Scaling Patterns and Ecological Correlates of Postcranial Skeletal Robusticity in *Canis* and *Ursus*: Implications for Human Evolution

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

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Abstract

There has been a trend toward decreasing skeletal robusticity in the genus *Homo* throughout the Pleistocene, culminating in the gracile postcrania of living modern humans. This change is typically attributed to changing tool technologies and subsistence patterns among human groups. However, other mammalian groups also experience a similar change in their postcranial strength over the same time period. It is proposed in this dissertation that ecological variables are correlated with measures of postcranial strength and may be a better explanation for Holocene skeletal gracilization in humans, as well as in other mammalian genera. This hypothesis is investigated through a close examination of the scaling patterns in two extant genera, *Canis* and *Ursus*, and a comparison of scaling patterns and relative strength of different species of *Canis*, including a fossil species that provides information about temporal change. Measurements of limb length, joint surface area, bone diameter, and strength measurements derived from radiographic images of long bone midshafts of North American specimens of *Canis*, (including the fossil *Canis dirus*) and *Ursus* were collected. Scaling patterns of the cross-sectional variables on limb length and joint surfaces were analyzed for the interspecific and intraspecific samples.

The first hypothesis tested was that *Canis* scales with geometric similarity of cross-sectional variables on bone length and body mass, and the *Ursus* scales with elastic

similarity. Larger *Canis* have relatively stronger postcrania than smaller *Canis*. The primary way in which this strength is achieved in larger individuals is through a relatively shortening of the bone length. The second hypothesis tested was that postcranial strength is correlated with ecological variables. To investigate this hypothesis, scaling patterns of different species of *Canis* were compared, including the fossil dire wolf. The results show that the dire wolf is relatively stronger than its living congenerics. There is also a strong relationship between the ratio of prey body mass to predator body mass and relative strength for these species. Carnivores that are hunting animals much larger than themselves must have postcranial skeletons that are strong enough to withstand the loading of the skeleton that occurs during hunting, taking down, and processing large herbivores.

Dedication

For Carolyn, who is a very old soul.

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1. Introduction

One of the most recognizable evolutionary trends associated with recent modern humans is the decrease in postcranial skeletal robusticity of the skeleton relative to Pleistocene members of the genus *Homo* (Boule, 1911-13; Weidenreich, 1941; Endo and Kimura, 1970; Day, 1971; Trinkaus 1976, 1984; Lovejoy and Trinkaus, 1980; Kennedy, 1983; Ben-Itzhak et al., 1988; Trinkaus and Ruff, 1989; Ruff et al., 1993). Holocene postcranial skeletal gracilization is an evolutionary trend that demands an explanation in order to better understand the ecological conditions that shaped our evolution, as well as to understand the adaptive and phylogenetic relationships among all the different hominin groups that existed during the Pleistocene. There is a tendency among paleoanthropologists to identify human traits as unique and propose and accept unique explanations for these traits, i.e., explanations that cannot be applied to any other species (Cartmill, 1990). In trying to explain the decrease in skeletal robusticity seen in hominins, many researchers have proposed some version of the "technology hypothesis of skeletal gracilization". This hypothesis states that increasing tool complexity lessened somatic energy expenditure because the tools were doing the work previously done by muscles, which reduced the mechanical loading on the skeleton, and was therefore the driving force behind gracilization (Bridges, 1989, 1991; Ruff and Larsen, 1990; Ruff et al., 1991; Ruff et al., 1993; Trinkaus et al., 1994).

The aim of this project is to interpret gracilization of the postcranial skeleton in modern humans in the broader context of mammalian adaptation and evolution through an evaluation of a new "ecological hypothesis of skeletal gracilization". This hypothesis posits that ecological factors, such as environmental productivity and how this productivity affects resource availability and procurement, will correlate with postcranial measures of bone strength in mammals. I will study scaling patterns within two non-primate mammalian genera (*Canis* and *Ursus*) and an evaluation of how ecological variables correlate with bone strength and robusticity. Mechanically relevant variables include diaphyseal length, the area of the femoral head, the midshaft diameter, the second moment of area, and the polar moment of inertia. The area of the femoral head is used to estimate body size. The other variables are used to estimate relative bone strength and skeletal robusticity. The two genera to be examined, *Canis* and *Ursus*, offer a look at two closely related groups that differ significantly in such factors as their body mass, resource procurement strategies, geographical distribution, and locomotion. Because of these differences, these taxa allow study of a range of factors that contribute to postcranial skeletal strength.

An appropriate definition of skeletal robusticity is fundamental to interpreting variation in this feature within and between species. Skeletal robusticity is a term that has been used to describe a number of different morphologic features and can be quantified in several ways. For example, we distinguish australopithecines as either "gracile" or "robust" on the basis of craniodental features (Dart, 1925; Broom, 1938, Broom and Robinson, 1949, 1950; Robinson, 1954, 1961; Grine, 1987). Similarly, if one were to say "Neandertals were robust" to a group of anthropologists some would think of prominent cranial features such as brow ridges, a sagittal crest, occipital bun, or extreme cranial thickness. Others would think of long bone shaft thickness, muscle scar markings, long bone cross-sectional dimensions or joint size and morphology (Schwalbe, 1901; Boule, 1911-13; Howell, 1951; Endo and Kimura, 1970; Ruff et al., 1993). The term "robust" is not a precise term, which can lead to a great deal of confusion when discussing the implications and probable causes of skeletal robusticity.

It is important to use measurements of skeletal strength that are consistent and meaningful in a functional context. Therefore, skeletal robusticity is quantified in this study by variables that describe the cross-sectional dimensions of the femur, humerus and tibia in terms of their ability to resist external loads. These measurements reflect what is known about the functional adaptation of bone to its loading environment. There are many studies that confirm that some relationship exists between mechanical loading and cross-sectional dimensions (Roux, 1881; Kummer, 1972; Lanyon, 1973; Lanyon et al., 1975 Goodship et al., 1979; Lanyon et al., 1979; Carter et al., 1980; Pauwels, 1980; Woo et al., 1981; Lanyon et al., 1982; Martin and Burr, 1982; Currey, 1984; Rubin, 1984; Frost, 1985; Rubin and Lanyon, 1982, 1985; Frost, 1987; Lanyon, 1987; Martin and Burr, 1989; Rubin et al., 1994; Trinkaus et al., 1994; Lieberman et al., 2001). Although studies have shown that it is difficult to assign a direct causal relationship between such specific details of size and shape as anterior-posterior diameter compared to medial-lateral diameter and the loading history of a bone (Judex et al., 1997; Demes et al., 1998; Demes, 2007), overall measures of bone strength that incorporate the shape of a bone's cross-section have been shown to provide good discernment of locomotor groups in several mammalian orders (Demes et al., 1991; Jungers and Burr, 1994).

The use of cross-sectional dimensions as a descriptive characteristic of hominin bone was first employed by Endo and Kimura's (1970) description of the skeleton of the Amud man (*Homo neanderthalensis*, Israel. Cross-sectional dimensions model the bone as a beam and apply engineering principles to determine the strength of the structure (Lovejoy et al., 1976). This technique has been used in numerous studies over the past 30 years (Burr et al., 1981; Larsen, 1981; Kimura and Takahashi, 1982; Ruff and Hayes, 1983; Ruff et al., 1984; Ruff and Runestad, 1992; Ruff et al., 1993; Daegling, 1993; Larsen, 1995; Trinkaus et al., 1999; Ruff et al., 1999; Bridges et al., 2000; Ledger et al., 2000; Lieberman et al., 2004; Pearson and Lieberman, 2004; Stock and Shaw, 2007).

The two categories of cross-sectional variables used in this dissertation are 1) the polar moment of inertia (J), and its component variables, the second moments of areas (I_{ap} and I_{ml}) of the bone in two perpendicular planes at midshaft and 2) the anterior-posterior and medial-lateral diameters of the bones at midshaft. The polar moment of inertia measures the strength of a bone in torsion and is expressed in millimeters to the fourth power. It is the sum of the two perpendicular second moments of area, which measure the strength of the bone in bending. A detailed explanation of these variables is available in Chapter 3. The anterior-posterior and medial-lateral diameters at midshaft are less accurate measures of bone strength, but are commonly used in comparative studies of bone strength and have been shown to correlate well with bending strength

(Stock and Shaw, 2007). Mid-shaft diameter is measured from the external surfaces of the bone. It is used in this study because it allows for a greater sample size due to restrictions imposed by the x-ray machine, and it allows for the inclusion of a fossil species for which x-ray data were not available. These cross-sectional dimensions, when regressed onto limb length, can demonstrate general shape changes that may occur with changes in body mass; when regressed onto body mass, they can provide information about mechanical loading; and when standardized for body mass and compared across groups, they illustrate variation within groups that may be attributed to environmental or ecological factors.

Hominin gracilization is typically explained as the result of increasing technological sophistication that lessened the amount of somatic energy required to procure resources (Brace, 1962, 1979, 1991; Brace et al., 1987; Brose and Wolpoff, 1971; Frayer, 1980, 1984; Ruff et al., 1984; Smith, 1985; Brock and Ruff, 1988; Bridges 1989, 1991; Mellars, 1989; Ruff and Larsen, 1990; Ruff et al., 1991; Ruff et al., 1993; Trinkaus et al., 1994; Churchill et al., 1996). This hypothesis rests on the assumption that reduced somatic energy is associated with reduced loading of the postcranial skeleton. A reduction in loading experienced by bone results in a reduction in the cross-sectional dimensions of bone in two ways. The first is that bone is not stimulated to grow as it would be under a loading regime of high magnitude strains. The second is that disuse can result in the atrophy of a bone's cortical dimensions (Carter, 1984; Frost, 1987). However, the link between technology and robusticity is highly speculative because there is no actual evidence of reduced loading resulting from improved tool technology or changing subsistence patterns in pre-industrial populations. In fact, there are examples of populations becoming *more* robust throughout time as their subsistence strategies changed from hunter-gatherers to agriculturalists (Larsen, 1997; Ruff, 2000a, 1987a and b, Ruff et al., 1994; Ruff and Larsen, 1990; Bridges, 1989), a finding that is at odds with the prevailing gracilization through technology hypothesis.

The explanation of skeletal gracilization related to technology assumes that there are changes in bone strength due to mechanical loading during the lifetime of the individual. However, it is also possible that Holocene gracilization is the result of a release of the selective pressure that had been maintaining robust skeletons in this lineage. For example, strong skeletons in Neandertals may have been selected for by the the possibility of traumatic injury resulting from close range hunting of large herbivores, a risk that is confirmed in the fossil record by the prevalence of healed long bone fractures among Neandertal remains, a pattern mirrored in a modern day group that also has close interactions with large herbivores, rodeo workers (Berger and Trinkaus, 1995). The extinction of large-bodied herbivores at the end of the Pleistocene could have eliminated the selective pressure among *Homo* for more robust skeletons.

There are three substantial flaws with the acceptance of the hypothesis that recent human gracilization, both cranial and postcranial, is a result of technological and subsistence changes that reduced the amount of work necessary for resource procurement. Firstly, this explanation does not fit with all the data on postcranial robusticity that we have about human evolution. The fossil record does not provide evidence for a close association between skeletal robusticity and technological sophistication. Secondly, it does not explain the geographic variation in robusticity seen in modern human populations. And lastly, it sets humans apart from other animals that show variability in skeletal robusticity yet do not utilize tool technology. When humans exhibit anatomical patterns that are consistent with those found in other groups of mammals, it is instructive to look for commonalities among all the groups when seeking an explanation for that trait (Cartmill, 1990).

Patterns of variation in postcranial skeletal robusticity among fossil hominins are complex, as illustrated in Table 1 and Figure 1. This table and figure demonstrate that there is not a linear temporal trajectory of decreasing robusticity within hominins. The overall pattern, despite small deviations, is that Holocene modern humans are less robust than all examples of Pleistocene hominins. Attempts to explain Holocene gracilization as resulting from increased reliance on tool use often ignore the more subtle variation within the Pleistocene that fail to support this hypothesis (Ruff et al., 1993; Churchill et al., 1996). For example, among late Pleistocene modern humans, there is variation in postcranial skeletal robusticity. Grevettian humeral shafts are modestly robust compared with earlier late archaic Europeans and later Late Upper Paleolithic humans (Churchill et al., 1996; Trinkaus, 2005). This mid-Upper Paleolithic population (21-27kya) exhibited a greater amount of dietary diversity than seen previously in the archaeological record (Richards et al., 2001), and experienced a population expansion

(Pettitt, 2000). A higher concentration of people in a given area means that the resources available to each person are reduced, forcing the population to work harder and/or search farther for subsistence. Again, this demonstrates that bone strength did not follow a simple temporal trajectory based on technology. Tool kits were changing and advancing through the late Pleistocene in Europe (Straus, 1993) and the variation in upper limb bone strength does not reflect these changes.

Table 1: Comparisons of femoral strength of hominin fossils. 'J femur' gives the raw value of J, expressed in mm4; 'J femur stand.' = 'J femur'/((femur length ^ 5.33) * 10^12)) for modern humans and = J femur/(1.28*(femur length^5.33) * 10^12)) for Neandertals

Species	Specimen	age	J femur (mm^4)	J femur standard. (no units)	SE, range	body mass (kg)	femur length (mm)	Citation
P. robustus	SK 82	1.6-1.8ma	52,899				310	1, 2, 3
P. robustus	SK 97	1.6-1.8ma	55,007					2, 3
H. habilis	OH 62	1.8ma	10,995				~280	4, 5
H. erectus	KNM-ER 736	1.7ma	116,628	480.1		62	500	6, 7
H. neanderthalensis	St. Cesaire 1	200-35kya	86,575	890.5		59.7-79.9	386-416	6, 9
H. sp and H. erectus	Average			816.3	25.9, 750-919			8
H. neanderthalensis	Tabun C1	200-35kya	39,168					10
H. neanderthalensis	Shanidar 4	200-35kya	89,258	894.2			404	11
***H.* sp**	Berg Aukas	130kya	103,085	590.1		93	470	6, 12
H. neanderthalensis	Ehringsdorf 5		102,449					13
	Qafzeh 8	100kya	102,428	670.6			458.3	13
H. neanderthalensis	Amud 1	45kya	90,471	464.4			458	13
H. neanderthalensis	Shanidar 5	70kya	99,703	725.3			429	13
H. neanderthalensis	Shanidar 6	70kya	45,134	765.5			366	13
H. neanderthalensis	Tabun1	120kya	39,168	467.1			391	13
H. sapiens	Qafzeh 3	100kya	51,842	786.0			391.5	13
H. sapiens	Qafzeh 9	100kya	94,614	751.4			442	13
H. sapiens	Skhul 4	90kya	52,731/56672	321.4			464.5	13

H. sapiens	Skhul 5	90kya	80,874/91,363	427.9			477	13
H. sapiens	Skhul 6	90kya	58,923	438.1			447.5	13
H. sapiens	Skhul 7	90kya	41,505	381.7			430	13
H. neanderthalensis	Tabun 3	120kya	23,971					13
H. sapiens	Ave. (n = 5)	200-35kya		570.9	48.7, 400-829			8
H. sapiens	Average	35-15kya		549	83.8, 315-797			8
H. sapiens	Iceman	5200bp	37,219	435.5		61	411	14
H. sapiens	N = 63	recent		457.4	5.8, 243-848			8
H. sapiens	Australian Aborigines male (n = 19)			302.4	90.5			15
H. sapiens	Australian Aborigines female (n = 8)			259.5	70.1			15

References for Table 1: 1. Lovejoy and Heiple, 1970; 2. Vrba, 1985; 3. Ruff et al., 1995; 4. Johanson et al., 1987; 5. Ruff, 2009; 6. Trinkaus et al., 1999; 7. Anton, 2003; 8. Ruff et al., 1993; 9. Vandermeersch, 1984; 10 McCown and Keith, 1939; 11. Trinkaus, 1983; 12. Grine et al., 1995; 13. Trinkaus and Ruff, ; 14. Ruff et al., 2006; 15. Carlson et al.,

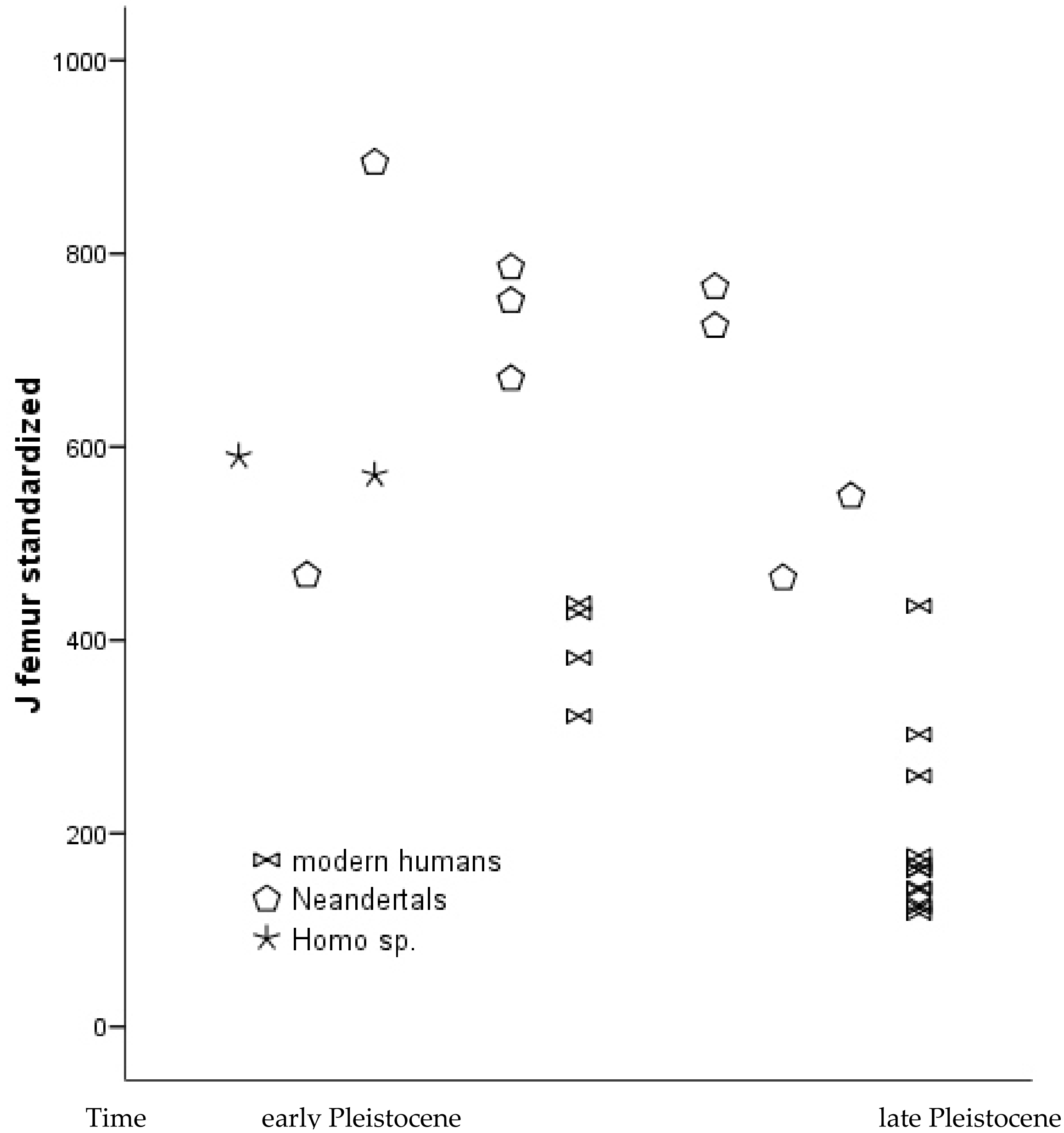


Figure 1: Postcranial skeletal robusticity in *Homo* over time (time on X axis is not to scale)

There is also evidence that even among modern human groups, measures of skeletal robusticity do not always follow the patterns predicted by the tool technology hypothesis. A series of studies on prehistoric Georgia populations (Larsen, 1997; Ruff, 2000a, 1987a and b, Ruff et al., 1994; Ruff and Larsen, 1990; Bridges, 1989) yielded conflicting results about the effect of subsistence change on patterns of postcranial skeletal robusticity. These studies documented temporal change in a population that was experiencing a transition from hunter-gatherer subsistence strategy to agriculture. Surprisingly, the hunter-gatherer population, which preceded the agriculturalists, had less robust postcrania than the agriculturalists. This example highlights the difficulty of using robusticity based on cross-sectional dimensions as an indicator of habitual behavior or subsistence activity. In discussing the apparent contradictions in the expectations for this fossil group, Stock (2006:195) suggests that "other mechanical factors may override subsistence strategy in their influence on the morphology of the femoral diaphysis, and may explain the lack of concordance among earlier studies of the relationship between subsistence strategy and robusticity".

A third flaw in the technology hypothesis is that there are non-primate taxa (*Connochaetes* and *Bison*) that also undergo postcranial gracilization in the Holocene (Churchill et al., 2000; Lewis, 2004). This suggests that humans were not the only species experiencing morphological change in this direction during the early Holocene. These observations warrant a closer look at whether this is a trend common to most mammalian groups, and if so, whether there are ecological correlates that can be applicable to non-human groups. Most mammalian groups experienced a reduction of body mass at the beginning of the Holocene, a phenomenon attributed to the changing global climate. With warming temperatures, mammals became smaller, as predicted by

Bergmann's Rule. This body mass reduction was a result of both the extinction of large-bodied forms (Kurtén, 1965), and body mass reduction over time within lineages (Davis, 1981; Avery, 1982; Guthrie, 2003). Within the genus *Homo*, body mass also decreased during this time (Ruff et al., 1997). The species with the largest documented body mass, *H. neanderthalensis* (76+/- 1.4 kg), went extinct during the Late Pleistocene. *H. sapiens* decreased in size from 66.6+/- 2.2 kg (Skhul-Qafzeh) to 58.2 +/- 1 (modern human sample) (Ruff et al., 1997). In this way, hominins follow the pattern of other mammals in body mass reduction trends. It may be that skeletal robusticity is also linked to the changing global climate and the body mass reduction that resulted from it. One thing is certain, however; wildebeest and bison did not become skeletally gracile because their tool kits became more sophisticated.

An alternative hypothesis is that aspects of ecology can predict patterns in postcranial skeletal robusticity. This idea has been explored in scaling studies among mammals, including anthropoid primates (Biewener et al., 1988; Demes et al., 1991; Demes and Jungers, 1993; Jungers and Burr, 1994), and more recently with studies on modern human variation (Churchill and Morris, 1998; Stock and Pfeiffer, 2004). However, other than the work on modern humans, there are few studies of the relationship between skeletal robusticity and ecological factors among closely related species that vary significantly in terms of subsistence strategy. The research presented here will test this idea further by examining the scaling patterns of variables that measure skeletal robusticity and bone strength relative to estimated body mass among species and genera that differ in locomotion, hunting strategy, diet, and prey preference. Consistent relationships between bone strength scaling and these ecological variables will be taken as evidence of a significant ecological signal in the functional adaptation of the bones.

1.1 Mechanical and Ecological Hypotheses

Several studies have outlined the differential scaling patterns of strength-related variables in different lineages of mammals (McMahon, 1975; Alexander, 1977; Alexander, Jayes et al., 1979; Prothero and Sereno, 1982; Biewener, 1983; Bertram and Biewener, 1990; Alexander and Pond, 1992; Christiansen, 1999a and b) (see Chapter 2 for details). It has been proposed that small and large mammals scale differently with regard to these variables (Economos, 1983; Bertram and Biewener, 1990; Christiansen, 1999a and b). Bertram and Biewener (1990) proposed that 100kg is the weight at which there would be differences in allometric scaling between small and large mammals. They propose that mammals under 100kg will scale with geometric similarity of length on diameter (scaling exponent of 1) and that mammals over 100kg will scale with elastic similarity (scaling exponent of .67). Therefore, all else being equal, the *Canis* group, which is smaller in body mass, may be expected to scale similarly to humans, a group that is also less then 100kg. *Ursus* may be expected to show a different scaling pattern because the species mean for two of the three groups included in this sample are larger than 100kg. Black bears, while still larger in body mass than all of the *Canis*, actually fall below the 100kg size limit proposed by Bertram and Biewener (1990). Because the regressions of Bertram and Biewener were done with larger taxonomic groups, it will be interesting to see if black bears scale with the other bears. According to the predictions of Bertram and Biewener (1990), the black bears should scale similarly to wolves rather than with their congenerics. The differential scaling hypothesis (Table 2) will be tested through the comparison of RMA regression slopes for bone diameter to the moment arm during bending (bone length) and an approximation of body mass (joint surfaces or cranial dimensions) as the independent variables. There are several possible outcomes of this test. First, the predictions of Bertram and Biewener will be upheld, and *Canis* will scale with geometric similarity and *Ursus* with elastic similarity. Another possibility is that *Canis* will scale with elastic similarity and *Ursus* with geometric similarity. A third possibility is that *Canis* and *Ursus* show neither pattern of geometric or elastic similarity. Gaining a greater understanding of how animals of different body masses scale at the level of the genus will lead to more informed interpretation of scaling patterns of extinct and extant *Homo*.

The second hypothesis (Table 3) that will be tested centers around the differences between species in the same genus in order to more fully answer questions about variation in postcranial skeletal robusticity within the genus *Homo*. Modern human skeletal gracilization has often been assumed to be the result of changing technologies (Brace, 1962, 1979, 1991; Brose and Wolpoff, 1971; Frayer, 1980, 1984; Ruff et al., 1984; Smith, 1985; Brock and Ruff, 1988; Bridges 1989, 1991; Mellars, 1989; Ruff and Larsen, 1990; Ruff et al., 1991; Ruff et al., 1993; Trinkaus et al., 1994; Churchill et al., 1996).

However, the effect of ecological variables, particularly the availability and type of resources has rarely been considered. In addition to changing technologies throughout the Pleistocene and Holocene among hominins, there were also great fluctuations of climate and temperature, proven determinates of certain morphological dimensions in mammals. I propose that differences in ecological conditions, that are influenced by climate and many other factors, are also determinates of bone strength in mammals. One potentially important variable is productivity. Productivity is measured in kilocalories and is the amount of calories available from plant material in a given area (Uchijima and Seino, 1985; Raich et al., 1991; Mittlebach et al., 2001).

In areas of low productivity, I predict that mammals that hunt (including *Canis* and *Homo*) will have more robust bones than the same species in areas of high productivity. The greater bone strength of predators in areas of low productivity is predicted because a) herbivores (prey) are relatively larger in areas of low productivity (Best, 1981; Murphy, 1985; Klein, 1986) and b) herbivores are less numerous in areas of low productivity. The ways in which these factors can influence bone strength in carnivores (*Canis* and *Homo*) is multifold. For example, predators in low productivity environments like high latitude cold areas may have to hunt large prey and thus may experience higher magnitude strains when they take down large mammals (compared to hunting smaller mammals). Similarly predators in low productivity environments may have to range further in search of prey. They may experience more frequent bone loading and they may have to travel faster to cover the ground in a single day and thus experience higher magnitude forces.

One way to test this hypothesis is to look at the geographic distribution of a measure of bone strength within a restricted taxonomic group. In order to test this possibility, all specimens of *Canis* for which there was geographic data associated with the remains, will be examined for a relationship between latitude (as a substitute for productivity) and a dimensionless measure of strength that is independent of body mass or limb length. The dimensionless measure of strength that is used in these analyses is a modified version of Alexander's (1989) index of athletic capability. This is further explained in Chapter 5. There are, of course, limitless numbers of ways to group species and populations in order to look at different correlates of productivity, so this is just a first step towards a more comprehensive understanding of these variables and the relationship between productivity and bone strength.

Another way to test this hypothesis is to look at temporal change in relative bone strength within a genus. This method is also used in this research, through the inclusion of a fossil species, *Canis dirus*, a North American Pleistocene species of wolf. This species is not ancestral to modern wolves, but its relationship to living wolves is similar to that of the Neandertals to living modern humans. Thus, this research will look at temporal patterns within a genus that has extinct and extant members that are similar morphologically and ecologically. On the basis of a limited amount of evidence, including data from hominins (Ruff et al., 1993), wildebeest (Churchill et al., 2000) and bison (Lewis, 2004), there appears to be a mammalian trend of gracilization in the Holocene. If, as is suggested by these examples, postcranial gracilization in the Holocene was a general mammalian trend, and not a hominin-specific trend, then *Canis* should also follow this pattern. According to the ecological hypothesis, more gracile skeletons are predicted for Holocene mammals because the warmer temperatures of this time result in more productive environments than those that were seen during the ice ages of the Pleistocene. Specific questions to be addressed are outlined in Table 3.

Table 2: Hypothesis #1 Strength Scaling Patterns (including an evaluation of Differential Scaling Hypothesis of Bertram and Biewner, 1990)

hypothesis	Questions	tests	sample	expectation
Mammals over 100kg in body mass will scale differently than mammals under 100kg. Geometric/elastic similarity	Are there shape changes in limb bones in relation to bone length in *Canis* and *Ursus*?	RMA regressions of cross-sectional variables on bone length	*Canis* (under 100kg) and *Ursus* (over 100kg)* *except *U. americanus*	*Canis* will scale with geometric similarity, *Ursus* with elastic similarity
	How does bone strength scale with body mass in *Canis* and *Ursus*?	RMA of x-sec variables on proxy for body mass	*Canis and Ursus*	Both genera will scale with isometry.
	Are there differences in the modified index of athletic capability) between *Canis* and *Ursus*?	Mann-Whitney U test for differences in index of athletic capability	*1. C. lupus, C. latrans, C. rufus* *2. U. americanus, U. arctos, U. maritimus*	Larger *Canis* and *Ursus* will have larger indices than smaller *Canis* and *Ursus*

Table 3: Hypothesis #2 (Ecological hypothesis)

hypothesis	Questions	tests	sample	expectation
Carnivores in areas of high productivity will have relatively stronger postcrania than carnivores living in areas of low productivity	Do Pleistocene *Canis* have greater cross-sectional dimensions than Holocene *Canis*?	Relationship of cross-sectional variables relative to body mass and bone length	*C. latrans, C. lupus, C. rufus C. dirus*	*C. dirus* will be relatively more robust
	Does latitude correlate with bone strength in extant *Canis*?	Graphical representation of potential relationship between latitude and index of athletic capability of the femur	*Canis* (extant)	Individuals at higher latitudes will have higher indices than those at lower latitudes

2. Background

In order to fully appreciate and understand how variation in scaling patterns of non-primate mammals can inform hypotheses about human evolution, I provide an overview of expected scaling patterns in mammals from a biomechanical perspective, and a brief exploration of bone as a structure and how it responds to loading, hormonal, and nutritional stimuli.

At the very least, a bone must be strong enough to support the body mass of the individual during locomotion. Mammalian skeletons tend to be stronger than necessary for this task by a factor of 2-4, which is known as the safety factor of the bone (Yamada, 1970; Reilly and Burstein, 1975; Currey, 1984; Biewener, 1993). Whether considering static or dynamic forces acting on the skeleton, body mass is typically assumed to be a crucial factor determining the magnitude of bone loading.

Allometry is the differential scaling of body parts. A number of researchers have proposed that bone cross-sectional dimensions should increase in proportion to the loads they experience rather than in geometric proportion to bone length or body mass (McMahon, 1975). This is because, in the absence of behavioral modification, in order for a bone to maintain its structural integrity as the body mass of an animal increases, it would have to increase its dimensions at a greater rate than it increases bone length or body mass (Galileo, 1637). However, the biological reality is that bone cross-sectional dimensions do not keep pace with body mass across large orders of magnitude of size and, thus, potentially do not keep pace with the loads they experience (Alexander, 1977). This leads to the idea that large animals have relatively weak bones and must modify their behaviors in order to prevent fracture (Alexander, 1977; Alexander et al., 1979).

