysis presented here.

5.3.6 Phylogenetic Comparative Analysis

I used phylogenetic generalized least squares (PGLS) multiple regression to test multiple models of correlation. With these models I sought to determine whether the variation in dietary and climatic ecology were sufficient to predict the variation in locomotor specialization I see in mouse–related rodents. With the R computational software, I used the gls function in the 'nlme' package to perform PGLS with univariate pPCA limb data (pPC2 only as an indicator of locomotor specialization), and the procD.pgls function in the 'geomorph' package to perform the PGLS with multivariate pPCA limb data (pPC2-5 together as an indicator of locomotor specialization).

I randomly resampled the taxa in my dataset to assess model sensitivity and reduce the effect of outliers. Bootstrapping was not used, as sampling with replacement would be incompatible with the phylogenetic structure of the data. Each nlme model was calculated on 100 of the 127 total taxa, and this was repeated 1000 times. Each geomorph model was also set to compile results over 1000 iterations.

Locomotor specialization was the dependent variable in this analysis. My independent ecological traits were represented as continuous variables: diet specialization was represented by the proportion of total food sources a species has been shown to eat, the physical properties of the substrate are represented by the mean global aridity index for all georeferenced occurrences of each species. λ here is an error term that incorporates the non–independence of these taxa according to the structure of their phylogenetic tree (Pagel, 1999). I tested the following combination of independent variables for their ability to predict the observed pattern of variation in limb specialization:

1. Aridity + λ
2. Diet + λ
3. Aridity + Diet + λ

4. Aridity * Diet + λ (including the interaction of the predictor variables)

5.4 Results

5.4.1 Substrate Analysis

This sand in deserts differs from the sand found on beaches, due to differences in erosion processes (Pettijohn *et al.*, 1987). Beach sand is created by water erosion, which rounds out the edges of the sand particles, and results in a larger and more uniformly–sized particles. Furthermore, beach sand often contains water, which alters the physical properties of the granular solid. Desert sand, on the other hand, is the result of wind erosion, which creates much smaller dust particles of irregular shape (eolian sand). Following rainfall, the dust creates a mud, which dries into a crust on the surface of the ground. This crust can be easily broken, restoring the soft and powdery consistency of the dust (Pettijohn *et al.*, 1987). Thus, the surface strength of eolian sand often shows a bimodal distribution: one mode representing the strength of the crust, and another mode representing the strength of the loose flowing sand (Hanks, 1960). In the natural habitat of each bipedal rodent, there was a top crust and loose sand underneath. The greatest difference between the surface strength of the two substrates was in the Australian *Notomys*, and the smallest difference was between the North American *Dipodomys*. Loose sand in the natural habitat of jerboas, in Xinjiang, People's Republic of China, had the lowest surface strength, as it provided barely any resistance to the penetrometer. Based on the variation in these substrate surface strength readings, each species of bipedal rodent likely encounters a wide range of terradynamics as it moves through its natural habitat.

Table 5.2: *Penetrometer readings in the native ranges of bipedal rodents, in kg/cm^2. These readings represent approximate unconfined shear strength. The maximum value is 0.28 with the low–strength soil adapter foot.*

	Crust 1	Crust 2	Loose 1	Loose 2
***Dipodomys* 1**	0.11	0.09	0.06	0.08
***Notomys* 1**	0.19	0.16	0.08	0.10
***Notomys* 2**	0.28	0.22	0.09	0.13
***Jerboa* 1**	0.13	0.09	0.05	0.00

The distribution of particle size in desert ecosystems illustrates the difference from artificial sands (Figure 5.4). The *Dipodomys spp.* natural habitats have the most narrow distributions, with the greatest mass at 125 μm for both localities. *Notomys spp.* natural habitats show a broader distribution that peaks between 125 and 250 μm. In contrast, the artificial sands (Artificial 1 sampled from a beach volleyball court, and Artificial 2 sampled from playground sand) show

sharp peaks at 250 μm, with almost no particles below 63 μm. These data suggest that sand in the natural habitats of bipedal rodents have surprisingly similar ranges of particle sizes. Importantly, these substrates exhibit different terradynamics than the artificial sand and beach sands that have more consistent particle sizes. Therefore laboratory experiments quantifying the effect of sand on rodent locomotion should ideally use sand from the natural habitat, rather than commercially available or beach sand.

5.4.2 Climatic Niche Modeling

Table 5.3: *The principal factors contributing to the niche models of bipedal rodents.*

	First	Second	Third	Fourth	Fifth	Sixth
All Bipeds	Aridity	Bio3	Bio19	Bio14	Bio4	Bio9
Dipodidae	Bio18	Aridity	Bio6	Bio3	Bio14	Bio15
Heteromyidae	Bio2	Bio18	Bio19	Bio11	Bio14	Aridity
Notomys	Aridity	Bio3	Bio17	Bio6	Bio4	Bio18

I found that each group of small bipedal desert rodent had a slightly different set of climatic variables that defined their climatic niche. These include Aridity, Bio2 (Mean Diurnal Range), Bio3 (Isothermality), Bio4 (Temperature Seasonality), Bio6 (Min Temperature of Coldest Month), Bio9 (Mean Temperature of Driest Quarter), Bio11 (Mean Temperature of Coldest Quarter), Bio14 (Precipitation of Driest Month), Bio15 (Precipitation Seasonality), Bio17 (Precipitation of Driest Quarter), Bio18 (Precipitation of Warmest Quarter), and Bio19 (Precipitation of Coldest Quarter).

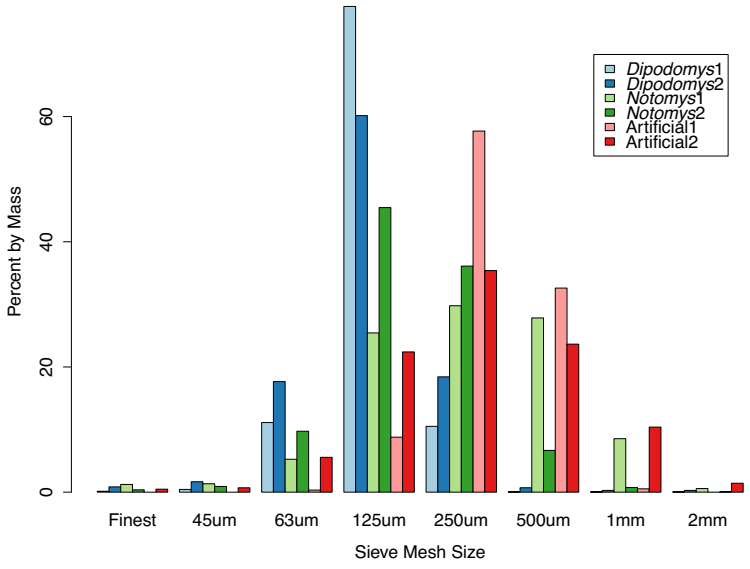


Figure 5.4: *Distribution of sand particle size, sampled from the natural habitats of* Dipodomys spp. *in shades of green and of* Notomys spp. *in shades of blue, compared to the particle size distribution of two types of artificial sand in shades of red.*

When all bipedal rodents were grouped together, aridity was the predominant variable associated with the locations of bipedal rodents. I used climatic niche modeling to determine how similar the climate of each group of bipedal rodents is to each other, and to determine whether there are other regions where the climate would be suitable for bipedal rodent survival.

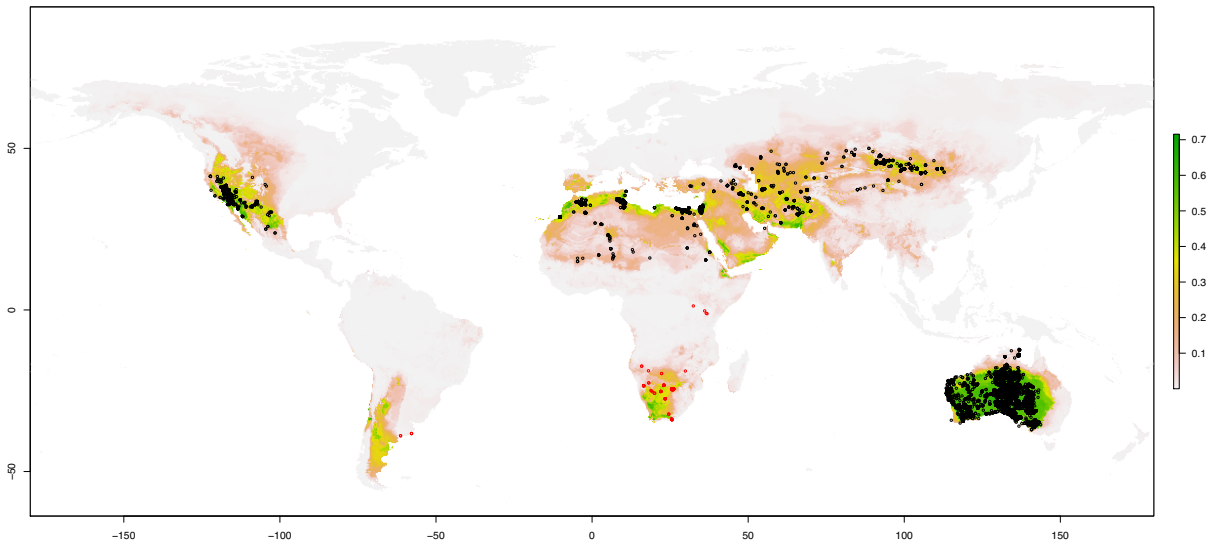


Figure 5.5: *Global niche model based on the occurrences of small bipedal desert rodents (black dots), using the 19 Bioclim variables and Aridity Index. The colored areas indicate locations where the climate is likely suitable for bipedal desert rodents, based on their current occurrences. Red dots indicate occurrences of extinct bipedal marsupial* Argyrolagus spp. *in South America, and the larger bipedal rodent* Pedetes spp. *in Sub–Saharan Africa that were not incorporated in the niche model.*

The niche models based on each group of bipedal rodents differed in their ability to predict the occurrences of other bipedal rodents. The Dipodidae niche model predicted the ranges of the bipedal rodents in North America and Australia. The North American and Australian niche models were able to predict the occurrence of the each other, but neither model showed suitable ranges matching the occurrence of dipodids. The combined bipedal rodent niche overestimated the native range of each group of bipedal rodent, including regions in Canada for Heteromyidae, regions in India and Southeast Asia for Dipodidae, and regions in Queensland for *Notomys sp.* (Figure 5.5). Each model found locations with suitable climates for bipedal rodents in South America and Subsaharan Africa.

The *Notomys spp.* niche was unable to predict the occurrences of jerboas, but showed suitable

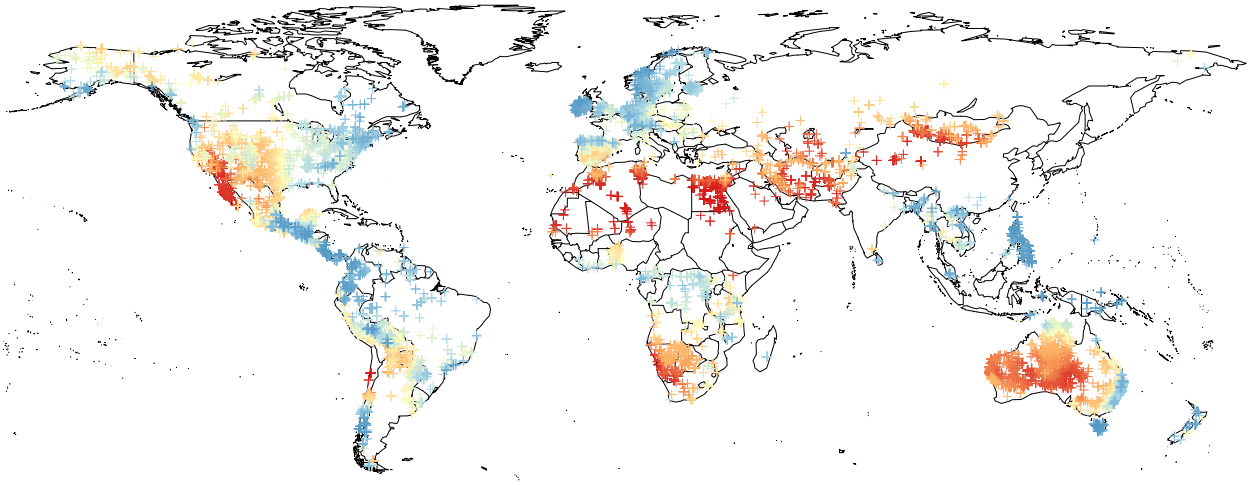


Figure 5.6: *Occurrences for all taxa included in this study, with aridity values of each location represented by color. Warmer colors are more arid, cooler colors are less arid.*

climates in North and South America, Subsaharan Africa, and South Asia. The heteromyid niche weakly predicted occurrences in all continents congruent with occurrences of bipedal taxa. The dipodid niche was able to strongly predict the occurrences of all bipedal taxa, though it overestimated the northern boundary of the heteromyid range.

Based on these results, I selected Aridity Index as the climatic independent variable for the generalized least squares model (Figure 5.6), as it was the only factor that was a primary factor in the niche of each group of bipedal rodent, and was the dominant factor in the combined bipedal rodent niche. Lower aridity values represent more arid habitats, and higher values represent more humid habitats. The set of aridity values for all rodents in the dataset ranged from 0 to 78700, with a mean of 7549 and a median of 6822. The localities for all bipedal rodent communities were below 1400, which was in the lowest quartile of the total dataset.

5.4.3 Hindlimb Morphology

Variation in the hindlimb best fit a multi–peak Ornstein–Uhlenbeck model (OUM), indicating distinct optima for ancestral common ancestors, derived murids, and derived dipodids (Figure 5.7 A). This pattern of evolution can be observed when a group of animals undergo adaptive evolution in response to a change in selective pressures. Fig. 5.7 B shows that the best fit OUM model are able to achieve the observed murid and dipodid trait means (dashed lines) when simulated over

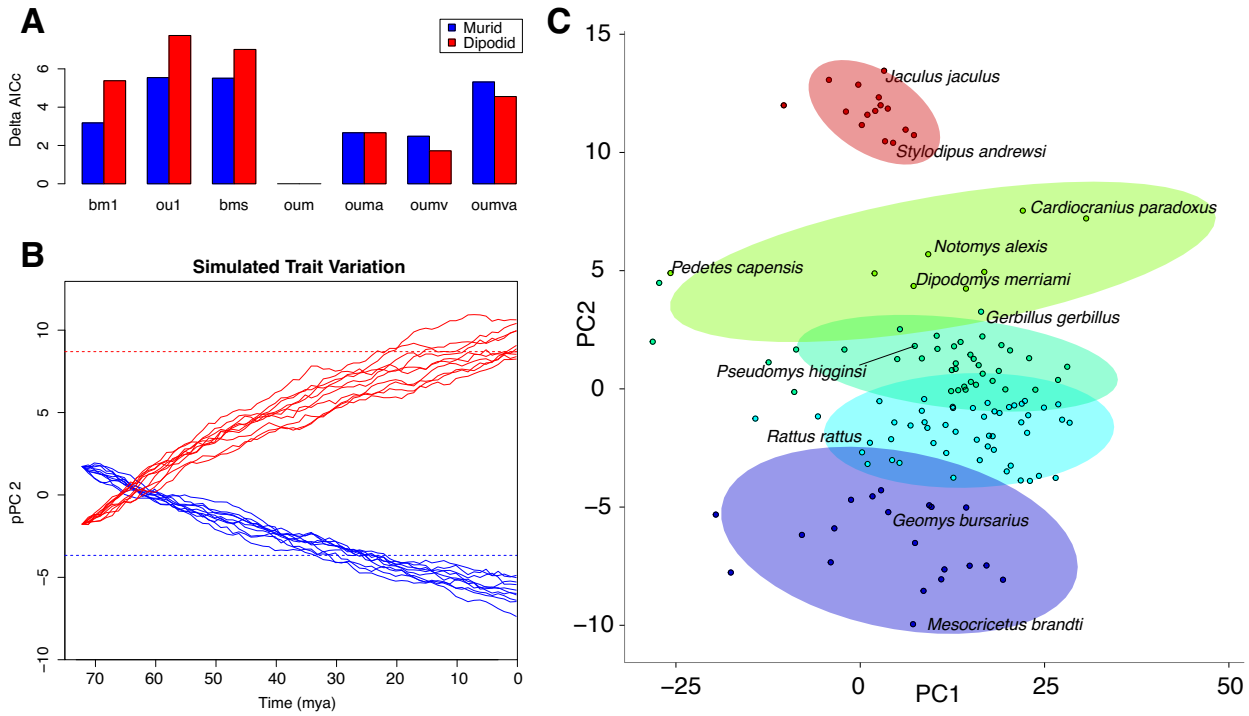


Figure 5.7: *A) Delta Akaike Information Content (corrected for small sample sizes) scores for each model of evolution. The lowest values indicate the model that best fits the data. B) Simulated evolution of murid and dipodid pPC2 values using the parameters derived from the OUM model. Observed means of pPC2 for each group are shown by the horizontal dashed lines. C) Groups of pPC2 plotted as a function of pPC1, with five clusters identified (by a kmeans clustering algorithm). Groups identified using pPC2, 3, 4, 5. pPC2 is used as the indicator of locomotor specialization. pPC1 aligns strongly with variation in body size. The shaded circles represent 95% confidence intervals.*

the amount of time since these two families diverged (~73mya).

Chapter 1 shows that a Phylogenetically–weighted Principal Components Analysis on limb lengths provides a suitable metric for estimating locomotor specialization. To obtain pPC2 values for each taxon, I performed this analysis with the larger dataset collected for this chapter (Fig 5.7 C). A kmeans clustering analysis was able to discern the obligately bipedal dipodid rodents as their own morphotype regardless of the number of clusters specified. The facultatively bipedal dipodids, heteromyids, and *Notomys alexis* form their own cluster, along with one species of gerbil. Aside from this one gerbil, the sympatric quadrupedal rodents clustered separately from the obligately and facultatively bipedal rodents (Figure 5.7 C).

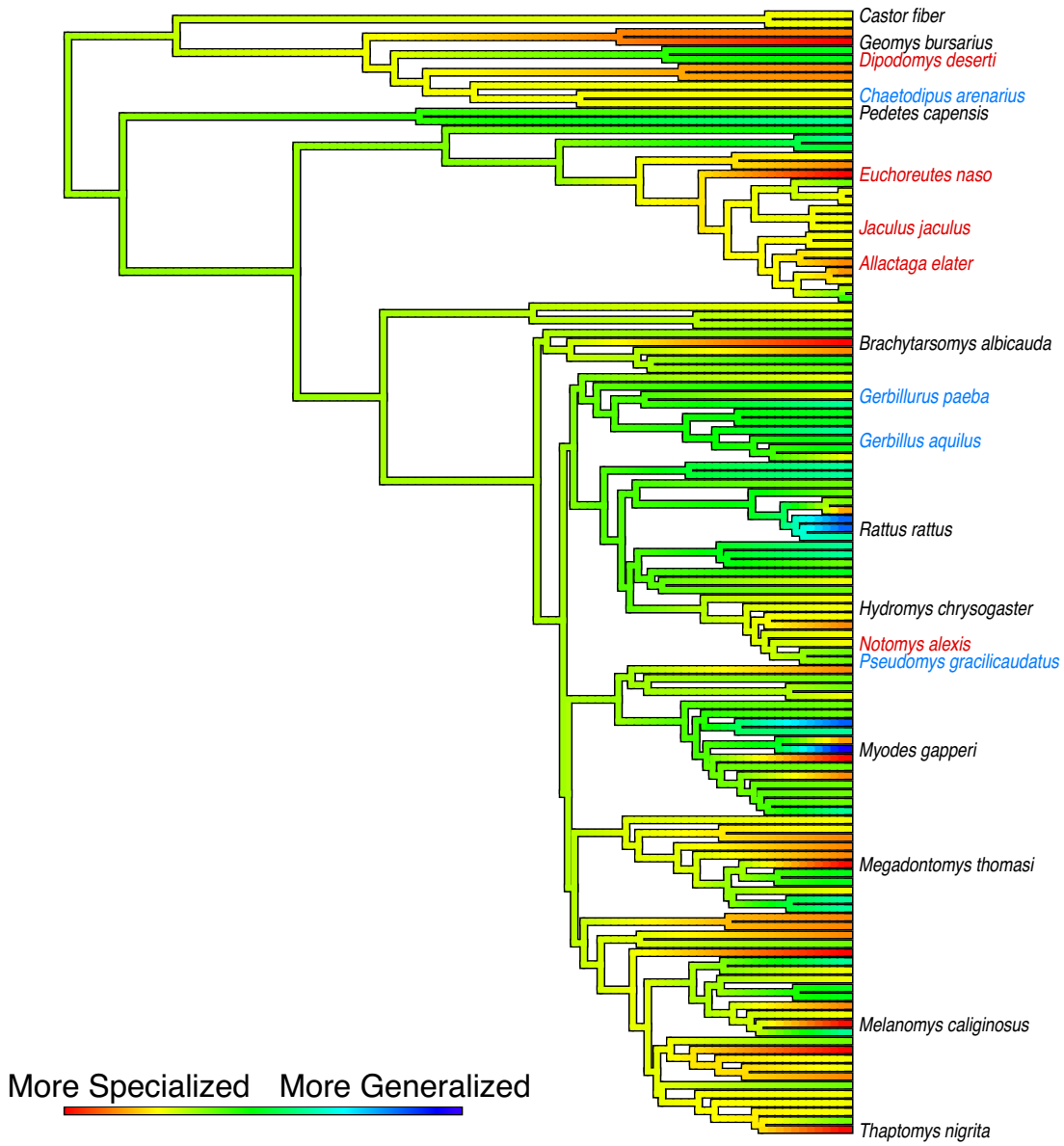


Figure 5.8: *Diet specialization as a continuous trait on a phylogeny, showing the ancestral state reconstruction based on maximum likelihood. Only notable species are listed for clarity; see Fig. 5.3 for the complete list of names. The names of small bipedal desert rodents are shown in red, and the names of sympatric quadrupedal desert rodents are shown in blue.*

5.4.4 Diet Specialization

Rodents are incredibly diverse in their feeding behaviors, and in the tasks for which they use their jaws, making it difficult to characterize the functional morphology of their jaws with a single metric (Figure 5.8). Phylogenetic relationships provide little information about diet specialization

in this clade ($\lambda = 0.40$). For example, Myomorpha includes tooth diggers (genus *Thomomys*), burrowing rodents whose lips close behind their teeth so that they can dig with their incisors without ingesting the soil (Parr *et al.*); others (genus *Paucidentomys*) completely lack molar teeth, and only eat worms and other soft invertebrates (Esselstyn *et al.*, 2012); even others (genus *Hydromys*) use their teeth to pry open shelled invertebrates (Parr *et al.*). This group also includes beavers (genus *Castor*) that shred through hard wood. The distinct functional requirements of these myriad feeding strategies make it difficult to meaningfully represent diet specialization with a single axis of morphological variation. Therefore I have used reports of stomach contents data to determine the diversity of foods eaten by each species.

True rats (genus *Rattus*) have the most diverse diets, which is no surprise considering the wide range of localities and climates that they have invaded (Table D.2). Equally diverse in their diet is the opportunistic herbivore *Myodes gapperi* that must subsist on various plant and fungal resources in their highly fluctuating habitat. The most restricted diets show no overlap, and include insectivores (*Euchoreutes*, *Melanomys*), frugivores (*Brachytarsomys*, *Megadontomys*), folivores specializing on leaves (*Thaptomys*), and tuber eaters (*Ellobius*, *Geomys*) (Table D.2).

The most derived bipedal rodents have quite specialized diets, and feed on seeds, grain, and tubers. Many of the quadrupedal rodents sympatric to the bipedal rodents show slight broadening of their dietary specialization, with the exception of the heteromyid species pair. *Dipodomys spp.* show a broader diet than sympatric *Chaetodipus spp.* and *Perognathus spp.* In general, quadrupedal desert rodents supplement their diets with insects or green vegetation (Table D.2).

5.4.5 Model Results

Surprisingly, none of the models were able to predict the observed variation in locomotor morphology to even a significance level of $\alpha = 0.1$ (Table 5.4). In general, the effect of diet was slightly more significant than the effect of aridity, and this effect was diminished when an interaction factor was included (Table 5.4, Model 4). The omission of the residual hindlimb length variation encompassed by pPCs 3:5 resulted in slightly stronger correlation with diet, and had nearly no effect on the correlation with aridity, except in the model that allowed interaction of predictor variables.

5.5 Discussion

Table 5.4: *The mean p–values for the generalized least squares models. The geomorph models output p–values averaged over the 1000 iterations as a part of the function. I averaged the p–values output from each of the 1000 nlme model iterations.*

Model	Factor	geomorph (pPC2:5)	nlme (pPC2)
1	Aridity	0.677	0.664
2	Diet	0.258	0.123
3	Aridity	0.641	0.659
	Diet	0.258	0.124
4	Aridity	0.685	0.551
	Diet	0.291	0.157
	Interaction	0.764	0.477

All of the climatic niche models showed that the arid ecosystems in South America and Sub–Saharan Africa are potentially suitable climates for small bipedal rodents. Notably, a bipedal marsupial *Argyrolagus spp.* inhabited nearby locations in South America during the Pliocene around 5 million years ago (Simpson, 1970) (Figure 5.5). Climate modeling for the Pliocene indicates that *Argyrolagus spp.* likely inhabited arid environments (Figure 5.9) (Haywood *et al.*, 2013). South American caviomorph rodents were sympatric with the bipedal marsupial, and continue to inhabit South American deserts. Desert–adapted caviomorphs, such as *Octomys mimax*, show only slight morphological convergence to the bipedal myomorph rodents, likely due to the short amount of time since the extinction of *Argyrolagus spp.* (less than 5 mya) and the rockier terrain compared to the deserts with more derived bipedal rodents (Mares, 1975). Cricetines inhabiting these deserts show even less desert–adapted traits, which corresponds to their more recent invasion of the ecosystem (Leite *et al.*, 2014).

Pedetes spp., also called springhare or springhaas, are large bipedal myomorph rodents that inhabit Sub–Saharan Africa. Due to the significant difference in the dynamics of hopping between small bipedal rodents and the much larger bipedal macropodids, it is difficult to predict the dynamics of this bipedal hopper of intermediate size (Biewener and Blickhan, 1988; Alexander and Vernon, 1975) (Ch. 2). Videos of springhare hunting suggest that these rodents inhabit semi–arid ecosystems with grass and scrub vegetation, and use a hopping gait that is more periodic and linear than the convergent forms examined in this thesis (Figure 5.10). The locomotion and ecology of springhares qualitatively resemble the medium–sized bipedal hopping marsupials of Australia, such as bilbies, quokkas, and potoroos (Van Dyck *et al.*, 2012). Further biomechanical and

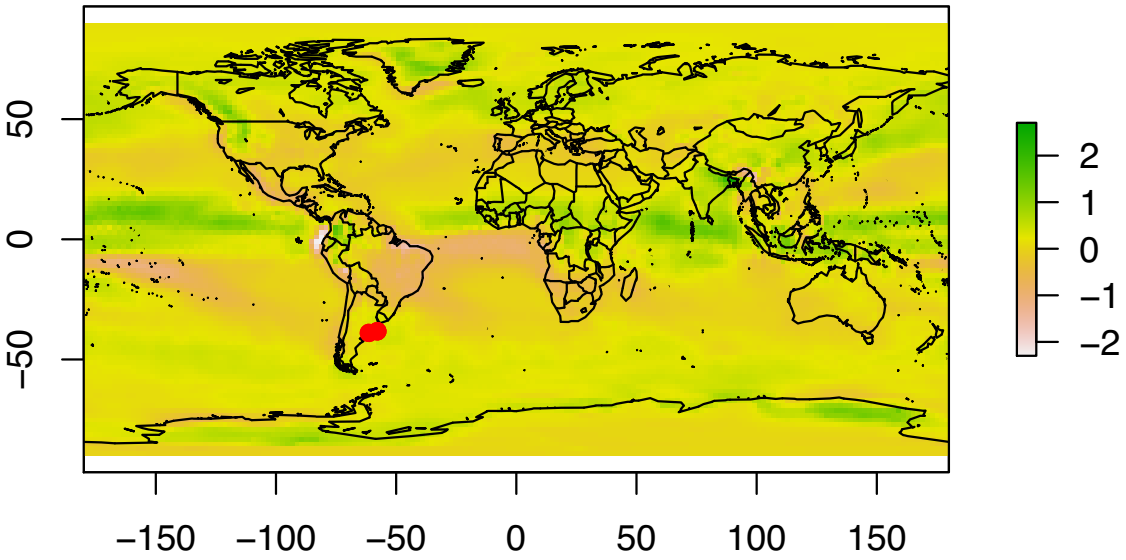


Figure 5.9: *Model of global precipitation in the Pliocene, showing multi–model annual means showing the mean total precipitation increase in mean precipitation compared to pre–industrial values. Areas colored in green encountered more precipitation in the Pliocene than in the present, areas colored in peach encountered less precipitation in the Pliocene than in the present, and areas colored in yellow show minimal change in precipitation between the Pliocene and the present. Locations of* Argyrolagus spp. *fossils are shown in red, in areas with minimal increase in precipitation from pre–industrial values (Haywood et al., 2013).*

ecological investigation can reveal the ecological niches occupied by bipedal hopping mammals across a range of sizes that span multiple orders of magnitude.

The restriction of the smallest bipedal hopping mammals to the most arid desert ecosystems suggests that ricochetal hopping is a biomechanically advantageous strategy for small mammals that interact with a granular substrate. The musculo–skeletal architecture of small bipedal rodents favors the rapid production of large forces (Biewener and Blickhan, 1988) (Ch. 2). When a rapid force is applied to a granular substrate, the particles temporarily pack together and resist forces much like a solid. This is called effective solidification, and is used by sea turtles and lizards to produce ground–reaction forces necessary for locomotion (Li *et al.*, 2012; Mazouchova *et al.*, 2010). The repeated evolution of bipedal hopping in desert ecosystems strongly suggests that these animals use effective solidification of granular media to enable rapid locomotion.

Furthermore, granular substrate can dissipate forces by displacing particles. This would be particularly useful for animals that escape predators with rapid or unpredictable maneuvers. The excess force produced during rapid accelerations can be absorbed by the granular substrate, rather than becoming excess ground–reaction forces that cause injury to the limb. Investigating

the biomechanical interactions between rodent feet and granular substrate will reveal how the physical properties of the natural habitat determines the evolution of locomotion.

While the hindlimb measurements accurately reflect the locomotor specializations of myomorph rodents, the ways in which a skull can be specialized are much more diverse and cannot be encompassed by a single axis of variation (Samuels, 2009; Swiderski *et al.*, 2000). While the physical properties of food items can greatly determine skull morphology, the skull is a multi–functional system that is shaped by its myriad uses. In Myomorpha alone, rodent skulls are important tools for manipulation of the ecosystem (digging by *Thomomys spp.* and woodworking by *Castor spp.*) or acute sensing (*Dipodomys spp.* and Dipodidae). Because of these confounding factors determining skull morphology, this study used descriptions of stomach contents and feeding habits to characterize the dietary ecology of these rodents.



Figure 5.10: *The escape trajectory of a springhare startled from a stationary position in its natural habitat. The light streaks are the reflection of infrared light from the eye extracted from 20 frames of video, and overlaid onto the same image. The springhare hops with a trajectory approximately perpendicular to the direction of videography. Video recorded at 30 fps by AirArmsHuntingSA (2015).*

The greatest drawback to this method is that it cannot distinguish between diets that are equally specialized on different foods. This can obscure important differences in trophic ecology. Rodents specializing on roots, insects, and vertebrates clearly differ in their diel cycles, metabolic rates, and vulnerability to predation (Price, 1978). Another drawback is that this method does not account for which food sources are available in their ecosystem. Very little meaning can be derived from the fact that a desert rodent does not choose to eat crustaceans or fish. Thus, this method overestimates the diet specialization for rodents in less diverse habitats.

These drawbacks can be addressed with more focused and quantitative techniques. Isotope analysis has been shown to accurately identify trophic level, resource use, and sources of dietary moisture in heteromyid rodents (Smiley *et al.*, 2015). It is also possible to infer competition and

to standardize the diet specialization based on available resources by comparing the results of isotope analyses within groups of sympatric species. Isotope analysis is particularly suited for this taxonomically diverse study, as it can be performed on museum specimens and does not require field–based data collection.

5.5.1 Alternative Hypotheses

The lack of a significant correlation suggests that the specialization of diet may not be the predominant factor that distinguishes bipedal from quadrupedal niches within desert ecosystems. Food tray experiments in the natural habitat indirectly show that kangaroo rats and jerboas forage in open areas more frequently than their quadrupedal counterparts (Brown *et al.*, 1994; Kotler, 1984b). However, it is unknown whether this resource partitioning is due to competition or a physical incompatibility between the morphology of a rodent and the microhabitat. One study suggests that more derived bipedal jerboas have a difficult time navigating densely vegetated areas (Schropfer *et al.*, 1985), but few studies have quantitatively tracked rodent locomotion and interaction with the natural habitat. The small size, relatively long and fragile limbs and tail, frequent sandbathing, burrowing, and rapid changes in acceleration during saltation make it difficult to make field–based recordings of individual trajectories using traditional (spool–and–line, colored dust, radiotransmitter) methods (Anderson *et al.*, 1988; Goodyear, 1989; Daly *et al.*, 1992b). Advances in remote sensing technology will be essential to determining how individual movements affect microhabitat preference and foraging patterns, to distinguish bipedal from quadrupedal desert rodent ecology.

Climate shows very little power to predict the locomotor morphology of rodents, which is evidence of the variety of niches that myomorph rodents occupy in each ecosystem. In fact, myomorph rodents are one of the most morphologically, ecologically, and taxonomically diverse groups of mammals (Fabre *et al.*, 2012). Due to the radical variation in traits with each additional sample, phylogenetically generalized least squares analysis (which requires high sample size for adequate statistical power) may not be the most appropriate approach to test these hypotheses.

Since the degree of bipedality corresponds to the time since bipedality evolved, it is possible that the *Notomys spp.* and bipedal heteromyids represent transitional forms that will eventually

completely converge upon the jerboa. This hypothesis would follow the Ornstein–Uhlenbeck model of evolution towards an optimum that best fits the morphological variation present in the Dipodidae clade. Alternatively, the selective pressures favoring the evolution of bipedality in each of these ecosystems may be distinct enough that each rodent has achieved the stable optimum for their unique ecosystem. I can test whether similar ecological factors were present when bipedality evolved in each group, instead of testing for the ecological factors that correlate to the current ranges of bipedal rodents. A concentrated changes test can be used to address this more historical question by searching for signals of correlated evolution (Maddison, 1990). This method still depends on understanding the differences in bipedal and quadrupedal desert rodent ecology, as stated above.

Finally, it is possible that bipedality evolved in each desert ecosystem in response to vastly different selective pressures. In that case, these rodents would represent a non–adaptive convergence. However, this does not imply that bipedalism is not an adaptation in each case. On the contrary, the punctuated equilibrium pattern of evolution found in Dipodidae suggests that bipedalism in this group is an adaptation that enabled rapid speciation in this clade (Ch. 1). If each group adaptively evolved bipedal locomotion in response to different selective pressures, further investigation would reveal a greater set of associated fitness benefits than previously expected. The expanded utility of bipedal ricochetal locomotion at small scales would be especially beneficial for engineers drawing inspiration from biology to design small–scale robotics.

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Conclusion

Nearly every aspect of animal survival requires movement, making locomotion an important determinant of animal fitness. Because locomotor performance is governed by myriad genetic, developmental, behavioral, and environmental factors it is often difficult to establish the adaptive nature of a locomotor trait. This dissertation demonstrates that studies conducted as part of an integrative investigation provide valuable insight into the complex evolutionary history of locomotor adaptation.

By examining the patterns of morphological evolution in a group that includes quadrupedal, facultatively bipedal, and obligately bipedal rodents, I developed hypotheses regarding the mechanisms that govern hindlimb morphology. This comparative framework is particularly valuable for directing developmental and genetic investigation of limb evolution.

While Chapter 4 shows that the multiple jerboa gaits exhibit distinct dynamic characteristics, our assertion that these gaits are used to enhance trajectory unpredictability is only theoretical. We plan to track both center of mass and footfall pattern simultaneously in an open arena to determine whether each gait is associated with distinct maneuvers. Interactions with the physical aspects of the natural habitat may also explain their legendary maneuverability. Granular substrate undoubtedly affects the locomotor performance of bipedal rodents. Personal observations throughout the duration of my doctoral research suggest that jerboas are less willing to perform extreme accelerations and redirections on hard surfaces because the hair on the plantar side of their feet causes them to slip and fall. It is also possible that the effective solidification of the granular substrate aids in turning. Turning jerboas exhibit significant roll–axis rotations while making quick turns, causing their legs to make contact with the ground at extreme lateral angles. If solidification occurs in response to the direction of the foot, then the granular substrate

would provide ground reaction forces oriented toward the center of mass, creating a "banking" effect. This effect could explain why bipedal rodent locomotion is more subdued in a laboratory environment, and would fit nicely with the "ricochetal" characterization of their saltation.

The elongate and ornamented tail of bipedal rodents likely enhances stability and maneuverability during the aerial phase of locomotion. Because the total angular momentum must be conserved in a solid body, the tail can be whipped around to produce body rotations during the aerial phases of hopping locomotion (Libby *et al.*, 2012b). It has been suggested that jerboas use their tails to produce yaw rotations, to reorient the body in the direction of the next turn (Hatt, 1932). This would theoretically enable the jerboa to limit the lateral forces required to perform rapid turns while in contact with the substrate. In support of this theory, bipedal rodents including jerboas have reduced lateral musculature. Furthermore, bipedal rodents that have had their tails surgically removed are unwilling to move quickly, and turn end over end when leaping (Bartholomew and Caswell, 1951). The tail is also swung vigorously when dropped, suggesting that they capable of inertial maneuvering (Jusufi *et al.*, 2008). Developing methods to examine the movement of these highly articulated tails in conjunction with their footfall patterns will be important to understanding how these rodents generate such erratic trajectories.