There are several theoretical predictions of how bone cross-sectional dimensions should scale with body mass. Geometric similarity predicts isometry of scaling. Galileo (1637) was the first to recognize that bone diameter would have to increase at a faster rate in order to support the increased body mass of larger animals. Thus, in order to maintain structural similarity, bone diameters would need to increase at greater rate than that of body mass. This is not the case across many taxa that include many orders of magnitude of size. Large animals compensate for the increased body mass through postural or behavioral adaptations that help to moderate the stresses on bone. Several studies have since offered support for geometric similarity (Alexander et al., 1979; Biewener, 1983; Economos, 1983; Polk et al., 2000)

Elastic similarity, proposed by McMahon (1975) predicts that there exists an allometric relationship between bone cross-sectional dimensions and bone length and body mass. This relationship is based on elasticity being the principal determinate of long bone structural integrity. This expectation of elastic similarity is that bone length increases at 2/3 the rate of bone diameter, and body mass increases at 5/8 the rate of bone diameter (McMahon, 1975; Stahl and Gummerson, 1967). Both of these expectations are theoretical, and there are, of course, other factors that determine bone strength and scaling patterns among mammals. The prediction of elastic similarity is upheld in some groups (Selker and Carter, 1989). However, a number of studies have shown that mammals scale with geometric, not elastic similarity (Alexander et al., 1979; Biewener, 1983; Economos, 1983). The finding that elastic similarity in bovids is highly dependent on sample composition more than anything else (Scott, 1985) is an indication that there are factors in addition to resistance to bending that influence the scaling patterns of long bones. Even within some of these studies, there are different scaling patterns for different groups (Alexander et al., 1979), which then result in the need for special explanation for these groups, or for an alternative theory about the scaling patterns of mammals.

Economos (1983) proposed that large and small animals scale differently from one another. I refer to this here as the Differential Scaling Hypothesis. This suggestion followed a study by Alexander in which a large animal group (Bovidae) scaled with elastic similarity, while all other groups scaled with close to geometric similarity (Alexander, 1977; Alexander et al., 1979). However, a follow-up study of Bovidae rejected elastic similarity as the main type of scaling for this group (Scott, 1985), casting doubt on the utility and applicability of elastic similarity. Across a broad range of mammals, geometric similarity holds true (Alexander, 1977), but within smaller groups, a much more complex pattern emerges. Animals with a larger body mass are more subject to the effects of gravity than are animals with a smaller body mass (Economos, 1983), and their skeletons might be expected to reflect this constraint. Therefore, elastic similarity may be the pattern seen in larger animals, but geometric similarity is the pattern seen in smaller animals. The idea of differential scaling for small and large animals has been shown to be true for other groups of mammals as well (Bertram and Biewener, 1990; Christiansen, 1999). Most of these studies look at taxonomic groups that encompass a broad range of species with different locomotor styles, body plans, and body sizes. When smaller taxonomic groups that are more restricted in body mass and locomotion are studied, the scaling patterns that they show are sometimes different from the patterns seen at high taxonomic levels (Heinrich and Biknevicius, 1998). When interpreting scaling patterns of groups of mammals, it is important to consider how the composition of the group may affect scaling patterns. For example, a group than encompasses several orders of magnitude of body mass and different types of locomotor patterns in its sample will have scaling pattern that reflect these differences. Large animals adapt to loads differently than small animals, and their bones will reflect this fact. Alternatively, a group that is more restricted in body mass and locomotor type will exhibit differences that reflect individual variation among its members in other variables, such as mechanical loading patterns that are tied to activity level or resource acquisition.

The size and shape of bone is a function of many different factors. Understanding how mechanical loading affects bone deposition, and, as a result, cross-sectional dimensions, is crucial to understanding how bone strength differs between groups and what factors can account for these differences. The postcranial skeleton grows in length by depositing bone to replace a cartilaginous precursor. Bone is laid down by osteoblasts, and bone is destroyed by bone-eating osteoclasts (Currey, 1984). The process of depositing and removing bone is continuous throughout life, although the rate of each of these processes and the regions of the skeleton at which they occur may vary over time.

There are two ways that a bone can become robust. One way is for the bone to become shorter, reducing the moment arm for external loads generated during locomotion and other body movements. The other way is for more bone to be deposited at a particular site along the shaft of the bone, reducing the internal stresses engendered by external loads. The most efficient place for this to occur is on the periosteal surface of the bone. According to beam theory, bone laid down on the periosteal surface contributes more to the overall strength and integrity of the structure than bone that is laid down on the endosteal surface because it also increases the external dimensions of the bone. For example, since second moments of area are calculated as the product of a unit area and the squared distance of that area from a neutral axis, bone deposited on the periosteal surface will result in greater strength values than the same amount of bone deposited on the endosteal surface (see Chapter 2 for further explanation).

The body of literature pertaining to the response of bone to mechanical stimuli is extensive, and sometimes contradictory. While the fact that loading can result in morphological changes in bone is not disputed, the importance of loading relative to other factors is in question (Bertram and Schwarz, 1991). These authors point out that studies investigating the effect of loading on bone assume a priori that Wolff's Law

(Wolff, 1892), which attempts to describe a predictable relationship between load and trabecular bone orientation, is valid, and design experiments that will prove it, ignoring any other explanations for the same results. However, despite criticisms related to experimental design, and the fact that there are likely to be several mechanical stimuli that operate to shape and reshape bone under different circumstances, there is considerable evidence that bone is reinforced in response to mechanical loading (Roux, 1881; Kummer, 1972; Lanyon, 1973; Lanyon et al., 1975; Turner et al., 1975; Goodship et al., 1979; Lanyon et al., 1979; Carter et al., 1980; Pauwels, 1980; Woo et al., 1981; Lanyon et al., 1982; Martin and Burr, 1982; Currey, 1984; Rubin, 1984; Frost, 1985; Rubin and Lanyon, 1982, 1985; Frost, 1987; Lanyon, 1987; Martin and Burr, 1989; Kimmel, 1993; Rubin et al., 1994; Trinkaus et al., 1994; Lieberman et al., 2001). Thus it is possible to draw broad conclusions about activity level of organisms or groups of organisms on the basis of differences in cross-sectional dimensions because of how bone changes in response to loading. The idea that cortical bone distribution should reflect mechanical loading was first expressed by Roux (1881; summarized in Roesler, 1981). Although eclipsed in name recognition by Wolff's Law, Roux's recognition of the relationship between bone and loading is more applicable to cross-sectional studies of bone adaptation than Wolff's Law. In particular, Roux's suggestion that mechanical stress is a stimulus to bone cells is an underlying principle in most anthropological studies of cross-sectional geometry. Roux did not articulate *how* mechanical loading stimulated bone cells, and answering this question has been an active area of research in the late 20th century. Before reviewing the experimental and observational studies, it is important to mention how Wolff's Law fits into this discussion.

Wolff's Law is commonly cited in reference to studies about bone changing in response to mechanical stimuli, but its use in these contexts is usually inappropriate. Wolff's hypothesis focused on the orientation of trabecular bone, and he sought mathematical formulae that would predict how this bone would respond to changes in the direction of principal stresses. He predicted that cortical bone would respond similarly to changes in stress, and that these changes would be predictable. In this last part, Wolff was shown to be in error, leading to a call in recent years to throw out Wolff's Law as an outdated idea that has no place in scientific research (Bertram and Schwartz, 1991). In response to criticisms of certain aspects of bone adaptation/mechanical loading studies, Ruff et al. (2006) distinguish between the "strict version" of Wolff's Law and the "general version" of Wolff's Law. The strict version is Wolff's attempt to mathematically predict trabecular bone orientation through the direction of loading in the bone. The general version of Wolff's Law simply states that mechanical loading influences bone shape. Ruff et al. (2006) point out that most criticism of Wolff's Law are leveled against the strict version, but the more general version is sometimes caught in the cross-fire. However, implicit in the general version as stated above, is the assumption that there is a simple cause and effect sequence between loading and bone form. This is not the case, for a number of reasons. First, bone is not adapted solely for the purpose of movement. The skeleton also provides an internal support system for the body, serves as a calcium bank, provides protection for vital organs and is a site for the manufacture of blood cells (Currey, 1984). Secondly, there are numerous factors, such as hormones, nutritional state, age and genetics (Lieberman, 1996) that mediate the amount and distribution of bone modeling or remodeling. This being the case, is there anything that can be said about the relationship between bone loading and the action of bone cells?

There have many studies over the past 30 years that attempt to resolve the question of how bone is stimulated to model or remodel, and the circumstances under which remodeling takes place. Bone has been demonstrated to change during the lifetime of an individual, making it ideal for studying the effect of the environment on the individual. However, there is no agreement about how the bone is stimulated to add or subtract bone. It is largely understood that strain magnitude plays a role in stimulating bone growth, but there are many other factors that can influence this process including strain frequency, piezoelectricity, hormones, age, and nutritional status.

Strain magnitude is the amount of deformation experienced by bone as a result of loading that has surpassed normal stress levels. It is expressed as $\Delta L/L$ (change in length / original length). For example, a bone that experiences bending strain will lengthen on the side of the bone that is in tension, and shorten on the side of the bone that is in compression. The percentage of change in length is expressed as strain magnitude. There are many experimental and observational studies that confirm that activity can causes changes in bone morphology by stimulating the removal or deposition of bone (Biewener et al., 1986; Woo et al., 1981; Rubin and Lanyon, 1984, 1985; Corruccini and Beecher, 1982, 1984; Bouvier and Hylander, 1981; Yamada and Kimmel, 1991). It is hypothesized that bone responds to activity in order to maintain strength to resist normal forces on the bone while maintaining a safety factor in the effect of unusually large loads. In a simple model, strain causes bone deposition until bone reaches a level that is sufficient to withstand this strain. The sensitivity of bone cells to strain-related stimulus is not infinite, and usually ceases after 20-30 minutes of exercise (Robling et al., 2002). Experimental studies go even further and claim that bone is sensitive to up to 30 loading cycles. Any more than this, and the effect is the same. Thus, loading a bone 31 times will have the same effect, in terms of the osteogenic response of the cells to the strain, as loading a bone 31000 times. In the absence of strain, bone resorption will occur so that this optimum strain level is maintained (Carter, 1984; Frost, 1987). There are several flaws with this model, which has led to criticism and repudiation of the entire strain-deposition/resorption model. One flaw is that there is no explanation as to *how* strain stimulates bone deposition, or how the absence of strain stimulates resorption. A second flaw is that there is evidence that bone does not respond to strain in a localized manner by depositing bone in the area of greatest strain, as would be expected by this model, but instead responds systemically to a particular stimulus or stimuli by acting on the entire skeleton. A third flaw is that this model does not take into account mediating factors such as hormones, diet and age.

Observational studies also demonstrate the importance of activity-related stimuli to bone cross-sectional dimensions. In a study on adult tennis players, a high degree of bilateral asymmetry was noted in the humerus (Jones et al., 1977), a finding that paralleled the finding of bilateral asymmetry in the upper limb of Neandertals (Trinkaus et al., 1994). These levels of individual asymmetry can exceed population level asymmetry (Trinkaus et al., 1994), making a strong argument that bone deposition is a result of regular activity and that the observed differences between closely related species, or populations of the same species can be attributed to mechanical loading. Systemic responses cannot account for bilateral asymmetry of the upper limb; especially since this asymmetry is not mirrored in the lower limb. The sample of tennis players studied by Jones et al. (1977) included individuals who began playing tennis as children or adolescents. These individuals showed a greater degree of asymmetry than those who began their tennis playing later in life. It is likely that most of the asymmetry seen in the human upper limb is a result of loading that occurred prior to adulthood and is maintained by regular activity throughout life.

Strain frequency has recently been shown to be an important stimulant of bone growth (Fritton et al., 2000). Typically, high strain frequency is experienced at low strain magnitude, and low strain frequency is experienced at high strain magnitude (Fritton et al., 2000). This means that activities such as standing or walking, which are characterized by low strain magnitude, can cause bone remodeling because of their high strain frequency (Jankovich, 1972; Flieger et al., 1998; Rubin et al., 2002; Tanaka et al., 2003; Ward et al., 2004; Judex et al., 2007). The way in which high frequency strain influences bone cells is proposed to be through fluid pressure gradients within the bone (Cowin 1995; Qin et al., 2003). However, most of the studies pertaining to strain frequency demonstrate that frequency has its greatest effect on cancellous bone, not cortical bone (Rubin et al., 2002).

Adding further to the confusion about the effect of strain magnitude or frequency on bone deposition is the fact that there are several mediating factors that are important to bone growth. Hormones have been shown to mediate the response of bone to activity (Lieberman, 1996). Estrogen deficiency has a profound effect on bone, resulting in the resorption of bone on the endosteal surface, particularly in women who are experiencing menopause. The level of circulating estrogen and estrogen receptors mediates the response of bone to strain (Zaman et al., 2000; Lee et al., 2003). Growth hormone (GH), and its effector hormone, insulin-like growth factor-1, are essential for normal bone growth. Individuals who are deficient in one or both of these hormones fail to grow normal skeletons and are usually shorter in stature than average (Laron, 2004; Guevara-Aguirra et al., 1993) and skeletal maturity is delayed (Brasel et al., 1965; Kornreich et al., 2008). However, these deficiencies lead to shorter bones due to problems at the growth plate. Structurally, the bones of individuals with these hormone deficiencies have sufficient cortical area to withstand the loads that they are subject to (Bachrach et al., 1998; Bikle et al., 2001; Kornreich et al. 2008). Low levels of growth hormone are associated with thin cranial vaults (Pirinen et al., 1994). A test of the hypothesis that levels of growth hormone can affect cranial width as a systemic effect demonstrated that levels of this hormone had more of an effect on cranial width than strain (Lieberman, 1996). It is proposed that since secretion of GH is prompted by exercise (Borer, 1980; Poehlman and Copeland, 1990; Felsing et al., 1992), activity has a systemic, rather than a localized effect on bone growth. If this is the case, then it may explain the greater robusticity of Pleistocene *Homo* in all areas of the skeleton.

Age is another important factor to consider when looking at cross-sectional variables. It is likely that the most active period of bone growth and deposition occurs in adolescence (Jones et al., 1977; Lieberman et al., 2003; Pearson and Lieberman, 2004). Bone, though a dynamic and ever-changing structure, undergoes relatively little change during adulthood. Menopause causes both a reduction of estrogen and high remodeling of bone, which reduces the bone mineral content, leading to a loss of strength and a higher incidence of fractures in older women (Aaron et al., 1987; Van der Linden et al., 2001; Manolagas, 2000). It had been thought that modeling only occurred during growth, while remodeling occurred during both growth and adulthood. This may not be the case, however. Studies have demonstrated that adults do add bone on the periosteal surface (Rubin and Lanyon, 1985; Jaworski and Uhthoff, 1986). This means that bone cross-sectional dimensions can reflect adult activities or activity levels.

One of the criticisms of cross-sectional studies of bone is that most long bone growth occurs during the juvenile period, and very little modeling of bone happens in the adult skeleton. This is true to an extent, but modeling can still occur in adults, although usually on the endosteal surface (Ruff et al., 1994). Bone is most responsive to mechanical loading during growth. In a longitudinal study covering almost 18 years, bone cross-sectional mechanical properties were tested for correlations to body mass*limb length, muscle mass, and stature (Ruff, 2003). The results demonstrate that for the femur, cross-sectional properties are closely correlated with the product of body mass and limb length throughout the growth period. This indicates that mechanical loading (body mass) during locomotion is stimulating bone growth. In contrast, the humerus, which in humans is unloaded during locomotion, and not subject to regular loads, did not show a correlation between strength and body mass*limb length. In addition, bone strength velocity (section modulus/body mass * limb length) of the humerus and femur during ontogeny corresponded to the change in locomotor style from crawling to walking (Ruff, 2003). The humerus strength velocity peaked early, followed by a decline. The femur strength velocity increased greatly around the time an individual would begin to walk.

Bone growth and cross-sectional change throughout the life of an individual is a complex subject area that is influenced by a number of different factors. Although there is a relationship between mechanical loading and bone deposition, the relationship is not predictable and cannot account for all of the variation that is seen in mammals. There are a number of other factors that mediate bone's response to loading. Consideration of these factors, including age, hormones, nutrition and the type of loading, when evaluating variation in postcranial robusticity is crucial to gaining a full understanding and appreciation for this variation. It was not possible, in the research presented here, to account for all of these factors. In an effort to maintain consistency of the sample so that there was not a great deal of variation in age, nutrition, or hormonal states, the only individuals included were wild adults that did not exhibit any pathologies of the skeleton. There may be some variation exhibited in measures of skeletal strength that are not entirely reflecting mechanical loading, but the assumption will be made that the major differences seen in skeletal strength among the animals sampled here is due to loading.

3. Materials and methods

3.1 Materials

Specimens used in this research were extant and fossil members of the genus *Canis* (wolves and coyotes), and extant members of the genus *Ursus* (bears). Both of these genera are carnivorans and possess a generalized skeleton, making them good for intraspecific or intrageneric comparisons (Alexander et al., 1979; Flynn et al., 1988). This sample came from collections housed at the Smithsonian Institute (SI), the American Museum of Natural History (AMNH), the Museum of Comparative Zoology (MCZ), and the North Carolina Science Museum (NCSM). These mammalian groups were chosen for several reasons. Each group exhibits interspecific variability in size, dietary choice and habitat, while maintaining similarities in body type and mode of locomotion. This allows for comparisons of postcranial skeletal strength that can focus on body mass, prey size, ecological variables and address the core questions of this dissertation.

All individuals included in this study were adults, as determined by complete epiphyseal fusion, and non-captive individuals, as determined by catalogue information included with the specimen.

Table 4: Body mass estimates of each species from the literature

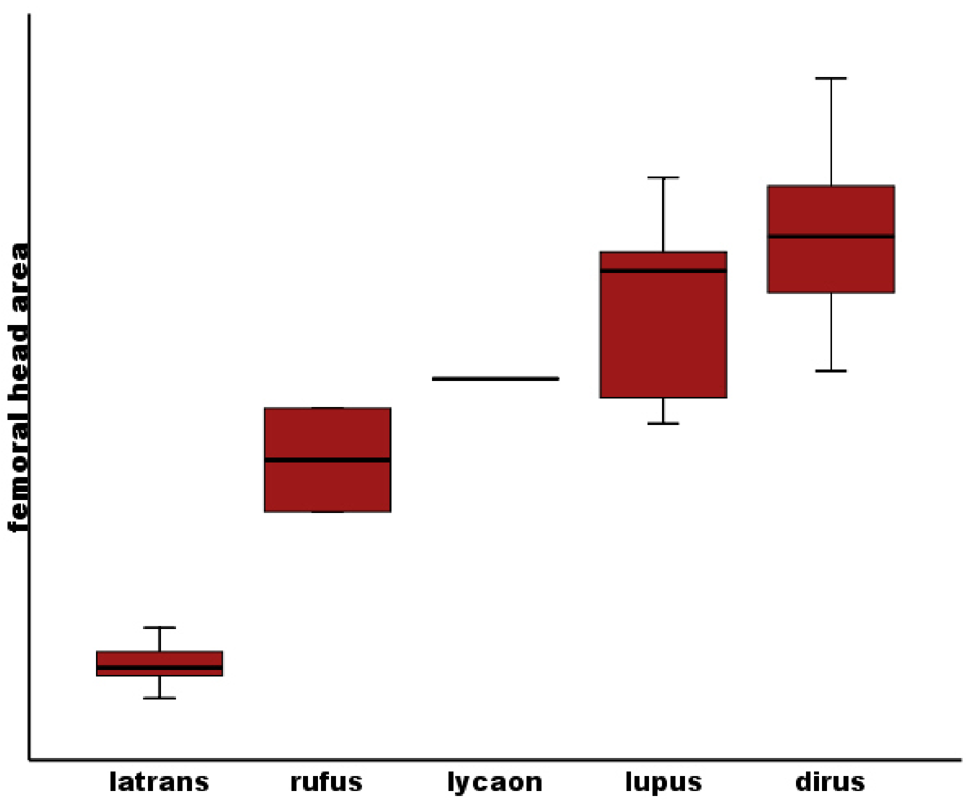
Species	Body mass	Reference
Canis latrans	14 kg	Macdonald, 1984
Canis lupus	45 kg	Macdonald, 1984
Canis lycaon	35 kg	Wilson et al., 2000
Canis rufus	30 kg	Macdonald, 1984
Canis dirus	55 kg	Anyonge and Roman, 2006; Van Valkenburgh and Koepfli, 1993
Ursus americanus	50 - 86 kg	Pieklilek and Burton, 1975; McLean and Pelton, 1990; Hall, 1981

Ursus arctos	100 -600 kg	LeFranc et al., 1987; Blanchard, 1987; Kingsley et al., 1988; Nowak and Paradiso, 1983;
Ursus maritimus	200 -680 kg	Demaster and Stirling, 1981

3.1.1 Canis

Four extant and one fossil *Canis* species were included in this study. All the individuals in this genus came from North American sites. Table 6 provides a summary of the sample of *Canis* used in this dissertation. The geographic distribution and population sizes of the species studied here have recently experienced dramatic change. In North America, gray wolves could historically be found in every region of the continent (Mech, 1970; Carbyn, 1987). Extermination efforts by humans to eliminate the threat of the gray wolf to livestock reduced their range to the western US and Canada (Young and Goldman, 1944). This once numerous species has been completely eliminated in some areas and is endangered in many others. In contrast, the coyote, the smaller relative of the gray wolf, has been able to take advantage of the areas left unoccupied by the gray wolf and now flourishes in the eastern US and Canada.

Canids first appeared in North American during the Miocene, about 9-10 million years ago (Xiaoming et al., 2004). They soon diversified and expanded to every continent (except Antarctica) (Rook, 1992; Tedford and Qiu, 1996). There are 14 genera in this family. This study focuses on the North American species of one of these genera, *Canis*, a group that includes wolves, coyotes, jackals and dogs. *Canis* was chosen for this study because of several ecological and behavioral similarities that it shares with hominins. Both canids and hominins are top hunters in their ecosystems, live and hunt in groups and are highly social and highly intelligent. Thus, if there were variation in postcranial skeletal robusticity that resulted from different ecological variables, then it would be reasonable to assume that canids and hominins vary in similar ways with regard to these variables. A brief description of the sample composition, natural history, physical characteristics, behavioral traits, and relationships with closely related groups is provided here for each species included in this research. This genus also is considerably diverse in terms of body mass. Figure 2 illustrates the relative sizes of each of the five species included here based on femoral head area.



272.9mm² 513.2mm² 610.1mm² 703.9mm² 767.2mm²

Figure 2: Body mass estimate using femoral head area (mm²) for *Canis* (boxes indicate 95% confidence intervals, whisker the total range)

The species included in this study are closely related members of the genus *Canis*. Figure 3 illustrates the phylogenetic position of each of these species. The gray wolf, *C. lupus* evolved in Eurasia from *C. etruscus* about 800kya (Nowak, 1979). Around 300 kya, *C. lupus* began migrating into North America following the Bering Land Bridge. The coyote had first appeared in North America about a million years ago, likely a descendent of the North American species *C. lepophagus* (Nowak, 1979). Two of the species in this study, the red wolf (*C. rufus*) and the eastern timber wolf, (*C. lycaon*) were once thought to be hybrids of the gray wolf and the coyote. Recent genetic studies have shown that both of these species have recently diverged from the coyote (Vila et al., 1999). The fossil dire wolf, *C. dirus* first appeared in North America around 100kya, likely a descendent of the South American *C. ambrusteri*. Throughout the Pleistocene, canids were subject to population expansion and contraction that followed glacial cycles (Vila et al., 1999). Gray wolves, which tend to prefer forest habitats, often experienced habitat fragmentation during the cooling cycles (Mech, 1970; Carbyn, 1987; Voigt and Berg, 1987), although their population numbers were relatively high during this time. It is only recently that their numbers have declined, largely due to eradication of populations through hunting by humans. The dire wolves went extinct at the end of the Pleistocene when the Pleistocene megafauna that served as their prey disappeared from the landscape. Larger, heavier, and slower than gray wolves and coyotes, they were not able to effectively compete for swifter, smaller prey.

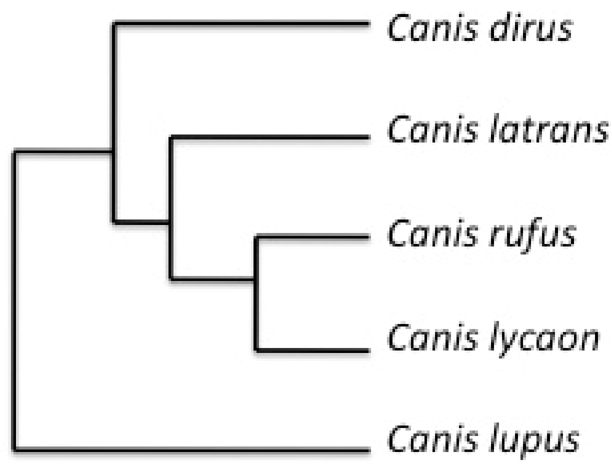


Figure 3: Cladogram showing the relationships of the *Canis* species used in this study. (Nowak, 1979; Kurtén and Anderson, 1980; Nowak, 1995; Vila et al., 1999; Wilson et al., 2000; Wilson et al., 2003). Please note that the final result is the compilation of morphological and genetic data that not each of these authors support

3.1.1.1 *Canis latrans* (Say 1823)

The sample of coyote (n=25), *Canis latrans*, came from collections at the AMNH and the NCSM. This sample consisted of 6 females, 12 males, and 7 of indeterminate sex. The majority of these specimens came from North Carolina, Nevada, and Arizona. Only one was from Canada. The dates of collection for this sample range from 1887-1997.

Coyotes evolved from the North American *Canis lepophagus* about 1 million years ago (Nowak 1979; Kurtén and Anderson, 1980). Coyotes were outnumbered by gray wolves in North American during the Pleistocene, but have recently expanded their range and population size exponentially to occupy nearly all of North America (Nowak, 1979; Voigt and Berg, 1987). It is not estimated that there are 7 million coyotes in North America (Lehman and Wayne, 1991).

Coyotes are the smallest of all the *Canis* species included in this study. Body mass estimates for the coyote differ by geography and range from 9.8 kg (Hawthorne, 1971) to 20.4 kg (Silver and Silver, 1969). Table 5 offers a more comprehensive look at the published body mass estimates for this species, as well as all the other species included in this research. Due in part to their recent rapid range expansion, there are significant differences in body mass between coyotes from the western US and coyotes from the eastern US, particularly New England and eastern Canada (Lawrence and Bossert, 1975; Hilton, 1978; Thurber and Peterson, 1991). The eastern coyotes are significantly larger than the western coyotes, and a t-test of the means of these two groups from the sample used in this study confirms this difference. A comparison of a body mass approximation of the western and eastern coyotes in this study using only those individuals from Arizona, Nevada, New York and North Carolina, demonstrated that there was a significant difference in body mass between the eastern and western groups ($t = 2.558$, $DF = 16$, $p = 0.021$ for unlogged data) ($t = 2.772$, $DF = 16$, $p = 0.014$ logged data) using a geometric mean that included femur length, femur midshaft ap, femur midshaft ml, femoral head area, humerus length, distal humeral breadth, tibia length, ulna length, skull width across canines, skull width across postorbital processes, skull width across occipital condyles, palate width, and mandibular height.

Many reasons have been proposed for this increase in body mass among eastern coyotes, including hybridization with *C. lupus* (Hilton, 1978; Lawrence and Bossert, 1975; Voigt and Berg, 1987), selection response (Bergmann's Rule) and greater resources (McNab, 1971; Schmitz and Kolenosky, 1985; Geist, 1987a; Thurber and Peterson, 1991). Of these three explanations, the abundant resources leading to body mass increase has the most evidence to back it up (Thurber and Peterson, 1991). *C. latrans* shows a higher amount of phenotypic variability than other canids (Young and Jackson, 1951), and so it is not surprising that one of the changes associated with their occupation of a new environment is an increase in body mass.

3.1.1.2 *Canis rufus* (Bailey 1905)

Nine specimens of *Canis rufus*, the red wolf, were included in this study, from the NCSM, the SI and the AMNH. This sample consisted of 5 females, 3 males, and one of unknown sex. Seven of these individuals came from Texas, and one came from North Carolina. The earliest collection date is 1853 for this sample, with the majority of individuals collected in the mid 20th century.

The phylogenetic position of the red wolf, *C. rufus*, was subject to recent debate, which included its validity as a species and whether or not it should be protected under the Endangered Species Act of 1973 (Young and Goldman, 1944; Wayne and Jenks, 1991; Gittleman and Pimm, 1991). It has been proposed that this species is a hybrid of the gray wolf and the coyote (Mech, 1970), although this view does not receive much support from other researchers (Nowak, 1979). A canonical discriminant analysis of skull measurements of these three species shows that *C. rufus* does indeed form a distinct population that is distinguishable from the coyote and the gray wolf (Nowak, 1992). However, the most recent molecular evidence indicates that this species is a hybrid of the gray wolf and the coyote (Brownlow, 1996). More specifically, there are no alleles unique to red wolves (Roy et al., 1994). However, this species is a distinct breeding population most closely related to the coyote (Vila et al., 1999) and is considered here as a distinct species. The red wolf, which once ranged extensively throughout the United State, went extinct in the wild in 1980 (Cohn, 1987).

The red wolf was largely eradicated in most of its range during the 19th and 20th centuries and reduced to less than 100 individuals by 1970. A program to reintroduce the red wolf to the Alligator River National Wildlife Refuge in North Carolina began restoring captive red wolves to the wild in 1987 (Phillips and Parker, 1988). Three of the specimens in this sample are from the Alligator River National Wildlife Refuge in North Carolina, a captive population that was reintroduced to the wild in 1987. This species is intermediate in size between *Canis lupus* and *Canis latrans*.

The red wolf is larger in body mass than the coyote (Table 4, Figure 2), but it overlaps somewhat with the other *Canis* presented here. This is not unexpected and there are other morphological and behavioral traits that distinguish the two groups. Red wolves are generally narrower through the body than gray wolves, and have a distinct reddish coloring to them (Paradiso and Nowak, 1972). They are active at night and hunt small to medium sized prey, including white tailed deer. Their current range is restricted to swampy or mountainous regions, their historical range having been restricted by human growth. Red wolves typically live in small family groups, although larger packs have been observed (Lawrence and Bossert, 1975).

3.1.1.3 *Canis lycaon* (Wilson et al. 2000)

There are seven specimens of *Canis lycaon*, the eastern timber wolf in this sample that consisted of specimens from the AMNH, the SI and the MCZ. Two of these are females, and the others are of indeterminate sex. All individuals included here are from Ontario in eastern Canada.

Commonly known as the eastern timber wolf, this species used to range throughout the northeastern US and eastern Canada. It has largely disappeared from the US, but populations remain in Canada, where it shares its range with the coyote. Like the red wolf, the eastern timber wolf was also long believed to be a hybrid of the gray wolf and the coyote, one that specialized in northeastern US and eastern Canada timber environments. Recent molecular studies indicate that this species of wolf, traditionally classified as a subspecies of *Canis lupus*, is distinct from that lineage and has its own evolutionary history in North America (Wilson et al., 2000; Wilson et al., 2003). This species is capable of interbreeding with the gray wolf, but it is genetically more similar to the coyote (Wilson et al., 2000). In fact, there is speculation that the larger coyotes in this region are the result of interbreeding with the timber wolf (Gompper, 2002). Deer, ranging in size from 90-250 lbs, is the typical prey species of the eastern timber wolf, although these wolves tend to hunt old or injured animals on the smaller end of this size range.

3.1.1.4 *Canis lupus* (Linneas 1758)

There are 24 *C. lupus*, 11 males, 8 females and 5 of unknown sex. The geographic range is broad, with individuals from Mexico to Anchorage, Alaska and Alberta, Canada. Six individuals are from Wood Buffalo National Park in Alberta, the site of Lu Carbyn's (1987) study of the relationship between the wolf and the bison. Other locations from which this sample comes are Minnesota, Kansas, Maine, Montana, Nebraska and Colorado. All of the *C. lupus* included here were collected during the last 155 years. The gray wolf is the largest of the extant wolf species, and the one with the greatest range variability. The gray wolf was previously much more prevalent, especially in the eastern US and Canada, but was hunted to extinction in these areas, to be largely replaced in its ecological niche by the smaller coyote. There are numerous subspecies of the gray wolf. For this research, the species was not divided up by subspecies.