It is necessary to examine the neuromotor control of locomotion in rodents to understand how jerboas are the only bipedal rodent to use multiple gaits. Recently, researchers have discovered that the mutation of a stop codon in the DMRT3 gene expands the range of gaits, including asymmetric gaits, used by horses (Andersson *et al.*, 2012). Furthermore, they found that a knockout in mice disrupted the coordination of their limb movements. Future work should investigate the evolution of the DMRT3 gene in the rodent clade to determine if there is any association with the evolution of bipedality and gait use.

To verify the adaptive nature of bipedal locomotion, one must demonstrate the causal effect on fitness (Losos, 2011; Arnold, 1983). Chapter 4 shows that bipedality is correlated with more unpredictable trajectories and with less thigmotaxis. However, unpredictability in rodents is confounded with dimensionality and speed. Demonstrating a causal relationship between trajectory unpredictability and predator evasion ability requires direct observation of prey that can vary trajectory unpredictability independently. Bio–inspired robots are an incredibly appropriate tool for performing this experiment. By programming a baited robot to independently vary

each aspect of locomotion, we can observe the resulting predation success. This use of bio–inspired robotics with natural predators would be a valuable system for testing various aspects of locomotion for their effect on prey fitness.

Once a causal relationship is established between trajectory entropy and predator evasion ability, entropy values can be used as a trait in comparative analyses to infer the ecology of extinct or rare taxa. In combination with other traits, it may be possible to statistically reconstruct the predation strategies that extinct prey evolved to evade, or the microhabitats that extinct prey preferred. In this vein, I propose that the precise quantification of neuromotor and behavioral traits will provide valuable insight into the ecology of extinct taxa when examined in a comparative phylogenetic framework.

Finally, social interactions between conspecifics can provide more information regarding the niche that bipedal rodents occupy in their respective ecosystems. My graduate work has been informed by the unique opportunity to study each member of this convergence in the context of its natural habitat. In particular, the deserts of Australia are especially taxonomically rich, and bipedal rodents must compete with other native rodents, invasive rodents, and small marsupials for limited resources. I plan to construct a long–term passive observation system to individually identify and track communities of small nocturnal mammals. This infrastructure could reveal how bipedal rodents differ from other small mammals in their microhabitat use, social cooperation, aggression, predator evasion ability, and migration. Recent advances in sensing, tracking, and big data management make it possible to study the locomotion and behavior of an entire community of organisms *in situ*.

The convergence of three groups of desert rodents on bipedal locomotion presents a complex and exciting system for the integration of biomechanics with ecology, evolution, and behavior. In an attempt to chip away at this metaphorical iceberg, my dissertation has utilized classical techniques of gross morphological dissection and skeletal morphometrics, recently established methods to characterize the dynamics of locomotion and to reconstruct the ancestral states of anatomical and ecological traits, and has developed novel methods to characterize non–steady–state locomotion. I am excited to continue examining systems that exhibit remarkable patterns of biomechanics, evolution, and ecology using the integrative approach I espouse in this dissertation.

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Appendix A

Appendix to Chapter 1

A.1 Supplemental Figures[1]

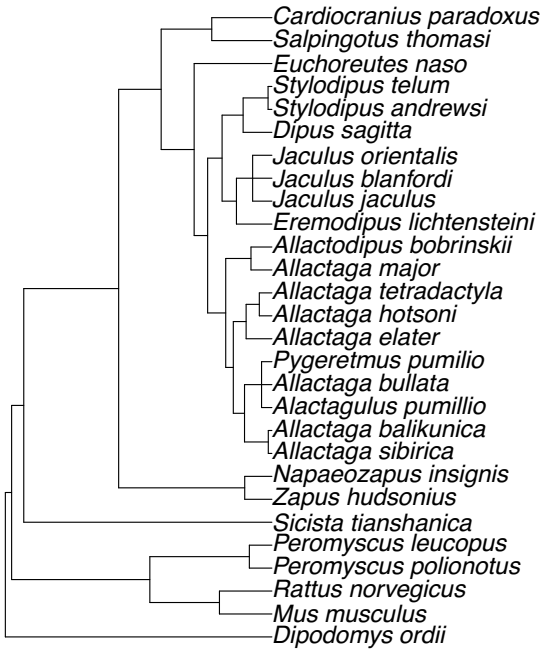


Figure A.1: *Time–Calibrated phylogeny of Dipodoidea*

Time–calibrated phylogeny of Dipodoidea generated by processing the Nexus file below using Mr. Bayes. 23 Dipodoid and 5 outgroup taxa were included in this phylogeny. Supports Figure 1.3B.

[1]Screenshots of supplemental videos are included as supplemental figures.

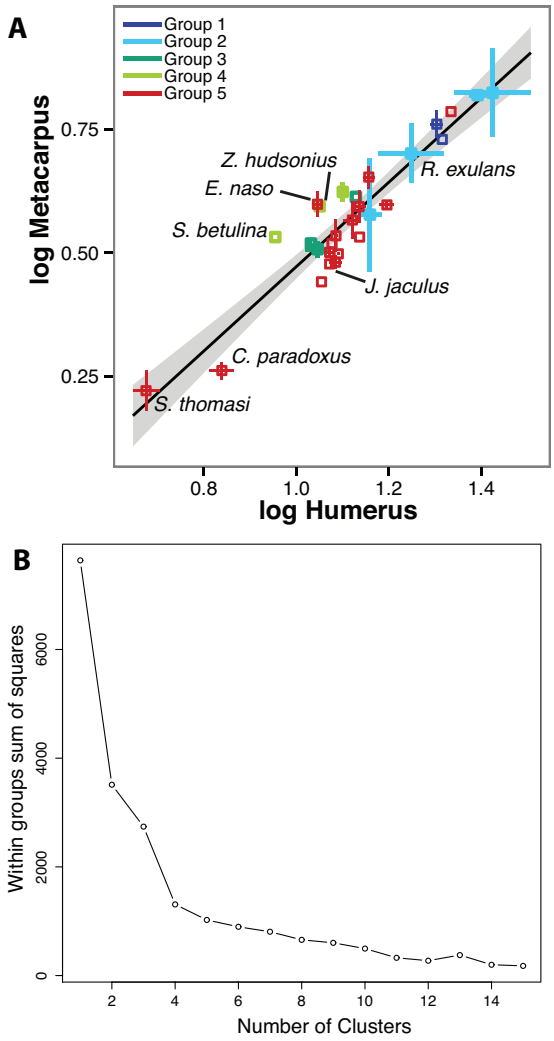


Figure A.2: *Forearm allometry and root means squared*

A) The humerus and third metacarpal scale near-isometrically for the ecomorphs identified by our clustering analysis. Log-log plot of the allometric scaling of humerus versus metacarpus. Linear regression: slope= 0.853, $p = 1.322e - 13$, adjusted $R^2 = 0.878$. Colors correspond to ecomorph groups identified in Figure 4B. Grey shading indicates 95% confidence interval, and vertical and horizontal lines represent variation one standard deviation away from the mean. B) Root means squared analysis illustrates the variation in limb proportions by pPC 2, 3, and 4 is best described using five clusters (least change in slope of the line after five clusters). Supports Figure 1.4.

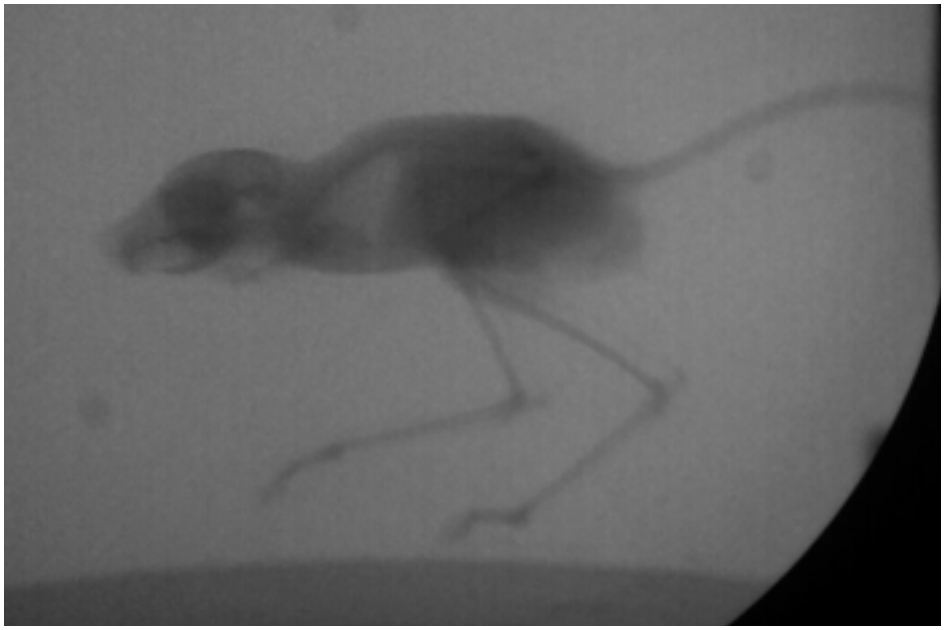


Figure A.3: *Lateral x–ray screenshot of* J. jaculus

Screenshot of lateral view of an X–ray fluoroscopic movie of *J. jaculus* moving along a narrow trackway used for Figure 1.1A.

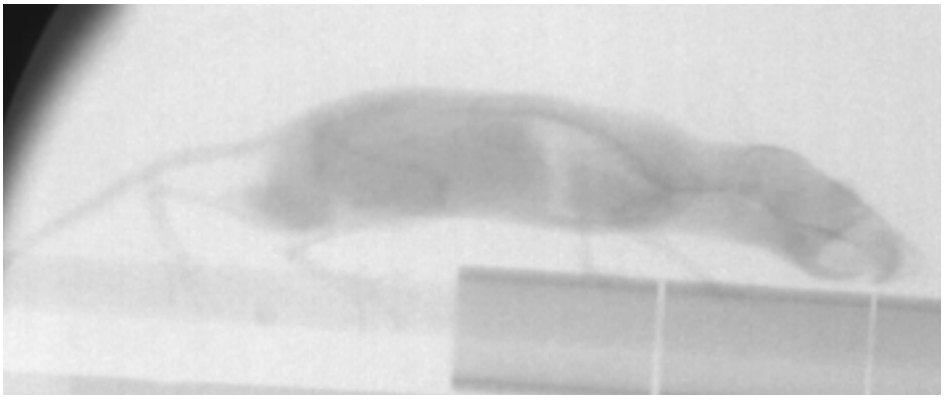


Figure A.4: *Lateral x–ray screenshot of* P. maniculatus

Screenshot of lateral view of an X–ray fluoroscopic movie of *P. maniculatus* moving along a narrow rod used for Figure 1.1B.

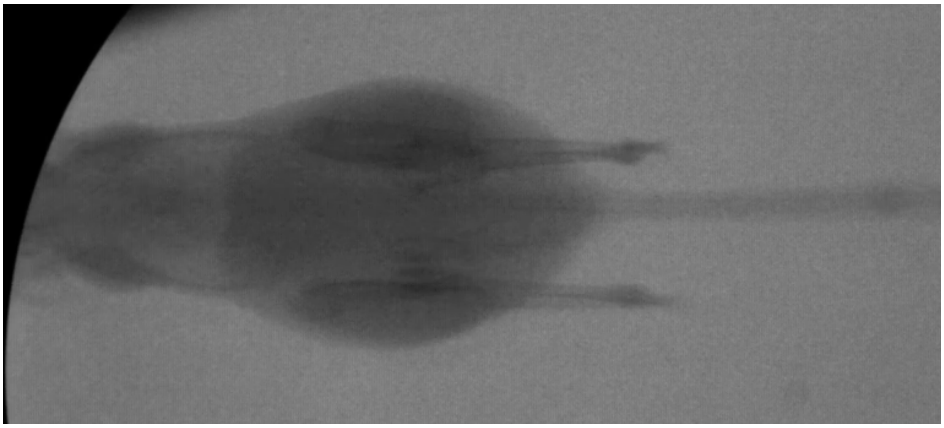


Figure A.5: *Dorso–ventral x–ray screenshot of* J. jaculus

Screenshot of dorsoventral view of an X–ray fluoroscopic movie of *J. jaculus* moving along a narrow trackway shows hindlimbs directly below the body.

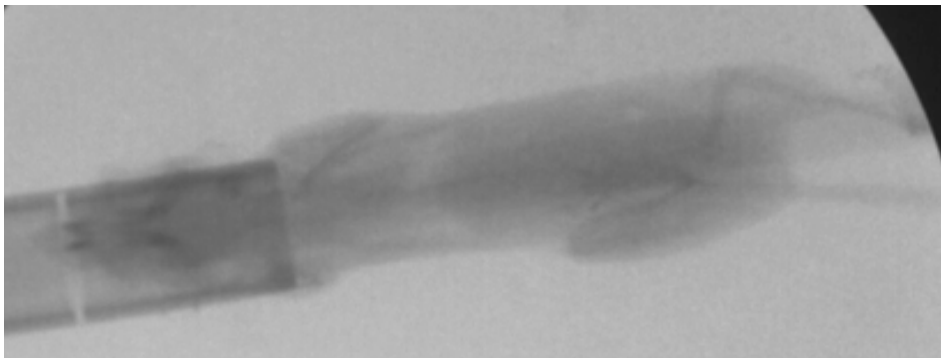


Figure A.6: *Dorso–ventral x–ray screenshot of* P. maniculatus

Screenshot of dorsoventral view of an X–ray fluoroscopic movie of *P. maniculatus* moving along a narrow rod shows hindlimbs in a laterally sprawled position.

A.2 Supplemental Tables[2]

Table A.1: *All measurements and museum catalog numbers for specimens used in Chapter 1.1*

Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsal	Locomotion	Museum Number
Acomys russatus	15.95			21.71	23.31	7.9	Generalist	MCZ 61401
Acomys russatus	15.05			20.18	22.51	6.03	Generalist	MCZ 61721
Acomys russatus	14.18	15.62	3.46	17.17	20.23	6.76	Generalist	MCZ 60929
Acomys russatus	13.74	17.34	5.08	19.62	23.35	7.67	Generalist	MCZ 61039
Acomys russatus	15.41	17.11	3.06	20.08	23.9	7.86	Generalist	MCZ 61721
Allactaga balikunica	12.27	19.83	3.4	29.97	46.19	30.72	Bipedal	MSB 227346
Allactaga balikunica	12.05	19.78	3.18	30.23	46.27	30.31	Bipedal	MSB 227352
Allactaga balikunica	12.21	19.78	3.7	31.28	46.94	29.97	Bipedal	MSB 227444
Allactaga bullata	13.34	20.64	4.06	32.64	47.65	32.32	Bipedal	MSB 225083
Allactaga bullata	14.14	21.5	3.59	33.94	47.13	31.61	Bipedal	MSB 225920
Allactaga bullata	13.53	21.1	4.13	33.81	47.13	31.25	Bipedal	MSB 225875
Allactaga elater	11.33	16.48	2.76	29.55	43.32	30.36	Bipedal	MSB 67489
Allactaga major	21.6	29.1	6.1	54	73.9	48.8	Bipedal	AMNH MO-227
Allactaga sibirica	14.2	21.4	4.4	34.2	50.2	33.7	Bipedal	AMNH M-55978
Allactaga sibirica	14.8	23.5	4.4	37.5	55.7	35.4	Bipedal	AMNH M-55980
Allactaga sibirica	13.76	21.56	4.82	33.52	48.94	34.44	Bipedal	MSB 215129
Allactaga sibirica	14.28	21.53	4.23	34.64	48.79	33.05	Bipedal	MSB 215135
Allactaga sibirica	14.68	22.01	4.66	36.21	50.8	34.7	Bipedal	MSB 216247
Allactaga tetradactyla	12.3	18.3	3.1	30.2	45.4	30.4	Bipedal	KLC Alct-1
Allactaga tetradactyla	11.8	17.7	3	29.2	43.8	29.2	Bipedal	KLC Alct-2
Allactaga tetradactyla	11.9	17.9	3.1	29.8	44.7	29.9	Bipedal	KLC Alct-3
Allactaga tetradactyla	12.6	18.9	2.9	31.6	47	31.6	Bipedal	KLC Alct-4
Allactaga tetradactyla							Bipedal	KLC Alct-6
Anomalurus beecrofti	62.17			70.94	70.62	15.65	Glider	MCZ 43043
Anomalurus beecrofti	60.96			70.16	72.25	15.68	Glider	MCZ 43042
Cardiocranius paradoxus	7.05	12.45	1.87	13.89	19.71	11.9	Bipedal	MSB 2250151
Cardiocranius paradoxus	6.43	11.54	1.74	14.21	20.18	12.18	Bipedal	MSB 199763
Cardiocranius paradoxus	7.55			14.84	21.98	12.96	Bipedal	MSB 215992
Cardiocranius paradoxus	7.24	12.68	1.87	14.53		13.5	Bipedal	MSB NK192352
Castor canadensis	54.12			69.18	87.3	42.48	Semi-aquatic	MCZ 60986
Castor fiber	63.63			79.78	104.49	50.71	Semi-aquatic	MCZ 19559
Dipodomys ordii	13.97			25.83	35.38	17.21	Fac Biped	MCZ 51502
Dipodomys peninsularis	13.43			27.79	38.99	17.88	Fac Biped	MCZ 52961
Dipodomys spectabilis	19.34			35.97	49.89	22.02	Fac Biped	MCZ 61209
Dipodomys spectabilis	17.94			32.84	47.74	21.07	Fac Biped	MCZ 59480
Dipus sagitta	12.57	19.67	3.33	31.26	45.31	29.31	Bipedal	MSB 199720
Dipus sagitta	13.7	20.32	3.86	33.45	46.88	30.43	Bipedal	MSB 224212
Dipus sagitta	13.4	20.19	3.88	31.34	46.03	31.82	Bipedal	MSB 214383
Euchoreutes naso	11.24	18.83	4.13	21.58	35.28	25.86	Bipedal	MSB 227347
Euchoreutes naso	10.97	18.63	3.8	22.03	35.01	24.39	Bipedal	MSB 227319
Geomys bursarius	20.99			35.68	34.51	12.43	Fossorial	MCZ BOM-7092
Jaculus blanfordi	13.7	21.2	3.4	33.1	52.4	36.7	Bipedal	AMNH M-212113
Jaculus jaculus	11.8	19	3	28.6	46.6	33.2	Bipedal	KLC
Jaculus orientalis	15.3	21.8	3.9	39.1	56.2	40.8	Bipedal	AMNH M-70004
Jaculus orientalis	16.1	22.8	4	40.4	58.9	39	Bipedal	AMNH M-70096

[2]Supplemental tables differ slightly from published supplemental tables to conform to formatting necessary for this dissertation.

(continued)

Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsal	Locomotion	Museum Number
Jaculus orientalis							Bipedal	USNH 308384
Mesocricetus auratus	23.46			29.17	26.89	6.77	Semi-fossorial	MCZ 61023
Mesocricetus auratus	21.13	22.47	6.31	24.99	23.39	6.4	Semi-fossorial	MCZ 61029
Mesocricetus auratus	20.06	21.47	5.8	24.65	22.48	7.01	Semi-fossorial	MCZ 61030
Mesocricetus auratus	19.47	20.4	5.78	22.38	21.33	6.38	Semi-fossorial	MCZ 61031
Mesocricetus auratus	19.85	21.86	5.63	23.22	22.4	6.93	Semi-fossorial	MCZ 61032
Mesocricetus auratus	20.14	21.3	5.3	23.31	22.5	6.41	Semi-fossorial	MCZ 61033
Mesocricetus brandti	25.13			28.54	27.17	6.18	Semi-fossorial	MCZ 57584
Mesocricetus brandti	24.36			31.08	31.28	6.33	Semi-fossorial	MCZ 58130
Microtus arvalis	11.81			12.55	15.52	5.73	Generalist	MCZ BOM-7168
Microtus mexicanus	12.76			15.42	18.16	6.14	Generalist	MCZ 46523
Microtus pennsylvanicus	17.72			20.61	24.78	8.53	Generalist	MCZ 59227
Mus musculus	11.5	13.3	3.4	15.2	17.3	7.5	Generalist	MCZ 62121
Mus musculus	11.62	13.74	3.15	15.52	17.82	8.6	Generalist	MSB 6668
Mus musculus	10.11	12.56	3.18	13.2	15.81	7	Generalist	MSB 6667
Mus musculus	11.28	13.39	3.13	14.64	16.98	7.18	Generalist	MSB 4584
Napaeozapus insignis							Fac Biped	MCZ 64235
Napaeozapus insignis	12.6	15	4.5	18	23.5	14	Fac Biped	AMNH 74849
Napaeozapus insignis	12.7	14.9	4.1	18.8	23.8	13.7	Fac Biped	MCZ 64327
Napaeozapus insignis	12.8	15	4.1	18.7	23.7	13.5	Fac Biped	MCZ 64328
Napaeozapus insignis	12.3	14.8	4.1	18.4	23.5	13.1	Fac Biped	MCZ 64329
Pedetes capensis	43.09			80.55	118.42	49.07	Large Bipedal	MCZ 62930
Peromyscus leucopus	13.6	16.1	4.1	18.3	21.6	8.3	Semi-arboreal	MCZ 62065
Peromyscus leucopus	13.3	16.4	4.1	17	20.8	8.7	Semi-arboreal	MCZ 62088
Peromyscus polinotus	10.8	13.9	3.3	14	16.6	7.3	Generalist	MCZ 66103
Peromyscus polinotus	10.7	13.5	3.3	13.8	16.6	7.8	Generalist	MCZ 66104
Pygeretmus pumilio	11.9	16.86	3.22	29.46	42.04	26.75	Bipedal	MSB 67482
Pygeretmus pumilio	11.87	17.16	3.21	29.37	42.27	25.57	Bipedal	MSB 67483
Pygeretmus pumilio	11.63	16.99	3.07	29.22	41.13	26.12	Bipedal	MSB 67484
Rattus exulans	15.58	19.57	4.62	22.17	26.33	10.25	Generalist	CFS 3744
Rattus exulans	16.92	20.76	4.56	22.04	28.34	11.68	Generalist	CFS 3746
Rattus exulans	22.48	26.99	6.14	30.79	33.8	11.81	Generalist	CFS 3740
Rattus exulans	16.59	19.86	4.91	22.74	27.14	9.57	Generalist	CFS 3742
Rattus norvegicus	32.2	35.6	8.4	42.7	45.7	16.3	Generalist	MCZ 61403
Rattus norvegicus	33.75	36.96	8.07	44.04	48.05	15.65	Generalist	MSB 89172
Rattus norvegicus	30.23	33.39	7.14	39.29	40.94	14.99	Generalist	MSB 92698
Rattus norvegicus	27.72			33.88	39.69	15.59	Generalist	MCZ 6019 FS
Rattus norvegicus	23.36	26.59	6.52	28.15	32.36	12.33	Generalist	MCZ 62277
Rattus norvegicus	24.55	26.41	6.44	29.93	35.52	11.37	Generalist	MCZ 62278
Rattus norvegicus	20.01	21.21	4.49	22.65	26.78	12.11	Generalist	MCZ 62279
Rattus norvegicus	24.77	28.84	6.37	28.68	34.11	12.23	Generalist	MCZ 62285
Rattus rattus	25.2	27	6.7	33.1	36.9	12.8	Generalist	MCZ 62631
Rattus rattus	23.51	29.16	6.62	35.86	38.29	13.75	Generalist	MSB 57181
Rattus rattus	25.3	27.09	6.44	33.15	36.48	12.98	Generalist	MSB 56007
Rhizomys pruinosus	41.87			48.14	45.05	14.04	Fossorial	MCZ 35935
Salpingotus thomasi	5	9.1	1.8	10.3	15.1	8.2	Bipedal	AMNH 244431
Salpingotus thomasi	4.8	8.4	1.7	9.6	15	8.6	Bipedal	AMNH 244432
Salpingotus thomasi	4.4	7.5	1.5	8.4	14.2	7.9	Bipedal	AMNH M-244429
Sicista betulina							Semi-arboreal	MVZ 176617
Sicista betulina	9	11.4	3.4	11.5	14.9	6.8	Semi-arboreal	AMNH M-206585
Spalax ehrenbergi	20.68	27.95	5.36	22.03	22.56	6.75	Fossorial	MCZ 61642

(continued)

Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsal	Locomotion	Museum Number
Spalax ehrenbergi	20.58			21.76	22.44	6.05	Fossorial	MCZ 61642
Spalax ehrenbergi	19.18			19.7	20.08	4.2	Fossorial	MCZ 61381
Spalax ehrenbergi	19.42			20.03	21.47	5.09	Fossorial	MCZ 61389
Stylodipus andrewsi	12.26	18.65	3.15	31.63	41.63	27.17	Bipedal	MSB 216102
Stylodipus andrewsi	12.38	18.73	3.14	31.28	41.29	27.2	Bipedal	MSB 227215
Stylodipus telum	11.94	17.61	3.3	30.15	40.99	25.79	Bipedal	MSB 67492
Thomomys bottae	24.23			28.9	28.69	9.93	Fossorial	MCZ 21093
Thomomys bottae	23.02			27.29	28	12.07	Fossorial	MCZ 21203
Thomomys bottae	22.51			25.23	28.2	8.89	Fossorial	MCZ 52884
Thomomys umbrinus	19.85			23.69	23.93	9.83	Fossorial	MCZ 6304
Zapus hudsonius	10.8	12.5	4	15.3	20.4	12	Fac Biped	AMNH 5403
Zapus hudsonius	11.4	13.3	3.8	17.5	22.3	13.4	Fac Biped	MCZ 64342
Zapus hudsonius	11.3	13.4	3.9	17.6	22.6	13.5	Fac Biped	MCZ 66116
Zapus hudsonius	11.4	13.5	4	17.2	22.1	13.4	Fac Biped	MCZ 66114

Table A.2: *Vertebral body lengths of* Jaculus jaculus *and* Sicista betulina *in mm. Ratios of vertebrae show enlargement, but no clear changes in the relative sizes of the vertebrae.*

Vertebra	***J. jaculus***	**Ratio** $n/n-1$	***S. betulina***	**Ratio** $n/n-1$
T1	1.5	1	0.57	1
T2	1.52	1.01	0.99	1.74
T3	1.75	1.15	1.11	1.11
T4	1.83	1.05	1.19	1.08
T5	1.97	1.07	1.17	0.98
T6	2.12	1.08	1.28	1.09
T7	2.04	0.96	1.28	1.01
T8	2.21	1.08	1.33	1.03
T9	2.4	1.08	1.43	1.08
T10	2.7	1.13	1.42	0.99
T11	2.88	1.07	1.41	1
T12	2.51	0.87	1.5	1.06
T13 (not in J. j.)	-	-	1.81	1.21
Average thoracic	2.12	-	1.27	-
L1	2.86	1.14	2.11	1.17
L2	3.25	1.14	2.37	1.12
L3	3.77	1.16	2.45	1.04
L4	4.2	1.11	2.61	1.06
L5	4.19	1	2.42	0.93
L6	3.7	0.88	2.37	0.98
L7 (not in S. b.)	3.13	0.84	-	-
Average lumbar	3.59	-	2.39	-
Thoracic/lumbar	0.59	-	0.53	-

Table A.3: *Hindlimb morphotype classifications for all 51 species of Dipodoidea.*

Family	Genus	Metatarsal Fusion	Hind Digits	Group in Fig 1.5	Morphotype
Sicistinae	*Sicista* (13 sp)	None	5	Quadruped	A
Zapodidae	*Eozapus* (1 sp)	None	5	Basal facultative	B
	Napaeozapus (1 sp)	None	5	Basal facultative	B
	Zapus (3 sp)	None	5	Basal facultative	B
Cardiocraniinae	*Salpingotus* (5 sp)	None	3	Basal pygmy biped	C
	Salpingotulus (1 sp)	None	3	Basal pygmy biped	C
	Cardiocranius (1 sp)	None	5	Basal pygmy biped	D
Euchoreutinae	*Euchoreutes* (1 sp)	Partial	5	Basal biped	E
Allactaginae	*Allactaga tetradactyla*	Full	4	Derived biped	F
	Allactaga (11 sp)	Full	5	Derived biped	G
	Pygeretmus (3 sp)	Full	5	Derived biped	G
Dipodinae	*Dipus* (1 sp)	Full	3	Derived biped	H
	Eremodipus (1 sp)	Full	3	Derived biped	H
	Jaculus (3 sp)	Full	3	Derived biped	H
	Stylodipus (3 sp)	Full	3	Derived biped	H
	Paradipus (3 sp)	Full	3	Derived biped	H

Morphotype designations correspond to Figure 1.2

Table A.4: *Loadings of bone elements in the phylogenetic Principal Components Analysis in Figure 1.4*

Bone	PC1	PC2	PC3	PC4
Humerus	-0.927962659	0.356347462	0.105019557	-0.02954119
Femur	-0.988392059	0.106862461	-0.062804684	0.087847158
Tibia	-0.988676775	-0.061289937	-0.119702004	-0.066582349
Metatarsal	-0.905125775	-0.415083981	0.091664625	0.00708643

Table A.5: *Species scores with the phylogenetic Principal Components in Figure 1.4*

Species	PC1	PC2	PC3	PC4
Allactaga sibirica	-0.833498727	-10.35657937	-1.06648016	0.880361456
Allactaga major	-10.39899369	-9.765816326	-1.038119269	0.938893537
Allactaga bullata	0.702943694	-10.06921166	-1.035308625	1.068422691
Allactaga elater	3.442629678	-11.33156407	-1.354898378	1.155256564
Allactaga tetradactyla	2.618551426	-10.76311821	-1.303189771	0.803366754
Jaculus jaculus	2.428835486	-11.96420373	-1.019793281	0.230172191
Jaculus blanfordi	-0.740042387	-11.4972549	-0.972631483	0.295664309
Stylodipus andrewsi	3.452682919	-9.502045937	-1.287213984	1.706944543

(continued)

Species	PC1	PC2	PC3	PC4
Dipus sagitta	1.587425245	-10.08717732	-1.069563948	0.936617127
Euchoreutes naso	7.902322257	-10.23825472	0.33567902	-0.138128795
Salpingotus koslovi	30.28733374	-7.963214022	-1.32157391	0.614203907
Cardiocranius paradoxus	20.82912937	-7.920307289	-0.749194601	0.977086321
Zapus hudsonius	16.27731228	-4.411206318	1.593165947	0.608551562
Napaeozapus insignis	14.28267712	-3.752875384	1.603025726	0.50488667
Sicista betulina	26.19246792	-0.825554552	1.066899444	0.187256716
Microtus pennsylvanicus	13.82091084	3.128606717	0.50192181	-0.288222943
Microtus mexicanus	21.50728549	3.18689337	0.118065083	0.194682335
Microtus arvalis	24.68966035	2.924844468	1.262136072	-0.309368234
Mesocricetus brandti	10.13057769	9.039933305	-1.737488265	0.561997069
Mesocricetus auratus	13.6100043	7.012090742	0.019907347	1.170157765
Peromyscus leucopus	17.50003803	0.878632183	0.505103325	0.346229223
Peromyscus polionotus	22.64682191	-0.065587696	1.226285782	0.619878336
Rattus exulans	10.32243591	1.31378492	0.006553186	0.251760162
Rattus rattus	4.656035714	2.156644903	-0.057864511	0.432177148
Rattus norvegicus	2.710245132	2.754811174	0.63694964	-0.017983533
Mus musculus	21.93967027	0.269771598	1.082439015	0.825438403
Acomys russatus	17.27645196	3.459604153	-0.634706936	0.54861346
Spalax ehrenbergi	17.04856928	8.609635305	-0.384676429	0.085116147
Rhizomys pruinosus	-3.430436863	6.667702878	0.911769789	0.625133264
Anomalurus beecrofti	-11.81791689	8.941832207	-1.070598583	-0.50411194
Pedetes capensis	-20.24209142	-4.157693636	-1.701977913	-1.121037362
Thomomys bottae	8.521456161	4.065084169	1.219275488	0.517551453
Thomomys umbrinus	11.69965665	3.171629521	1.786969911	1.002643689
Geomys bursarius	5.07194447	1.995062152	-1.066298917	1.981288997
Dipodomys ordii	7.538328416	-4.805912605	-0.934676363	0.357178695
Dipodomys spectabilis	0.608328366	-4.281753454	-1.476500694	-0.185439194
Castor canadensis	-17.81466575	-1.029094077	2.041696055	-1.054662598
Castor fiber	-21.87861557	-1.210462642	2.120834544	-1.490736905

Table A.6: *ANCOVA for allometric scaling regression lines of quadrupeds and the most derived bipeds.*

	model	**Lh**	α	$\beta 2$	$\beta 3$	$\beta 4$	R^2	**s.e.** α	**s.e.** $\beta - 2$	**s.e.** $\beta - 3$	**s.e.** $\beta - 4$	λ	**p value**	**Pref for 2 lines**
Interlimb	1 line	19.2	0.34	1.07	-	-	0.95	0.22	0.06	-	-	1	3.99E-14	-
	2 lines	36.17	0.07	1.07	1.13	-0.09	1.00	0.07	0.02	0.29	0.08	1.00E-07	4.32e-21	4.00e-8
Intralimb	1 line	32.67	0.06	0.79	-	-	0.79	0.13	0.09	-	-	1	1.88E-08	-
	2 lines	40.71	0.12	0.65	0.03	0.24	0.98	0.1	0.07	0.23	0.15	1.00E-07	1.30E-15	3.00E-03

Table A.7: *Statistical analysis of association of log(element length) with the nodes demonstrating punctuated evolution of the hindlimb*

Punctuation Model	**Lh**	α	$\beta 2$	R^2	**s.e.** α	**s.e.** $\beta - 2$	λ	**T-value**	**d.f.**	**Pval**	**Order**	**Critical Value**	**Adj Pval**
Tibia	24.17	0.90	0.07	0.76	0.07	0.01	1.00E-07	9.13	24.00	1.41E-09	1.00	1.67E-03	8.45E-09
Femur	21.44	0.86	0.06	0.66	0.08	0.01	1.00E-07	7.06	24.00	1.33E-07	2.00	2.00E-03	6.63E-07
MetaT	22.46	0.68	0.05	0.29	0.16	0.02	1.00	3.29	24.00	1.56E-03	3.00	2.50E-03	0.01
Ulna	24.11	0.97	0.03	0.16	0.13	0.01	0.96	2.26	24.00	0.02	4.00	3.33E-03	0.05
Humerus	19.29	0.84	0.03	0.15	0.15	0.02	0.92	2.17	24.00	0.02	5.00	0.01	0.04
MetaC	19.40	0.42	0.02	0.05	0.15	0.02	0.95	1.19	24.00	0.12	6.00	0.01	0.12

A.3 Supplemental Experimental Methods

Nexus file for tree constructed of 28 Myomorpha including 23 Dipodoidea.

```
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---------- ; End;
    begin mrbayes;
    [This block sets up several different partitions that could be used in the analysis of this dataset.
Note that Ibalia is selected as the outgroup; the default outgroup is the first taxon in the matrix.]
    outgroup Dipodomys_ordii;
    charset A2AB = 1-504;
    charset CNR1 = 505-982;
    charset GHR = 983-1629;
    charset IRBP = 1630-2165;
    charset LCAT = 2166-2545;
    charset BRCA1 = 2546-3196;
    charset vWF = 3197-3729;
    charset ATP7a = 3730-4319;
    charset CREM = 4320-4795;
    charset RAG2 = 4796-5254;
    charset DMP1 = 5255-5741;
    partition Names = 11:  A2AB, CNR1, GHR, IRBP, LCAT, BRCA1, vWF, ATP7a, CREM, RAG2, DMP1;
    set partition=Names;
    lset applyto=(all) nst=6 rates=invgamma;
    [Unless the parameters are explicitly unlinked, they will be shared across partitions.  The unlink
command is used to unlink the parameters.]
    unlink shape=(all) pinvar=(all) statefreq=(all) revmat=(all);
    [ADD A CLOCK RATE]
    constraint root = 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28;
    constraint ingroup = 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 23 24 25 26 27 28;
    constraint Dipodidae = 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 23 24 25 26 27 28;
    constraint mouse.rat = 1 2;
    constraint cardiocraniine = 19 23;
    constraint Dipodinae.Allactaginae = 6 7 8 9 10 11 12 13 15 16 17 18 24 25 26 27 28;
    constraint Jaculus = 15 16 27;
    [constraint <name of constraint> <type of constraint> = <taxa>]
    prset topologypr = constraints(root, ingroup, Dipodidae, mouse.rat, cardiocraniine, Dipodinae.Allactaginae,
Jaculus);
    [node calibrations.  The offset exponential distribution has its expectation at the minimum age
and mean.  That is, the offsetexponential(300,325) has the minimum 300 and an exponential mean of 325.
branch lengths in millions of years]
    calibrate root = offsetexponential(55.8, 59); [Calibrations taken from Date-a-Clade]
    calibrate Dipodidae = offsetexponential(43, 47); [Calibrations taken from Wu et al 2012, PLoS One]
c alibrate mouse.rat = offsetexponential(7.3, 9); [Calibrations taken from Wu et al 2012, PLoS One]
    calibrate cardiocraniine = offsetexponential(9, 11); [Calibrations taken from Wu et al 2012, PLoS
One]
```

```
    calibrate Dipodinae.Allactaginae = offsetexponential(10.5, 13); [Calibrations taken from Wu et al
2012, PLoS One]
    prset applyto = (all) ratepr = variable;
    prset brlenspr = clock:  uniform; [need uniform clock when you include fossil species]
    prset nodeagepr = calibrated;
    prset clockratepr = normal(0.2, 0.02);
    [normal(mean, variance)]
    prset clockvarpr = igr;
    prset Igrvarpr = exponential(0.8);
    [The following line allows rates to vary across partitions]
    prset ratepr=variable;
    mcmcp ngen=10000000 nchains=4 nruns=2 printfreq=1000 samplefreq=1000;

    end;
```

Appendix B

Appendix to Chapter 2

B.1 Supplementary Tables

Table B.1: *Morphometric data for hindlimb tendons.*

Tendon	Mass (g)	Length (mm)	Area (mm^2)	Flexor Moment Arm(mm)	Extensor Moment Arm(mm)
Plantaris	0.006	46.688	0.119	1.900	-
Digital Flexor	0.014	47.050	0.271	1.900	-
Achilles	0.017	19.906	0.784	-	4.820

Table B.2: *Hindlimb muscle morphometric data geometrically scaled for a jerboa of mass 62.72g.*

Muscle	Mass (g)	Fiber Length (mm)	Pennation Angle (deg)	MTP Arm (mm)	Ankle Arm (mm)	Knee Arm (mm)	Hip Arm (mm)
Plantaris	0.1	7.1	8	1.15	4.52	1.96	
Digital Flexors	0.06	7.25	15	1.08	1.58		
Medial Gastroc	0.2	4.39	15		4.52	2.02	
Lateral Gastroc	0.22	5.15	18		4.52	2.02	
Soleus	0.02	7.16	5		4.47		
Rectus Femoris	0.18	9.35	16			3.33	5.75
Vastus Lateralis	0.43	13.21	11			3.33	
Vastus Medialis	0.13	9.98	10			3.33	
Vastus Intermedius	0.02	5.3	5			3.33	
Biceps Femoris	0.87	32.26	10				5.79
Gluteus Medius	0.19	11.23	0				3.42
Gluteus Medialis	0.02	6.65	0				3.42
Gluteus Minimus	0.06	8.63	0				3.42
Adductor Magnus	0.56	23.01	3				10.52
Semitendinosus	0.07	23.46	3				11.32

Appendix C

Appendix to Chapter 4

C.1 Supplementary Methods for Continuous Entropy Calculation

Note, we make substantial use of measure theory and the unfamiliar reader may wish to consult Folland (2013) for an introduction.