The gray wolf, *Canis lupus*, is the largest living canid and is described as 'hypercarnivorous' (Van Valkenburg, 1989), meaning that this species consumes animal flesh almost exclusively and is considered a dietary specialist. The gray wolf hunts in packs and regularly takes prey much larger than itself (Mech, 1970). The smallest species reported as prey for the gray wolf is the beaver. Lu Carbyn (2003), in *The Buffalo Wolf*, describes a pack of 17 wolves preying on a bison calf that they had successfully chased and isolated from the pack. When hunting large prey, the wolf will attack mostly at the hindquarters in order to bring the animal down. It will then proceed with disemboweling and attacking other areas. In a description of this hunt, Carbyn (2003) provides a glimpse of how an individual wolf must work to successfully bring down a very large mammal. "This time a large wolf braced its hind legs firmly on the ground and clawed itself up onto the calf, gripping the calf's back with its teeth. The wolf repositioned itself, and once more I could see the teeth sink into the calf's rump." (Carbyn, 2003:7-8). With large prey such as this, the wolves will often simply rip the prey apart bit by bit, an exhausting struggle that can last hours.

This species occupies the largest and most diverse geographic range of any mammal, save for humans (and a rat or mouse), making it an ideal species to investigate the effect of environmental factors on morphological variation. Its historical range was all of North America, much of Europe and Asia. Extermination of the gray wolf due to hunting in the US has reduced their range considerably (Leonard et al., 2005). This species is making a comeback in numbers in the western US, and is still widespread in Canada.

3.1.1.5 *Canis dirus* (Leidy 1858)

The Pleistocene dire wolf, *Canis dirus*, is the only fossil species included in this research. All of the individuals from this study come from the Rancho La Brea tar pits and are housed at the University of California Museum of Paleontology in Berkeley, CA. There is an extensive collection of isolated skeletal elements available for study. All of the *C. dirus* sampled here were not catalogued or assigned specimen numbers. There is no information available about the sex of any of the individuals sampled here, and there would be no reliable way to determine this. For each limb element (femur, humerus and tibia), 20-40 bones were randomly selected and measured for length, midshaft diameters, and joint surface area variables.

The dire wolf was a large-bodied wolf that flourished during the Pleistocene and preyed upon the megafauna that characterized the North American landscape at that time. Several authors have suggested, on the basis of craniodental morphology, that the dire wolf was hypercarnivorous (Van Valkenburgh and Koepfli, 1993). Their prey included mastodon, bison, horse, camel, ground sloth (Kurtén and Anderson, 1980). The Pleistocene climate in coastal California was milder than most other areas of the continent, and constituted a 'refugium' of sorts for many large mammals (Johnson, 1977). The rich faunal diversity of this area was captured in the fossil deposits of the La Brea Tar Pits. Morphologically, the dire wolf is larger overall than the gray wolf, but with relatively shorter limbs and a smaller brain (Kurtén, 1984; Van Valkenburgh and Ruff, 1987). Gray wolves entered North America by crossing the Bering Land Bridge approximately 300,000 years ago (Leonard et al., 2002). The dire wolf, in contrast, likely evolved from a South American canid and first made its appearance in the fossil record 100-130,000 years ago (Leonard et al., 2002). These two species, and the coyote, were contemporaneous in Pleistocene North America (Kurtén and Anderson, 1980). The extinction of the megafauna that were prey for the dire wolf, such as horse, mastadon, camel and bison (Fox-Dobbs et al., 2007) at the terminal Pleistocene led to the demise of the dire wolf, which were not able to compete with its smaller cousins for smaller, fleeter prey species (Dundas, 1999).

Table 5: Summary of extant *Canis* sample

specimen #	species	sex	location
AMNH 123036	latrans	female	Colorado, White River Dry Fork
AMNH 123183	latrans	unknown	
AMNH 1306	latrans	male	Arizona: Fort Verde
AMNH 1316	latrans	female	Fort Verde Arizona
AMNH 1317	latrans	male	Fort Verde Arizona
AMNH 131833	latrans	male	NM Colfax Co., La Guilla Meadows
AMNH 141153	latrans	male	Nevada: 8 mi W. Panaca Benn Springs
AMNH 141161	latrans	male	Nevada: 8 mi W. Panaca Benn Springs
AMNH 141166	latrans	female	Nevada: 8 mi W. Panaca Benn Springs
AMNH 141170	latrans	female	Nevada: 8 mi W. Panaca Benn Springs
AMNH 142360	latrans	unknown	Sioux City, Nebraska
AMNH 166693	latrans	unknown	NY: Bronx Co., Van Cortland Park
AMNH 28197	latrans	unknown	Canada: British Columbia; Alsek River
AMNH 5021	latrans	unknown	Montana: Big Porcupine Creek
AMNH 99653	latrans	male	NY: Franklin County, Belmont
MCZ 59348	latrans	male	
MCZ 59701	latrans	female	
MCZ 59686	latrans	female	
MCZ 60129	latrans	unknown	
MCZ 60058	latrans	female	
MCZ 60059	latrans	male	
MCZ 60610	latrans	male	
MCZ 60611	latrans	unknown	
MCZ 60970	latrans	male	
MCZ 60985	latrans	male	
MCZ 61020	latrans	male	
MCZ 61425	latrans	male	
MCZ62077	latrans	male	
MCZ 62027	latrans	male	
MCZ 61897	latrans	female	
MCZ 62624	latrans	male	
MCZ 62195	latrans	male	
MCZ 61415	latrans	female	
MCZ 63141	latrans	female	
MCZ 50913	latrans	male	
MCZ 63142	latrans	male	
NCSM 7164	latrans	unknown	Craven/Jones City Line, NC
NCSM 7823	latrans	male	Tyrrell City, NC
NCSM 8191	latrans	male	Henderson Co, NC

NCSM 8183	latrans	male	Cherokee Co, NC
NCSM 5251	latrans	male	
NCSM 8326	latrans	unknown	Haywood Co
NCSM 8325	latrans	female	Caswell Co,NC
NCSM 8204	latrans	female	Hyde Co, NC
NCSM 8187	latrans	male	Bertle/Washington
NCSM 8205	latrans	male	
NCSM 2450	latrans	female	Smithfield Johnston CO
AMNH 134940	lupus	male	Minn: Cook County, Swamper Lake
AMNH 134941	lupus	male	Minn: Cook county, South Lake
AMNH 134944	lupus	female	Minn: Cook County, Pike Lake
AMNH 98225	lupus	female	Alberta: Wood Buffalo, Snake River
AMNH 98226	lupus	male	Alberta: Wood Buffalo, Snake River
AMNH 98227	lupus	female	Alberta: Wood Buffalo, Snake River
AMNH 98230	lupus	male	Alberta: Wood Buffalo, Snake River
AMNH 98231	lupus	male	Canada: Alberta, Wood Buffalo
AMNH 98232	lupus	female	Alberta: Wood Buffalo, Snake River
MCZ 267	lupus	unknown	Kansas
MCZ 268	lupus	unknown	Kansas
MCZ 59176	lupus	unknown	Alberta, Banff National Park
MCZ 62506	lupus	female	Maine: Russel Pond
USNM 173882	lupus	male	
USNM 269140	lupus	male	
USNM 271651	lupus	male	Montana: Three Forks
USNM 324994	lupus	male	Anchorage
USNM 530900	lupus	female	
USNM A00977	lupus	female	Montana, Fort Union
USNM A01308	lupus	male	Fort Kearny Nebraska
USNM A01384	lupus	unknown	Mexico: Matamoras
USNM A02567	lupus	male	Colorado, Platte River
USNM A03497	lupus	unknown	Montana, Missouri River
USNM A49978	lupus	female	
AMNH 134942	lycaon	female	Minnesota: Cook County, South Lake
MCZ 326	lycaon	unknown	
MCZ 51378	lycaon	female	Ontario
MCZ 56610	lycaon	unknown	Ontario: Kapuskasing
MCZ 56611	lycaon	unknown	Ontario: Kapuskasing
MCZ 56612	lycaon	unknown	Ontario: Kapuskasing
USNM 268194	lycaon	unknown	Eastern Canada
AMNH 100225	rufus	unknown	Mississippi: Biloxi, Harrison Co line
NCSM 6338	rufus	male	NC Dare City ARNWR release project
USNM 135445	rufus	unknown	Texas
USNM 249694	rufus	female	Texas Parker County
USNM 273254	rufus	female	Angleton TX
USNM 273254	rufus	female	Angleton TX
USNM 273255	rufus	male	Hallettsville TX

USNM 274107	rufus	female	Angleton TX
USNM 348063	rufus	unknown	New Morgue Cave near Huntsville, AL

3.1.2 *Ursus*

The genus *Ursus* was chosen because the species in this genus represent a wide range of ecological, behavior, and morphological diversity. Unlike *Canis*, in which the species sampled here are similar in ecology and locomotion, differing mainly in body mass, *Ursus* is a quite variable genus in which comparisons across groups are more likely to yield conclusions linked to ecological factors than morphological features. There are three species included in this study, and a more complete description of the individuals in the sample can be seen in Table 7. This sample encompasses a wide range of body mass (Table 6, Figure 4), but each group is distinct.

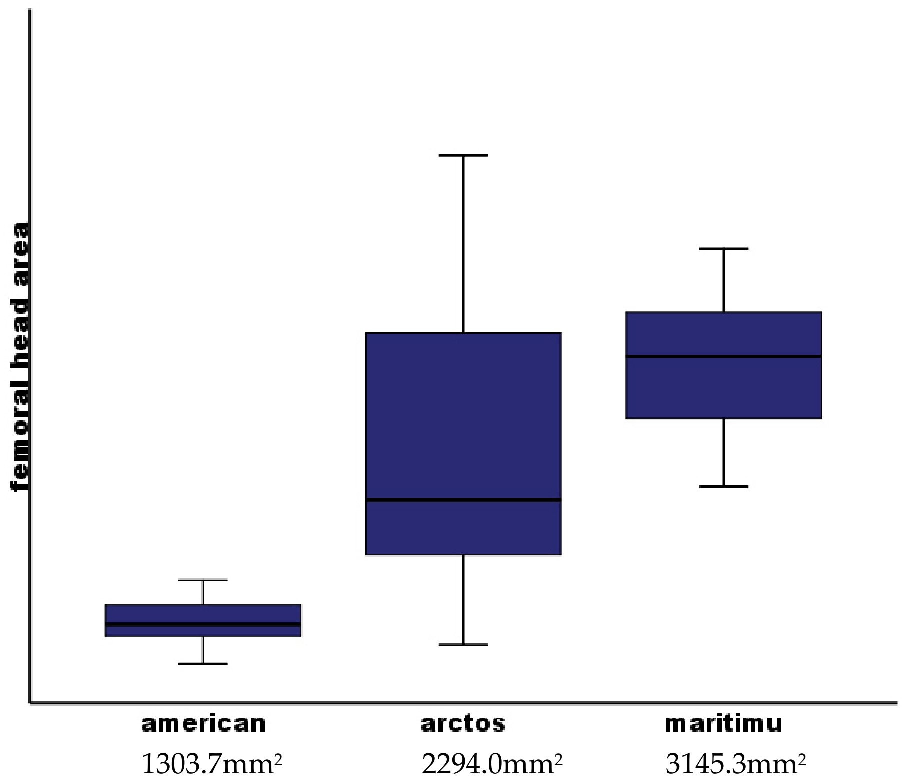


Figure 4: Femoral head area for the three species of *Ursus* (boxes represent 95% confidence intervals, whiskers the total range of sample)

3.1.2.1 *Ursus americanus* Pallas 1780

The black bear, *Ursus americanus*, is the smallest of the extant *Ursus* species. There are as many as 16 recognized subspecies of black bears in North America (Hall, 1981). There are 14 individual black bears in this sample (3 males, 1 female, and 10 of indeterminate sex) from the SI and AMNH. Most of these individuals were collected from the eastern US. There are also two from Alaska, one from Idaho, one from Wyoming and one from New Mexico. This species has the greatest geographic distribution of the three ursids included here.

Black bears are widely distributed throughout North America. They first appeared in the fossil record during the mid-Pleistocene (Kurtén and Anderson, 1980).

There was an increase in body mass in this lineage during the Pleistocene, then a decrease during the Holocene (Kurtén and Anderson, 1980). Black bears are omnivorous and are opportunistic foragers (Boileau et al. 1994; Maehr and Brady 1984; Noyce et al. 1997; Smith et al. 1994). They also hunt on occasion, usually taking small mammals or white-tailed deer or moose (Austin et al., 1994; Kunkel and Mech, 1994). Black bears often live alongside brown bears, but competition between the two species is limited due to differences in resource selection and habitat preferences (Aune, 1994). This is a solitary species, like the other *Ursus* species, with no natural predators, aside from humans.

3.1.2.2 *Ursus arctos* Linnaeus, 1958

The grizzly bear, *Ursus arctos*, is represented by 19 individuals (8 males, 5 females, and 6 of indeterminate sex) from the SI and the AMNH. Geographically, the sample includes individuals from Alaska, Wyoming, California, British Columbia, Washington and the Northwest Territories. The age range of the sample is 4 years to 35 years old. They were collected in 19th and 20th centuries. In terms of body mass, there is a wide range among this species, with the largest individuals coming from Alaska, and specifically Kodiak Island.

Grizzly bears historically occupied much of western North America, including Mexico. They are presently prevalent in Alaska and Canada and in managed population in the western US (Servheen, 1990). There are also populations of grizzly bears in Eurasia, but none of the individuals sampled here come from outside of North America.

The grizzly bear first appears in the fossil record 500,000 years ago and shares a common ancestor with the cave bear, *Ursus spelaeus* (Kurtén, 1968). Grizzly bears are omnivorous and opportunistic feeders (Bunnel and Hamilton, 1983; LeFranc et al., 1987; Nowak and Paradiso, 1983). They also prey actively on moose (Ballard et al., 1981; Larsen et al., 1989), caribou and wild boar (Danilov, 1983). Grizzly bears are solitary animals, but are not territorial (Le Franc et al., 1987; Murie, 1985). Compared with the other groups in this study, the grizzly bear is considerably larger than the black bear, but similar to it ecologically. It is more similar to the polar bear in terms of body mass, but differs from this species ecologically.

3.1.2.3 *Ursus maritimus* Phipps, 1774

There are eight polar bears (1 female, 3 males and 4 of indeterminate sex), *Ursus maritimus*, sampled in this research. All are from either Alaska or Canada, although polar bears are found also in circumpolar areas of Europe and Russia. Most of the individuals were collected in the latter half of the 20th century, and one was collected at the end of the 19th century.

The polar bear is a specialized species that diverged from the brown bear 200,000 years ago and is superbly adapted to a circumpolar environment (Kurtén, 1964). The polar bear varies greatly in size, with a latitudinal cline observed (Manning, 1971). Ranges of body mass for this species are included in Table 5. This species is highly sexually dimorphic, with males up to three times as large as females (DeMaster and Stirling, 1981). Ecologically, this bear is very different from the other bear species. It is highly carnivorous and does the majority of its hunting through 'still-hunting' (Stirling and Latour, 1978), which essentially involves waiting next to a breathing hole for a seal to surface. This is obviously a far different hunting style than the active group hunting that is undertaken by the wolf species discussed earlier. The polar bear primarily hunts ringed seals (Stirling and McEwan, 1975; Stirling and Archibald, 1977) and have also been observed scavenging the carcasses of large marine mammals including whales and walruses (Russell, 1975; Heyland and Hay, 1976).

The polar bear is also highly specialized with regards to its locomotion. This species lives on land, but possesses many adaptations to swimming in the arctic waters. Polar bears are capable of swimming vast distances. These factors, combined with its unique hunting style, make the polar bear distinct in many respects from the other species of bears included here.

Table 6: Summary of *Ursus* sample

specimen #	species	sex	location
AMNH 128521	americanus	unknown	Maine
AMNH 70357	americanus	unknown	Gulf of St. Lawrence
AMNH 90334	americanus	unknown	Florida
AMNH 24157	americanus	unknown	
AMNH 164283	americanus	unknown	Alaska: Galhunda Valley
AMNH 45149	americanus	male	Alaska: Prince William Sound
AMNH 120843	americanus	unknown	Idaho; Fremont Co. RR Ranch
USNM 308296	americanus	female	W. Virginia Buchhannon
USNM 269999	americanus	unknown	
USNM 255072	americanus	male	New Mexico
USNM 283630	americanus	unknown	Wyoming: Yellowstone Nat. Park
USNM 303193	americanus	unknown	Pennsylvania
USNM 2359	americanus	unknown	
USNM 219285	americanus	male	Alaska: Cook's Inlet
USNM 216206	arctos	male	Alaska: Chichagof Island
USNM A16624	arctos	unknown	California McCloud River
USNM 199252	arctos	male	Alaska: Cape Douglas
USNM 218229	arctos	male	
USNM 283629	arctos	unknown	Wyoming - Yellowstone Nat. Park
USNM 301690	arctos	female	Wyoming - Yellowstone Nat. Park
USNM 269998	arctos	male	
AMNH 128463	arctos	unknown	British Columbia
AMNH 21802	arctos	male	Alaska Peninsula
AMNH 135504	arctos	unknown	Alaska
AMNH 135502	arctos	male	Alaska: Canoe Bay Alaska Pen
AMNH 34903	arctos	unknown	Alaska: Chichagof Island
USNM 203761	arctos	female	Wyoming
USNM 243786	arctos	male	Washington; Holman Pass
USNM 021691	arctos	female	
USNM 008125	arctos	unknown	NW Territories; Franklin Bay
USNM 007188	arctos	male	NW Territories; Anderson River
USNM 265076	arctos	female	Alaska: St Lawrence
USNM 252303	arctos	female	Alaska: Kodiak Island
USNM 271322	arctos	male	
AMNH 125407	horribilis	female	British Columbia: Robb Lake Pass
AMNH 45150	horribilis	female	Yukon: Whitehorse
AMNH 100039	maritimus	unknown	Alaska
AMNH 215283	maritimus	female	
USNM 275121	maritimus	unknown	Canada; NW Terr. Bylot Island
USNM 260231	maritimus	male	South of Franz Joseph Land
USNM 218230	maritimus	unknown	
USNM 275124	maritimus	unknown	Canada: NW Terr. Devon Island
USNM 275117	maritimus	male	Bylot Island
USNM A16739	maritimus	male	Alaska: Goglaamie Village

3.2 Methods

3.2.1 Data collection

This section will describe the data collection procedure for a specimen for which all postcranial elements were available, and for which x-rays were taken. Not all specimens had all of the available elements, and there were a number of individuals, especially in the *Ursus* group, for which it was not possible to take x-rays due to logistical problems. Table 8 defines each variable that was measured in this study. Table 8 describes the units of each of these variables, any modifications that were done, and the resulting units of the variables that were used in subsequent regressions.

Table 7: Definition of variables

Variable	Definition	reference (if any)
femur length	"the size of the vector parallel to the longitudinal axis from the proximal point of the femoral head to the midpoint between the distal points of the two condyles" (502)	Egi, 2001
femoral head area	Superior-inferior and medial-lateral lengths of the femoral head	Rafferty, 1996
distal femur	"sum of medial and lateral condyles" (504)	Egi, 2001
femur midshaft ml diameter	Midshaft is determined by ½ of femur length; medial-lateral diameter is perpendicular to the long axis of the femur as defined above as femur length	
femur midshaft ap diameter	Midshaft diameter perpendicular to the medial-lateral diameter	
humerus length	"most proximal point of the humeral head to the mid-point between the most distal points of the trochlea and capitulum" (502)	Egi, 2001
distal humeral breadth	"sum of the capitulum and trochlea" (504);	Egi, 2001
humerus ap diameter	Midshaft diameter perpendicular to the medial-lateral diameter	Bertram and Biewener, 1990
humerus ml diameter	ML diameter is parallel to long axis of distal humerus; midshaft is 50% of length of bone	
tibia length	"proximal and distal points of tibial length are set as the anterior edge of the condyles and the mid-point of the talar articular surface, respectively" (502)	Egi, 2001
proximal tibial breadth	Maximum breadth of the tibial plateau posterior to the tibial condyles in the medial-lateral direction	
tibia midshaft ap diameter	Midshaft diameter perpendicular to the medial-lateral diameter	
tibia midshaft ml diameter	ML diameter is parallel to the long axis of the proximal tibial surface; midshaft is 50% of length	

I first examined each specimen to make sure that it was skeletally mature by checking that all epiphyses were fused and that there were no deciduous teeth (if cranial remains were available). Next, I made sure that there were no pathologies (bone disease, healed fractures, extreme porosity) that would possibly alter measures of postcranial robusticity either through a shape change in the bone or through systemic influences on bone biology. If I deemed the specimen suitable after these examinations, I would record all the information on the catalogue card. This always included a museum specimen number and species. It often also included the date it was collection, its location, who the collector was, body mass, and notes about its collection.

The next step was to take the postcranial measurements using a variety of instruments. The lengths of the long bones were measured using an osteometric board or, for the largest of the *Ursus* individuals, a homemade osteometric board, consisting of millimeter graph paper and a flat vertical edge on either side. A description of the linear measures of each bone can be found in Table 8. Once bone length was ascertained, the diameters of each bone were measured at midshaft in both the anterior-posterior and medial-lateral dimensions (following Biewener, 1983; Bertram and Biewener, 1990). These measurements were taken using Mitutoyo digital calipers. The calipers had a maximum length of 150mm, and were used for many postcranial and cranial measurements. The medial-lateral plane corresponds to the medial-lateral axis of the distal joint surface for the femur and humerus, and the proximal joint surface of the tibia. The anterior-posterior plane is found at 90º to that plane. The bones were aligned with a flat surface, usually a table, so that these planes were as close to the actual planes as possible. Femoral head area was calculated by the product of the length of the joint surface in the superior-inferior direction and the width of the joint surface in the anterior-posterior direction (Rafferty, 1996). Maximum dimensions were used in these cases. The distal femoral breadth was likewise measured as the maximum width of the distal femur on its inferior surface. The distal humeral breadth was also measured in this manner. The proximal tibial breadth was measured as the widest breadth of the tibial plateau in the medial-lateral direction.

X-rays were available for much of the *Canis* group, and few of the *Ursus*. The settings of the machine were different for each group due to the differences in bone width. Biplanar radiographs of femora were taken using an Acoma Super 80 portable x-ray unit. The settings used on Kodak Industrex MX125 film were 15kvp, 70 MA for 8 seconds for the *Canis* sample and 30-40 seconds for the *Ursus* sample. The settings for the x-ray for each genus were determined by trial and error. The x-ray film was individually packaged and so it was possible to use the machine in the collections room of each museum without moving specimens to a special facility. Each femur and humerus was oriented with the long axis of the distal joint surface parallel to the ground; the tibia was oriented with the long axis of the proximal joint surface parallel to the ground. X-rays taken with the bone in this orientation provided the medial-lateral measurements. The bone was then rotated 90º. The x-rays taken from this orientation provided the anterior-posterior measurements (Ruff and Hayes, 1983).

Once back at Duke, the x-rays were developed in one of two ways. The department of radiology at Duke University Medical Center had a processor that they allowed me use of to develop the x-rays. Many of the sheets of film were developed in this manner. However, this was 'old' technology, and the processor was not maintained because there were better radiological options available (i.e. digital film) for the hospital. Therefore, when this machine broke, I had to develop the remainder of the film in a dark room. Developing chemicals specific to the type of film were used and the resulting images were comparable to those that were obtained by using the processor. Cortical bone width, total bone diameter, and medullary cavity diameter were measured directly on the x-rays using digital calipers (Stock, 2002; O'Neill and Ruff, 2004). These dimensions were then used to calculate bone strength.

3.2.2 Determination of bone strength

Variations of cross-sectional dimensions of bone have been used to describe behavioral and locomotor differences between groups of animals. For the analyses here, three different measures of estimating bone strength were used. The second and polar moments of area of a bone (I and J), and the anterior-posterior and medial-lateral diameters, all at the midshaft of the bone were used to estimate or approximate bone strength. A summary of these measurements, including their units and any adjustments to the variable can be found in Table 9.

The second moments of area describe the bending (I) and torsional (J) strength of a bone around an axis or centroid using mechanical principles that model the bone as a hollow beam (Timoshenko and Gere, 1972; Lovejoy et al., 1976; see also Daegling, 1989 for a cautionary approach). The use of these variables depends on the assumption that the structural properties of bone are the main determinant of strength and that the material properties of bone remain relatively constant or do not have much effect on the variation of the overall strength of the bone. This assumption has been upheld by experimental studies (Woo et al., 1981; Lanyon et al., 1982; Martin and Burr, 1982; Rubin, 1984; Frost, 1985; Rubin and Lanyon, 1982, 1985; Frost, 1987; Lanyon, 1987; Martin and Burr, 1989; Rubin et al., 1994; Trinkaus et al., 1994).

The formulas to calculate I and J use the ellipse model method (Ruff, 1989, 1995; Biknevicius and Ruff, 1992; Ohman, 1993; Runestad et al., 1993; Lazenby, 1997, 1998):

$I_{ap} = (\pi/64)*[(\text{ML diameter}*\text{AP diameter}^3) - (\text{ML med. cavity}*\text{AP med. cavity}^3)]$

$I_{ml} = (\pi/64)*[(\text{AP diameter}*\text{ML diameter}^3) - (\text{AP med. cavity}*\text{ML med. cavity}^3)]$

$J = I_{ml} + I_{ap}$

An explanation of exactly what I and J measure is demonstrated in Figure 5. These variables determine strength by calculating the amount and distribution of cortical bone around a neutral axis. Lieberman (2001) pointed out that in a living, moving individual, the neutral axis is constantly changing. Despite this fact, the strength of a bone can be measured using this method and model and the results of the relative strength measured can be compared with like measurements from closely related species.

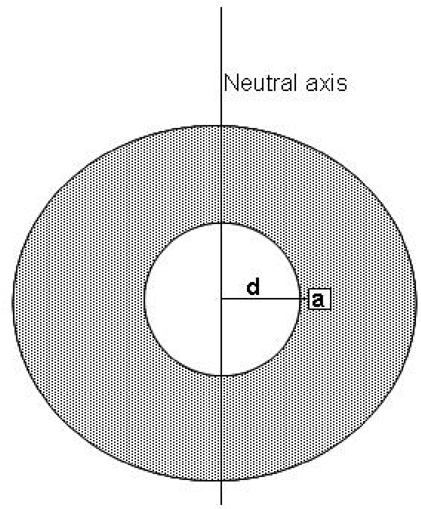


Figure 5: The second moment of area is measured by the area of unit of bone multiplied by the square of its distance from the neutral axis.

The section modulus (Z) is calculated by dividing the second moment of area (I) in a particular plane by half of the bone width of that plane at the level from which the cross-section was measured (that is midshaft here in all cases). Half of bone width in the plane being measured is used to approximate the maximum distance from the neutral axis of the bone. This is only an approximation, and not a real value because the neutral axis of a bone is constantly changing (Lieberman, 2001). Adding bone tissue on the periosteal surface will make a bone stronger than if bone tissue were added in the medullary cavity. The section modulus minimizes this effect, which, in larger animals, will have a heavy influence on measures of bone strength. Some researchers view the section modulus as a more accurate and useful representation of bone strength that the second moment of area measurements.

The final estimate of bone strength that is used here is the medial-lateral and anterior-posterior diameters of each bone at midshaft. In the absence of x-ray or CT resources, bone midshaft diameters can be used to approximate bending strength in a particular plane (Stock and Shaw, 2007). Although this method is not as accurate as those using the x-rays, it is a good substitute and allows for a larger sample to be included in these analyses. Due to the method in which the second moments of area are measured (as the product of a unit area and the square of the distance of that unit from the neutral axis of a bone), bone deposition on the periosteal surface will have a stronger impact on measures of bone strength than bone deposited on the medullary surface. Therefore, midshaft diameters are a suitable, although not ideal, substitute for actual bone strength.

Table 8: Units of measurement and modifications of variables used (all data were logged after any modifications)

variable	units of measurement	modifications	units of measurement after modifications
bone length	mm	none	mm
bone diameter (anterior-posterior and medial-lateral)	mm	none	mm
femoral head area	mm^2	square root	mm
joint surface breadth (distal humeral and proximal tibial)	mm	none	mm
I	mm^4	fourth root	mm
J	mm^4	fourth root	mm

3.2.3 Analysis

The use of a Model II regression, reduced major axis (RMA) is used in all analyses. RMA assumes that there is error in both variables. The use of this type of regression is more appropriate for biological data for which there is error, than are Model I regression techniques such as least-squares (Aiello, 1992; Sokal and Rohlf, 1981). SPSS was used for all statistical analyses. All data for regression analyses were logged. RMA was done using a script in SPSS syntax that used a bootstrapping algorithm to find the until the best fit line of the data that minimized the squared distance of each point from the line. It stopped taking iterations when no more improvement could be made. Significance of the coefficient was determined through the loss function, which calculated the squared distance of each data point from the regression line. This was subsequently subtracted from 1 to get a p-value. 95% confidence intervals were calculated (Jolicoeur and Mosimann, 1968). Estimates of slopes were considered significantly different from the null hypothesis of isometry if the 95% confidence intervals did not include isometry.

4. Results

4.1 Summary statistics

The raw values of mean, standard deviation, and number of specimens for each variable, categorized by species and sex are provided in Tables 10 through 15. There are a considerable number of specimens of unknown sex included in this sample. Among *Canis* and *Ursus*, males are generally larger than females. The 'unknown' sex category has values that are intermediate between the male and female groups in many cases. The exceptions to this are provided in Table 17. Within *Canis*, there is one species, *C. lycaon*, for which there are no known males. It is expected that the unknown group will have larger mean values than the female group, under the assumption that it contains some male specimens. This is borne out in most cases, again summarized in Table 17.

Due to availability at the museums, the number of individuals for each category varies depending on the element being measured. Individuals were included even if one or more skeletal element was missing or damaged in order to maximize the sample size. Data on the postcrania for these specimens are included because they can be used in analyses of single-element scaling (e.g., tests that are designed to investigate temporal trends through the inclusion of the fossil dire wolf). Each dire wolf specimen is a single isolated element for which there were no associated remains.

Table 9: *Canis* femoral variables (raw data)

species	sex		femur length	femoral head area	distal femoral breadth	femur midshaft ml	femur midshaft ap	IML femur	IAP femur	j femur
dirus	unknown	Mean	247.4	771.3	46.1	19.9	19.4			
		Std. Deviation	9.4	87.4	2.8	1.0	1.1			
		N	47	46	45	47	47			
	Total	Mean	247.4	771.3	46.1	19.9	19.4			
		Std. Deviation	9.4	87.4	2.8	1.0	1.1			
		N	47	46	45	47	47			
latrans	female	Mean	170.1	265.3	26.7	11.6	11.4	751.1	750.2	1,501.4
		Std. Deviation	3.3	11.4	0.8	0.6	0.5	172.8	135.4	295.0
		N	6	6	6	6	6	11	11	11
	male	Mean	176.9	271.3	28.1	11.6	11.6	899.9	904.1	1,804.0
		Std. Deviation	8.8	23.4	1.8	0.8	0.6	240.3	235.8	464.1
		N	11	11	11	11	11	20	20	20
	unknown	Mean	175.5	281.9	27.9	11.5	11.1	809.0	818.0	1,627.0
		Std. Deviation	11.7	47.1	2.5	0.9	1.2	216.5	196.7	407.5
		N	7	7	7	7	7	13	13	13
	Total	Mean	174.8	272.9	27.7	11.6	11.4	835.9	840.2	1,676.0
		Std. Deviation	9.0	29.8	1.9	0.7	0.8	222.5	209.2	421.8
		N	24	24	24	24	24	44	44	44
lupus	female	Mean	227.0	691.1	42.1	16.8	17.1	3,761.0	3,641.6	7,402.6
		Std. Deviation	15.19	92.3	2.1	1.3	2.0	1,697.0	1,542.9	3,228.0
		N	8	4	4	8	8	8	8	8
	male	Mean	235.6	714.1	43.1	17.3	17.5	3,909.6	3,802.7	7,712.3
		Std. Deviation	21.7	125.7	1.9	1.3	2.1	1,364.5	1,234.9	2,571.7
		N	11	5	5	11	11	9	9	9
	unknown	Mean	215.2			15.5	14.9	2,589.5	2,561.4	5,150.9
		Std. Deviation	17.7			1.6	1.3	1,250.0	1,074.7	2,308.3
		N	5			5	5	5	5	5
	Total	Mean	228.5	703.9	42.6	16.8	16.8	3,555.5	3,462.0	7,017.6
		Std. Deviation	19.8	106.0	2.0	1.5	2.1	1,502.9	1,360.0	2,846.2
		N	24	9	9	24	24	22	22	22

lycaon	female	Mean	227.0	610.1	38.7	15.5	15.9	3,049.1	1,165.4	4,214.5
		Std. Deviation	2.8			2.3	1.1	1,084.3	1,129.3	45.1
		N	2	1	1	2	2	2	2	2
	unknown	Mean	234.4			16.4	16.8	3,203.2	3,017.2	6,220.4
		Std. Deviation	18.7			1.4	1.8	538.2	679.5	1,200.3
		N	5			5	5	4	4	4
	Total	Mean	232.3	610.1	38.7	16.2	16.6	3,151.8	2,399.9	5,551.8
		Std. Deviation	15.8			1.6	1.6	644.4	1,202.7	1,392.0
		N	7	1	1	7	7	6	6	6
rufus	female	Mean	202.3			14.3	13.6	1,676.4	1,672.6	3,349.0
		Std. Deviation	5.2			1.8	1.0	707.9	761.1	1,462.7
		N	4			4	4	4	4	4
	male	Mean	205.0	574.8	41.4	14.9	15.6	2,124.1	1,776.4	3,900.5
		Std. Deviation	18.4			1.5	2.2	2,278.8	1,877.2	4,156.0
		N	2	1	1	2	2	2	2	2
	unknown	Mean	214.7	451.6	35.5	14.7	14.4	2,368.8	2,540.5	4,909.3
		Std. Deviation	14.2			1.2	1.1	227.8	230.2	448.6
		N	3	1	1	3	3	3	3	3
	Total	Mean	207.0	513.2	38.5	14.6	14.3	2,006.7	1,985.0	3,991.7
		Std. Deviation	11.7	87.1	4.2	1.4	1.4	978.3	920.0	1,880.4
		N	9	2	2	9	9	9	9	9
Total	female	Mean	205.0	451.5	33.4	14.6	14.6	2,046.2	1,856.3	3,902.4
		Std. Deviation	27.1	221.1	7.8	2.5	2.8	1,679.1	1,579.9	3,182.5
		N	20	11	11	20	20	25	25	25
	male	Mean	206.1	419.4	33.3	14.5	14.7	1,852.7	1,801.9	3,654.5
		Std. Deviation	32.8	219.1	7.5	3.0	3.3	1,607.9	1,515.9	3,114.9
		N	24	17	17	24	24	31	31	31
	unknown	Mean	235.0	702.0	43.5	18.2	17.8	1,735.3	1,725.2	3,460.6
		Std. Deviation	25.6	188.2	6.8	3.0	3.0	1,162.1	1,107.6	2,261.9
		N	67	54	53	67	67	25	25	25
	Total	Mean	223.4	609.8	40.0	16.7	16.5	1,876.2	1,795.0	3,671.2
		Std. Deviation	30.9	235.3	8.5	3.4	3.4	1,495.3	1,407.6	2,871.0
		N	111	82	81	111	111	81	81	81

Table 10: *Canis* humeral variables (raw data)

species	sex		humerus length	distal humeral breadth	humerus midshaft ml	humerus midshaft ap	hum iml	hum iap	j humerus
dirus	unknown	Mean	222.6	34.5	23.5	19.0			
		Std. Deviation	8.4	1.7	1.6	1.1			
		N	29	28	29	29			
	Total	Mean	222.6	34.5	23.5	19.0			
		Std. Deviation	8.4	1.7	1.6	1.1			
		N	29	28	29	29			
latrans	female	Mean	155.8	19.3	11.5	12.6	999.2	654.4	1,653.7
		Std. Deviation	3.2	0.5	0.8	0.4	165.7	41.5	190.8
		N	6	6	6	6	4	4	4
	male	Mean	164.9	20.3	11.6	13.1	1,058.5	637.5	1,696.0
		Std. Deviation	8.7	1.3	0.7	0.7	68.7	52.9	113.7
		N	11	11	11	11	5	5	5
	unknown	Mean	162.8	19.9	11.3	13.1	938.7	584.2	1,522.9
		Std. Deviation	9.9	1.5	1.3	1.6	162.4	31.2	171.7
		N	7	7	7	7	4	4	4
	Total	Mean	162.0	19.9	11.5	13.0	1,003.4	626.3	1,629.7
		Std. Deviation	8.6	1.2	0.9	1.0	133.1	50.1	163.1
		N	24	24	24	24	13	13	13
lupus	female	Mean	213.0	32.0	18.1	20.4	7,916.0	5,090.1	13,006.0
		Std. Deviation	19.0	3.3	1.5	2.5	4,127.2	2,556.4	6,683.6
		N	8	4	4	4	2	2	2
	male	Mean	222.6	33.3	20.0	19.6	5,220.1	2,939.6	8,159.7
		Std. Deviation	21.2	3.0	3.5	1.9			
		N	11	5	5	5	1	1	1
	unknown	Mean	201.6						
		Std. Deviation	18.1						
		N	5						
	Total	Mean	215.0	32.7	19.2	20.0	7,017.3	4,373.2	11,390.6
		Std. Deviation	20.7	3.0	2.8	2.1	3,307.5	2,193.0	5,492.2
		N	24	9	9	9	3	3	3

lycaon	female	Mean	213.5	27.9	16.2	17.6			
		Std. Deviation	0.7						
		N	2	1	1	1			
	unknown	Mean	219.6						
		Std. Deviation	16.5						
		N	5						
	Total	Mean	217.9	27.9	16.2	17.6			
		Std. Deviation	13.8						
		N	7	1	1	1			
rufus	female	Mean	183.8						
		Std. Deviation	10.0						
		N	4						
	male	Mean	188.0	29.9	16.6	18.9			
		Std. Deviation	18.4						
		N	2	1	1	1			
	unknown	Mean	197.3	26.8	15.7	18.4			
		Std. Deviation	16.3						
		N	3	1	1	1			
	Total	Mean	189.2	28.4	16.1	18.6			
		Std. Deviation	13.6	2.2	0.7	0.4			
		N	9	2	2	2			
Total	female	Mean	190.1	24.7	14.3	15.9	3,304.8	2,133.0	5,437.8
		Std. Deviation	28.5	6.5	3.4	4.1	4,022.5	2,560.2	6,582.0
		N	20	11	11	11	6	6	6
	male	Mean	193.3	24.7	14.4	15.4	1,752.1	1,021.2	2,773.3
		Std. Deviation	32.2	6.5	4.3	3.3	1,700.1	941.0	2,640.7
		N	24	17	17	17	6	6	6
	unknown	Mean	210.1	31.5	21.0	17.9	938.7	584.2	1,522.9
		Std. Deviation	23.7	6.1	5.1	2.6	162.4	31.2	171.7
		N	49	36	37	37	4	4	4
	Total	Mean	201.4	28.5	18.1	16.9	2,131.0	1,328.9	3,459.9
		Std. Deviation	28.4	7.0	5.7	3.2	2,711.1	1,710.2	4,418.7
		N	93	64	65	65	16	16	16

Table 11: *Canis* tibial variables (raw data)

species	sex		tibia length	proximal tibial breadth	tibia midshaft ml	tibia midshaft ap	tib iml	tib iap	J tibia
dirus	unknown	Mean	239.4	49.2	19.3	19.6			
		Std. Deviation	11.6	2.7	1.3	1.8			
		N	20	20	20	20			
	Total	Mean	239.4	49.2	19.3	19.6			
		Std. Deviation	11.6	2.7	1.3	1.8			
		N	20	20	20	20			
latrans	female	Mean	181.8	29.4	11.0	10.9	999.2	654.4	1,653.7
		Std. Deviation	2.8	0.4	0.2	0.2	82.9	20.8	95.4
		N	7	7	7	7	4	4	4
	male	Mean	187.4	30.9	11.2	11.4	1,058.5	637.5	1,695.0
		Std. Deviation	7.1	2.1	0.5	0.7	30.7	23.6	50.8
		N	11	11	11	11	5	5	4
	unknown	Mean	183.9	30.7	11.5	11.4	938.7	584.2	1,522.9
		Std. Deviation	12.8	2.6	1.1	1.1	81.2	15.6	85.9
		N	7	7	7	7	4	4	4
	Total	Mean	184.5	30.4	11.2	11.3	1003.4	626.3	1,629.7
		Std. Deviation	9.1	2.1	0.7	0.8	37.0	13.9	45.2
		N	24	24	24	24	13	13	13
lupus	female	Mean	235.9	45.8	16.1	18.2	7916.0	5090.1	13,006.0
		Std. Deviation	19.5	1.6	1.5	0.9	291.8	1,807.7	4,726.0
		N	8	4	4	4	4	4	4
	male	Mean	243.8	46.6	16.9	17.6	5,220.1	2,940.0	8159.7
		Std. Deviation	21.9	2.1	1.5	1.8	408.7	538.4	1,984.8
		N	11	5	5	5	4	4	4
	unknown	Mean	214.5						
		Std. Deviation	13.9						
		N	5						
	Total	Mean	235.1	46.2	16.5	17.8	7,017.3	4,373.2	11,390.6
		Std. Deviation	22.1	1.8	1.5	1.4	1,910.0	1,266.1	3171.0
		N	24	9	9	9	8	8	8

lycaon	female	Mean	234.5	41.5	13.8	14.8	2,071.0	1,922.4	3,993.4
		Std. Deviation	6.4						
		N	2	1	1	1	1	1	1
	unknown	Mean	234.4						
		Std. Deviation	17.4						
		N	5						
	Total	Mean	234.4	41.5	13.8	14.8	2,071.0	1,922.4	3,993.4
		Std. Deviation	14.4						
		N	7	1	1	1	1	1	1
rufus	female	Mean	210.0						
		Std. Deviation	6.1						
		N	4						
	male	Mean	212.5	42.0	15.7	17.9			
		Std. Deviation	17.7						
		N	2	1	1	1			
	unknown	Mean	226.3	39.7	15.0	15.8	2,685.4	2,378.6	5,064.0
		Std. Deviation	14.3						
		N	3	1	1	1	1	1	1
	Total	Mean	216.0	40.8	15.4	16.8	2,685.4	2,378.6	5,064.0
		Std. Deviation	12.8	1.7	0.5	1.5			
		N	9	2	2	2	1	1	1
Total	female	Mean	213.8	36.3	13.1	13.8	2,767.7	2,392.1	5,159.8
		Std. Deviation	27.8	8.4	2.7	3.7	2,065.8	1,783.4	3,828.9
		N	20	11	11	11	8	8	8
	male	Mean	215.4	36.2	13.1	13.6	2,352.2	1,021.2	2,773.3
		Std. Deviation	31.7	7.7	2.9	3.2	2,059.2	384.2	1078.1
		N	24	17	17	17	8	8	8
	unknown	Mean	225.0	44.2	17.2	17.4	1,024.8	985.1	2,009.9
		Std. Deviation	24.2	8.6	3.6	3.9	931.5	781.8	1,709.8
		N	40	28	28	28	5	5	5
	Total	Mean	219.6	40.2	15.1	15.6	2,194.5	1,328.9	3,459.9
		Std. Deviation	27.6	9.1	3.8	4.1	1,906.5	427.5	1,104.7
		N	84	56	56	56	21	21	21

Table 12: *Ursus* femoral variables (raw data)

species	sex		femur length	Femoral head area	distal femoral breadth	femur midshaft ml	femur midshaft ap	Iml	Iap	J femur
americanus	female	Mean	291.0	1,071.3	50.3	24.6	20.9	10,264.2	13,946.7	24,210.9
		Std. Deviation								
		N	1	1	1	1	1	1	1	1
	male	Mean	332.3	1,401.2	60.3	31.1	24.4	20,330.8	33,554.6	53,885.4
		Std. Deviation	22.6	181.4	4.9	0.8	1.6	5,510.1	5,142.8	10,652.9
		N	3	3	3	2	2	2	2	2
	unknown	Mean	324.7	1,297.1	56.7	27.0	23.3	17,640.3	24,779.7	42,420.0
		Std. Deviation	28.4	147.4	4.5	2.2	1.5	5,412.9	10,149.1	15,562.0
		N	9	9	9	3	3	2	2	2
	Total	Mean	323.9	1,303.7	57.1	27.9	23.3	17,241.3	26,123.1	43,364.4
		Std. Deviation	27.0	163.9	4.9	3.0	1.7	5,651.3	9,896.7	15,376.0
		N	13	13	13	6	6	5	5	5
arctos	female	Mean	360.7	1,711.9	65.0	30.6	26.0	21,723.8	37,973.5	59,697.4
		Std. Deviation	40.3	377.3	7.2	4.9	3.5	15,906.0	33,500.0	49,406.0
		N	7	7	7	5	5	2	2	2
	male	Mean	443.3	2,756.6	82.8	38.1	30.3	44,434.7	63,370.4	107,805.1
		Std. Deviation	90.8	743.3	9.5	5.9	5.2	30,457.5	25,858.0	56,315.5
		N	8	8	7	6	6	2	2	2
	unknown	Mean	404.8	2,368.9	74.6	31.1	29.6	36,352.8	62,752.5	99,105.3
		Std. Deviation	67.7	914.1	14.5	5.8	10.2			
		N	5	5	5	2	2	1	1	1
	Total	Mean	404.8	2,294.0	74.1	34.1	28.6	33,734.0	53,088.1	86,822.1
		Std. Deviation	76.5	800.5	12.5	6.3	5.3	20,645.9	25,261.8	45,042.6
		N	20	20	19	13	13	5	5	5
maritimus	female	Mean	364.0	2,161.9	80.6					
		Std. Deviation								
		N	1	1	1					
	male	Mean	460.7	3,427.0	88.6	39.1	32.3	45,983.9	65,627.7	111,611.6
		Std. Deviation	36.3	772.6	7.0	4.5	4.6			
		N	3	3	3	3	3	1	1	1

	unknown	Mean	454.8	3,191.4	88.5	42.0	33.1	78,359.7	117,509.0	195,868.7
		Std. Deviation	41.6	547.5	10.4	5.1	3.2	49,085.2	80,932.9	130,018.2
		N	4	3	3	3	3	2	2	2
	Total	Mean	445.6	3,145.3	87.4	40.5	32.7	67,567.7	100,215.2	167,783.0
		Std. Deviation	47.0	707.7	7.8	4.6	3.6	39,421.8	64,593.3	104,013.4
		N	8	7	7	6	6	3	3	3
Total	female	Mean	353.3	1,690.7	65.1	29.6	25.1	17,904.0	29,964.6	47,868.5
		Std. Deviation	42.0	427.6	9.8	5.0	3.7	13,049.0	27,450.9	40,499.9
		N	9	9	9	6	6	3	3	3
	male	Mean	423.2	2,609.8	79.0	37.1	29.8	35,103.0	51,895.6	86,998.6
		Std. Deviation	84.8	948.1	13.3	5.5	5.1	20,536.6	21,329.4	41,681.8
		N	14	14	13	11	11	5	5	5
	unknown	Mean	375.8	1,946.6	67.6	33.6	28.6	45,670.6	69,466.0	115,136.5
		Std. Deviation	69.7	917.0	15.5	8.0	6.3	39,477.9	61,863.2	101,260.4
		N	18	17	17	8	8	5	5	5
	Total	Mean	387.1	2,121.2	70.8	34.2	28.3	35,198.4	53,592.4	88,790.9
		Std. Deviation	74.3	907.6	14.6	6.8	5.4	28,441.8	42,410.8	70,566.2
		N	41	40	39	25	25	13	13	13

Table 13: *Ursus* humeral variables (raw data)

species	sex		humerus length	distal humeral breadth	humerus midshaft ml	humerus midshaft ap	Iml humerus	Iap humerus	J humerus
americanus	female	Mean	262.0	43.2	24.4	26.5	15,939.9	15,949.8	31,889.7
		Std. Deviation							
		N	1	1	1	1	1	1	1
	male	Mean	281.7	55.6	29.1	33.6	48,751.1	42,174.9	90,926.0
		Std. Deviation	19.0	3.5	2.4	3.5	29,145.0	22,522.2	51,667.2
		N	3	3	2	2	2	2	2
	unknown	Mean	284.1	51.3	26.9	31.3	38,138.8	31,347.4	69,486.3
		Std. Deviation	26.6	3.9	1.1	2.7	15,722.9	10,101.2	25,824.1
		N	9	9	3	3	2	2	2
	Total	Mean	281.9	51.7	27.2	31.3	37,943.9	32,598.9	70,542.8
		Std. Deviation	23.9	4.7	2.2	3.5	21,298.4	16,378.4	37,628.5
		N	13	13	6	6	5	5	5
Arctos	female	Mean	306.4	60.0	30.7	34.6	74,045.7	79,910.9	153,956.5
		Std. Deviation	36.7	5.7	4.1	5.3			
		N	7	7	5	5	1	1	1
	male	Mean	377.9	76.5	38.6	41.3	64,094.4	79,272.4	143,366.8
		Std. Deviation	47.5	9.4	8.2	8.7			
		N	8	8	6	6	1	1	1
	unknown	Mean	343.2	67.8	31.7	35.2	78,076.9	65,997.7	144,074.6
		Std. Deviation	55.9	11.6	6.9	4.8			
		N	6	5	3	3	1	1	1
	Total	Mean	344.1	68.5	34.3	37.6	72,072.3	75,060.3	147,132.7
		Std. Deviation	54.1	11.2	7.3	7.2	7,197.1	7,854.9	5,920.2
		N	21	20	14	14	3	3	3
maritimus	female	Mean	322.0	65.2					
		Std. Deviation							
		N	1	1					
	male	Mean	389.0	85.7	35.6	46.1	98,694.0	68,307.9	167,001.9

		Std. Deviation	30.3	4.1	4.3	7.1			
		N	3	3	3	3	1	1	1
	unknown	Mean	379.3	84.9	37.8	46.4	166,421.1	142,010.3	308,431.4
		Std. Deviation	29.3	9.8	6.5	3.6	102,137.9	113,505.0	215,642.8
		N	4	4	3	3	2	2	2
	Total	Mean	375.8	82.7	36.7	46.3	143,845.4	117,442.8	261,288.2
		Std. Deviation	33.5	9.8	5.1	5.1	82,128.3	90,842.5	172,969.2
		N	8	8	6	6	3	3	3
Total	female	Mean	303.2	58.7	29.6	33.3	44,992.8	47,930.4	92,923.1
		Std. Deviation	35.7	7.8	4.5	5.8	41,087.0	45,227.3	86,314.3
		N	9	9	6	6	2	2	2
	male	Mean	359.6	74.0	36.0	41.2	65,072.6	57,982.5	123,055.2
		Std. Deviation	56.7	12.9	7.2	8.2	28,945.8	22,853.8	48,572.8
		N	14	14	11	11	4	4	4
	unknown	Mean	322.8	63.4	32.1	37.7	97,439.4	82,542.6	179,982.0
		Std. Deviation	54.0	15.7	6.7	7.5	83,072.8	79,959.1	162,692.3
		N	19	18	9	9	5	5	5
	Total	Mean	330.9	66.0	33.2	38.1	76,133.9	67,318.5	143,452.4
		Std. Deviation	55.1	14.4	6.8	7.9	60,419.0	56,076.3	115,691.8
		N	42	41	26	26	11	11	11

Table 14: *Ursus* tibial variables (raw data)

species	sex		tibia length	proximal tibial breadth	tibia midshaft ml	tibia midshaft ap	Iml tibia	Iap tibia	J tibia
americanus	female	Mean	230.0	58.4	18.6	23.7	11,527.0	6,534.9	18,061.9
		Std. Deviation							
		N	1	1	1	1	1	1	1
	male	Mean	256.3	66.9	20.3	30.9	22,851.7	11,012.1	33,863.8
		Std. Deviation	11.6	5.1	0.9	0.3	7,442.7	2,510.4	9,953.2
		N	3	3	2	2	2	2	2
	unknown	Mean	250.3	63.3	21.0	25.1	21,154.4	13,865.6	35,020.0
		Std. Deviation	20.4	4.0	2.2	1.9	2,280.6	470.9	1,809.8
		N	9	9	3	3	2	2	2
	Total	Mean	250.2	63.8	20.4	26.8	19,907.8	11,258.1	31,165.9
		Std. Deviation	18.5	4.5	1.7	3.5	6,149.7	3,261.6	8,920.8
		N	13	13	6	6	5	5	5
arctos	female	Mean	268.3	72.1	23.1	31.0	45,909.7	23,130.6	69,040.3
		Std. Deviation	29.2	8.6	4.3	3.6			
		N	7	7	5	5	1	1	1
	male	Mean	321.9	90.2	25.9	36.7	53,335.5	30,424.3	83,759.8
		Std. Deviation	40.2	12.9	3.7	11.7	19,239.9	11,481.2	30,721.1
		N	7	7	5	5	2	2	2
	unknown	Mean	298.2	81.8	22.4	29.4	35,449.3	21,294.6	56,743.9
		Std. Deviation	44.9	15.6	2.3	2.3			
		N	5	5	2	2	1	1	1
	Total	Mean	295.9	81.3	24.1	33.1	47,007.5	26,318.4	73,325.9
		Std. Deviation	42.8	14.1	3.8	8.1	13,964.9	8,184.0	22,021.6
		N	19	19	12	12	4	4	4
maritimus	female	Mean	266.0	84.1					
		Std. Deviation							
		N	1	1					

	male	Mean	343.3	101.4	29.7	41.5			
		Std. Deviation	20.3	11.5	4.8	3.3			
		N	4	4	4	4			
	unknown	Mean	337.5	100.0	28.6	40.5			
		Std. Deviation	29.8	9.2	4.7	3.1			
		N	4	4	3	3			
	Total	Mean	332.1	98.8	29.2	41.1			
		Std. Deviation	33.3	10.6	4.3	3.0			
		N	9	9	7	7			
Total	female	Mean	263.8	71.9	22.4	29.8	28,718.3	14,832.8	43,551.1
		Std. Deviation	28.3	9.9	4.3	4.4	24,312.2	11,734.9	36,047.2
		N	9	9	6	6	2	2	2
	male	Mean	313.9	88.4	26.2	37.4	38,093.6	20,718.2	58,811.8
		Std. Deviation	43.9	16.5	4.9	8.6	21,251.1	13,101.6	34,314.5
		N	14	14	11	11	4	4	4
	unknown	Mean	283.0	76.6	24.2	32.0	25,919.4	16,341.9	42,261.3
		Std. Deviation	46.5	17.6	4.7	7.6	8,409.3	4,302.0	12,607.4
		N	18	18	8	8	3	3	3
	Total	Mean	289.3	79.6	24.7	33.8	31,952.1	17,951.6	49,903.7
		Std. Deviation	45.6	16.9	4.8	7.9	17,205.8	9,666.4	26,746.7
		N	41	41	25	25	9	9	9

4.2 Test for sex differences

This is a mixed sample of males and females and so the first step in analyzing this data is to determine whether there is significant sexual dimorphism in any of the raw or derived variables used in the analyses. Tables 10-15 provide the raw data for the variables used in this dissertation. Sex was unknown for a large number of individuals. One way to look at size distribution according to sex is to see where the unknown category of individuals falls relative to known male and female groups. Table 17 is an illustration of the unknown groups relative to the known groups. The expectation is that each unknown group would be a mix of males and females, and thus the means for this group would fall between the means for the males in the females. However, in some cases, the unknowns are larger or smaller than both males and females; additionally, there are a few cases in which the female group mean for a particular variable is larger than the male group mean. These results attest to the high variability of the sample groups used here, partly attributable to the wide geographic range from which the samples came.

Using the data provided in Tables 10-15, the Mann-Whitney U test was used to test for differences between males and females for each species. The results are summarized in Table 16. There are very few instances in which these data show significant size dimorphism between males and females. This is likely due to a combination of small sample size and high variability in each group, since there is documented sexual dimorphism in each species sampled for this dissertation.

Within *Canis*, there are two species (*Canis latrans* and *Canis lupus*) that exhibit considerable amounts of sexual dimorphism in this sample. *C. latrans* males and females are significantly different in measures of humerus length and tibia length. *C. lupus* does not demonstrate significant dimorphism in any of the postcranial measurements. There was no significant dimorphism in the other two extant species. Although the sample sizes of *C. latrans* and *C. lupus* are comparable (and small), the standard deviation of the means of the *C. lupus* variables is higher than that of *C. latrans* in nearly every case. This pattern indicates that there is considerable variability among the postcranial variables of gray wolves because the standard deviations are large. Because of this high amount of variability, combined with the small sample size, it is difficult to detect sexual dimorphism within this sample. There are differences in body mass between male and female *C. lupus* (Mech, 1974), but there is considerable overlap because of the high amount of geographic diversity in body mass among this species. Since the sample here is not restricted geographically, there differences between the sexes are obscured slightly with regards to the body mass differences that might otherwise be apparent in a sample group from a tighter geographic range.

The species with the most amount of sexual dimorphism in the sample is *Ursus arctos*. Grizzly bears are highly dimorphic, and also show geographic variation in body mass (Servheen, 1990). Due to the small sample size of *U. maritimus*, there are no significant differences between the sexes in polar bears. However, this species is known to be highly sexually dimorphic (DeMaster and Stirling, 1981). The largest male polar bears can be up to three times as large in body mass and the smallest female polar bears. As with the *C. lupus* sample, the high amount of variability in body mass inherent in this species makes detecting sex differences difficult. The great range in body mass possible in both males and females, combined with the small sample size (1 known female, 3 known males) contribute to the absence of statistically significant sex differences between the groups. There are several variables for which the unknown sample group of *U. maritimus* is greater in size than both the male and female groups (see Table 17). The unknown group may consist mostly or entirely of males, but given the size range of this species, it is not possible to say this for sure.

A close examination of possible sexual size dimorphism in this sample is important for understanding the composition of the sample group, but with a small sample size that encompasses a wide geographic range, it may not be possible to detect the dimorphism in every case. The regressions and other analyses done in Chapters 4 and 5 of this dissertation should not be adversely affected by sexual dimorphism in the sample, whether or not it was detected by these tests, because each variable tested is tested for scaling patterns on another measurement, either bone length or femoral head area, from that same individual. In addition, the use of individual specimens for analysis instead of species means will allow any patterns of sexual dimorphism to be detected.

Table 15: Mann Whitney U test for differences between the sexes - only significant results reported.

Species (female, male)	femur length	distal femoral breath	femoral head area	midshaft ml	humerus length	tibia length
C. latrans (6, 11)	ns	ns	ns	ns	0.02	0.04
C. lupus (8, 11)	ns	ns	ns	ns	ns	ns
U. arctos (6, 7)	0.02	0.01	0.01	0.03	0.01	0.01

Table 16: *Canis* and *Ursus* unknown sex categories relative to known males and females

	unknown	latrans	lupus	rufus
femur	larger	femoral head		femur length, Iap, Iml, J
	smaller		Femoral length, midshaft ap, Iml, Iap, J	
humerus	larger			humerus length
	smaller	midshaft ml, Iml, Iap, J	humerus length, midshaft ml*,	
tibia	larger	tibia ml, tibia ap,		tibia length
	smaller	Iml, J	tibia length	

	unknown	americanus	arctos	maritimus
femur	larger			midshaft ml***, midshaft ap***, Iml***, Iap***, J***
humerus	larger	humerus length	Iml****, J****	midshaft ml***, midshaft ap***, Iml***, Iap***, J***
	smaller		Iap	
tibia	larger	midshaft ml, Iap, J		
	smaller		midshaft ml, midshaft ap, Iml, Iap, J	

*intermediate, but males are smaller than females	**no unknowns, but males are smaller than females	***no females, but unknowns are larger than males	****unknowns are larger than both, but females are larger than males

4.3 Are there skeletal shape differences within genera?

A change in bone shape that accompanies size increases or decreases is allometry (Gould, 1966). As body mass increases in mammals, the cross-sectional area of long bones must bear proportionally greater weight because body mass increases to the third power whereas cross-sectional area increases to the second power. Theoretically, bone stresses can be reduced through either an increase in cross-sectional dimensions thereby increasing the area over which load is distributed, through decreasing the bending moment arms (i.e., by having proportionally shorter long bones) thereby reducing the bending moment acting at each cross-section, or through changing behavior such that external loads are reduced.

Changes in bone shape are evaluated here from reduced major axis regressions of mid-shaft diameter relative to bone length. All values are logged. These regressions will determine whether bone diameters and bone lengths increase at the same rate, or whether there are shape differences that accompany size increases, which would indicate allometry. The first set of contrasts in this section examines size related shape changes in bone diameter scaling relative to bone length in large versus small mammals. Section 4.4.2 will discuss these results in the context of the geometric and elastic similarity hypotheses with reference to the predictions of Bertram and Biewener (1990) and the results obtained in several other mammalian scaling studies (Demes, Jungers and Selpien, 1991; Jungers and Burr, 1998; Heinrich and Biknevicius, 1998; Christiansen, 1999a).

The second set of contrasts in this section examines the scaling patterns of mechanical strength variables (I and J) relative to bone length. An understanding of shape changes in bone will provide a context in which to evaluate how a bone adapts to its mechanical environment through bone strength as measured at the midshaft of the bone. Therefore, there is an exploration of bone strength, expressed as second moments of area and polar moment of area, on bone length accompany the regressions of the diameters on bone length. I and J are measured in mm^4, and in these analyses the fourth root of this variable was taken, and the log of the fourth root was used in the regression, along with the log of bone length. These regressions are expected to follow the same patterns as those of bone diameters on bone length, based on the high correlation between bone diameter and second and polar moment of area (O'Neill and Ruff, 2002; Stock and Shaw, 2007). Although body mass is not used as the independent variable in any of these analyses, it is, of course, positively correlated with long bone length in the *Canis* and *Ursus* sample. An evaluation of both diameters and mechanical strength measures compared to body mass will come in section 4.5.

By convention, the null hypothesis for evaluating shape changes in bone is geometric similarity (Alexander et al., 1979). Geometric similarity means that cross-sectional diameter and bone length increase at the same rate. If they do increase at the same rate, this indicates isometry of scaling of these variables. An isometric increase, though, is generally interpreted to signify that the bones are relatively weaker because the loads they incur are a function of body mass (which increases to the 3rd power), but the ability to resist the loads is a function of cross-sectional area, (which increases to the 2nd power). Thus, positive allometry of bone diameter on bone length is necessary for maintaining strength as size increases, but there is no consensus as to how much positive allometry is enough.