Notation

Given an element $y \in \mathbb{R}^{n \times m}$, let $[y]_{ij}$ denote the (i,j)-th component of y. We use the same convention for elements belonging to any multidimensional vector space. By $\mathbb{N}$ we denote the nonnegative integers and let $\mathbb{N}_k^n$ refer to those $\alpha \in \mathbb{N}^n$ with $|\alpha| = \sum_{i=1}^n [\alpha]_i \leq k$. Every polynomial on $\mathbb{R}^n$ with $x = (x_1, \ldots, x_n)$, can be expanded in the monomial bases via:

$$p(x) = \sum_{\alpha \in \mathbb{N}^n} p_\alpha x^\alpha \tag{C.1}$$

where $x^\alpha = x_1^{\alpha_1} \cdots x_n^{\alpha_n}$ and $(p_\alpha)_{\alpha \in \mathbb{N}^n}$ is the vector of coefficients of p.

Optimization Problem 4.6

Solving this optimization problem requires finding an object defined on a continuum. Fortunately, one can prove (refer to Lemma C.1) that this optimization problem has a solution parameterized by a finite-dimensional vector. That is, this optimization problem has a solution of the following

form:

$$f^*(\boldsymbol{\lambda}^*, x) = \exp(\sum_{\alpha \in \mathbb{N}^3_{2k}} \lambda^*_\alpha x^\alpha), \tag{C.2}$$

where $\boldsymbol{\lambda}^*$ is a real-valued vector of size $\binom{3+2k}{2k}$ whose α-component is denoted by λ^*_α where $\alpha \in \mathbb{N}^3_{2k}$. By searching for the dimensional vector $\boldsymbol{\lambda}^*$ that maximizes the differential entropy while matching the empirical moments, one has solved for the continuous probability distribution that best describes the empirical data while presuming the least about the data.

Proof. There exists a finite vector $\boldsymbol{\lambda}^* = (\lambda^*_\alpha)_{|\alpha| \leq 2k} \in \mathbb{R}^{\binom{n+2k}{2k}}$ such that:

$$f^*(\boldsymbol{\lambda}^*, x) = \exp(\sum_{\alpha \in \mathbb{N}^n 2k} \lambda^*_\alpha x^\alpha), \tag{C.3}$$

is a solution to Problem (4.6). □

Proof. Suppose $g \in L^1([-1,1]^n)$ has moments with order less than or equal to $2k$ that are identical to f^* which is given by Equation (C.3):

$$\begin{aligned}
\boldsymbol{H}(g) &= -\int_{[-1,1]^n} g(x) \ln\left(g(x)\frac{f^*(\boldsymbol{\lambda}^*, x)}{f^*(\boldsymbol{\lambda}^*, x)}\right) dx && \text{(C.4)}\\
&= -KL(g||f^*) - \int_{[-1,1]^n} g(x) \ln f^*(\boldsymbol{\lambda}^*, x) dx && \text{(C.5)}\\
&\leq -\int_{[-1,1]^n} g(x) \left(\sum_{\alpha \in \mathbb{N}^n_{2k}} \lambda^*_\alpha x^\alpha\right) dx && \text{(C.6)}\\
&= -\sum_{\alpha \in \mathbb{N}^n_{2k}} \lambda^*_\alpha m_\alpha && \text{(C.7)}\\
&= -\int_{[-1,1]^n} f^*(\boldsymbol{\lambda}^*, x) \left(\sum_{\alpha \in \mathbb{N}^n_{2k}} \lambda^*_\alpha x^\alpha\right) dx && \text{(C.8)}\\
&= -\int_{[-1,1]^n} f^*(\boldsymbol{\lambda}^*, x) \ln f^*(\boldsymbol{\lambda}^*, x) dx && \text{(C.9)}\\
&= \boldsymbol{H}(f), && \text{(C.10)}
\end{aligned}$$

where in the second line KL denotes the Kullback–Leibler Divergence Cover and Thomas (2012) which is always nonnegative and the fourth line follows since g and f have identical moments for all moments with order less than or equal to $2k$. □

As a result of Lemma C.1, Equation (4.6) reduces to the concave finite-dimensional optimization problem:

$$\sup_{\lambda \in \mathbb{R}^{\binom{n+2k}{2k}}} \left\{ \sum_{\alpha \in \mathbb{N}^n_{2k}} \widehat{m}_\alpha \lambda_\alpha - f_d(\boldsymbol{\lambda}) \right\}, \tag{C.11}$$

where $f_d : \mathbb{R}^{\binom{n+2k}{2k}} \to \mathbb{R}$ is defined as:

$$f_d(\boldsymbol{\lambda}) = \int_{[-1,1]^n} f(\boldsymbol{\lambda}, x) dx. \tag{C.12}$$

For $\boldsymbol{\lambda} \in \mathbb{R}^{\binom{n+2k}{2k}}$ we denote the $\alpha \in \mathbb{N}^n$ moment of $f(\boldsymbol{\lambda}, x)$ as $\widetilde{m}_\alpha(\boldsymbol{\lambda})$ where:

$$\widetilde{m}_\alpha(\boldsymbol{\lambda}) = \int_{[-1,1]^n} x^\alpha f(\boldsymbol{\lambda}, x). \tag{C.13}$$

Given $\boldsymbol{\lambda} \in \mathbb{R}^{\binom{n+2k}{2k}}$ one can compute $\widehat{m}_\alpha(\boldsymbol{\lambda})$ using numerical integration. To solve Problem (C.11), one can implement Newton's Method Lasserre (2009) as described in Algorithm 1. To apply Newton's method one must compute the Hessian of f_d which follow from the following lemma:

Proof. The Hessian $\nabla^2 f_d : \mathbb{R}^{\binom{n+2k}{2k}} \to \mathbb{R}^{\binom{n+2k}{2k} \times \binom{n+2k}{2k}}$ is given by:

$$[\nabla^2 f_d(\boldsymbol{\lambda})]_{j,k} = \int_{[-1,1]^n} x^{j+k} f(\boldsymbol{\lambda}, x) dx = \widetilde{m}_{j+k}(\boldsymbol{\lambda}) \tag{C.14}$$

for all $j, k \in \mathbb{N}^n_{2k}$. □

Proof. This follows directly from the Fundamental Theorem of Calculus. □

Require: $\boldsymbol{\lambda}^0 \in \mathbb{R}^{\binom{n+2k}{2k}}$ and $\epsilon \in (0, \infty)$.
1: Set $j = 0$.
2: **loop**
3: Set $\boldsymbol{\lambda}^{j+1} = \boldsymbol{\lambda}^j + \left[\nabla^2 f_d(\boldsymbol{\lambda}^j)\right]^{-1} (\widehat{m} - \widetilde{m}(\boldsymbol{\lambda}^j))$
4: Replace j by $j + 1$.
5: **if** $\|\boldsymbol{\lambda}^{j-1} - \boldsymbol{\lambda}^j\|_2 \leq \epsilon$ **then**
6: **return** $\boldsymbol{\lambda}^j$.
7: **end if**
8: **end loop**

Algorithm 1: *Newton's Method for Computing the Maximum Entropy Distribution*

C.2 Supplementary Results

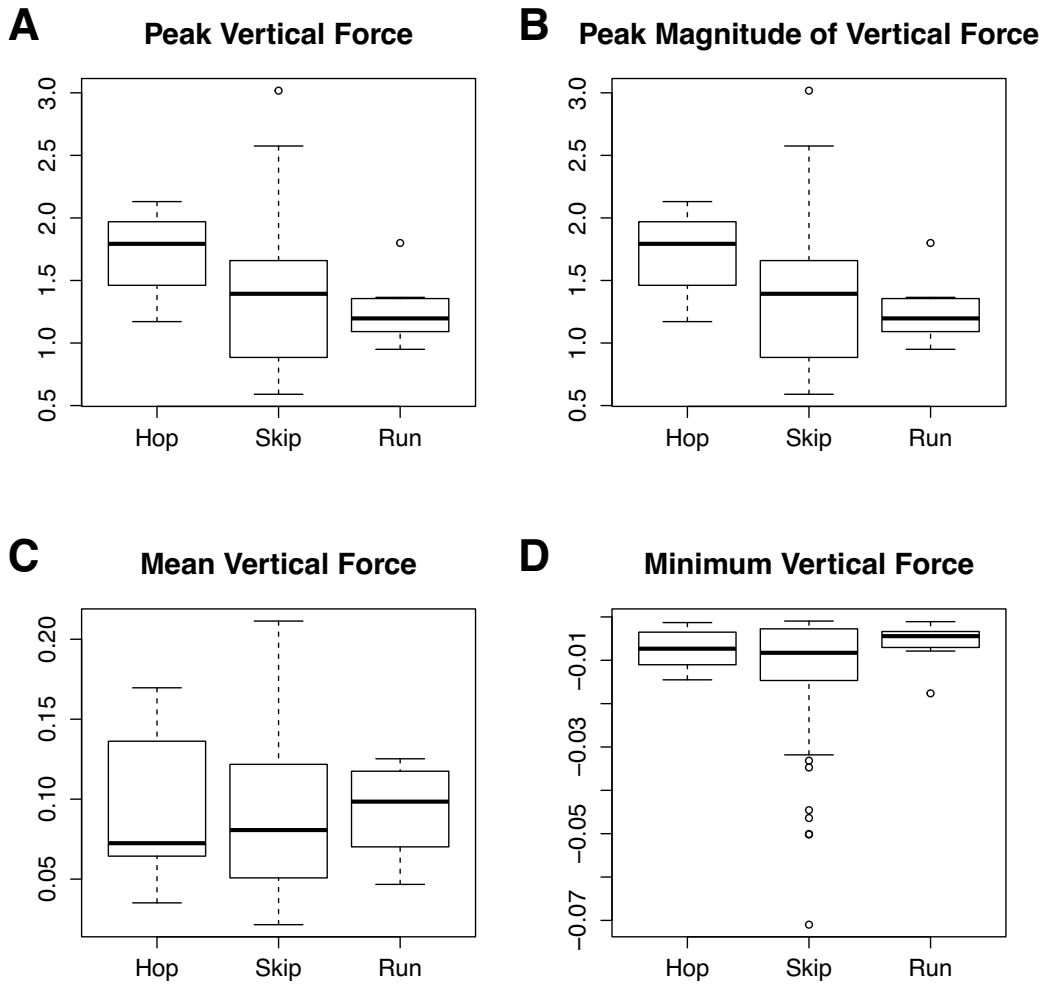


Figure C.1: *Components of vertical force sorted by gait. A) Peak vertical force trended towards significantly different between gaits ($p = 0.0876$), B) Peak magnitude of vertical force was exactly the same, indicating that positive vertical force was greater than the negative values of vertical force ($p = 0.0876$), C) Mean vertical force was not significantly different between gaits ($p = 0.997$), D) Minimum vertical force was near zero, indicating accurate balancing of bridges and minimal ringing, and was not significantly different between gaits ($p = 0.246$).*

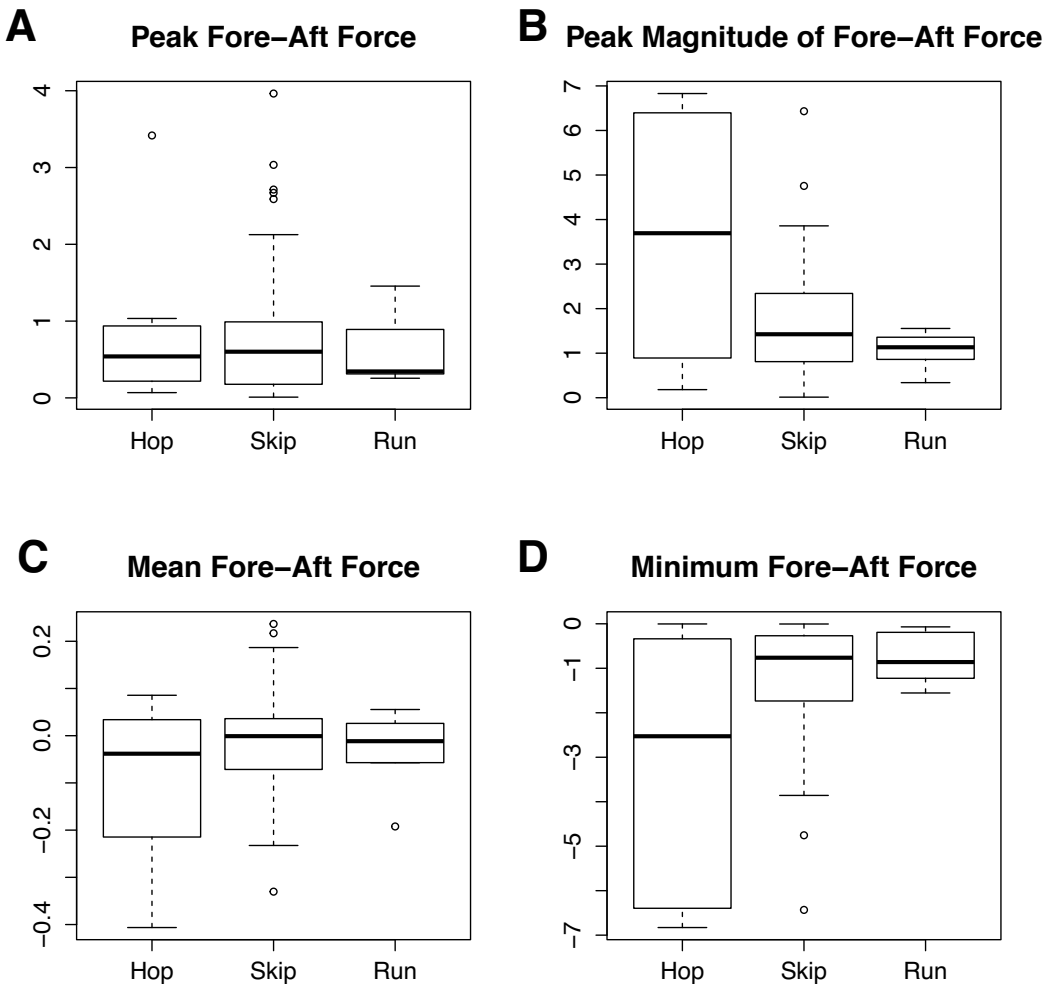


Figure C.2: *Components of fore-aft force sorted by gait. A) Peak fore-aft force did not differ significantly between gaits ($p = 0.801$), B) Peak magnitude of vertical force was highly significant, indicating that negative fore-aft force differs significantly between gait ($p = 0.000237$), C) Mean fore-aft force did not differ significantly between gait ($p = 0.135$), D) Minimum fore-aft force was highly significant ($p = 0.00148$), though not as significant as the magnitude of vertical force, indicating that both large negative and positive fore-aft forces contribute to the significant differences between gait.*

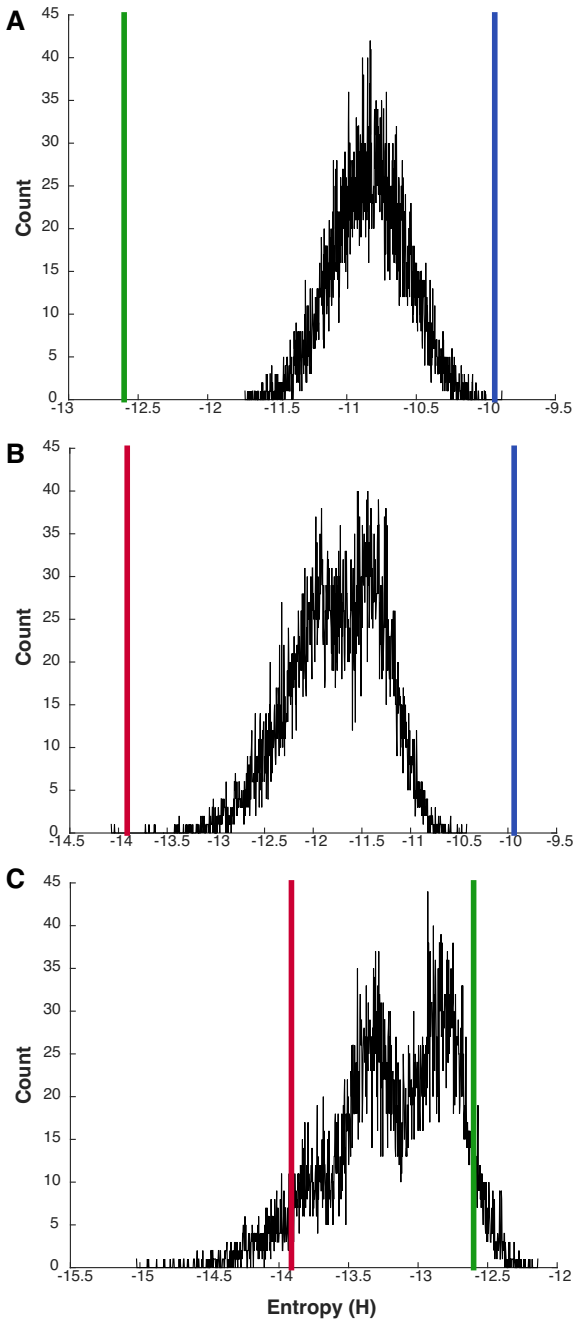


Figure C.3: *The sampling distribution of trajectory entropy for each unique combination of field species is illustrated. Vertical lines show the true value of entropy for each species. The proportion of samples in the corresponding tail of the distribution is the p–value for that species (Fisher's Exact Test.. A)* A. elater *in blue:* $p = 0.0002$, D. sagitta *in green:* $p = 0$, *B)* A. elater *in blue:* $p = 0$, Meriones sp. *in red:* $p = 0.0002$, *and C)* D. sagitta *in green:* $p = 0.0561$, Meriones sp. *in red:* $p = 0.0605$.

C.2.1 Detailed Light–Dark Box Results

Each animal performed 3 trials. The location of the dark box and the animal trial order were randomized prior to experimentation. The trials were performed throughout the periods in which their housing rooms were dark and illuminated (light cycle). We recorded the amount of time it took to capture each animal prior to experimentation to account for the stress of capture.