4.3.1 Results

Tables 17-19 summarize the results of reduced major axis regressions of the log of bone cross-sectional dimensions on the log of bone length for the femur, humerus and tibia of *Canis* and *Ursus*. The log of the fourth root of the strength variables, I and J were used so that the expected isometric slope of all regressions is 1. RMA was done using a script in SPSS syntax that took iterations of the data until the best fitting coefficients of the data were found. Significance of the coefficient was determined through the loss function, which calculated the squared distance of each data point from the regression line. This was subsequently subtracted from 1 to get a value equivalent to p-value. *Canis* scales with with significant positive allometry of cross-sectional dimensions on limb length (slope > 1) in all but one example (humeral Iap; slope 1.36; 95% CI 0.97 – 1.74). The confidence interval of this slope is very wide and isometry is included within its limits. The lack of clear positive allometry of this regression is due to the large confidence intervals, which are likely a result of very high variability of this sample. All of the midshaft diameters in *Canis* scale with positive allometry, which means that there is shape change of bone diameter relative to the bending moment load arm (bone length). Among *Ursus*, however, there is either of isometry or positive allometry for each regression of bone diameter on bone length. The femoral diameters and the humeral medial-lateral diameters scale with isometry, but the tibial diameters and the humeral anterior-posterior diameters scale with positive allometry. However, all of the bone strength variables in *Ursus* scale with statistical isometry for all three bones.

4.3.1.1 Femur

The null hypothesis for the scaling of cross-sectional diameter on bone length is isometry, which yields a predicted slope of 1. These results show that there is shape change of the femur in *Canis*, with longer femora having relatively thicker cross-sections than shorter femora (Table 18, Figures 6 and 7). In contrast, *Ursus* scales with isometry in both anterior-posterior and medial-lateral diameters on femur length (Table 18, Figures 6 and 7). There is no shape change of the femur detected in *Ursus* at different femur lengths.

Table 17: RMA regressions of femoral cross-sectional dimensions on femur length

X variable	Y variable	slope	intercept	CI slope	R^2	N
Femur length *Canis*	midshaft ml	1.33	-1.93	1.2 – 1.46	.929	86
	midshaft ap	1.43	-2.15	1.34 – 1.52	.958	86
	Iml	1.43	-2.49	1.32 – 1.54	.955	80
	Iap	1.41	-2.44	1.27 – 1.55	.897	80
	J	1.39	-2.33	1.28 – 1.51	.946	80
Femur length *Ursus*	midshaft ml	1.07	-1.24	0.90 – 1.24	.971	25
	midshaft ap	1.01	-1.16	0.87 – 1.15	.980	25
	Iml	1.02	-1.49	0.76 – 1.28	.989	13
	Iap	1.05	-1.52	0.81 – 1.29	.983	13
	J	1.03	-1.42	0.80 – 1.26	.986	13

The second moments of area (I) and polar moment of area (J) follow the same general scaling pattern as the midshaft diameters (Table 18, Figures 8, 9 and 10). Among *Canis*, there is positive allometry of femoral second moments of areas on femur length demonstrating that the larger animals in *Canis* not only have relatively wider bone diameters; they also have relatively greater strength of these bones relative to bone length. The medial-lateral diameter on femur length has a lower slope than the anterior-posterior diameter on femur length. This pattern is reversed for the second moments of area (Iml and Iap). This difference might mean that there is a structural constraint, such as a muscle, that limits bone growth in the medial-lateral direction, but that that limitation is compensated for in larger individuals through changes in the medullary cavity so that the bone is not compromised in bending strength in that direction. This change would be subsequently reflected in the scaling of the strength variables on bone length.

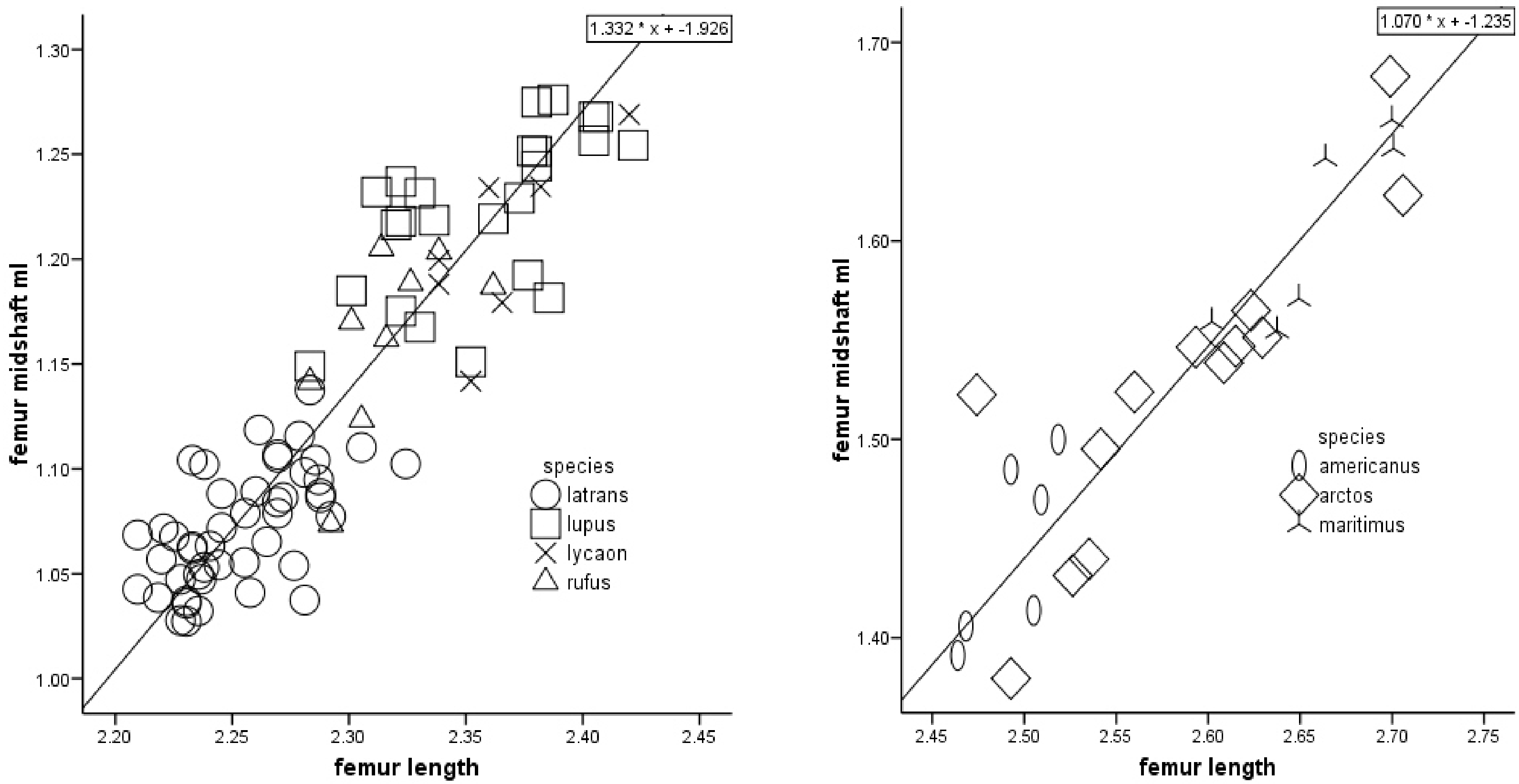


Figure 6: Femur midshaft medial-lateral diameter on femur length in *Canis* and *Ursus* (all units mm; data are logged)

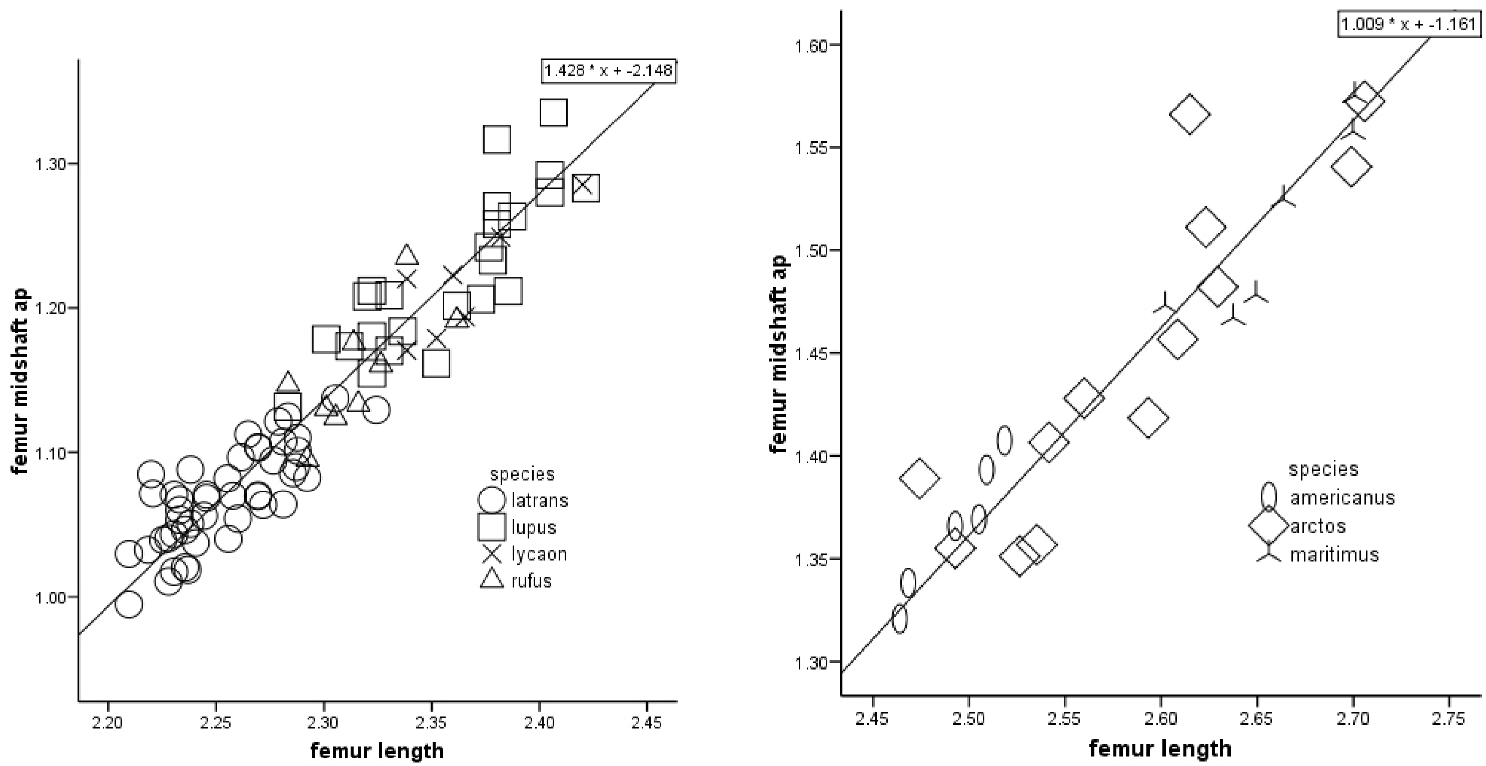


Figure 7: Femur midshaft anterior-posterior diameter on femur length in *Canis* and *Ursus* (all units mm; data are logged)

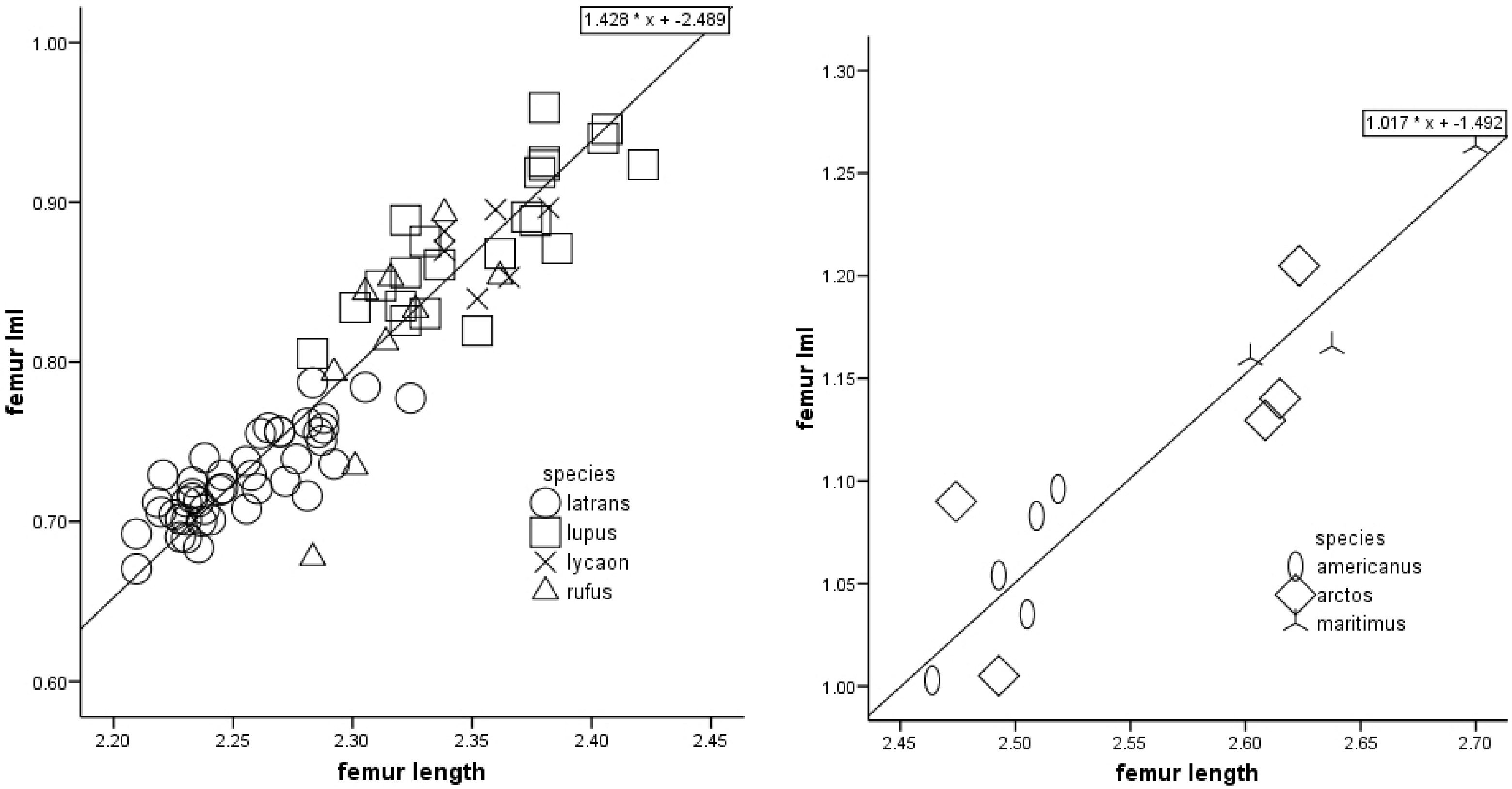


Figure 8: Femur Iml on femur length in *Canis* and *Ursus* (all units mm; data are logged)

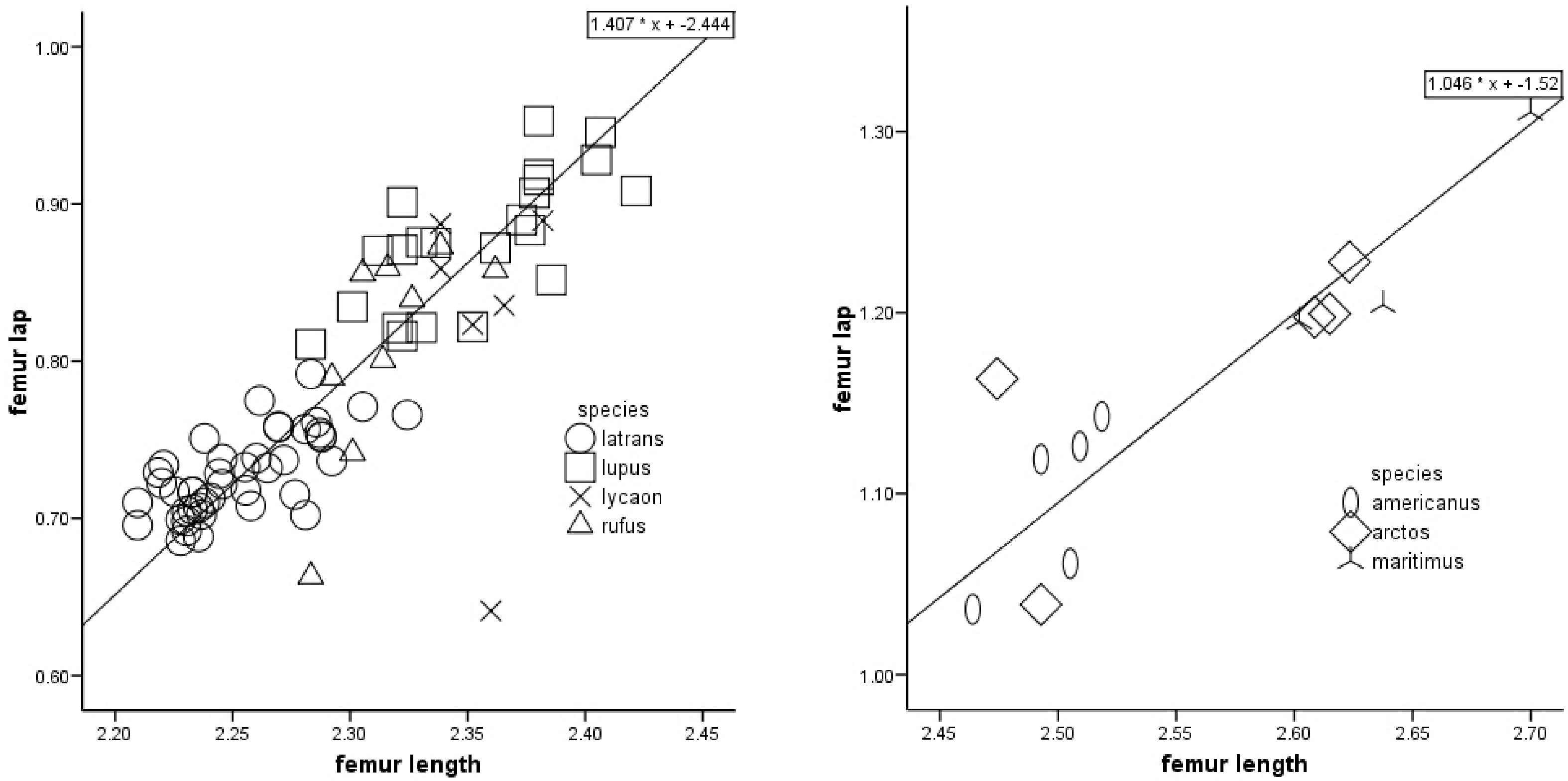


Figure 9: Femur Iap on femur length in *Canis* and *Ursus* (all units mm; data are logged)

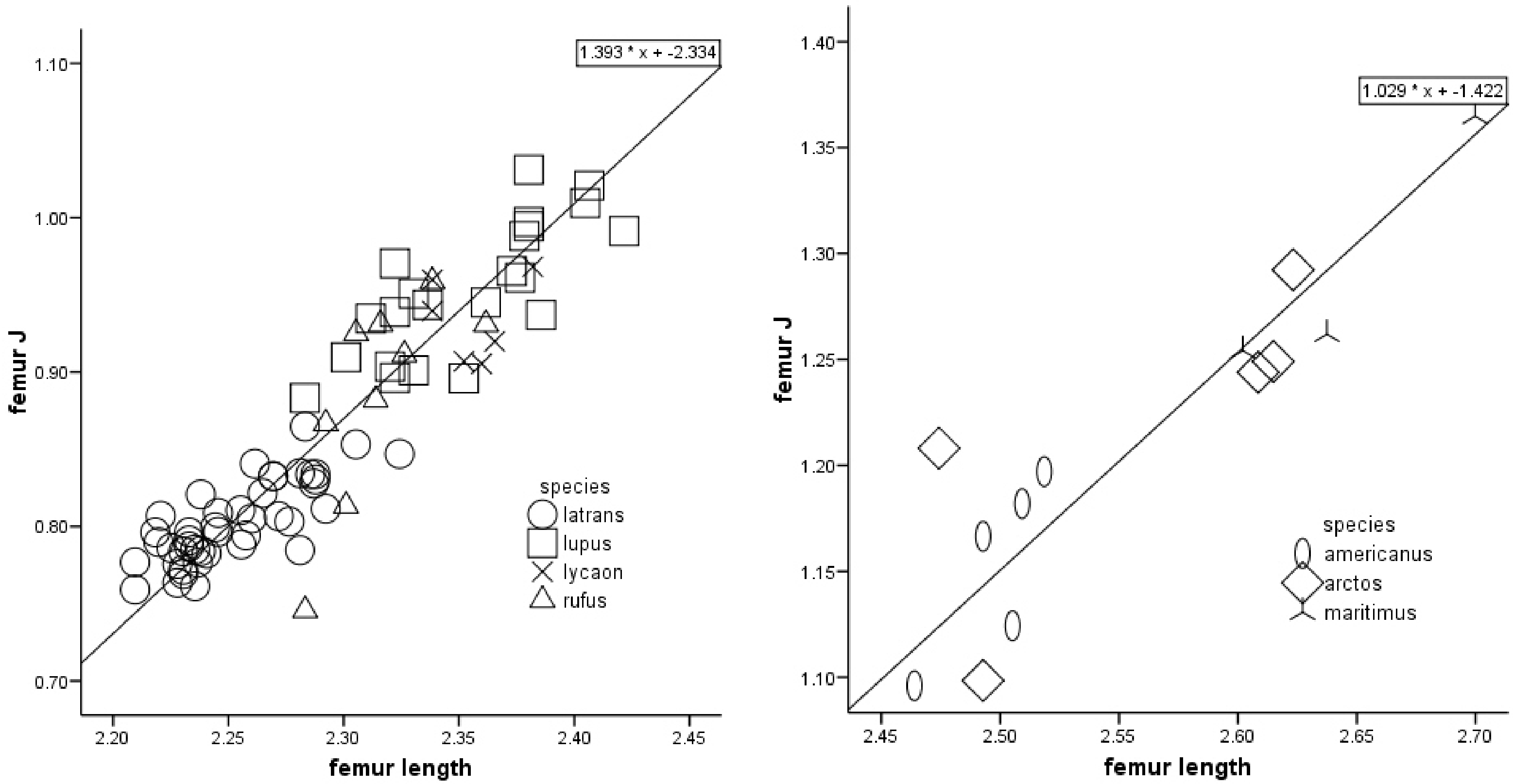


Figure 10: Femur J on femur length in *Canis* and *Ursus* (all units mm; data are logged)

4.3.1.2 Humerus

Table 18: RMA regressions of humeral cross-sectional dimensions on humerus length

X variable	Y variable	slope	intercept	CI slope	R^2	N
Humerus length *Canis*	midshaft ml	1.47	-2.19	1.32 – 1.62	.976	37
	midshaft ap	1.26	-1.66	1.11 – 1.40	.975	37
	Iml	1.37	-2.27	1.15 – 1.60	.995	16
	Iap	1.36	-2.28	0.97 – 1.74	.996	16
	J	1.36	-2.19	1.02 – 1.70	.996	16
Humerus length *Ursus*	midshaft ml	1.22	-1.55	0.95 – 1.50	.972	26
	midshaft ap	1.26	-1.61	1.09 – 1.44	.976	26
	Iml	1.24	-1.90	0.82 – 1.66	.991	11
	Iap	1.20	-1.82	0.83 – 1.57	.991	11
	J	1.18	-1.73	0.91 – 1.44	.993	11

Reduced major axis regressions of humeral cross-sectional dimensions on humerus length yield results that are far less consistent than those for the femoral regressions (Table 19 and Figures 11-15). Humeral midshaft diameters in *Canis* scale with positive allometry relative to humerus length. The humeral medial-lateral diameter has a higher slope than the anterior-posterior diameter. In *Ursus*, the scaling of humeral midshaft medial-lateral diameter on humerus length includes isometry in the 95% confidence intervals, but humeral midshaft anterior-posterior diameter scales with positive allometry relative to humerus length. In no cases among *Canis* is isometry included in the 95% confidence intervals in the slope of diameters on humerus length, which excludes isometry as the scaling pattern for this bone in this genus. One of the reasons that the results for the humeral regressions are less clear than those of the femur is that the deltoid tuberosity falls around the midshaft of the humerus in both genera, which may impact measures of bone diameter.

One interesting point is that the humeral midshaft anterior-posterior diameter scales nearly identically in *Canis* and *Ursus*. The slopes are identical and they only differ by .05 in the intercept. In the strength estimate (Iap), however, there is a difference between the two genera in both slope and intercept, although the confidence intervals overlap. This may mean that the diameter is not as reliable as a measure of bone strength, at least for the humerus. The humeral midshaft is complicated and difficult to measure due to the deltoid tuberosity. This finding is likely a reflection of anatomical variation surrounding this muscle scar than actual strength differences.

There is positive allometry of the second moments of area on bone length in both *Canis* and *Ursus*, but the confidence intervals reveal that some of these coefficients include isometry. The Iml and J measurements of the humerus in *Canis* scale with positive allometry that is significantly different from isometry. The Iap of *Canis* is not significantly different from isometry. This means that overall, longer bones have relatively greater bone strength, as measured solely by the cross-section, than do shorter bones. Bone length is also a factor in determining bone strength because if two bones have the same cross-sectional dimensions but different lengths, the longer bone will be weaker than the shorter bone. In these results, we see that bone strength is increasing at a greater rate than bone length. Without including body mass, it is not possible to say yet whether this greater bone strength comes from buttressing of the cortical midshaft, or through relatively shorter bones in individuals with a larger body mass. In *Ursus*, all of the slopes of bone strength on bone length are positively allometric, but they include isometry in the confidence interval, so an isometric relationship cannot be ruled out.

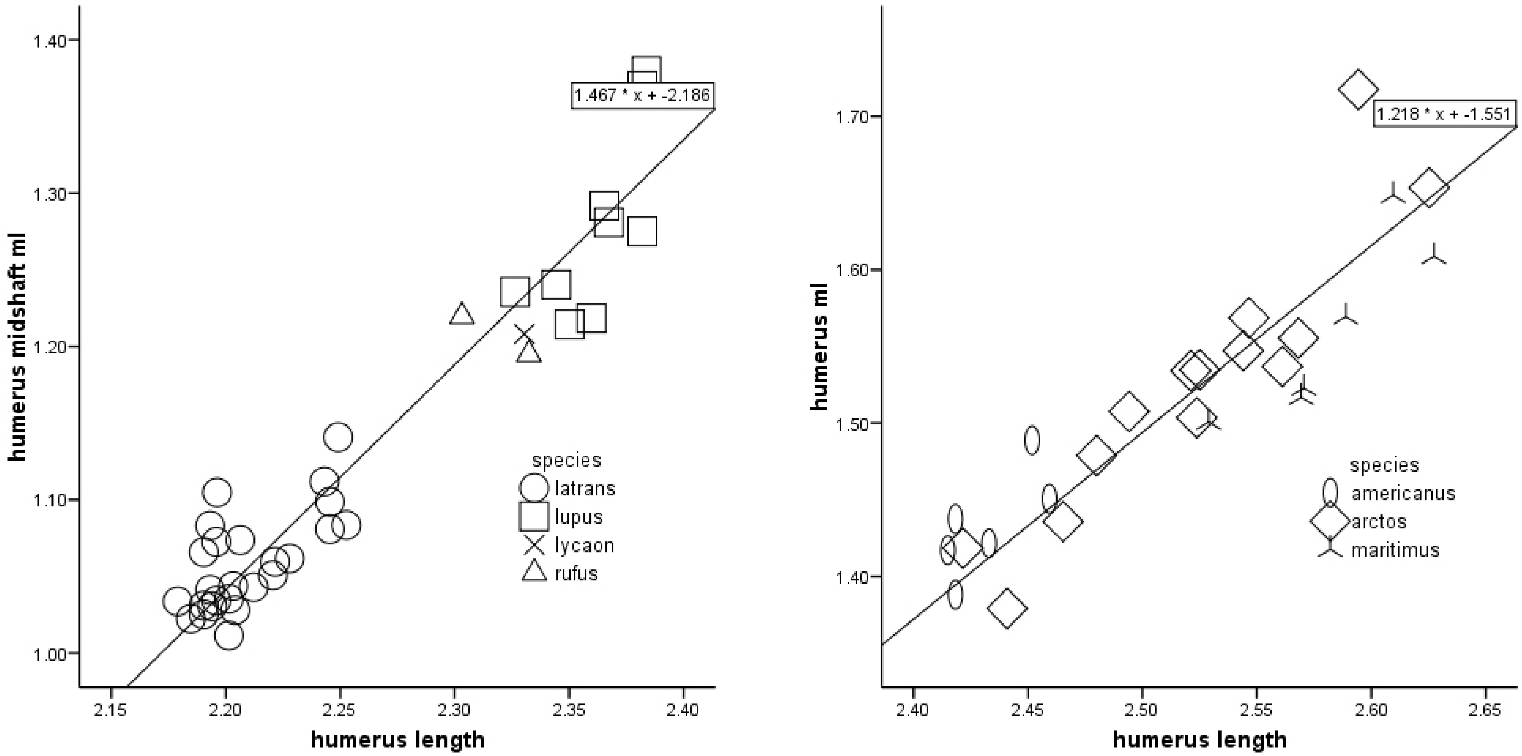


Figure 11: Humeral midshaft medial-lateral diameter on humerus length in *Canis* and *Ursus* (all units mm; data are logged)

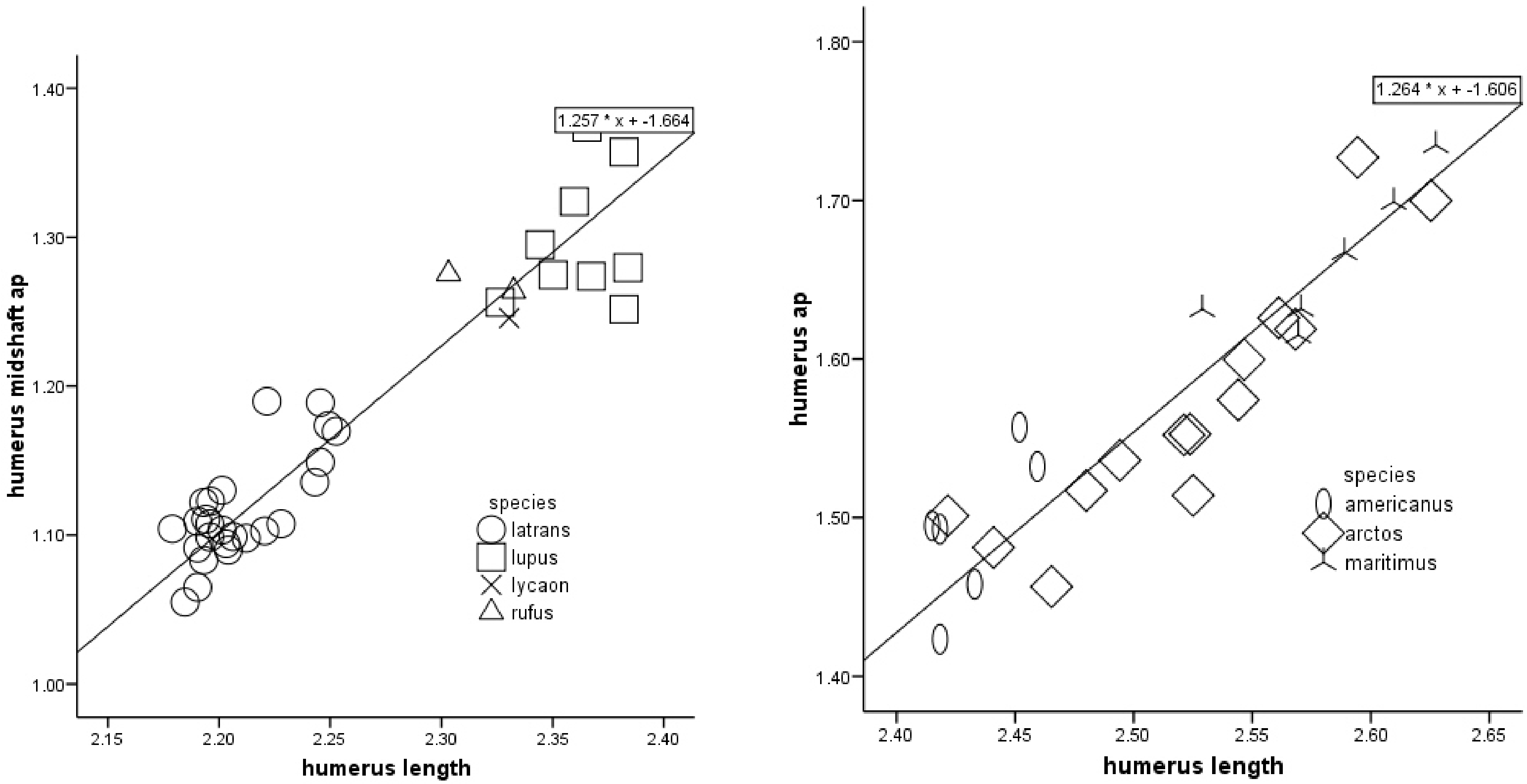


Figure 12: Humeral midshaft anterior-posterior diameter on humerus length in *Canis* and *Ursus* (all units mm; data are logged)