Species was the main determinant of microhabitat preference (Nested ANOVA) for the percentage of time spent in the exposed area and the number of times the animal returned to the box after a period of risk assessment. Variations specific to each individual and trial number, or acclimation to the experiment, were marginally significant determinants of behavior. We found that the box location, time it took to capture the animal, and the time in each animal's light cycle the experiment was performed had no measurable effect on the difference between species ($\alpha = 0.05$) on percentage of time spent in the exposed area, the number of times the animal went into the box, or the number of times the animal returned to the box after a period of risk assessment (Mixed–effects ANOVA). The percentage of time in risk–assessment only varied significantly with the combined effect of species and trial number.

Table C.1: *The level of significance for the effect of each independent variable on the behavior of animals in the Light–Dark Box experiment. The dependent variables are on the top row, and the independent variables and the type of model used are in the first column on the left. Symbols indicate first the effect of the Species, then the effect of the additional variable, and, if present, the mixed effects of Species and the additional variable. - indicates* $p > 0.1$, *. indicates* $0.1 > p > 0.05$, ** indicates* $0.05 > p > 0.01$, *** indicates* $0.01 > p > 0.001$, **** indicates* $0.001 > p > 0$. *All models were designed prior to viewing results.*

	% Exposed	% Risk Assess	% Out to In	% Risk to In
Species+Individual (Nested)	***,*	-,-	***,*	***,-
Species*Trial Number (Mixed)	**,.,-	-,-,*	.,-,-	***,-,-
Species*Capture Time (Mixed)	*,-,-	-,-,-	.,-,-	***,-,-
Species*Box Location (Mixed)	*,-,-	-,-,-	.,-,-	***,-,-

Appendix D

Appendix to Chapter 5

D.1 Supplementary Tables

Table D.1: *Morphological measurements and museum information for specimens used in Chapter 5, sorted by family.*

Family	Museum	Number	Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsus
Anomaluridae	MCZ	43042	*Anomalurus derbianus*	61.9	63.09	10.19	68.63	74.36	16.97
Calomyscidae	UMMZ	167675	*Calomyscus bailwardi*	12.63	15.08	3.39	16.74	20.92	8.09
Calomyscidae	UMMZ	167679	*Calomyscus bailwardi*	12.58	15.86	3.15	15.22	20.45	8.46
Calomyscidae	UMMZ	167677	*Calomyscus bailwardi*	12.54	15.55	3.15	17.44	19.98	7.96
Castoridae	MCZ	61275	*Castor canadensis*	72.84	102.18	17.81	20.75	83.11	120.24
Castoridae	MCZ	60986	*Castor canadensis*	54.28	79.41	18.04	66.53	87.32	42.98
Castoridae	UMMZ	83971	*Castor canadensis*	77.61	110.18	18.64	88.72	126.07	53.37
Castoridae	UMMZ	83970	*Castor canadensis*	54.37	74.29	18.22	60.66	83.58	34.13
Castoridae	MCZ	19559	*Castor fiber*	64.78	93.45	19.16	74.81	104.37	50.71
Cricetidae	UMMZ	157152	*Abrothrix olivaceus*	11.65	13.91	2.64	15.27	20.09	7.14
Cricetidae	UMMZ	157151	*Abrothrix olivaceus*	10.68	14.76	3.38	13.49	18.09	7.87
Cricetidae	UMMZ	160519	*Akodon aerosus*	12.56	16.87	4.4	15.49	21.53	9.26
Cricetidae	UMMZ	160515	*Akodon aerosus*	12.57	15.54	3.45	15.93	20.35	9.23
Cricetidae	UMMZ	160516	*Akodon aerosus*	11.8	15.65	3.61	14.44	19.8	8.9
Cricetidae	UMMZ	97680	*Arvicola sapidus*	18.65	24.5	5.4	20.58	26.93	11.02
Cricetidae	UMMZ	123305	*Auliscomys pictus*	11.96	14.41	3.67	14.65	19.1	7.8
Cricetidae	UMMZ	89977	*Baiomys musculus*	9.81	11.96	2.27	12.42	14.85	5.92
Cricetidae	UMMZ	86533	*Baiomys musculus*	9.39	11.18	2.44	11.55	14.04	5.31
Cricetidae	UMMZ	92576	*Baiomys musculus*	7.89	9.95	2.16	9.99	12.26	5.95
Cricetidae	UMMZ	89976	*Baiomys musculus*	8.64	10.96	2.76	10.75	13.7	5.86
Cricetidae	UMMZ	96291	*Baiomys musculus*	8.69	10.55	2.21	11.47	13.87	5.33
Cricetidae	UMMZ	125472	*Calomys callosus*	13.84	16.26	3.29	19.13	21.31	7.44
Cricetidae	UMMZ	125468	*Calomys callosus*	13.02	15.06	4.02	17.3	18.55	8.04
Cricetidae	UMMZ	125471	*Calomys callosus*	14.37	16.64	3.73	19.27	20.88	8.44
Cricetidae	UMMZ	125469	*Calomys callosus*	13.42	15.43	3.16	17.04	19.22	7.54
Cricetidae	UMMZ	125470	*Calomys callosus*	12.56	13.52	3.82	16.11	18.37	7.55
Cricetidae	UMMZ	111187	*Cricetus cricetus*	36.78	41.25	8.65	41.25	40.5	11.63
Cricetidae	UMMZ	100771	*Dicrostonyx hudsonius*	17.29	21.03	4.24	19.55	23.85	5.63
Cricetidae	UMMZ	118591	*Ellobius fuscocapillus*	16.89	19.71	5.16	18	19	5.62

(continued)

Family	Museum	Number	Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsus
Cricetidae	UMMZ	155931	*Graomys domorum*	18.56	22.01	5.16	25.31	29.72	11.53
Cricetidae	UMMZ	155929	*Graomys domorum*	18.75	23.15	4.74	26.11	29.68	11.91
Cricetidae	UMMZ	155034	*Graomys domorum*	18.41	22.41	4.55	24.82	29.2	10.87
Cricetidae	UMMZ	155930	*Graomys domorum*	17.35	21.23	4.46	23.17	28.06	12.04
Cricetidae	UMMZ	155933	*Graomys domorum*	16.84	20.14	4.25	24.03	28.39	10.75
Cricetidae	UMMZ	114214	*Handleyomys fuscatus*	13.59	16.16	4.43	19.04	22.29	10.54
Cricetidae	UMMZ	114217	*Handleyomys fuscatus*	12.31	14.79	4.62	16.05	19.74	9.13
Cricetidae	UMMZ	166255	*Holochilus brasiliensis*	21.7	26.87	5	29.13	33.69	13.62
Cricetidae	UMMZ	166256	*Holochilus brasiliensis*	21.18	26.46	5.78	28.38	35.27	14.76
Cricetidae	UMMZ	166257	*Holochilus brasiliensis*	23.54	26.12	5.64	33	36.63	14.13
Cricetidae	UMMZ	166258	*Holochilus brasiliensis*	21.42	24.61	4.89	28.91	33.51	15
Cricetidae	UMMZ	166267	*Holochilus brasiliensis*	23.47	27.97	5.26	33	36.74	14.79
Cricetidae	UMMZ	137010	*Hylaeamys megacephalus*	19.02	22.71	5.92	24.79	30.39	13.28
Cricetidae	UMMZ	137011	*Hylaeamys megacephalus*	18.82	23.03	4.6	24.92	30.82	12.91
Cricetidae	UMMZ	137012	*Hylaeamys megacephalus*	14.87	19.85	4.94	21.12	26.18	13.91
Cricetidae	UMMZ	137009	*Hylaeamys megacephalus*	14.77	18.83	5.33	19.28	24.67	12.07
Cricetidae	UMMZ	167700	*Hyperacrius wynnei*	11.88	15.08	4.06	12.83	16.85	5.73
Cricetidae	UMMZ	123538	*Lasiopodomys brandtii*	13.77	15.35	5.45	14.59	19.63	6.5
Cricetidae	UMMZ	101113	*Lemmus trimucronatus*	16.23	18.23	3.65	19.18	22.76	6.96
Cricetidae	UMMZ	101115	*Lemmus trimucronatus*	20.07	19.95	4.06	22.85	27.37	6.3
Cricetidae	UMMZ	101114	*Lemmus trimucronatus*	16.7	19.58	3.96	20.77	24.84	7.46
Cricetidae	UMMZ	101111	*Lemmus trimucronatus*	15.74	16.59	4.15	16.64	21.62	6.89
Cricetidae	UMMZ	115518	*Megadontomys thomasi*	22.82	24.28	5.22	26.93	30.96	9.43
Cricetidae	UMMZ	114226	*Megadontomys thomasi*	21.52	26.23	5.4	27.31	35.26	11.63
Cricetidae	UMMZ	114225	*Megadontomys thomasi*	21.41	26.01	5.17	27.38	34.4	11
Cricetidae	UMMZ	112276	*Melanomys caliginosus*	12.46	14.45	4.21	13.95	19.36	8.5
Cricetidae	MCZ	61023	*Mesocricetus auratus*	23.72	27.56	5.21	27.85	26.85	6.68
Cricetidae	MCZ	61029	*Mesocricetus auratus*	21.18	24.17	5.39	25.07	24.3	6.69
Cricetidae	MCZ	61030	*Mesocricetus auratus*	20.06	21.47	5.8	24.65	22.48	7.01
Cricetidae	MCZ	61032	*Mesocricetus auratus*	19.85	21.86	5.63	23.22	22.4	6.93
Cricetidae	MCZ	61033	*Mesocricetus auratus*	20.14	21.3	5.3	23.31	22.5	6.41
Cricetidae	MCZ	61031	*Mesocricetus auratus*	19.47	20.4	5.78	22.38	21.33	6.38
Cricetidae	MCZ	57584	*Mesocricetus brandti*	25.13	27.69	5.57	28.54	27.17	6.18
Cricetidae	MCZ	58130	*Mesocricetus brandti*	24.36	29.04	5.23	31.08	31.28	6.33
Cricetidae	MCZ	7168	*Microtus arvalis*	11.98	13.43	2.63	12.55	15.52	5.73
Cricetidae	MCZ	46523	*Microtus mexicanus*	14.08	16.06	3.18	15.25	17.63	6.27
Cricetidae	UMMZ	89423	*Microtus mexicanus*	12.37	14.92	3.72	13.89	18.61	7.02
Cricetidae	MCZ	59227	*Microtus pennsylvanicus*	17.7	20.43	4.16	20.33	23.98	8.3
Cricetidae	UMMZ	166227	*Myodes gapperi*	11.57	13.36	3.66	13.06	17.27	7.16
Cricetidae	UMMZ	167059	*Myodes gapperi*	12.75	15.05	4.25	14.57	18.56	7.67
Cricetidae	UMMZ	167066	*Myodes gapperi*	11.35	14.14	3.27	12.59	17.4	6.58
Cricetidae	UMMZ	167058	*Myodes gapperi*	11.19	13.23	3.73	12.19	16.61	7.14
Cricetidae	UMMZ	167060	*Myodes gapperi*	12.44	14.58	3.68	14.02	17.93	7.35
Cricetidae	UMMZ	160545	*Neacomys spinosus*	10.8	12.3	3.43	16.01	19.4	9.03
Cricetidae	UMMZ	137070	*Necromys lenguarum*	14.52	18.48	3.61	20.35	23.9	8.19
Cricetidae	UMMZ	137080	*Necromys lenguarum*	13.44	16.42	3.71	18.76	22.86	8.82
Cricetidae	UMMZ	137082	*Necromys lenguarum*	11.19	14.42	3.66	14.59	17.41	8.04
Cricetidae	UMMZ	137083	*Necromys lenguarum*	11.48	14.17	3.17	14.3	17.03	7.17
Cricetidae	UMMZ	137081	*Necromys lenguarum*	10.18	13.74	3.79	13.08	16.4	7.82
Cricetidae	UMMZ	137139	*Nectomys squamipes*	26.5	32.79	7.57	37.51	44.72	20.33
Cricetidae	UMMZ	137140	*Nectomys squamipes*	22.66	29.43	6.61	30.94	38.52	19.59

(continued)

Family	Museum	Number	Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsus
Cricetidae	UMMZ	123577	*Neodon juldaschi*	10.47	12.29	2.82	12.35	14.52	6.99
Cricetidae	MCZ	61183	*Neotoma albigula*	26.55	30.24	5.68	30.58	35.56	11.75
Cricetidae	UMMZ	107880	*Neotoma albigula*	29.02	32.39	6.16	34.76	37.6	11.69
Cricetidae	UMMZ	79068	*Neotoma albigula*	24.76	30.48	5.38	29.67	33.21	10.59
Cricetidae	MCZ	59215	*Neotomodon alstoni*	14.13	21.36	3.76	19.05	25.51	10.73
Cricetidae	UMMZ	89420	*Neotomodon alstoni*	12.39	18.48	3.79	17.04	23.23	10.05
Cricetidae	UMMZ	96227	*Neotomodon alstoni*	17.61	21.52	4.29	21.24	26.91	10.74
Cricetidae	UMMZ	96229	*Neotomodon alstoni*	14.42	20.71	4.55	19.38	24.74	10.17
Cricetidae	UMMZ	96230	*Neotomodon alstoni*	15.18	20.51	4.74	19.23	25.63	11.3
Cricetidae	UMMZ	96228	*Neotomodon alstoni*	14.36	21.08	4.29	19.11	25.72	10.6
Cricetidae	UMMZ	155923	*Nephelomys albigularis*	18.42	22.97	5.74	22.87	29.51	13
Cricetidae	UMMZ	155924	*Nephelomys albigularis*	18.93	22.18	4.54	25.1	30.98	13.2
Cricetidae	UMMZ	155920	*Nephelomys albigularis*	15.02	19.9	5.09	19.44	26.12	11.8
Cricetidae	UMMZ	155921	*Nephelomys albigularis*	14.78	18.63	5.53	18.65	25.55	12.22
Cricetidae	UMMZ	155922	*Nephelomys albigularis*	14.44	17.9	5.28	18.76	25.76	13.16
Cricetidae	UMMZ	126299	*Neusticomys monticolus*	12.86	16.16	3.72	15.15	23.14	10.63
Cricetidae	UMMZ	155789	*Neusticomys monticolus*	13.3	16.26	3.68	15.85	22.88	9.95
Cricetidae	UMMZ	155793	*Neusticomys monticolus*	13.55	16.49	4.39	16.34	23.96	9.51
Cricetidae	MCZ	37899	*Oecomys bicolor*	13.01	16.93	3.44	17.25	20.35	7.55
Cricetidae	UMMZ	160550	*Oecomys bicolor*	13.89	16.13	4.04	17.19	20.2	8.27
Cricetidae	MCZ	61800	*Oligoryzomys fulvescens*	12.75	17.16	4.29	17.37	21.8	10.58
Cricetidae	MCZ	61792	*Oligoryzomys fulvescens*	14.23	16.8	4.25	20.33	22.72	9.55
Cricetidae	UMMZ	137060	*Oligoryzomys chacoensis*	10.65	13.97	3.59	15.17	19.65	9.66
Cricetidae	UMMZ	125546	*Oligoryzomys chacoensis*	10.83	12.88	3.44	15.15	19.64	9.8
Cricetidae	UMMZ	125547	*Oligoryzomys chacoensis*	12.09	14.55	4.06	18.29	21.63	9.72
Cricetidae	UMMZ	125548	*Oligoryzomys chacoensis*	10.63	12.61	3.98	15.2	19.88	9.1
Cricetidae	MCZ	59445	*Ondatra zibethicus*	39.23	54.69	10.2	44.8	68.27	27.96
Cricetidae	MCZ	59446	*Ondatra zibethicus*	35.7	51.06	10.34	41.18	61.49	26.67
Cricetidae	UMMZ	89729	*Ondatra zibethicus*	39.76	54.39	11.52	45.52	63.61	26.72
Cricetidae	UMMZ	89728	*Ondatra zibethicus*	31.03	49.74	10.8	38.76	58.11	26.77
Cricetidae	UMMZ	158365	*Onychomys leucogaster*	12.78	17.5	4.35	15.15	18.88	7.9
Cricetidae	UMMZ	158363	*Onychomys leucogaster*	14.07	18.72	4.36	17.66	19.71	7.71
Cricetidae	UMMZ	158364	*Onychomys leucogaster*	13.84	18.46	4.28	17.02	20.35	7.91
Cricetidae	UMMZ	118220	*Oryzomys couesi*	17.1	19.71	4.39	22.36	27.28	12.48
Cricetidae	UMMZ	92595	*Oryzomys couesi*	14.05	17.61	4.3	19.66	24.13	11.2
Cricetidae	UMMZ	96303	*Oryzomys couesi*	13.5	15.67	3.91	17.43	22.4	10.3
Cricetidae	UMMZ	92590	*Oryzomys couesi*	14.69	16.66	4.23	20.16	24.94	11.51
Cricetidae	UMMZ	92591	*Oryzomys couesi*	14.33	17.19	4.26	18.99	23.35	11.69
Cricetidae	UMMZ	114086	*Osgoodomys banderanus*	15.71	18.55	4.34	20.37	25.06	10.02
Cricetidae	UMMZ	115519	*Ototylomys phyllotis*	21.75	26.19	5.75	28.11	35.67	11.79
Cricetidae	UMMZ	126088	*Oxymycterus delator*	19.1	24.16	5.04	26	28.21	9.98
Cricetidae	UMMZ	126085	*Oxymycterus delator*	18	22.45	4.37	24.74	26.07	8.84
Cricetidae	UMMZ	126086	*Oxymycterus delator*	17.87	22.76	4.91	23.5	25.38	9.47
Cricetidae	UMMZ	126089	*Oxymycterus delator*	14.06	17.81	4.72	18.07	20.12	8.54
Cricetidae	UMMZ	126087	*Oxymycterus delator*	14.38	18.32	4.73	18.96	22.2	9.06
Cricetidae	MCZ	62088	*Peromyscus leucopus*	13.3	16.4	4.1	17	20.8	8.7
Cricetidae	MCZ	62065	*Peromyscus leucopus*	13.6	16.1	4.1	18.3	21.6	8.3
Cricetidae	MCZ	66104	*Peromyscus polionotus*	10.7	13.5	3.3	13.8	16.6	7.8
Cricetidae	MCZ	66103	*Peromyscus polionotus*	10.8	13.9	3.3	14	16.6	7.3
Cricetidae	UMMZ	168395	*Phodopus sungorus*	15.4	19.76	3.12	17.99	20.8	4.45
Cricetidae	UMMZ	170500	*Phodopus sungorus*	14.21	18.74	3.4	16.79	19.64	4.81

(continued)