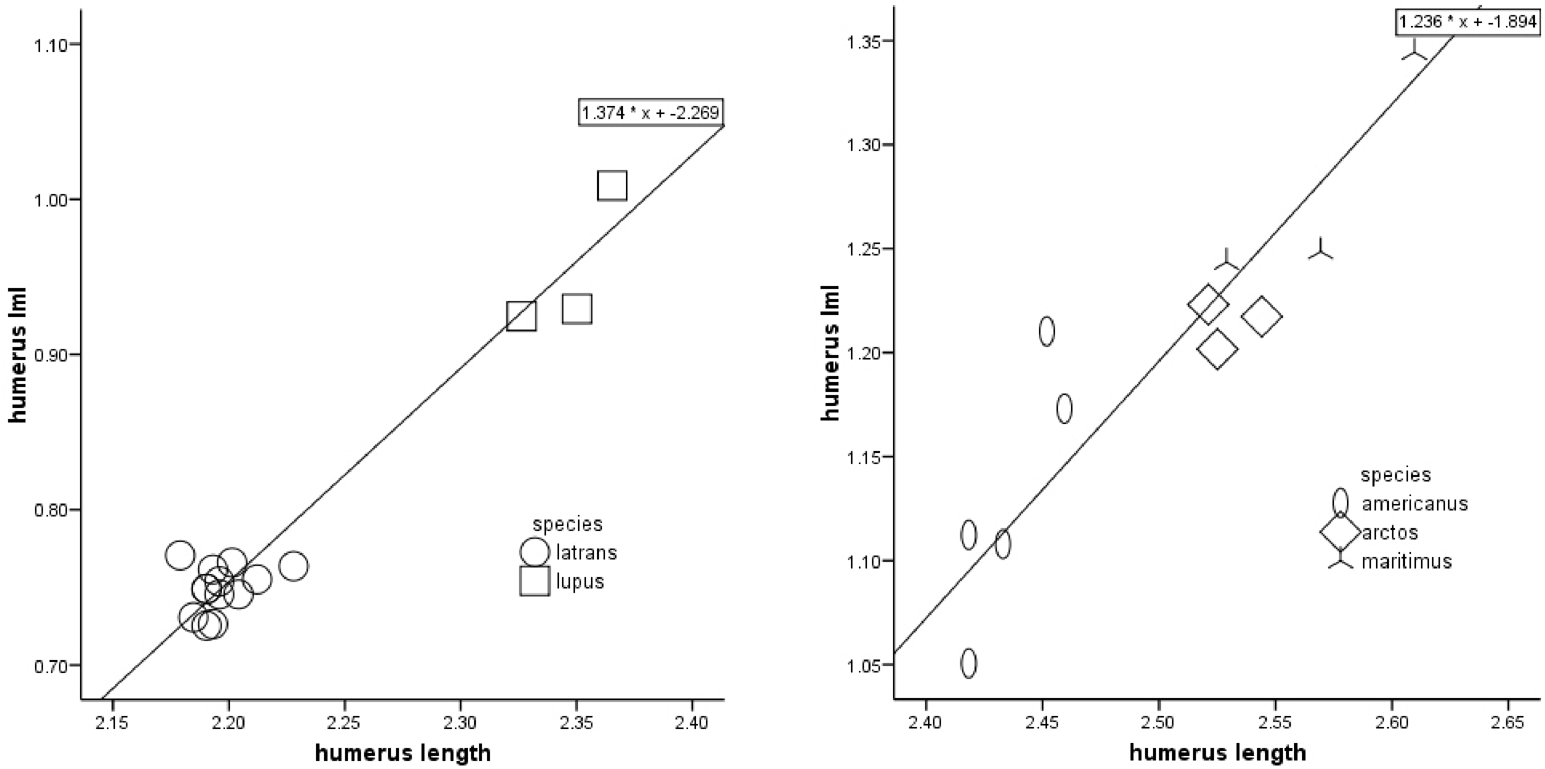


Figure 13: Humerus Iml on humerus length in *Canis* and *Ursus* (all units mm; data are logged)

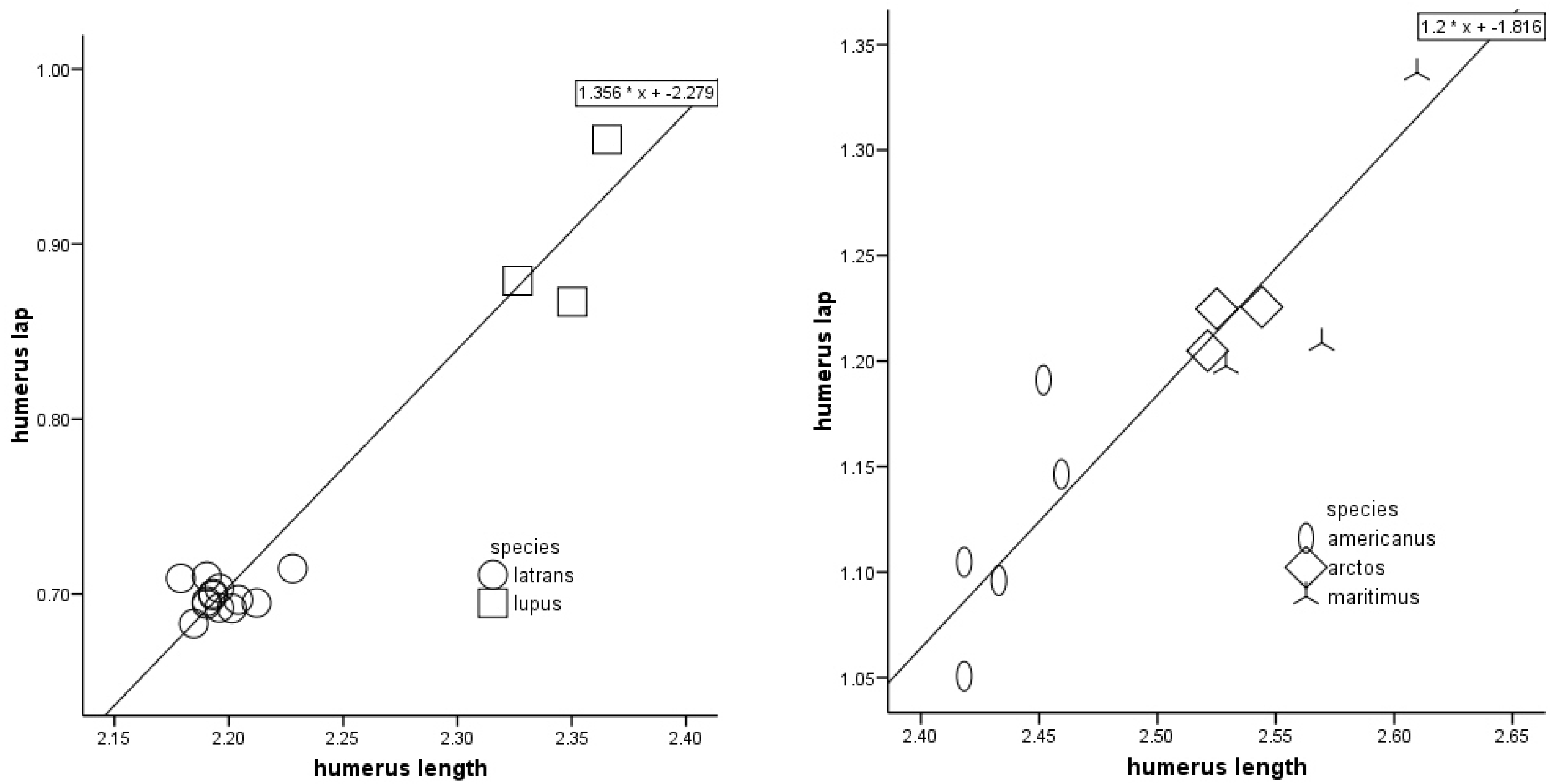


Figure 14: Humerus Iap on humerus length in *Canis* and *Ursus* (all units mm; data are logged)

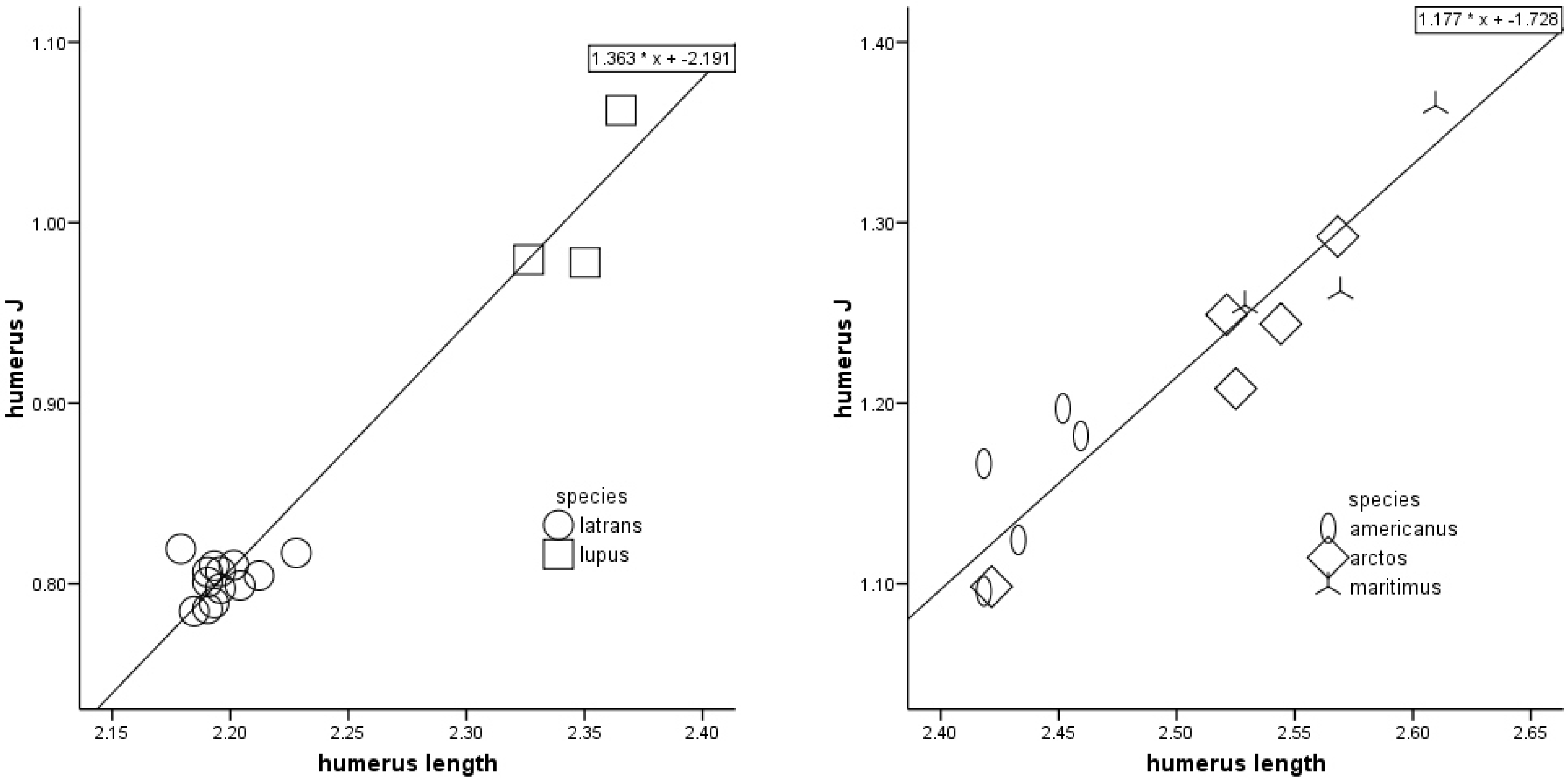


Figure 15: Humerus J on humerus length in *Canis* and *Ursus* (all units mm; data are logged)

4.3.1.3 Tibia

Table 19: RMA regressions of tibial cross-sectional dimensions on tibia length

Y variable	X variable	slope	intercept	CI slope	R^2	N
Tibia length *Canis*	midshaft ml	1.21	-1.69	1.09 – 1.32	.984	37
	midshaft ap	1.42	-2.17	1.24 – 1.60	.974	37
	Iml	1.31	-2.25	1.17 – 1.44	.991	21
	Iap	1.24	-2.09	1.11 – 1.37	.994	21
	J	1.27	-2.08	1.08 – 1.45	.994	21
Tibia length *Ursus*	midshaft ml	1.24	-1.66	1.05 – 1.43	.984	25
	midshaft ap	1.46	-2.07	1.17 – 1.75	.965	25
	Iml	1.19	-1.78	0.96 – 1.43	.998	9
	Iap	1.18	-1.81	0.87 – 1.48	.997	9
	J	1.18	-1.70	0.87 – 1.48	.998	9

The scaling of the tibial midshaft diameters on tibia length is the same for *Canis* and *Ursus* (Table 20, Figures 16-20). In fact, both the slopes and the intercepts are nearly identical in the two genera, and are not statistically different from each other (as determined by the 95% confidence intervals). There is positive allometry of both diameters on tibia length. What makes the consistency of these findings so remarkable is the fact that distal limb segments have observed to be more variable between individuals of the same species than proximal limb segments (Meadows, Jantz and Jantz, 1999; Holliday and Ruff, 2001). This reported variability is due in part to the effects of Allen's rule, which states that in colder climates, limbs will be relatively shorter than the limbs of conspecifics in warmer climates due to the need to maximize the surface area to volume ratio, thereby conserving heat (Allen, 1877). However, the consistency of the scaling relationship of these two related genera indicate that there is less variability of scaling patterns in this bone than there appears to be based on previous studies of bone length. The relationships of the cross-sectional dimensions to bone length appear to show little deviation from the pattern of positive allometry exhibited by both genera. It may be that the variability seen in the length of the distal limb segments is not a response to temperature, but a response to a mechanical need to support a particular body mass.

The scaling of the second moments of area on bone length in *Canis* show a consistent pattern of positive allometry that is statistically different from isometry. This pattern is the same as is seen for the femur and the humerus (with the exception of the Iap of the humerus). As tibia length increases in *Canis*, the bone strength in both the anterior-posterior and medial-lateral directions increases. Individuals with longer tibiae within this genus have relatively stronger tibiae than individuals with shorter tibiae. Among *Ursus*, there is a scaling exponent that suggests positive allometry, but isometry is included in the confidence intervals of measures of bone strength on bone length in the tibia. The pattern of strength scaling on tibia length in this genus also mirrors the results obtained for the femur and the humerus, with no exceptions. There is a scaling pattern that is not different from isometry of bone strength measures on bone length for the three limb bones sampled in this dissertation for the genus *Ursus*.

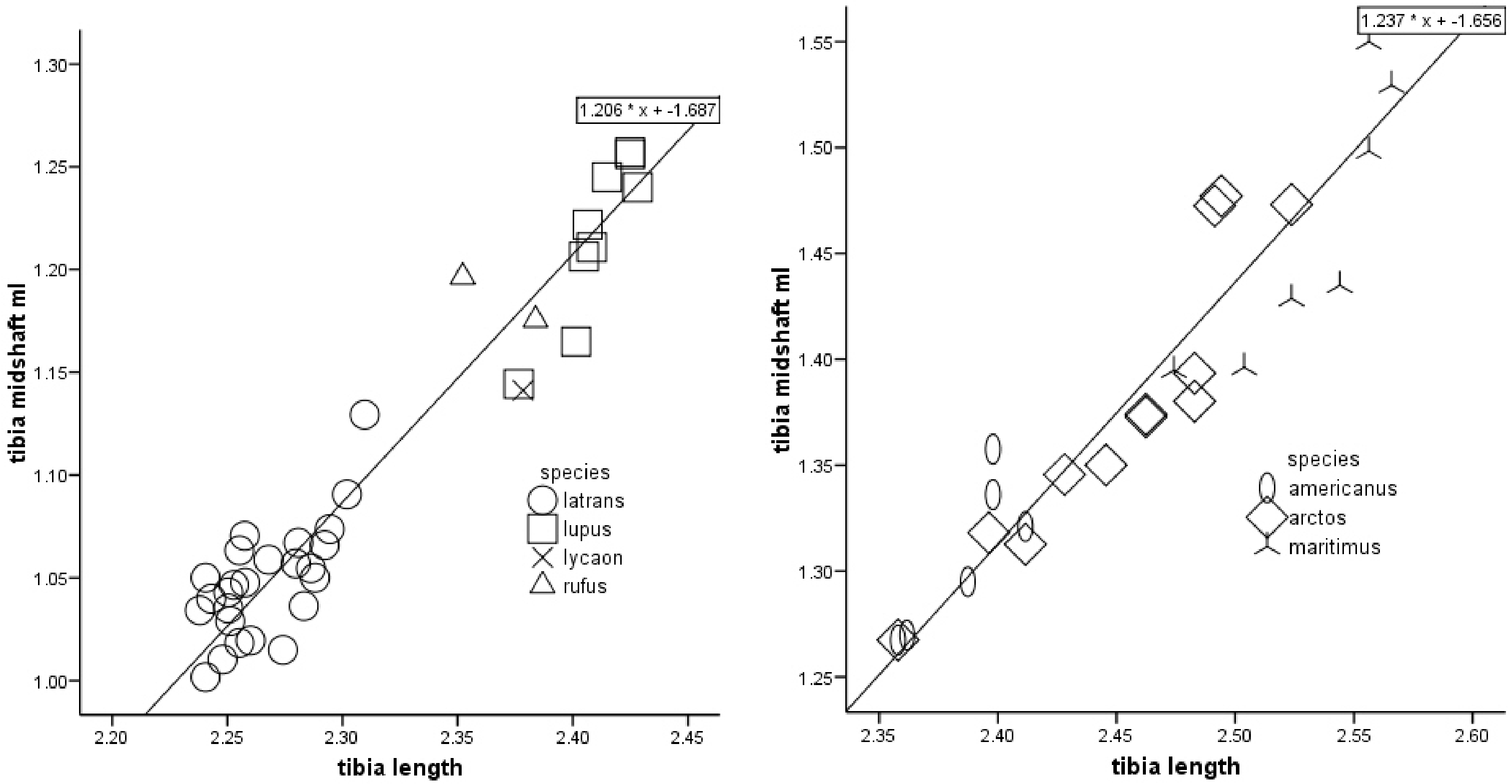


Figure 16: Tibial midshaft medial-lateral diameters on tibia length in *Canis* and *Ursus* (units in mm; all data logged)

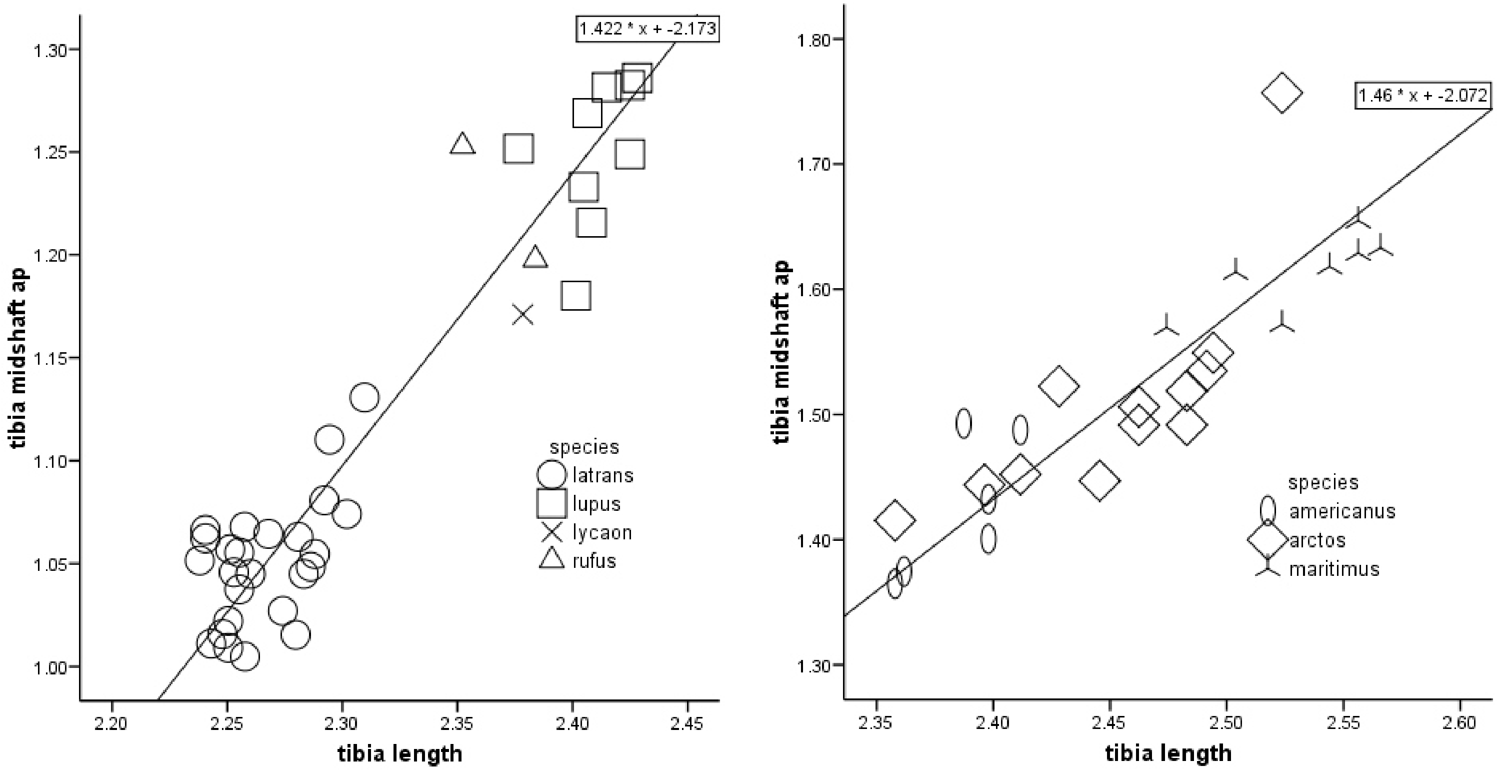


Figure 17: Tibial midshaft anterior-posterior diameters on tibia length in *Canis* and *Ursus* (units in mm; all data logged)

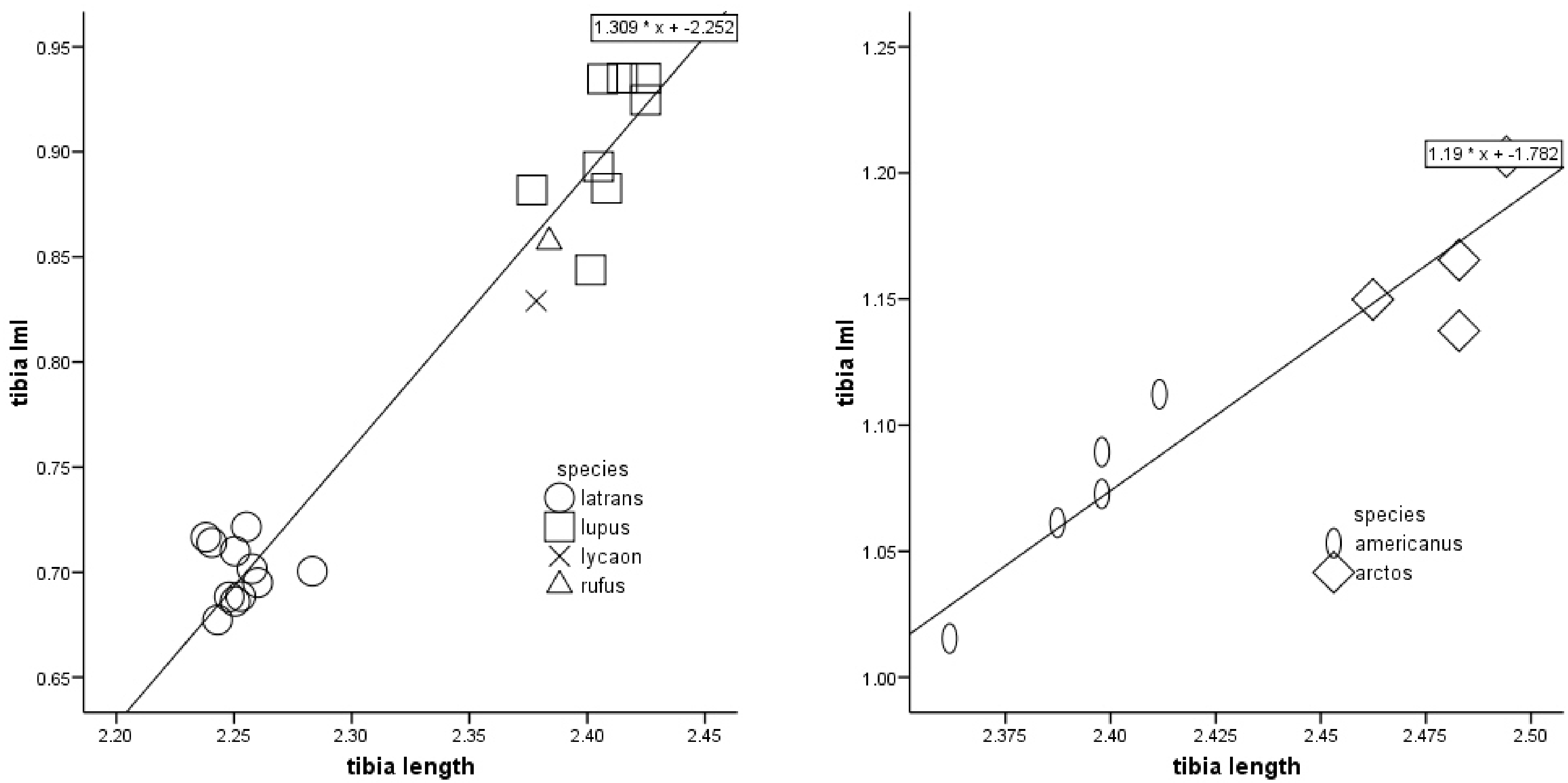


Figure 18: Tibia Iml on tibia length in *Canis* and *Ursus* (units in mm; all data logged)

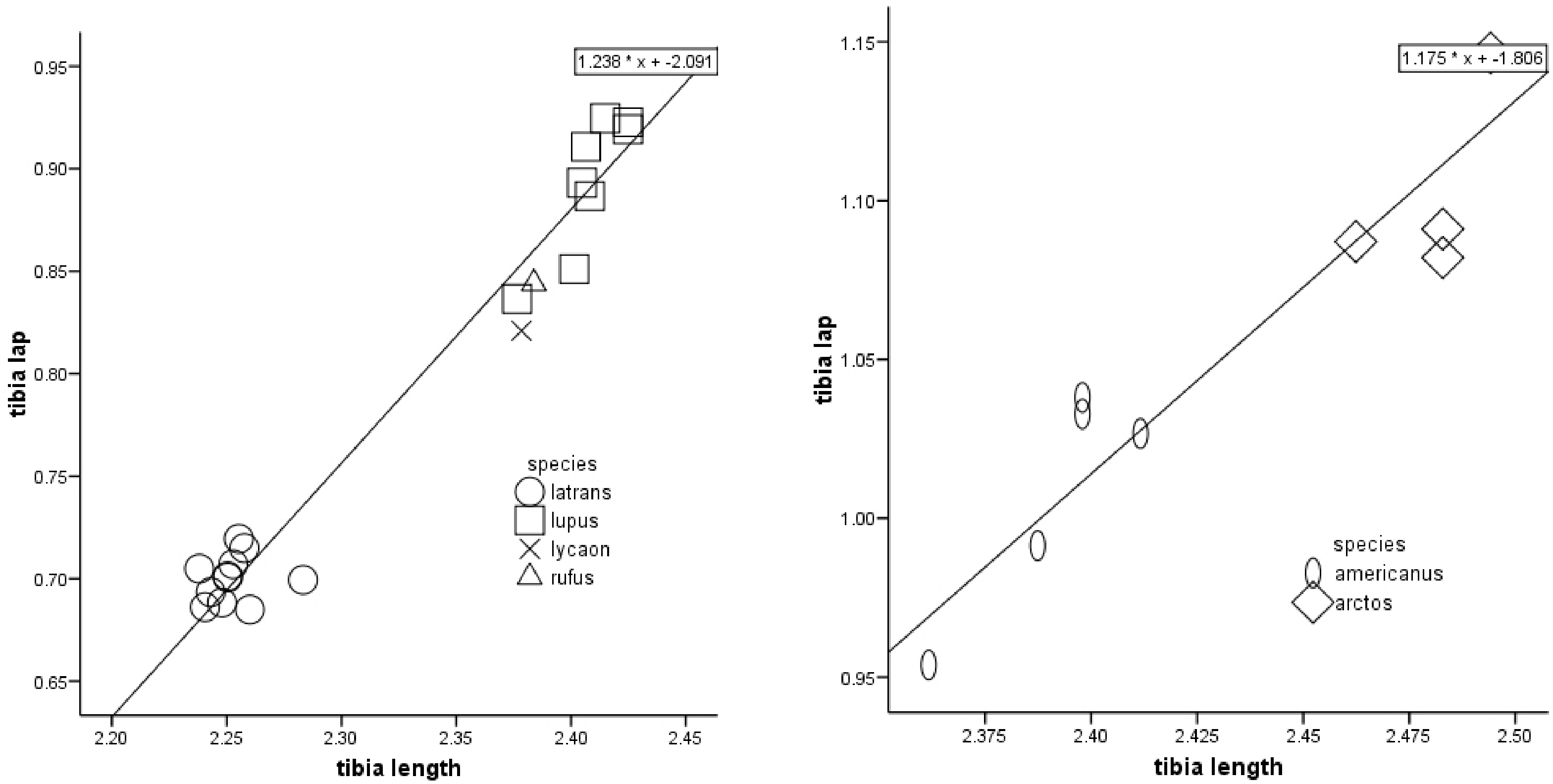


Figure 19: Tibia Iap on tibia length in *Canis* and *Ursus* (units in mm; all data logged)

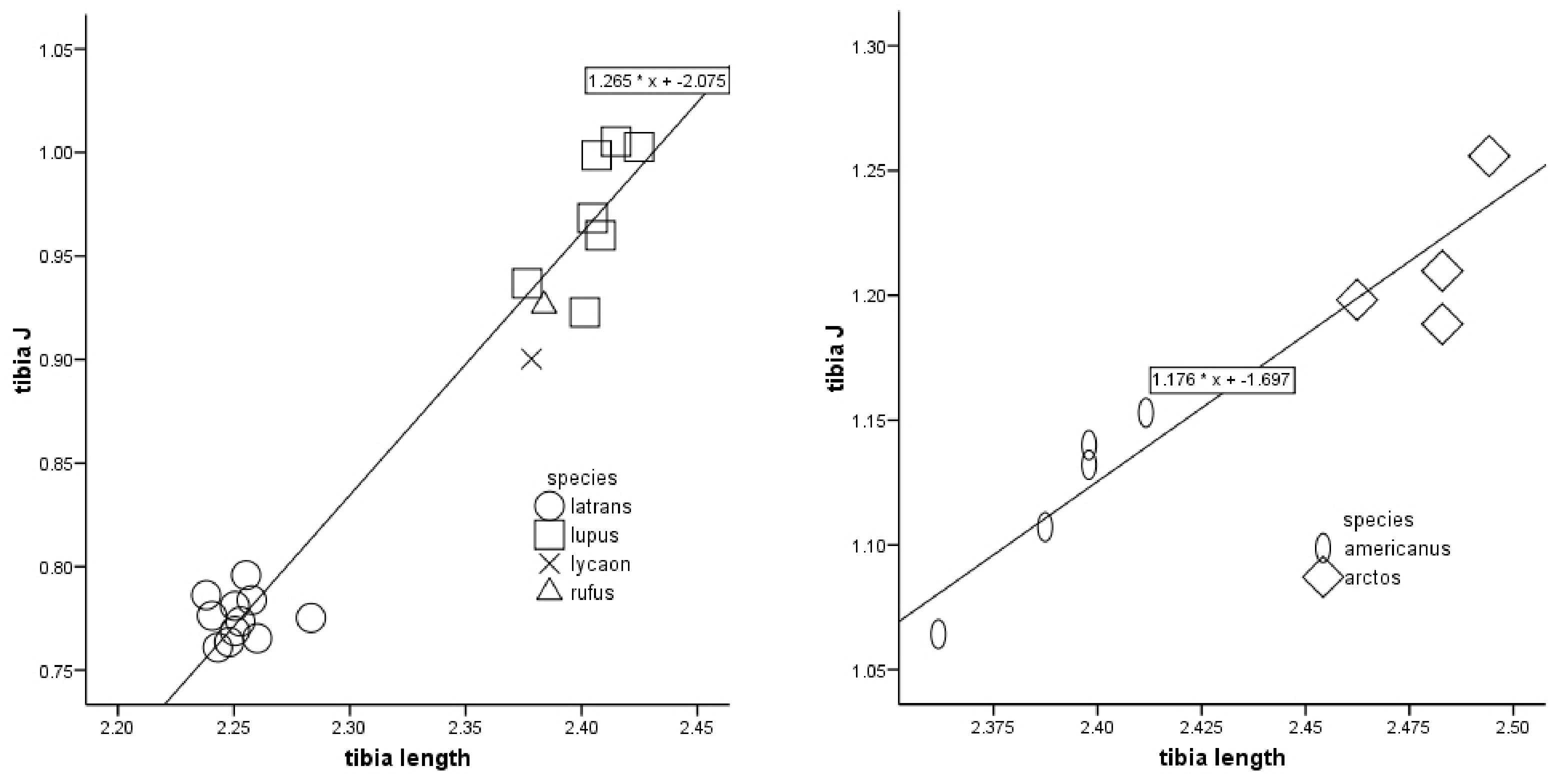


Figure 20: Tibia J on tibia length in *Canis* and *Ursus* (units in mm; all data logged)

4.3.2 Evaluation of elastic and geometric scaling hypotheses

The differetial scaling hypothesis of Bertram and Biewener (1990) predicts that small and large mammalian species will scale differently due to the different constraints imposed by body mass. Many examples of this differential scaling were outlined by studies of different taxa (Bertram and Biewener, 1990; Christiansen, 1999a) and it has been proposed that, due to predictable differences in the mechanics of quadrupedal locomotion in large compared to small animals, there are different scaling patterns for large and small animals (Economos, 1983; Bertram and Biewener, 1990; Christiansen, 1999a). The data presented in this section suggests that *Canis* and *Ursus* also follow different scaling patterns that may be related to body mass. These patterns will be evaluated in the context of the predictions of Bertram and Biewener (1990) and other studies of mammalian scaling patterns.

According to Bertram and Biewener (1990), the long bone length of small mammals (< 100 kg) should scale with geometric similarity, or isometry, relative to bone diameter (i.e., with a predicted slope of 1.0). By contrast, the long bone length of large animals should scale with elastic similarity, or negative allometry, relative to bone diameter (i.e., with a predicted slope of .675). Species of *Canis* weigh less than 100kg, the limit proposed by Bertram and Biewener (1990) that would differentiate large and small mammalian scaling patterns. Therefore, according to the model of Bertram and Biewener (1990), *Canis* bone length should scale relative to bone diameter with geometric similarity. The *Ursus* sample straddles the 100 kg threshold, making it difficult to evaluate the scaling patterns of this sample with respect to the differential scaling hypothesis. However, contrasts between large and small bears will be important to evaluate within the context of the differential scaling hypothesis and its potential to be present in a restricted taxonomic group.

The variables on the X and Y axes presented in the previous two sections were switched relative to the axes in the elastic similarity hypothesis as laid out by McMahon (1975), and relative to some other scaling studies (Bertram and Biewener, 1990; Christiansen, 1999a) because the aim of this dissertation is to investigate variation in skeletal robusticity and the factors that contribute to this variation. However, it is important to evaluate the predictions of the elastic and geometric similarity hypotheses using analyses that can be compared to other studies. In order to make these comparisons, another set of regressions using bone length as the dependent variable and bone diameter as the independent variable were done, reversing the axes of the previous section. These 'reverse regressions' for *Canis* and *Ursus* are reported in Table 20. The results of Bertram and Biewener (1990) are also reported. The results presented in this dissertation are from RMA regressions. In order to compare the results presented here with the least squares results of Bertram and Biewener (1990), the scaling exponent, or slope of the regression, was divided by the correlation coefficient (r). This modified scaling exponent is equivalent to the slope generated by the reduced major axis method (Sokal and Rohlf, 1995). The species means obtained by Bertram and Biewener (1990) for the species that are also used in this dissertation can be seen in Table 21. For nine variables and six species, there are only 16 instances in which the means obtained by Bertram and Biewener (1990) do not fall within the 95% confidence intervals presented for this dissertation data. Seven of those sixteen occur in the species *C. rufus* and five occur in *C. latrans*. Because these are variable species, and the sample sizes for these species of both Bertram and Biewener (1990) and this dissertation (in the case of *C. rufus*) are small, it is not surprising that their data fall outside the confidence intervals. Even in the cases in which their data are not within these confidence intervals, they are still very close to the confidence intervals. However, because most of the differences in the data occur in the genus *Canis*, and this is the genus for which there are fewer instances of similar results shared with Bertram and Biewener (1990), it is possible that data collected for the species means, and the small number of individuals in the sample is responsible for these differences. These data are also plotted along the regressions with the data presented here in order to see if there are large differences in the measures obtained by Bertram and Biewener (1990) that may influence the scaling patterns that they got for each group. These charts, with the Bertram and Biewener specimens labeled, can be found in Appendix A.

Among *Canis*, the femoral midshaft anterior-posterior diameter on femur length includes the slope of elastic similarity (0.71; CI 0.66 – 0.74) that is statistically different from isometry. The femoral midshaft medial-lateral diameter on femur length in *Canis* does not include elastic similarity in its confidence intervals, so this relationship exhibits neither elastic nor geometric similarity. However, this relationship is definitely trending towards elastic similarity rather than geometric similarity (slope of 0.75; CI 0.68 – 0.82). The femoral diameters of *Ursus* scale with geometric similarity. Bertram and Biewener (1990) obtained results of geometric similarity of scaling for both femoral diameters of Ursidae, and the medial-lateral diameter of Canidae.

Of the four regressions of bone diameter of the humerus in two genera, only one (humerus length on humeral medial-lateral diameter in *Canis*) supports one of the two proposed scaling patterns (elastic or geometric similarity) by exhibiting elastic similarity of scaling (slope of 0.68; CI 0.58 – 0.78). Humeral length diameter of *Canis* scales with neither elastic nor geometric similarity on anterior-posterior diameter. The results for *Ursus* show that the scaling of humerus length is consistent with both elastic and geometric similarity on anterior-posterior diameter (0.82; CI 0.61 – 1.03) and with elastic similarity on medial-lateral diameter (0.79; CI 0.65 – 0.93). Bertram and Biewener (1990) obtained resuls of elastic similarity of humerus length on medial-lateral diameter, and neither elastic nor geometric similarity (their exponent falling between the two theoretical scaling patterns) on anterior-posterior diameter for their sample of Ursidae, which included the same three species that are sampled in this dissertation. The results of those authors lend support for the scaling of elastic similarity for the medial-lateral diameter of the humerus of *Ursus*.

The scaling of the tibia is similar for both genera. Tibia length scales with elastic similarity on the anterior-posterior diameter of the tibia, but with neither elastic nor geometric similarity on the medial-lateral diameter for both genera in this dissertation.

Bertram and Biewener (1990) reported geometric similarity for the medial-lateral diameter of the femur in *Canis* and neither elastic nor geometric similarity for the anterior-posterior diameter. Bertram and Biewener (1990) also reported elastic similarity of tibia length on the anterior-posterior diameter on the tibia in the genus *Ursus*.

In summary, among *Canis*, the only result that is the same in this study and in Bertram and Biewener's (1990) study is that of the anterior-posterior humeral diameter on humeral length, which exhibits neither geometric nor elastic similarity. Bertram and Biewener (1990) obtained results of either geometric similarity or neither geometric nor elastic similarity for all *Canis* diameters, while the results of this dissertation were either elastic similarity, or neither elastic nor geometric similarity. It is important to remember that Bertram and Biewener (1990) sampled many species within the family Canidae, while this dissertation was looking at a single genus within that family, narrowing the taxonomic focus. A similar study of domestic dogs found a pattern similar to that of Bertam and Biewener (1990) for these same variables (Casinos et al., 1986). Casinos and colleagues (1986) tested geometric and elastic similarity hypotheses in domestic dogs, ranging in size from tiny terriers and Pomeranians to large mastiffs and wolfhounds, and found an overall pattern of geometric similarity in the scaling of long bone diameters to long bone length. Although this group is more constrained taxonomically than Bertram and Biewener's (1990) sample, the range of body mass between the largest and smallest specimen encompasses several orders of magnitude more than the sample of *Canis* in this dissertation, perhaps accounting for some of the difference in results.

Among *Ursus*, four of the six limb length on diameter regressions yield the same results as those from Bertram and Biewener (1990), the only exceptions being the humeral anterior-posterior diameter on humeral length and the tibial medial-lateral diameter on tibial length. Overall, there is a mixed result of geometric, elastic, both or neither scaling pattern for *Ursus*. Bertram and Biewener's (1990) sample of Ursidae included only the three species sampled in this dissertation, making the sample groups identical, which would explain why the results are more similar for this group than they are for the Canidae/*Canis* group. There is likely to be less variability in certain parameters, such as body shape and locomotion, when the taxonomic groups are smaller.

Although the results obtained here are not in agreement with the results of Bertram and Biewener (1990), there is support for the idea that the taxonomic level (or range of body size) from which the sample is taken can influence the results of the regressions. Because there are no clear definitions for taxonomic levels across groups, it is the idea that sampling from a larger group of related species that differ significantly in factors such as body mass, locomotion, and ecology, will yield very different results than those of a group that is more restricted in all of these variables. Heinrich and Biknevicius (1998) obtained results of elastic similarity for a small-bodied group (the mustelids), and surmised that geometric similarity was unusual for narrower sample groups. The sample group of Heinrich and Biknevicius (1998) was even smaller in body mass than the body mass of *Canis*, but the taxonomic levels of the two studies are comparable. Among closely related species that are similar in body shape and locomotor type, there may be different scaling expectations than for taxonomically broad samples of varying body types and locomotor styles.

Table 20: Bertram and Biewener (1990) species means; numbers in bold do not fall within the 95% confidence intervals of the species means for the data collected for this dissertation

species	femur length	femur ap	femur ml	humerus length	humerus ap	humerus ml	tibia length	tibia ap	tibia ml
Canis latrans	183.0	**12.79**	12.11	162.8	**15.74**	**13.1**	184.6	**13.54**	**12.2**
Canis lupus	237.4	17.67	17.11	213.1	20.95	16.72	233.4	18.12	16.21
Canis rufus	**193.6**	13.53	14.44	**173.9**	**14.74**	**14.31**	**194.2**	**14.29**	**13.45**
Ursus americanus	296.9	**21.18**	25.09	**255.6**	28.00	**24.83**	223.8	25.39	19.81
Ursus arctos	435.0	**34.32**	40.05	331.0	38.94	35.88	284.2	34.51	27.35
Ursus maritimus	457.5	33.39	38.64	380.6	45.50	37.42	318.4	40.78	33.40

Table 21: Regressions for comparison with Bertram and Biewener (1990), *Canis* and *Ursus*

	dependent v.	independent v.	slope	CI (*scaling)	B & B slope (95% CI), R^2	B & B RMA slope (*scaling)
Bone length (*Canis*)	femur length	femur ml	0.75	0.68 – 0.82 (N)	0.844 (+/- 0.112), 0.948	0.89 (G)
	femur length	femur ap	0.71	0.66 - 0.74 (E)	0.872 (+/- 0.102), 0.973	0.896 (N)
	humerus length	humerus ml	0.68	0.58 - 0.78 (E)	0.852 (+/- 0.123), 0.959	0.888 (G)
	humerus length	humerus ap	0.8	0.69 - 0.91 (N)	0.762 (+/- 0.108), 0.961	0.793 (N) – same
	tibia length	tibia ml	0.83	0.75 - 0.91 (N)	0.844 (+/- 0.139), 0.948	0.89 (G)
	tibia length	tibia ap	0.7	0.62 - 0.79 (E)	0.764 (+/- 0.123), 0.950	0.804 (N)
Bone length (*Ursus*)	femur length	femur ml	0.94	0.78 - 1.09 (G)	0.964 (+/- 0.286), 0.938	1.03 (G) – same
	femur length	femur ap	0.99	0.86 - 1.12 (G)	0.960 (+/- 0.147), 0.960	1.00 (G) – same
	humerus length	humerus ml	0.82	0.61 - 1.03 (B)	0.718 (+/- 0.241), 0.922	0.779 (B) – same
	humerus length	humerus ap	0.79	0.65 - 0.93 (E)	0.791 (+/- 0.092), 0.990	0.80 (N)
	tibia length	tibia ml	0.81	0.72 - 0.90 (N)	0.724 (+/- 0.245), 0.921	0.786 (B)
	tibia length	tibia ap	0.69	0.52 - 0.85 (E)	0.693 (+/- 0.186), 0.948	0.731 (E) - same

* G = geometric similarity; E = elastic similarity; B = both geometric and elastic similarity; N = neither geometric nor elastic similarity

4.3.3 Discussion

It is necessary to determine how organisms adapt mechanically to loading on their skeletons in order to explore questions about the relationship between ecological variables and postcranial bone strength. This section examined the scaling relationships between cross-sectional variables on bone length in the femur, humerus, and tibia of both *Canis* and *Ursus*. There were three goals of this section: a) to detect any bone shape changes with size increases within a genus, b) to explore the scaling relationship of bone strength on bone length and c) to test the geometric and elastic similarity hypotheses in the context of differential scaling proposed by Bertram and Biewener (1990).

The results of the regressions of bone diameters on bone length show that there is an overall pattern of positive allometry in *Canis* and isometry in *Ursus*. As bone lengths increased within *Canis*, bone diameters increased to a greater degree, resulting in bone shape differences between small and large individuals. The isometric pattern seen in *Ursus* indicates that the shape differences with increasing bone length in this genus are less pronounced than those of *Canis*. In order to determine whether the observed shape changes in *Canis* were due to shorter bones or thicker cross-sections in the larger animals, log of bone length was regressed onto the log of the square root of femoral head area, used here as a substitute for body mass (see section 4.4 for a detailed explanation of the use of femoral head area as a substitute for body mass). The log of the square root of femoral head area was used in this analysis, and the expected isometric slope is 1. In *Canis*, the observed slope of this regression is significantly lower than 1, a finding of negative allometry. This means that larger *Canis* have relatively shorter femora for their size than smaller *Canis*. Negative allometry of bone length on body mass is predicted by McMahon's (1973) theory of elastic similarity because of the mechanical advantage conferred by having shorter limbs. This suggests that the means by which larger *Canis* were able to increase relative bone strength is not through a relative increase of cortical bone dimensions, but through a relative decrease in bone length that acts to increase mechanical strength.

Variability in limb length among mammals is often attributed to Allen's Rule (Allen, 1877), which states that in colder climates, organisms will have relatively shorter limbs than conspecifics in warmer climates due to the necessity of minimizing heat loss in colder climates through minimizing surface area to volume ratios. The explanation for this phenomenon is the same as the explanation for organisms being larger in colder environments (Bergmann's Rule). However, some studies have challenged the idea that heat conservation is the driving force behind Bergmann's Rule and offered alternative explanations for this observation, such as seasonality, primary productivity, competition, threat of predation, and life history constraints that select for larger body mass (Rosenzweig, 1968, Ashton et al., 2000). There has not been as much research into Allen's Rule, but the shared explanation raises the possibility that Allen's Rule is also not temperature-driven, as has always been assumed (see also Niles, 1973). It may be that the shorter limbs seen in some organisms living in colder environments are a response to the mechanical need for stronger bones. The fact that the *Canis* sample group follows the pattern of relatively shorter limbs in larger individuals and the *Ursus* sample group does not indicates that there may be different selective pressure operating on limb length in these two groups, even though they overlap geographically and there are even more individuals from the *Ursus* group that are found at higher latitudes. One possibility is that larger *Canis* regularly hunt prey that are several times their own body mass. The larger stresses placed on the skeletons of the wolves because of the large body mass of the prey species results in a need for relatively stronger bones. These stronger bones can result from either a buttressing of the cortical area or a relative shortening of the limb. The strategy of *Canis* seems to be a shortening of the limb bone. For the data collected here, the mechanical strengthening explanation is stronger than the heat conservation explanation for shortened limbs because *Ursus* does not display the same relationship between bone length and body mass, despite the fact that many of the individuals in this sample are from higher latitudes and colder climates. If the heat conservation explanation for Allen's Rule were valid, there would be a relatively shortening of the limbs in this genus. This is not the case, however. There is an isometric relationship between bone length and femoral head area in the genus *Ursus* for the sample included here. This means that the high latitude polar bear and grizzly bears are not adapting to the colder environments through a shortening of their limbs, as predicted by Allen's Rule. They are becoming larger in body mass, and the cross-sectional dimensions of their long bones reflect this larger body mass in an isometric manner.

Bertram and Biewener (1990) proposed that at very large sizes, simple postural and locomotor adaptations were not enough to maintain bone strength and that limb shortening, resulting in extreme negative allometry, was necessary for a large organism to carry its own weight. This was demonstrated by the ceratomorphs, which have limb bones than are considerably shorter than would be predicted by geometric, or even elastic similarity. These results stand in contrast to the results of other large-bodied mammals, such as elephants, which have limb lengths that are relatively longer than those of the ceratomorphs (Alexander, Jayes et al., 1979; Bertram and Biewener, 1990; Christiansen, 1999). The longer limb lengths of elephants result in bones that are relatively more gracile (weaker), a phenomenon explained by the fact that elephants do not have a suspensory phase of locomotion (Hutchinson et al., 2003), thereby minimizing the amount of stress and strain put on their skeletons during locomotion. This is an example of a mechanical explanation for relatively short limbs.

The second and polar moments of area were also regressed onto bone length in order to explore how strength variables change with increasing bone length. All of the strength variables for *Canis* scale with positive allometry on bone length. All of the strength variables for *Ursus*, with the exception of humeral Iap (which scales with positive allometry), scale with isometry on bone length. The consistency of these results suggests that there is a functional difference in the loading patterns of larger *Canis* that is compensated for by a relative strength increase with bone length increases. Regressions of bone length on femoral head area (as a substitute for body mass) indicate that bone length has a negatively allometric relationship with body mass. This means that the relatively greater strength in longer bones among *Canis* is a result of a relative decrease in bone length among larger individuals. The next section (4.5) will directly explore the relationship between body mass and bone strength.

The final third set of analyses in this section evaluated two hypotheses related to scaling patterns in large and small mammals. The summary of the results of the tests of the geometric and elastic similarity hypotheses is provided in Table 20. Bertram and Biewener (1990) predicted that small mammals (under 100kg) would scale with geometric similarity, and that large mammals (over 100kg) would scale with elastic similarity). These predictions are not supported by the data presented in this dissertation. Bertram and Biewener (1990) showed that an across-species regression of bone length on bone diameters had a pattern of negative allometry that was due, in part, to the lower scaling exponents of the intrafamilial regressions of families at the larger end of the body mass spectrum. The results presented here of regressions with the axes reversed in order to compare with other studies (presented in the text of each preceding section), show a pattern opposite to what Bertram and Biewener (1990) found. In the results of this dissertation, the genus that was larger in body mass (*Ursus*) had scaling exponents that were larger (with the axes flipped to correspond to Bertram and Biewener (1990)) than those of the genus that was smaller in body mass (*Canis*).

Half of the regressions for *Canis* show a scaling pattern of elastic similarity. The other half of the regressions shows positive allometry, but fail to meet the criteria for elastic similarity. None show geometric similarity, contrary to expectations. Within *Canis*, there are bone shape differences between large and small individuals that are manifest in the relationship between bone diameter and bone length. Bone cross-sectional dimensions are relatively wider in longer bones than they are in shorter bones.

Within the genus *Ursus*, the results of the test of the elastic and geometric similarity hypotheses are more ambiguous (Table 20). There is a mixture of results, which is echoed in the comparison between this study and that of Bertram and Biewener (1990). The femoral midshaft diameters scale with geometric similarity on femur length. There are no clear results for the humerus (the anterior-posterior diameter scales with neither elastic nor geometric similarity, and the medial-lateral diameter is not statistically different from either scaling pattern). The tibial anterior-posterial diameter scales with elastic similarity (perhaps due to the irregular shape of the tibia), and the medial-lateral diameter does not show either pattern. Bertram and Biewener (1990) also obtained mixed results including elastic similarity, geometric similarity, and neither scaling pattern (Table 20) for the genus *Ursus*. This finding may be due to the size range of the *Ursus* sample, which ranges from black bears that may be under 100kg to polar bears, which may be as large as 600kg. At larger sizes, scaling patterns begin to change due to mechanical constraints, as evidenced by the curvilinear line that describes the true relationship of the cursorial Carnivorans in the Bertram and Biewener (1990) study.

The finding of elastic similarity of scaling for a small-bodied genus such as *Canis* is not unprecedented. Heinrich and Biknevicius (1998) studied the scaling pattern of mustelids and their results support a pattern of elastic similarity for this group, which covers a size range of two orders of magnitude with no species exceeding 32kg. This size range falls on the lower end of the *Canis* group, but the results are comparable to the results obtained here for *Canis*. Those authors suggested that the different scaling pattern that their data showed was a result of their sample being from a lower and less variable taxonomic group.

The range of body mass of the species included in the results of the regressions for the family Ursidae by Bertram and Biewener (1990) is slightly larger than the range of body mass of the species of *Ursus* included in this study. Their sample of Canidae included several species that were not included in this work. In addition, they used species averages for the regressions, and this study used individuals. These two factors may account for some of the discrepancies between the results of these two studies.

In summary, on the basis of regressions of cross-sectional diameters on bone length, a pattern of elastic similarity for *Canis* is not supported in all cases. There is no evidence for geometric similarity of scaling in *Canis*, and all results show positive allometry, meaning that bone diameters are increasing at a greater rate than bone lengths. Subsequent analyses of bone length show that this allometric relationship is the result of relatively shorter bones in larger individuals. Among *Ursus*, there is no clear pattern of either geometric or elastic similarity of bone diameters on bone length.

4.4 Scaling of cross-sectional dimensions on femoral head area as a substitute for body mass

The previous section provided evidence for bone shape change in the genus *Canis* on the basis of the relationship between cross-sectional dimensions and bone length in the femur, humerus, and tibia. In the genus *Ursus*, by contrast, there is no statistically significant bone shape change observed in the relationship between cross-sectional dimensions and bone length except in the case of the anterior-posterior diameter of the tibia. This section will explore the relationship between bone strength (measured by both diameter and second moments of area) and femoral head area (as a substitute for body mass) so that the mechanical considerations of the different saling patterns are more fully understood and accounted for.

The regressions presented here of the log of bone diameter and the log of the fourth roots of second and polar moments of area on the log of the square root of femoral head area (as a proxy measurement of body mass) will allow an interpretation of differences in mechanical adaptation that is expressed through cross-sectional strength. Actual body mass is obviously the best variable to use in this case, but actual body mass was known for less than a quarter of the sample. In the absence of actual body mass, an estimator or predictor of body mass is used in its place. Because the joint surfaces of long bones must bear the weight of the body during locomotion (Alexander, 1980), joint dimensions are the best estimators of body mass (Jungers and Susman, 1984). In a narrow taxonomic sample, there is often an isometric relationship between joint dimensions in body mass (Jungers and Susman, 1984; Egi, 2001). However, as more groups are added to a sample, and the taxonomic level goes up, the relationship between joint surface and body mass becomes allometric (Jungers, 1991). In the absence of actual body mass, and without a sample size sufficient to derive a significant regression formula that would be accurate for the groups sampled, the square root of femoral head area (superior-inferior diameter x cranial-caudal diameter) was used as a substitute for body mass. This is a geometric mean of the femoral head diameter. The taxonomic levels used in this dissertation are relatively narrow, and so it was deemed appropriate to use a direct measure of joint surface as a substitute for body mass. The square root of femoral head area was used throughout Chapter 4, regardless of which bones cross-sectional dimensions were being studied so that there is consistency of the body mass estimator. In Chapter 5, however, femoral head area could not be used for all bones because the *Canis dirus* sample consisted of isolated, unassociated skeletal elements. In these cases, the joint surface breadth of the tibia and humerus were used, again for the reason that joint surface dimensions are appropriate substitutes for body mass in narrow taxonomic samples.

Bones must be strong enough to bear the weight of the body during locomotion. From the previous section, it is evident that bone strength increases with positive allometry on bone length in *Canis*, but we don't know if that means the bones are stronger relative to body mass in larger animals, or relatively stronger overall (taking into account both bone length and body mass). Similarly, it is not clear yet whether *Ursus* long bones are stronger or weaker relative to the mechanical demands placed on the bones. This section will answer these questions through the exploration of the scaling of bone cross-sectional variables on body mass.

4.4.1 Results

Tables 23, 24 and 25 show the scaling exponent of reduced major axis regressions of the log of bone cross-sectional variables of the femur, humerus and tibia on the log of the square root of femoral head area. The square root of femoral head area and the fourth root of the second and polar moments of area were used in these regressions so that the expected isometric slope of each regression is 1. Significance was determined through the bootstrapping technique in SPSS described earlier. There are consistent results in both genera of isometric scaling of these variables. These results show that most femoral, humeral and tibial cross-sectional variables scale in a regular, predictable manner with body mass in both *Canis* and *Ursus*. The charts (Figures 21-35) that accompany these tables allow a side-by-side comparison of *Canis* and *Ursus* in these regressions. Although nearly all scaling exponents for both genera are not statistically different from 1 (isometry), it is interesting to note that in most cases, the *Canis* slope is higher than the *Ursus* slope. This may reflect the fact that larger animals must find alternate means (posture, behavior) of minimizing the strains on their bones and maintaining constant safety factors (Biewener, 1993), and the relationship of strength to body mass alone does not take these changes into account. Despite the small sample size, the results in *Ursus* are remarkably consistent across variables and skeletal elements.

4.4.1.1 Femur

Table 22: RMA regressions of femoral cross-sectional dimensions on femoral head area

Y variable	X variable (femur)	slope	intercept	CI slope	R^2	N
Femoral head area *Canis*	midshaft ml	0.87	-0.002	0.81 – 0.94	.961	37
	midshaft ap	1.02	-0.19	0.94 – 1.10	.956	37
	Iml	0.98	-0.47	0.91 – 1.05	.987	33
	Iap	0.93	-0.41	0.87 – 1.00	.982	33
	J	0.95	-0.36	0.90 – 1.02	.986	33
Femoral head area *Ursus*	midshaft ml	0.95	-0.05	0.77 – 1.14	.972	24
	midshaft ap	0.92	-0.07	0.71 – 1.13	.962	24
	Iml	0.87	-0.31	0.74 – 1.01	.995	13
	Iap	0.90	-0.31	0.76 – 1.03	.990	13
	J	0.88	-0.23	0.73 – 1.04	.993	13

The RMA regressions of the log of femoral cross-sectional dimensions on the log of the square root of femoral head area are shown in Table 23 and Figures 21, 22 and 23. All regressions are significant. With one exception (medial-lateral midshaft diameter of *Canis*), no results are statistically different from isometry. Most of the scaling exponents for both genera are trending towards negative allometry, but with the inclusion of isometry at the upper end of the confidence intervals. These same variables on femur length yielded results of isometry for *Ursus*, but significant positive allometry for *Canis* (Table 18). Bone shape changes due to allometric scaling occur in *Canis*, but the scaling cross-sectional dimensions and measurements of strength on body mass indicate that these variables, in body small and large individuals, reflect the body mass that they must support and transport on a daily basis.

These results of isometric scaling of cross-sectional dimensions on femoral head area in *Canis*, combined with the positive allometry of bone cross-sectional dimensions on bone length, and the negative allometry of bone length on femoral head area, make it possible to conclude that bone strength increases in this genus in larger individuals are due primarily to shortening the length of the bone rather than depositing more bone tissue about the cross-section. Since bone length shows very little bilateral asymmetry in humans (Churchill and Formicola, 1997), but there is bilateral asymmetry in cortical bone distribution (Jones et al., 1977) and cortical bone distribution can and does change within the lifetime of an individual (Ruff et al., 1994), both in response to activity, it may be suggested that the primary evolutionary mechanism for building stronger bones in *Canis* is not dependent on activity level during adult life. In other words, bone strength is mediated by bone length. This does not mean that there is not individual variation in cross-sectional strength occurring as a result of daily activity and loading placed on the bone, and the subsequent remodeling of this bone.

It is commonly assumed in studies of human postcranial robusticity that the primary way in which bone becomes stronger is through increased bone deposition that occurs as a result of activity. However, it may be that postcranial robusticity is a result of shorter limbs. This is a design strategy that emphasizes a 'conservation of materials'. Of the two strategies to make stronger bones, one involves the manufacture of *more* bone tissue (growing wider cross-sections) and one involves the manufacture of *less* bone (growing relatively shorter limbs). Among the *Canis* sample, larger individuals are relatively stronger than smaller individuals. This is accomplished through relatively shorter bones, which serves the dual purpose of making bones stronger and maximizing the surface-area to volume ratio (thereby decreasing heat loss). Maximizing bone strength through the shortening of limb length is less costly to an organism since fewer resources are needed, which would be an advantage in less productive, colder environments. It may be that the primary reason for shorter limbs is maximizing strength due to increasing mechanical loading and that heat conservation is a secondary result.

In *Ursus*, there is an isometric relationship of bone cross-sectional dimensions and second and polar moments of area on body mass, but there is also an isometric relationship between these variables and bone length, which suggests that bones in larger individuals are relatively weaker than bones in smaller individuals. Larger species can compensate for this relative reduction in strength through postural and behavioral adaptations that minimize the stresses on bones, and maintain constant safety factors (Biewener, 1982, 1993). It may be assumed, since there is an isometric relationship between these variables in *Ursus*, that there are some postural and behavioral differences observable between black bears and polar bears that may account for the relative weakness of polar bear skeletal elements. One obvious difference is that polar bears are adapted to a semi-aquatic habitat since their primary source of food comes from the ocean. There are changes and adaptations to the limbs to make them efficient swimmers. The different demands placed on the limb bones of these two species might account for the differences in how strong the bones are relative to body mass.