Family	Museum	Number	Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsus
Cricetidae	UMMZ	170501	*Phodopus sungorus*	14.48	17.61	3.25	16.96	19.34	4.42
Cricetidae	UMMZ	170499	*Phodopus sungorus*	13.84	18.3	3.22	16.47	18.66	4.95
Cricetidae	UMMZ	155992	*Phyllotis darwini*	16.44	20.67	3.62	22.65	28.55	10.84
Cricetidae	UMMZ	155990	*Phyllotis darwini*	11.49	14.72	4.03	15.26	19.57	9.25
Cricetidae	MCZ	50830	*Microtus pinetorum*	11.77	13.15	2.99	12.11	14.32	6.18
Cricetidae	MCZ	63085	*Microtus pinetorum*	12.05	13.21	3.05	11.38	14.25	5.18
Cricetidae	MCZ	63708	*Microtus pinetorum*	10.15	12.01	2.48	10.14	12.02	4.97
Cricetidae	UMMZ	100874	*Podomys floridanus*	16.24	20.62	3.94	20.53	25.22	11.4
Cricetidae	UMMZ	100875	*Podomys floridanus*	12.72	16.9	4.28	15.25	18.33	9.45
Cricetidae	UMMZ	133913	*Pseudoryzomys simplex*	14.54	18.09	3.99	20.91	25.02	11.27
Cricetidae	UMMZ	122557	*Reithrodontomys gracilis*	10.51	13.58	2.81	13.29	18.09	6.79
Cricetidae	UMMZ	111986	*Rheomys raptor*	13.78	16.08	4.09	16.6	22.89	10.53
Cricetidae	UMMZ	111985	*Rheomys raptor*	14.05	15.88	4.23	16.82	22.73	10.9
Cricetidae	UMMZ	137071	*Scapteromys tumidus*	19.08	24.41	5.71	26.26	31.7	15.26
Cricetidae	UMMZ	120005	*Scotinomys teguina*	10.73	12.87	3.1	13.12	17.36	7.33
Cricetidae	UMMZ	112235	*Scotinomys teguina*	10.77	13.35	3.42	13.3	17.51	7.65
Cricetidae	UMMZ	125149	*Scotinomys teguina*	9.35	12.24	2.92	11.62	16.57	7.24
Cricetidae	UMMZ	125144	*Scotinomys teguina*	10.01	12.41	3.01	12.09	15.92	6.48
Cricetidae	UMMZ	120004	*Scotinomys teguina*	9.69	12.79	3.2	12.33	17.08	7.57
Cricetidae	UMMZ	96306	*Sigmodon hispidus*	18.69	21.33	4.56	27.94	28.52	11.13
Cricetidae	UMMZ	100690	*Sigmodon hispidus*	16.88	20.07	4.42	22.48	26.19	11.67
Cricetidae	UMMZ	100691	*Sigmodon hispidus*	15.08	18.47	4.44	20.49	23.66	11.03
Cricetidae	UMMZ	92597	*Sigmodon hispidus*	11.86	13.66	3.29	14.47	18.27	7.03
Cricetidae	UMMZ	146833	*Synaptomys cooperi*	13.73	15.64	4.16	14.79	19.41	6.4
Cricetidae	UMMZ	160087	*Synaptomys cooperi*	13.63	15.41	3.07	14.95	19.21	5.88
Cricetidae	UMMZ	76423	*Synaptomys cooperi*	13.02	15.13	4.3	13.03	17.47	6.06
Cricetidae	UMMZ	122810	*Synaptomys cooperi*	11.22	13.44	2.85	11.63	14.89	5.69
Cricetidae	UMMZ	126068	*Thaptomys nigrita*	11.32	14.21	3.62	13.35	16.14	6.51
Cricetidae	UMMZ	126069	*Thaptomys nigrita*	11.31	14.5	3.12	13.19	16.53	7.18
Cricetidae	UMMZ	160580	*Thomasomys daphne*	11.38	16.74	3.87	12.87	22.33	8.73
Cricetidae	UMMZ	159340	*Tylomys nudicaudus*	31.26	32.73	7.61	40.42	41.96	12.06
Cricetidae	UMMZ	159341	*Tylomys nudicaudus*	30.67	34.13	6.47	40.18	41.92	12.13
Cricetidae	UMMZ	159342	*Tylomys nudicaudus*	27.35	30.6	7.26	32.93	36.69	12.47
Dipodidae	MSB	227346	*Allactaga balikunica*	12.27	19.83	3.4	29.97	46.19	30.72
Dipodidae	MSB	227352	*Allactaga balikunica*	12.05	19.78	3.18	30.23	46.27	30.31
Dipodidae	MSB	227444	*Allactaga balikunica*	12.21	19.78	3.7	31.28	46.94	29.97
Dipodidae	MSB	225083	*Allactaga bullata*	13.34	20.64	4.06	32.64	47.65	32.32
Dipodidae	MSB	225875	*Allactaga bullata*	13.53	21.1	4.13	33.81	47.13	31.25
Dipodidae	MSB	225920	*Allactaga bullata*	14.14	21.5	3.59	33.94	47.13	31.61
Dipodidae	MSB	67489	*Allactaga elater*	11.33	16.48	2.76	29.55	43.32	30.36
Dipodidae	UMMZ	118661	*Allactaga elater*	11.61	16.87	28.28	42.35	42.23	26.38
Dipodidae	UMMZ	118660	*Allactaga elater*	11.23	17.25	2.79	26.03	42.21	31.22
Dipodidae	UMMZ	118664	*Allactaga elater*	12.24	17.81	3.2	29.94	44.92	29.21
Dipodidae	UMMZ	118662	*Allactaga elater*	11.41	16.31	2.47	28.42	42.18	26.52
Dipodidae	USNM	341595	*Allactaga elater*	12.41	17.18	3	28.64	45.33	29.78
Dipodidae	UMMZ	118665	*Allactaga euphratica*	13.59	20.6	3.95	33.8	52.14	35.07
Dipodidae	AMNH	MO-227	*Allactaga major*	21.6	29.1	6.1	54	73.9	48.8
Dipodidae	UMMZ	123580	*Allactaga major*	20.29	26.69	5.43	45.51	66.99	47.94
Dipodidae	AMNH	M-55978	*Allactaga sibirica*	14.2	21.4	4.4	34.2	50.2	33.7
Dipodidae	AMNH	M-55980	*Allactaga sibirica*	14.8	23.5	4.4	37.5	55.7	35.4
Dipodidae	MSB	215129	*Allactaga sibirica*	13.76	21.56	4.82	33.52	48.94	34.44

(continued)

Family	Museum	Number	Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsus
Dipodidae	MSB	215135	*Allactaga sibirica*	14.28	21.53	4.23	34.64	48.79	33.05
Dipodidae	MSB	216247	*Allactaga sibirica*	14.68	22.01	4.66	36.21	50.8	34.7
Dipodidae	USNM	155194	*Allactaga sibirica*	16.01	23.44	4.68	39.12	57.36	40.74
Dipodidae	KLC	Alct-1	*Allactaga tetradactyla*	12.3	18.3	3.1	30.2	45.4	30.4
Dipodidae	KLC	Alct-2	*Allactaga tetradactyla*	11.8	17.7	3	29.2	43.8	29.2
Dipodidae	KLC	Alct-3	*Allactaga tetradactyla*	11.9	17.9	3.1	29.8	44.7	29.9
Dipodidae	KLC	Alct-4	*Allactaga tetradactyla*	12.6	18.9	2.9	31.6	47	31.6
Dipodidae	UMMZ	123528	*Allactodipus bobrinskii*	12.77	19.94	3.05	29.9	45.49	32.75
Dipodidae	UMMZ	123527	*Allactodipus bobrinskii*	11.66	18.51	3.12	27.46	44.15	30.67
Dipodidae	MSB	199763	*Cardiocranius paradoxus*	6.43	11.54	1.74	14.21	20.18	12.18
Dipodidae	MSB	2250151	*Cardiocranius paradoxus*	7.05	12.45	1.87	13.89	19.71	11.9
Dipodidae	MSB	199720	*Dipus sagitta*	12.57	19.67	3.33	31.26	45.31	29.31
Dipodidae	MSB	214383	*Dipus sagitta*	13.4	20.19	3.88	31.34	46.03	31.82
Dipodidae	MSB	224212	*Dipus sagitta*	13.7	20.32	3.86	33.45	46.88	30.43
Dipodidae	UMMZ	123529	*Dipus sagitta*	12.45	21.04	4.97	28.6	45.73	34.1
Dipodidae	UMMZ	123530	*Dipus sagitta*	14.19	21.75	4.33	31.32	48.13	33.84
Dipodidae	MSB	227319	*Euchoreutes naso*	10.97	18.63	3.8	22.03	35.01	24.39
Dipodidae	MSB	227347	*Euchoreutes naso*	11.24	18.83	4.13	21.58	35.28	25.86
Dipodidae	AMNH	M-212113	*Jaculus blanfordi*	13.7	21.2	3.4	33.1	52.4	36.7
Dipodidae	UMMZ	122753	*Jaculus blanfordi*	13.32	21.33	3.63	30.27	49.51	36.06
Dipodidae	UMMZ	123531	*Jaculus blanfordi*	13.04	20.67	3.2	29.77	48.82	35.48
Dipodidae	KLC		*Jaculus jaculus*	11.8	19	3	28.6	46.6	33.2
Dipodidae	UMMZ	101320	*Jaculus jaculus*	10.7	18.64	3.3	24.19	44.57	32.63
Dipodidae	AMNH	M-70004	*Jaculus orientalis*	15.3	21.8	3.9	39.1	56.2	40.8
Dipodidae	AMNH	M-70096	*Jaculus orientalis*	16.1	22.8	4	40.4	58.9	39
Dipodidae	UMMZ	99270	*Jaculus orientalis*	15.08	22.09	4.11	37.66	60.71	44.62
Dipodidae	MSB	67482	*Pygeretmus pumilio*	11.9	16.86	3.22	29.46	42.04	26.75
Dipodidae	MSB	67483	*Pygeretmus pumilio*	11.87	17.16	3.21	29.37	42.27	25.57
Dipodidae	MSB	67484	*Pygeretmus pumilio*	11.63	16.99	3.07	29.22	41.13	26.12
Dipodidae	UMMZ	123526	*Pygeretmus pumilio*	11.44	15.89	2.73	23.41	35.54	24.18
Dipodidae	UMMZ	123525	*Pygeretmus pumilio*	10.35	15.29	2.66	20.57	34.35	24.86
Dipodidae	UMMZ	118718	*Salpingotulus michaelis*	5.68	8.69	1.22	9.55	15.96	8.9
Dipodidae	UMMZ	118720	*Salpingotulus michaelis*	4.63	8.76	1.66	9.32	15.43	8.45
Dipodidae	UMMZ	118717	*Salpingotulus michaelis*	4.88	9.27	1.43	9.95	15.84	8.67
Dipodidae	UMMZ	118719	*Salpingotulus michaelis*	4.79	8.76	1.37	9.45	15.82	8.18
Dipodidae	AMNH	244431	*Salpingotulus thomasi*	5	9.1	1.8	10.3	15.1	8.2
Dipodidae	AMNH	244432	*Salpingotulus thomasi*	4.8	8.4	1.7	9.6	15	8.6
Dipodidae	AMNH	M-244429	*Salpingotulus thomasi*	4.4	7.5	1.5	8.4	14.2	7.9
Dipodidae	AMNH	M-206585	*Sicista betulina*	9	11.4	3.4	11.5	14.9	6.8
Dipodidae	UMMZ	122857	*Sicista betulina*	8.39	11.34	2.73	11.21	15.23	6.61
Dipodidae	MSB	216102	*Stylodipus andrewsi*	12.26	18.65	3.15	31.63	41.63	27.17
Dipodidae	MSB	227215	*Stylodipus andrewsi*	12.38	18.73	3.14	31.28	41.29	27.2
Dipodidae	MSB	67492	*Stylodipus telum*	11.94	17.61	3.3	30.15	40.99	25.79
Dipodidae	AMNH	74849	*Napaeozapus insignis*	12.6	15	4.5	18	23.5	14
Dipodidae	MCZ	64327	*Napaeozapus insignis*	12.7	14.9	4.1	18.8	23.8	13.7
Dipodidae	MCZ	64328	*Napaeozapus insignis*	12.8	15	4.1	18.7	23.7	13.5
Dipodidae	MCZ	64329	*Napaeozapus insignis*	12.3	14.8	4.1	18.4	23.5	13.1
Dipodidae	AMNH	5403	*Zapus hudsonius*	10.8	12.5	4	15.3	20.4	12
Dipodidae	MCZ	64342	*Zapus hudsonius*	11.4	13.3	3.8	17.5	22.3	13.4
Dipodidae	MCZ	66114	*Zapus hudsonius*	11.4	13.5	4	17.2	22.1	13.4
Dipodidae	MCZ	66116	*Zapus hudsonius*	11.3	13.4	3.9	17.6	22.6	13.5

(continued)

Family	Museum	Number	Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsus
Dipodidae	UMMZ	67805	*Zapus princeps*	10.75	13.72	4.1	16.49	22.36	12.98
Dipodidae	UMMZ	67802	*Zapus princeps*	11.57	15.41	3.87	17.32	23.16	12.65
Dipodidae	UMMZ	67807	*Zapus princeps*	11.92	15.46	3.71	17.7	23.26	13.41
Dipodidae	UMMZ	67806	*Zapus princeps*	10.95	13.85	3.92	16.11	22.28	13.02
Geomyidae	UMMZ	158358	*Geomys bursarius*	25.09	34.27	8.66	27.22	28.8	10.71
Geomyidae	UMMZ	54826	*Thomomys talpoides*	20.24	26.39	5.95	22.3	23.88	8.82
Heteromyidae	UMMZ	80771	*Chaetodipus arenarius*	10.65	13.37	2.27	14.22	17.44	7.85
Heteromyidae	UMMZ	80773	*Chaetodipus arenarius*	9.28	12.72	2.51	12.27	17.26	8.48
Heteromyidae	UMMZ	80776	*Chaetodipus arenarius*	9.39	12.24	12.54	13.06	16.77	8.35
Heteromyidae	UMMZ	76772	*Chaetodipus hispidus*	13.11	16.26	3.4	17.07	19.7	8.97
Heteromyidae	UMMZ	117537	*Dipodomys deserti*	16.56	25.08	3.83	30.61	46.09	19.42
Heteromyidae	UMMZ	117542	*Dipodomys deserti*	15.46	24.99	3.56	28.8	43.61	18.88
Heteromyidae	UMMZ	123560	*Dipodomys merriami*	14.37	21.94	3.62	25.63	35.71	15.44
Heteromyidae	UMMZ	123561	*Dipodomys merriami*	14.09	20.87	2.93	25.53	36.15	15.32
Heteromyidae	UMMZ	123562	*Dipodomys merriami*	12.11	20.05	2.76	23.97	33.74	16.41
Heteromyidae	UMMZ	95684	*Heteromys gaumeri*	15.8	19.52	4.98	21.64	24.94	13.41
Heteromyidae	UMMZ	94055	*Liomys irroratus*	15.47	18.07	4	21.41	24.34	12.6
Heteromyidae	UMMZ	89399	*Liomys irroratus*	14.08	17.57	3.88	19.13	21.83	10.43
Heteromyidae	UMMZ	158361	*Perognathus flavescens*	9.38	11.75	2.18	10.97	13.68	6.91
Heteromyidae	UMMZ	158362	*Perognathus flavescens*	9.87	12.65	2.48	11.53	14.51	6.62
Heteromyidae	UMMZ	76590	*Perognathus flavescens*	9.06	11.39	2.61	10.91	13.19	6.07
Muridae	MCZ	60929	*Acomys russatus*	14.18	15.62	3.46	17.17	20.23	6.76
Muridae	MCZ	61039	*Acomys russatus*	13.74	17.34	5.08	19.62	23.35	7.67
Muridae	MCZ	61721	*Acomys russatus*	15.41	17.11	3.06	20.08	23.9	7.86
Muridae	UMMZ	113425	*Aethomys chrysophilus*	19.18	22.7	4.94	24.59	29.91	12.54
Muridae	UMMZ	113426	*Aethomys chrysophilus*	16.53	21.33	4.82	21.19	26.71	11.22
Muridae	UMMZ	101173	*Apodemus ponticus*	15.55	17.56	3.89	19.86	23.32	9.99
Muridae	UMMZ	103286	*Apodemus ponticus*	15.15	17.62	3.96	19.69	23.7	11.17
Muridae	UMMZ	160314	*Apomys microdon*	14.79	19.95	4.3	21.11	30.63	12.25
Muridae	UMMZ	160315	*Apomys microdon*	15.49	19.3	4.9	21.59	29.6	13.02
Muridae	UMMZ	160318	*Apomys microdon*	14.06	18.1	4.57	19.29	28.89	13.41
Muridae	USNM	584421	*Bandicota bengalensis*	27.32	28.86	7.58	31.85	34.38	13.29
Muridae	USNM	584422	*Bandicota bengalensis*	25.72	29.3	7.29	29.4	33.49	13.01
Muridae	USNM	584423	*Bandicota bengalensis*	28.84	33.93	7.55	33.62	36.37	13.29
Muridae	USNM	255354	*Berylmys bowersi*	32.97	41.31	10.62	45.67	54.36	21.79
Muridae	USNM	458792	*Bullimus bagobus*	29.27	43.34	10.24	37.61	46.5	18.45
Muridae	UMMZ	118680	*Dipodillus dasyurus*	12.82	16.5	3.09	16.76	24.26	10.81
Muridae	UMMZ	118681	*Dipodillus dasyurus*	12.9	18.11	3.17	16.63	24.07	11.19
Muridae	UMMZ	122596	*Dipodillus dasyurus*	12.74	17.92	3.4	17.5	23.6	10
Muridae	UMMZ	122576	*Gerbillurus paeba*	12.5	17.73	2.82	18.1	25.73	10.65
Muridae	UMMZ	122579	*Gerbillurus paeba*	11.23	15.47	3.1	15.15	21.37	10.87
Muridae	UMMZ	122578	*Gerbillurus paeba*	11.23	15	3.15	14.87	21.74	10.17
Muridae	UMMZ	117676	*Gerbillus aquilus*	12.14	16.92	2.96	18.94	26.39	11.14
Muridae	UMMZ	118641	*Gerbillus aquilus*	12.96	17.85	3.4	19.41	26.58	11.19
Muridae	UMMZ	117657	*Gerbillus gerbillus*	10.91	15.39	3.16	15.09	23.86	10.7
Muridae	UMMZ	117656	*Gerbillus gerbillus*	11.09	15.9	3.35	16.32	24.79	10.81
Muridae	UMMZ	117653	*Gerbillus gerbillus*	11.37	17.08	3.03	17.11	25.76	11.61
Muridae	UMMZ	117654	*Gerbillus gerbillus*	10.69	15.06	3.17	15.09	23.4	10.39
Muridae	UMMZ	117655	*Gerbillus gerbillus*	10.94	16.05	3.35	15.45	24.97	11.05
Muridae	UMMZ	117651	*Gerbillus gerbillus*	10.64	16.7	3	15.24	24.18	12.1
Muridae	USNM	221203	*Hydromys chrysogaster*	30.09	36.35	10.8	41.1	52.8	24.73

(continued)

Family	Museum	Number	Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsus
Muridae	USNM	15315	*Hydromys chrysogaster*	32.1	38.52	10.34	42.83	58.89	23.96
Muridae	USNM	237715	*Hydromys chrysogaster*	33.05	39.55	10.98	45.4	55.07	24.55
Muridae	MCZ	62942	*Mastomys natalensis*	12.99	17.37	4.23	17.88	22.17	9.07
Muridae	MCZ	62943	*Mastomys natalensis*	12.43	16.64	3.49	16.56	21.34	9.03
Muridae	UMMZ	113443	*Mastomys natalensis*	14.77	19.1	8.69	11.74	15.26	2.98
Muridae	UMMZ	113445	*Mastomys natalensis*	12.95	16.74	3.57	16.88	21.16	8.53
Muridae	USNM	237787	*Melomys burtoni*	16.39	19.7	5.15	21.37	25.87	9.94
Muridae	USNM	284427	*Melomys burtoni*	17.13	19.68	5.77	21.04	25.84	9.83
Muridae	UMMZ	119154	*Meriones meridianus*	14.25	19.48	3.04	19.75	27.72	11.82
Muridae	UMMZ	118737	*Meriones meridianus*	14.53	21.18	3.73	21.93	30	12.91
Muridae	UMMZ	118738	*Meriones meridianus*	12.37	17.44	3.13	17.4	24.87	11.09
Muridae	UMMZ	118744	*Meriones meridianus*	11.93	17.6	3.32	16.78	22.35	10.77
Muridae	USNM	284349	*Mesembriomys gouldii*	43.87	50.91	12.99	52.91	66.44	24.24
Muridae	UMMZ	165051	*Micromys minutus*	9.21	11.01	2.07	11.37	14.29	5.26
Muridae	UMMZ	165052	*Micromys minutus*	9.31	11.17	2.09	11.86	14.82	6.51
Muridae	MCZ	62121	*Mus musculus*	11.5	13.3	3.4	15.2	17.3	7.5
Muridae	MSB	4584	*Mus musculus*	11.28	13.39	3.13	14.64	16.98	7.18
Muridae	MSB	6667	*Mus musculus*	10.11	12.56	3.18	13.2	15.81	7
Muridae	MSB	6668	*Mus musculus*	11.62	13.74	3.15	15.52	17.82	8.6
Muridae	UMMZ	121216	*Nesokia indica*	23.33	27.69	7.28	26.39	29.7	11.99
Muridae	UMMZ	167680	*Nesokia indica*	24.88	27.69	6.8	28.29	31.01	12.05
Muridae	WAM	24494	*Notomys alexis*	13.12	19.04	3.09	22.2	33.98	16.85
Muridae	WAM	25624	*Notomys alexis*	12.65	17.9	3.06	20.81	31.8	16.09
Muridae	UMMZ	118567	*Pachyuromys duprasi*	14.16	21.17	3.39	17.96	23.97	9.64
Muridae	UMMZ	178556	*Pachyuromys duprasi*	14.54	22.46	3.34	18.81	24.76	9.2
Muridae	UMMZ	118655	*Pachyuromys duprasi*	14.84	22.64	3.72	18.93	25.17	9.18
Muridae	UMMZ	178554	*Pachyuromys duprasi*	14.59	22.25	3.65	18.78	24.86	9
Muridae	UMMZ	118656	*Pachyuromys duprasi*	15.28	22.14	3.34	19.71	24.62	8.64
Muridae	USNM	573154	*Phloeomys cumingi*	40.05	38.86	10.23	42.44	45.94	13.34
Muridae	USNM	573509	*Phloeomys cumingi*	33.53	32.7	8.95	35.91	37.59	11.86
Muridae	UMMZ	177846	*Phloeomys pallidus*	63.83	70.57	17.12	67.46	70.96	23.17
Muridae	UMMZ	118708	*Psammomys obesus*	22.05	28.31	5.17	28.44	32.98	13.14
Muridae	UMMZ	118688	*Psammomys obesus*	21.74	26.11	5.05	27.84	31.3	13.01
Muridae	UMMZ	118684	*Psammomys obesus*	21.41	27.64	5.41	26.7	32.15	12.75
Muridae	UMMZ	118687	*Psammomys obesus*	19.89	24.94	4.46	25.43	30.7	12.48
Muridae	USNM	238500	*Pseudomys gracilicaudatus*	12.96	16.9	3.85	18.11	22.25	9.63
Muridae	USNM	238501	*Pseudomys higginsi*	16.74	20.81	5.7	20.62	30.78	14.31
Muridae	USNM	238509	*Pseudomys higginsi*	17.63	24.06	5.47	23.15	33.47	13.93
Muridae	CFS	3740	*Rattus exulans*	22.48	26.99	6.14	30.79	33.8	11.81
Muridae	CFS	3742	*Rattus exulans*	16.59	19.86	4.91	22.74	27.14	9.57
Muridae	CFS	3744	*Rattus exulans*	15.58	19.57	4.62	22.17	26.33	10.25
Muridae	CFS	3746	*Rattus exulans*	16.92	20.76	4.56	22.04	28.34	11.68
Muridae	MCZ	61403	*Rattus norvegicus*	32.2	35.6	8.4	42.7	45.7	16.3
Muridae	MCZ	62277	*Rattus norvegicus*	23.36	26.59	6.52	28.15	32.36	12.33
Muridae	MCZ	62285	*Rattus norvegicus*	24.77	28.84	6.37	28.68	34.11	12.23
Muridae	MCZ	62278	*Rattus norvegicus*	24.55	26.41	6.44	29.93	35.52	11.37
Muridae	MCZ	62279	*Rattus norvegicus*	20.01	21.21	4.49	22.65	26.78	12.11
Muridae	MSB	89172	*Rattus norvegicus*	33.75	36.96	8.07	44.04	48.05	15.65
Muridae	MSB	92698	*Rattus norvegicus*	30.23	33.39	7.14	39.29	40.94	14.99
Muridae	MCZ	62631	*Rattus rattus*	25.2	27	6.7	33.1	36.9	12.8
Muridae	MSB	56007	*Rattus rattus*	25.3	27.09	6.44	33.15	36.48	12.98

(continued)

Family	Museum	Number	Species	Humerus	Ulna	Metacarpal	Femur	Tibia	Metatarsus
Muridae	MSB	57181	*Rattus rattus*	23.51	29.16	6.62	35.86	38.29	13.75
Muridae	MCZ	57863	*Rhabdomys pumilio*	14.52	17.44	3.51	18	21.01	8.2
Muridae	MCZ	57864	*Rhabdomys pumilio*	14.49	17.87	3.69	18.33	21.82	8.41
Muridae	MCZ	62949	*Saccostomus campestris*	20.27	23.62	4.41	24.99	25.53	8.66
Muridae	UMMZ	118597	*Sekeetamys calurus*	16.68	21.87	3.34	21.42	28.62	12.33
Muridae	UMMZ	118601	*Sekeetamys calurus*	15.12	22.03	3.49	21.33	30.62	13.32
Muridae	UMMZ	122801	*Sekeetamys calurus*	16.61	24.3	3.92	23.17	33.83	13.25
Muridae	UMMZ	118600	*Sekeetamys calurus*	15.77	21.82	3.91	22.05	30.98	13.12
Muridae	UMMZ	119010	*Tatera indica*	16.89	23.04	3.93	24.28	33.08	16.28
Muridae	UMMZ	119013	*Tatera indica*	18.49	24.78	4.04	27.74	36.43	16.06
Muridae	UMMZ	119009	*Tatera indica*	17.17	22.76	3.87	25.97	35.22	15.47
Muridae	UMMZ	119012	*Tatera indica*	18.31	25.2	4.1	27.83	35.31	16.3
Muridae	UMMZ	119011	*Tatera indica*	15.13	20.91	3.83	23.06	29.9	14.69
Muridae	UMMZ	113433	*Thallomys nigricauda*	18.25	21.5	4.61	22.93	26.73	10
Muridae	USNM	284338	*Zyzomys argurus*	14.35	17.11	3.44	19.82	23.74	8.95
Muridae	USNM	284349	*Zyzomys argurus*	13.93	15.46	3.81	18.08	22.64	9.13
Nesomyidae	UMMZ	121019	*Beamys hindei*	22	28.15	5.74	26.15	28.3	8.08
Nesomyidae	MCZ	28642	*Brachytarsomys albicauda*	24.47	29.98	6.77	30.26	34.02	10.84
Nesomyidae	MCZ	28641	*Brachytarsomys albicauda*	24.88	31.28	6.18	29.2	35.81	11.03
Nesomyidae	MCZ	46261	*Brachyuromys betsileoensis*	19.7	24.79	5.39	25.08	29.22	11.83
Nesomyidae	UMMZ	113469	*Dendromus mesomelas*	7.82	12.27	1.86	9.43	15.05	6.57
Pedetidae	UMMZ	157202	*Pedetes capensis*	48.31	57.65	8.06	89.56	127.43	48.69
Spalacidae	MCZ	3617	*Cannomys badius*	24.63	28.16	8.59	24.77	24.45	7.17
Spalacidae	MCZ	35935	*Rhizomys pruinosus*	42	47.33	12.44	46.2	44.19	14.88
Spalacidae	MCZ	61642	*Spalax ehrenbergi*	20.68	27.95	5.36	22.03	22.56	6.75

Table D.2: *Diet information and sources for taxa included in Chapter 5, sorted by family. Reference codes: 1 is Nowak and Wilson (1999), 2 is Shenbrot et al. (2008), 3 is Balete et al. (2012), 4 is (Parr et al.), 5 is Pizzimenti (1980), 6 is Miljutin and Lehtonen (2008), 7 is Sokolov et al. (1996), 8 is Robovsky et al. (2008), 9 is Pinotti et al. (2011), 10 is Myers et al. (2016), 11 is Perrin et al. (1992), 12 is Patton (2015), 13 is Sahley et al. (2015). Blank "Total" values indicate no diet data available in the literature, and these values were predicted from the threshold model.*

Family	Species	Ref	Green	Root	Bark	Nut	Seed Grain	Flower	Fruit	Moss	Lichen	Fungus	Arth	Worm	Shell	Crust	Egg	Vert	Total
Anomaluridae	*Anomalurus derbianus*	1	x		x	x		x	x				x						Six
Calomyscidae	*Calomyscus bailwardi*	4	x			x	x	x											Four
Castoridae	*Castor canadensis*	1	x	x	x														Three
Castoridae	*Castor fiber*	1	x	x	x														Three
Dipodidae	*Allactaga balikunica*	1	x	x			x												Three
Dipodidae	*Allactaga bullata*	1	x	x			x												Three
Dipodidae	*Allactaga elater*	2	x				x												Two
Dipodidae	*Allactaga major*	1	x	x			x												Three
Dipodidae	*Allactaga sibirica*	2	x	x			x		x				x						Five
Dipodidae	*Allactaga tetradactyla*	1	x	x			x												Three
Dipodidae	*Allactodipus bobrinskii*	2	x				x						x						Three
Dipodidae	*Cardiocranius paradoxus*	2	x				x	x											Three
Dipodidae	*Dipus sagitta*	2	x	x			x		x										Four
Dipodidae	*Euchoreutes naso*	7											x						One
Dipodidae	*Jaculus blanfordi*	2	x	x			x												Three
Dipodidae	*Jaculus jaculus*	1	x	x			x												Three
Dipodidae	*Jaculus orientalis*	1	x	x			x												Three
Dipodidae	*Napaeozapus insignis*	1	x			x	x		x			x	x						Six
Dipodidae	*Pygeretmus pumilio*	2	x				x												Two
Dipodidae	*Salpingotulus michaelis*	1	x				x												Two
Dipodidae	*Sicista betulina*	2	x				x		x				x	x					Five
Dipodidae	*Stylodipus andrewsi*	1		x			x				x								Three
Dipodidae	*Stylodipus telum*	2	x	x			x												Three
Dipodidae	*Zapus hudsonius*	1				x	x		x			x	x						Five
Geomyidae	*Geomys bursarius*	1		x															One
Geomyidae	*Thomomys talpoides*	1	x	x															Two
Heteromyidae	*Chaetodipus arenarius*	1	x				x						x						Three
Heteromyidae	*Chaetodipus hispidus*	1	x				x						x						Three
Heteromyidae	*Dipodomys deserti*	1	x				x	x	x				x						Five
Heteromyidae	*Dipodomys merriami*	1	x				x	x	x				x						Five
Heteromyidae	*Heteromys gaumeri*	1	x				x												Two
Heteromyidae	*Liomys irroratus*	1	x				x												Two
Heteromyidae	*Perognathus flavescens*	1	x				x						x						Three
Nesomyidae	*Beamys hindei*	1					x		x										Two
Nesomyidae	*Brachytarsomys albicauda*	1							x										One
Nesomyidae	*Brachyuromys betsileoensis*	6																	
Nesomyidae	*Dendromus mesomelas*	1					x		x				x				x	x	Five
Nesomyidae	*Saccostomus campestris*	1				x	x		x				x						Four
Pedetidae	*Pedetes capensis*	1	x	x			x						x						four
Spalacidae	*Cannomys badius*	1	x	x			x												Three
Spalacidae	*Rhizomys pruinosus*	1	x	x			x		x										Four
Spalacidae	*Spalax ehrenbergi*	1		x			x						x						Three

(Continued)

Family	Species	Ref	Green	Root	Bark	Nut	Seed Grain	Flower	Fruit	Moss	Lichen	Fungus	Arth	Worm	Shell	Crust	Egg	Vert	Total
Cricetidae	*Abrothrix olivaceus*	1					x		x			x	x						Four
Cricetidae	*Akodon aerosus*	1	x									x	x	x					Four
Cricetidae	*Arvicola sapidus*	4	x	x				x	x										Four
Cricetidae	*Auliscomys pictus*	5	x										x						Two
Cricetidae	*Baiomys musculus*	1	x				x						x						Three
Cricetidae	*Calomys callosus*	5											x						One
Cricetidae	*Cricetus cricetus*	1	x	x			x							x					Four
Cricetidae	*Dicrostonyx hudsonius*	1	x		x			x	x										Four
Cricetidae	*Ellobius fuscocapillus*	4		x															One
Cricetidae	*Graomys domorum*	1	x				x		x										Three
Cricetidae	*Holochilus brasiliensis*	1	x												x				Two
Cricetidae	*Lasiopodomys brandtii*	4	x	x															Two
Cricetidae	*Lemmus trimucronatus*	4	x	x	x				x	x	x								Six
Cricetidae	*Megadontomys thomasi*	1							x										One
Cricetidae	*Melanomys caliginosus*	1							x										One
Cricetidae	*Mesocricetus auratus*	1	x				x		x									x	Four
Cricetidae	*Mesocricetus brandti*	4				x	x						x						Three
Cricetidae	*Microtus arvalis*	4	x	x		x	x												Four
Cricetidae	*Microtus mexicanus*	4	x	x		x	x												Four
Cricetidae	*Microtus pennsylvanicus*	4	x	x		x	x												Four
Cricetidae	*Microtus pinetorum*	4	x	x		x	x		x				x						Six
Cricetidae	*Myodes gapperi*	4	x	x	x	x	x		x		x	x	x						Nine
Cricetidae	*Neacomys spinosus*	4					x		x				x						Three
Cricetidae	*Necromys lenguarum*	10				x	x						x						Three
Cricetidae	*Nectomys squamipes*	1	x										x					x	Three
Cricetidae	*Neodon juldaschi*	8	x							x									Two
Cricetidae	*Neotoma albigula*	1	x	x										x					Three
Cricetidae	*Neotomodon alstoni*	4	x			x	x		x				x						Five
Cricetidae	*Neusticomys monticolus*	4											x						One
Cricetidae	*Oecomys bicolor*	12					x		x				x						Three
Cricetidae	*Oligoryzomys chacoensis*	1	x				x		x			x	x						Five
Cricetidae	*Oligoryzomys fulvescens*	1	x				x		x			x	x						Five
Cricetidae	*Ondatra zibethicus*	4	x												x	x		x	Four
Cricetidae	*Onychomys leucogaster*	1											x					x	Two
Cricetidae	*Oryzomys couesi*	1	x				x		x				x			x		x	Six
Cricetidae	*Osgoodomys banderanus*	1					x		x				x						Three
Cricetidae	*Ototylomys phyllotis*	1	x						x										Two
Cricetidae	*Oxymycterus delator*	1	x										x	x					Three
Cricetidae	*Peromyscus leucopus*	1				x	x		x				x	x				x	Six
Cricetidae	*Peromyscus polionotus*	1				x	x		x				x	x				x	Six
Cricetidae	*Phodopus sungorus*	1	x				x												Two
Cricetidae	*Phyllotis darwini*	5	x				x						x						Three
Cricetidae	*Podomys floridanus*	4				x	x					x	x	x					Five
Cricetidae	*Reithrodontomys gracilis*	4					x						x						Two
Cricetidae	*Rheomys raptor*	4											x	x					Two
Cricetidae	*Scapteromys tumidus*	1	x										x	x					Three
Cricetidae	*Scotinomys teguina*	4							x				x						Two
Cricetidae	*Sigmodon hispidus*	1	x										x			x	x		Four
Cricetidae	*Synaptomys cooperi*	4	x	x	x				x	x		x		x	x				Eight
Cricetidae	*Thaptomys nigrita*	9	x																One
Cricetidae	*Thomasomys daphne*	13	x				x					x	x						Four
Cricetidae	*Tylomys nudicaudus*	4			x						x								Two

(Continued)

Family	Species	Ref	Green	Root	Bark	Nut	Seed Grain	Flower	Fruit	Moss	Lichen	Fungus	Arth	Worm	Shell	Crust	Egg	Vert	Total
Muridae	*Acomys russatus*	1	x				x											x	Three
Muridae	*Aethomys chrysophilus*	1		x		x	x		x										Four
Muridae	*Apodemus ponticus*	1		x		x	x		x				x						Five
Muridae	*Apomys microdon*	3					x		x					x					Three
Muridae	*Bandicota bengalensis*	1				x	x												Two
Muridae	*Berylmys bowersi*	1	x				x						x	x					Four
Muridae	*Dipodillus dasyurus*	4	x				x						x						Three
Muridae	*Gerbillurus paeba*	11	x				x						x						Three
Muridae	*Gerbillus aquilus*	1	x	x		x	x						x						Five
Muridae	*Gerbillus gerbillus*	1	x	x		x	x						x						Five
Muridae	*Hydromys chrysogaster*	1													x	x		x	Three
Muridae	*Hyperacrius wynnei*	1	x	x															Two
Muridae	*Mastomys natalensis*	1	x				x						x						Three
Muridae	*Melomys burtoni*	1	x						x										Two
Muridae	*Meriones meridianus*	1	x	x			x		x				x						Five
Muridae	*Mesembriomys gouldii*	1				x	x						x						Three
Muridae	*Micromys minutus*	1	x				x						x				x		Four
Muridae	*Mus musculus*	1	x	x			x						x						Four
Muridae	*Nesokia indica*	1	x	x			x		x										Four
Muridae	*Notomys alexis*	1	x				x		x										Three
Muridae	*Pachyuromys duprasi*	1	x			x	x						x	x					Five
Muridae	*Phloeomys cumingi*	4	x	x	x	x	x		x										Six
Muridae	*Phloeomys pallidus*	4	x	x	x	x	x		x										Six
Muridae	*Psammomys obesus*	1	x			x	x						x	x					Five
Muridae	*Pseudomys gracilicaudatus*	1	x	x			x						x						Four
Muridae	*Pseudomys higginsi*	1	x	x			x						x						Four
Muridae	*Rattus exulans*	1	x			x	x		x				x	x					Six
Muridae	*Rattus norvegicus*	1	x			x	x		x				x	x			x	x	Eight
Muridae	*Rattus rattus*	1	x			x	x		x				x	x			x	x	Eight
Muridae	*Rhabdomys pumilio*	1		x			x		x				x		x		x		Six
Muridae	*Sekeetamys calurus*	4	x			x	x		x				x	x					Six
Muridae	*Tatera indica*	1	x	x			x						x				x	x	Six
Muridae	*Thallomys nigricauda*	1	x	x			x	x	x				x						Six
Muridae	*Zyzomys argurus*	1					x		x				x						Three