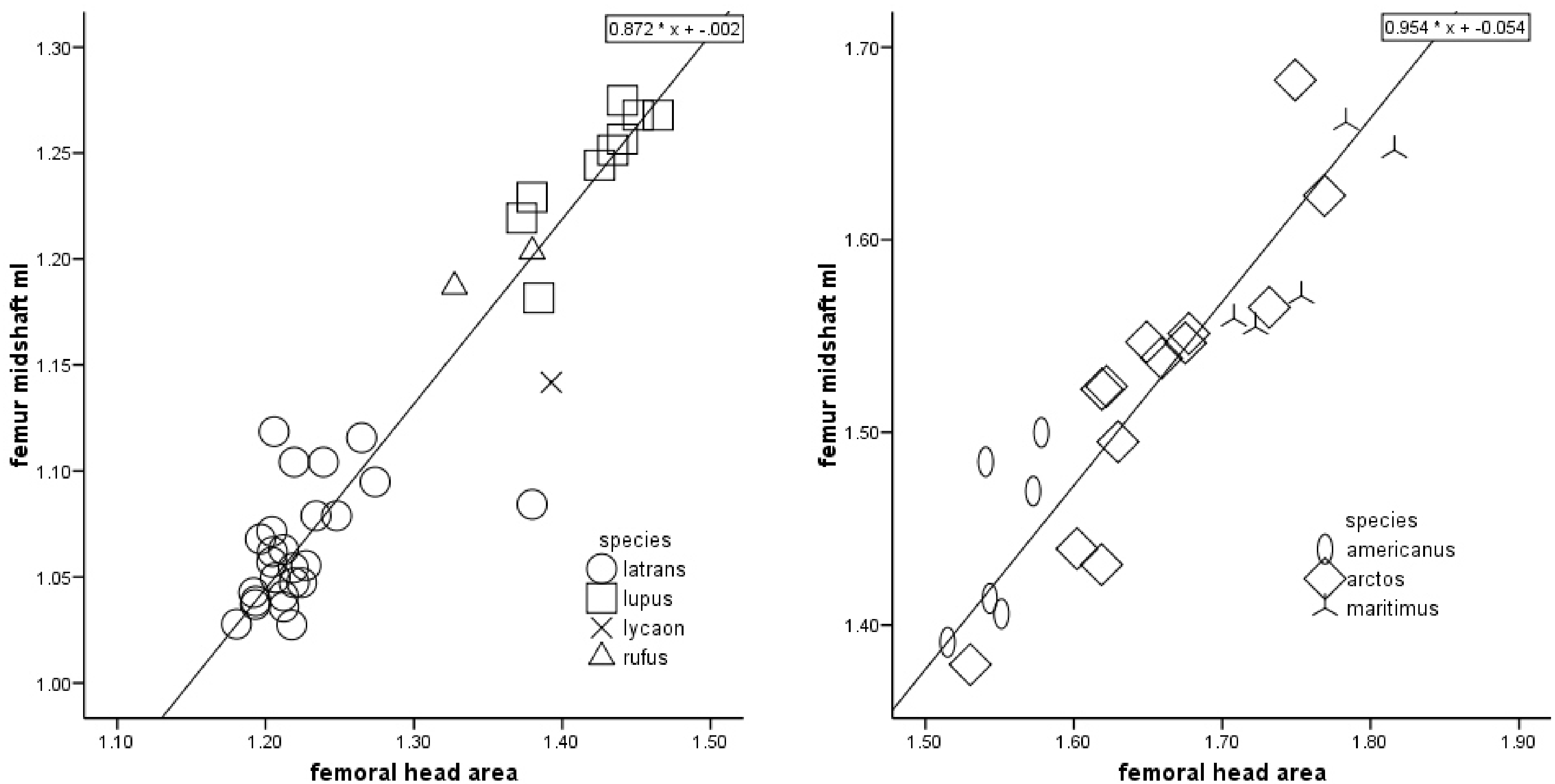


Figure 21: Femoral midshaft medial-lateral diameter on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

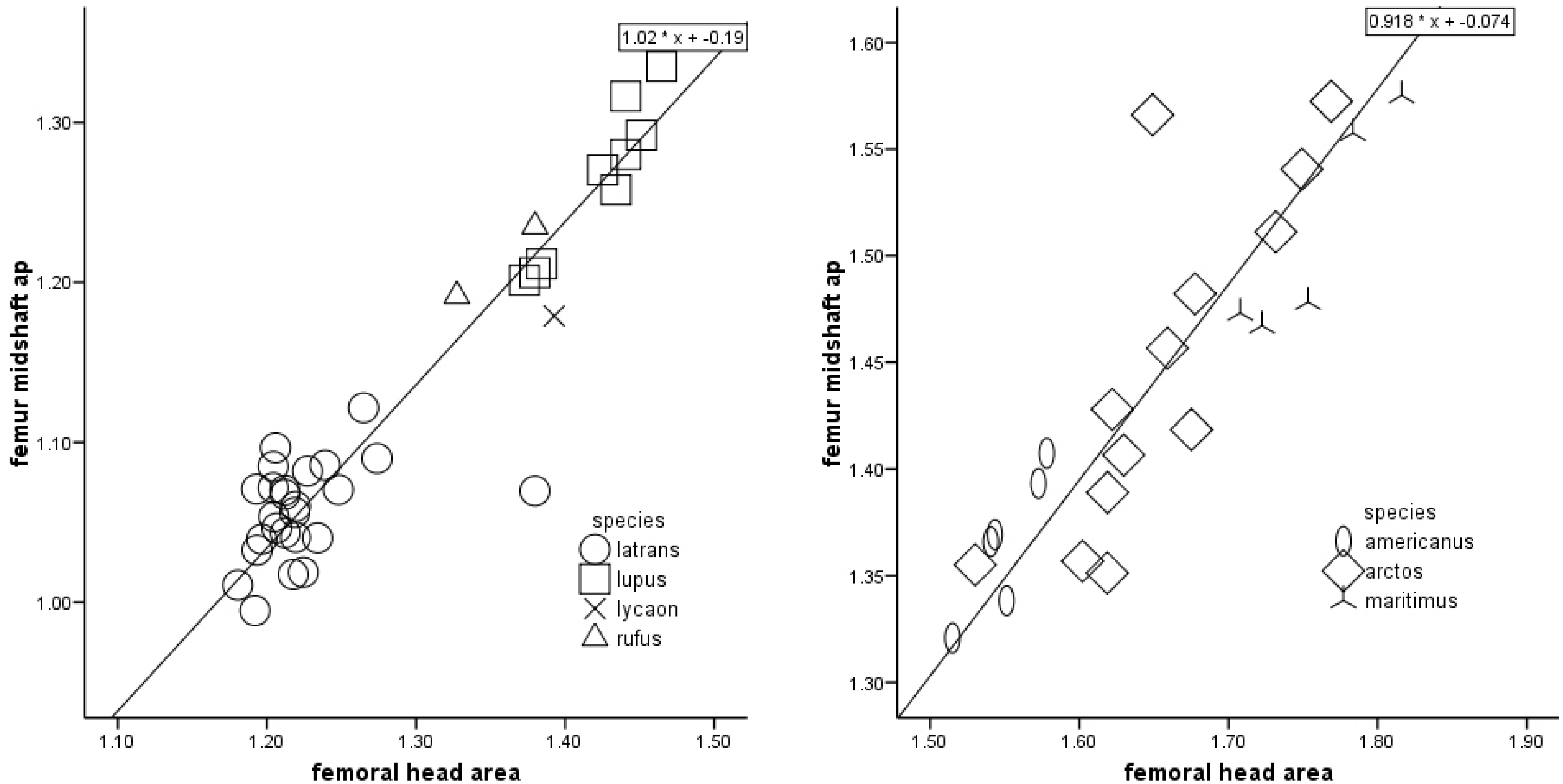


Figure 22: Femoral midshaft anterior-posterior diameter on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

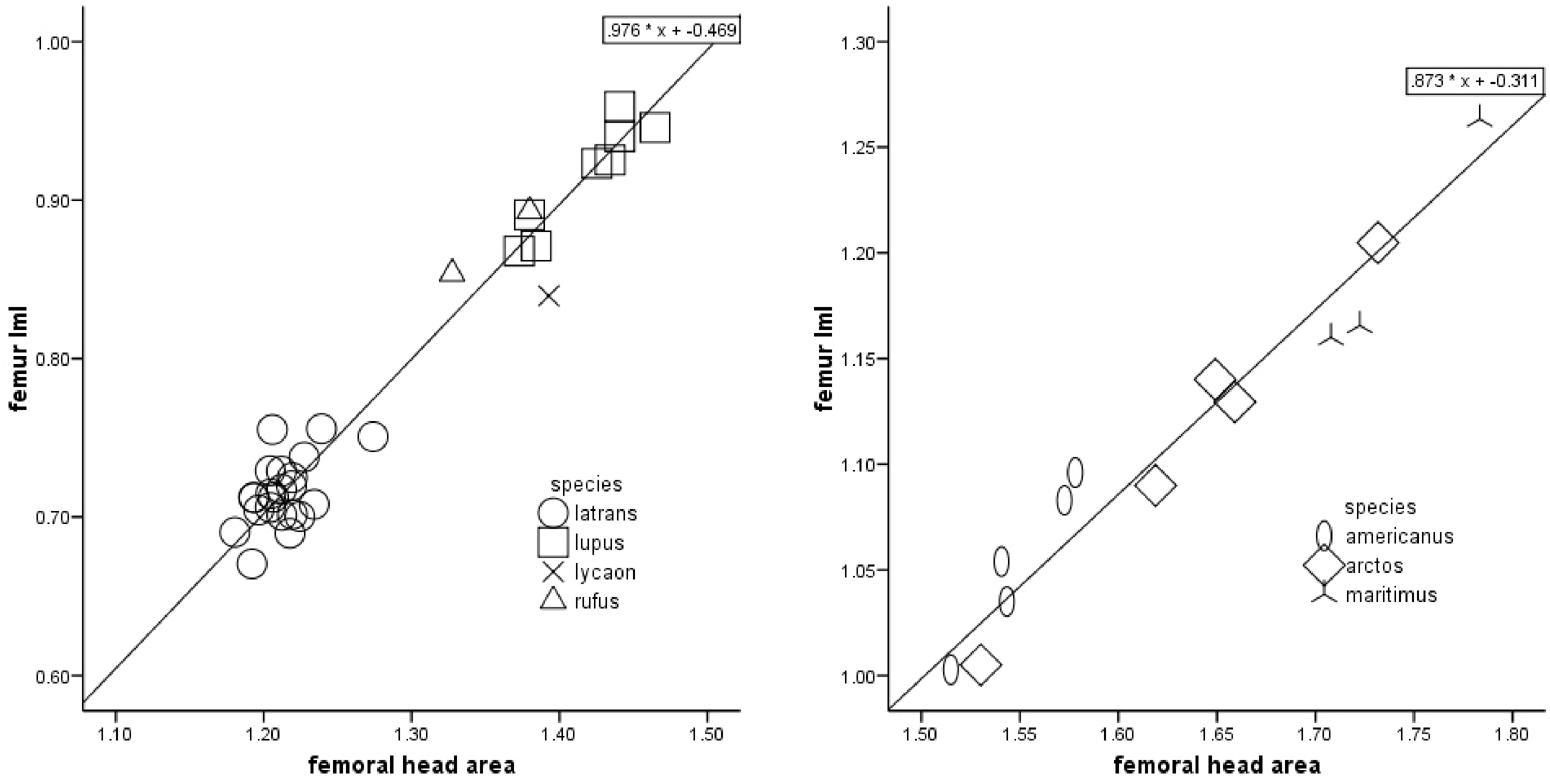


Figure 23: Femur Iml on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

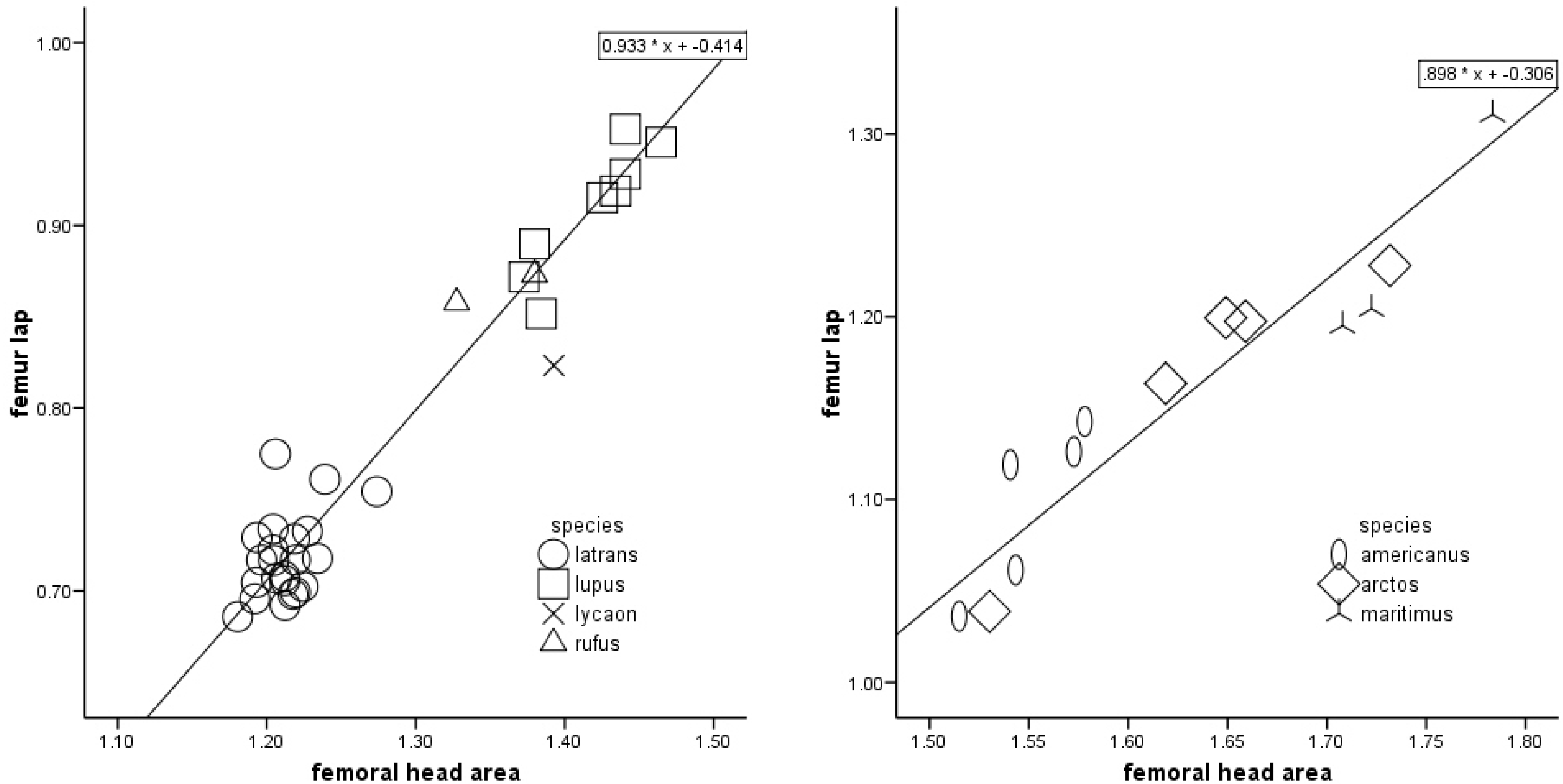


Figure 24: Femur Iap on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

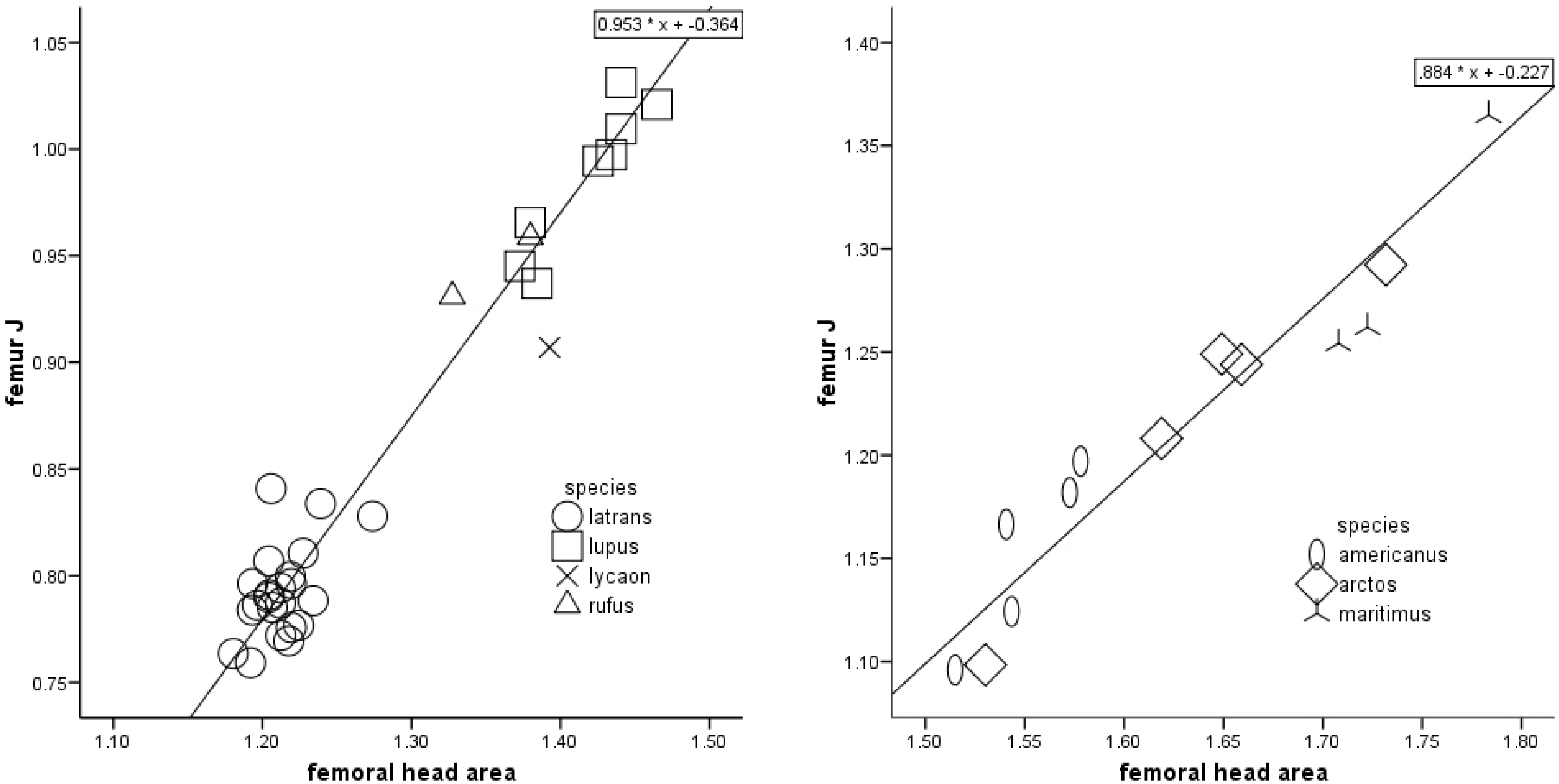


Figure 25: Femur J on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

4.4.1.2 Humerus

Table 23: RMA regressions of humeral cross-sectional dimensions on femoral head area

Y variable	X variable (humerus)	slope	intercept	CI slope	R^2	N
Femoral head area *Canis*	midshaft ml	1.1	-0.28	0.96 – 1.23	.945	37
	midshaft ap	0.94	-0.03	0.82 – 1.06	.956	37
	Iml	1.07	-0.55	0.98 – 1.17	.993	16
	Iap	1.06	-0.58	0.89 – 1.23	.997	16
	J	1.07	-0.48	0.88 – 1.25	.995	16
Femoral head area *Ursus*	midshaft ml	0.98	-0.10	0.73 – 1.23	.942	24
	midshaft ap	1.01	-0.09	0.81 – 1.21	.971	24
	Iml	0.94	-0.33	0.61 – 1.26	.991	11
	Iap	0.91	-0.30	0.74 – 1.07	.985	11
	J	0.92	-0.23	0.47 – 1.37	.993	11

The pattern of scaling for humeral cross-sectional dimensions on femoral head area (Table 24) shows little variation from that of the femoral dimensions on femoral head area. In this case, every cross-sectional variable for both *Canis* and *Ursus* scale with isometry on femoral head area. The anterior-posterior and medial-lateral diameters are increasing at a rate that keeps pace with increasing body mass (expressed by femoral head area). The sample size for the second moments of area for *Ursus* is small (only 11 individuals), but the results of these regressions are the same as the results of the regressions of bone diameters on body mass and these results are statistically significant. However, the wide confidence intervals of the *Ursus* sample are probably a result of the small sample size.

With one exception (the anterior-posterior diameter of the femur in *Canis*), all humeral diameters scale with a slightly higher scaling exponent than the corresponding femoral diameters. These results are similar to the results of Heinrich and Biknevicius (1998) who found that humeral dimensions in mustelids scale with a higher scaling exponent than the corresponding femoral dimensions. This means that the forelimb of larger individuals is strengthened, perhaps to bear a larger proportion of the body mass than the forelimb in smaller individuals. Heinrich and Biknevicius (1998) suggested that the higher exponent in the forelimbs meant that the hindlimb was becoming either longer or less flexed relative to the length or flexion of the forelimb. In order to test this hypothesis, RMA regressions of the femoral length on humeral length were done in order to see if there was an allometric relationship between the two. A finding of positive allometry (slope > 1) means that the femora in large individuals were longer, relative to the length of the humerus, than the femoral in smaller individuals. This test provides only provisional support for their hypothesis since it is only accounting for the length of the proximal sections of both limbs rather than of the entire limb.

The strength variables, Iap, Iml and J, also all scale with isometry on femoral head area. Like the bone diameters, all strength variables in the humerus have slightly higher scaling exponents than those of the femur, although none are different from isometry. This finding may be explained by prey capture techniques that require extensive use of the forelimbs. *Canis* hunt through chasing, often covering long distances, and attacking the prey in groups while biting at the hindquarters in an attempt to weaken and bring down the animal. This is different from the hunting style of felids, which are solitary hunters and grapple with their prey (Gonyea, 1976).

However, in *Canis*, the hunting of large animals results in the need for carcass processing and individuals may be bracing themselves with their forelimbs as they rip off pieces of meat for consumption and for sharing with other members of their pack. Bears, like felids, are solitary hunters and use a style of prey capture that relies heavily on forelimb strength. This explanation is merely speculatory, and more data and further testing would be needed to determine the role of prey capture in relative strength of the forelimb versus the hindlimb.

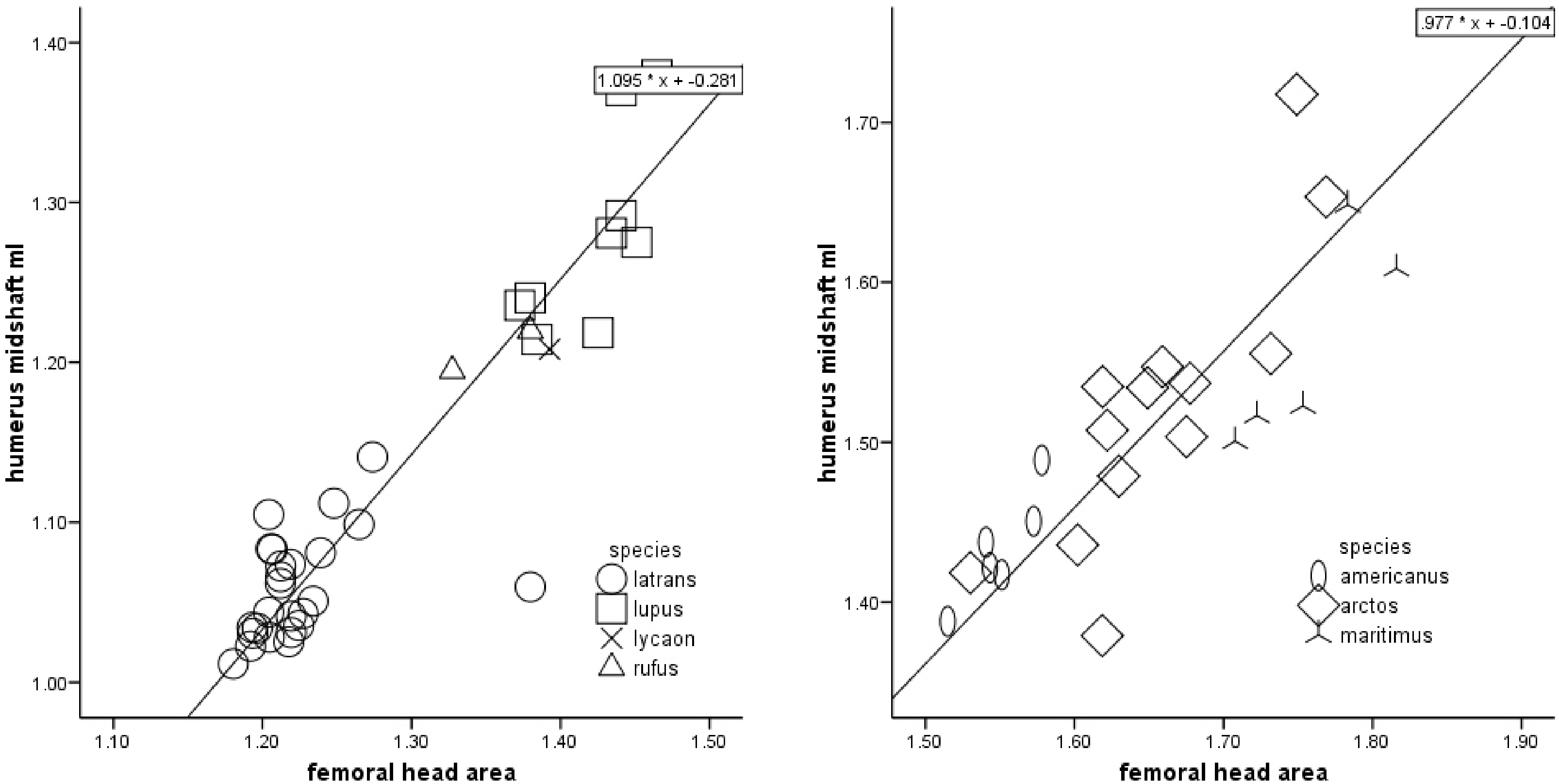


Figure 26: Humeral midshaft medial-lateral diameter on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

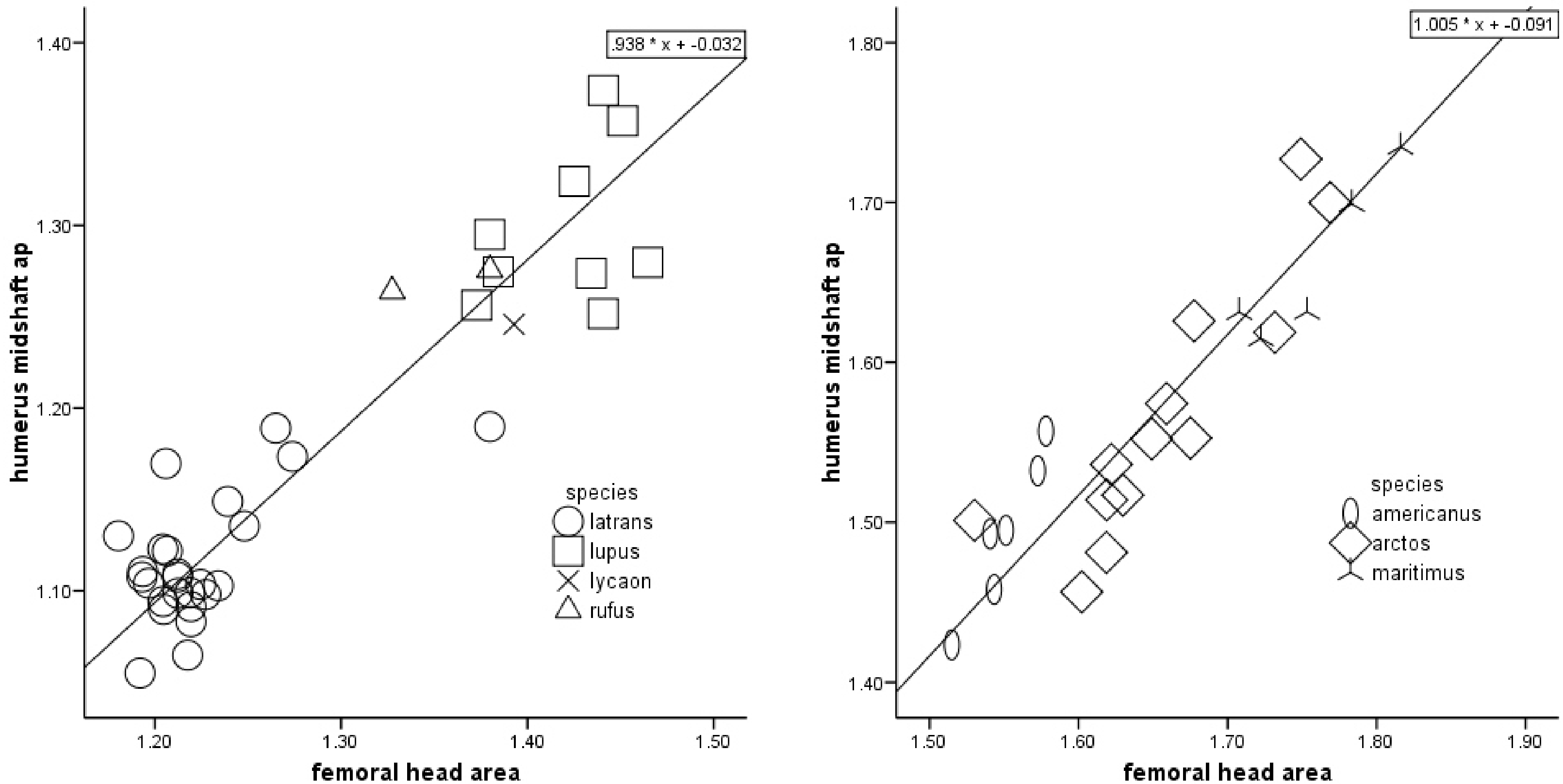
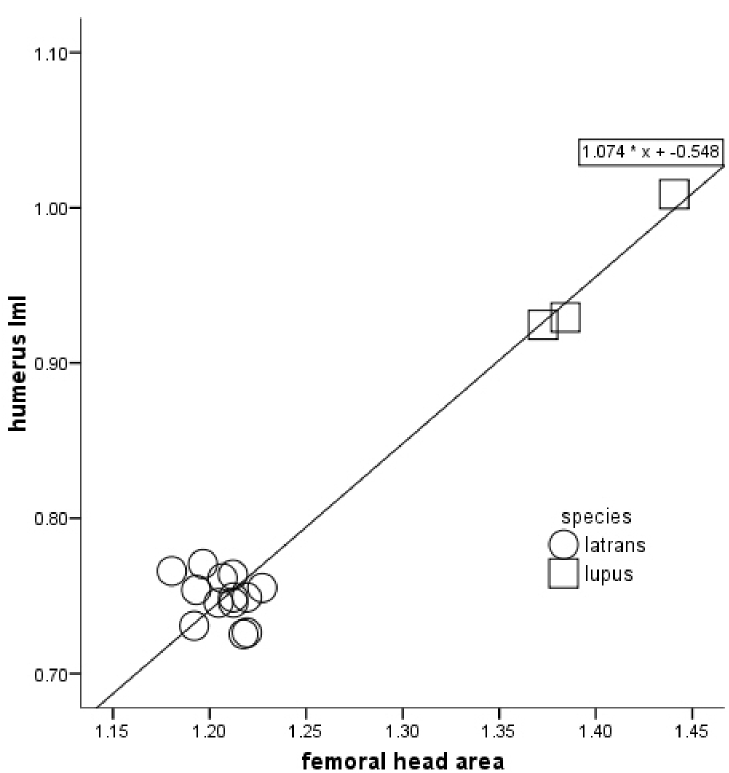


Figure 27: Humeral midshaft anterior-posterior diameter on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)



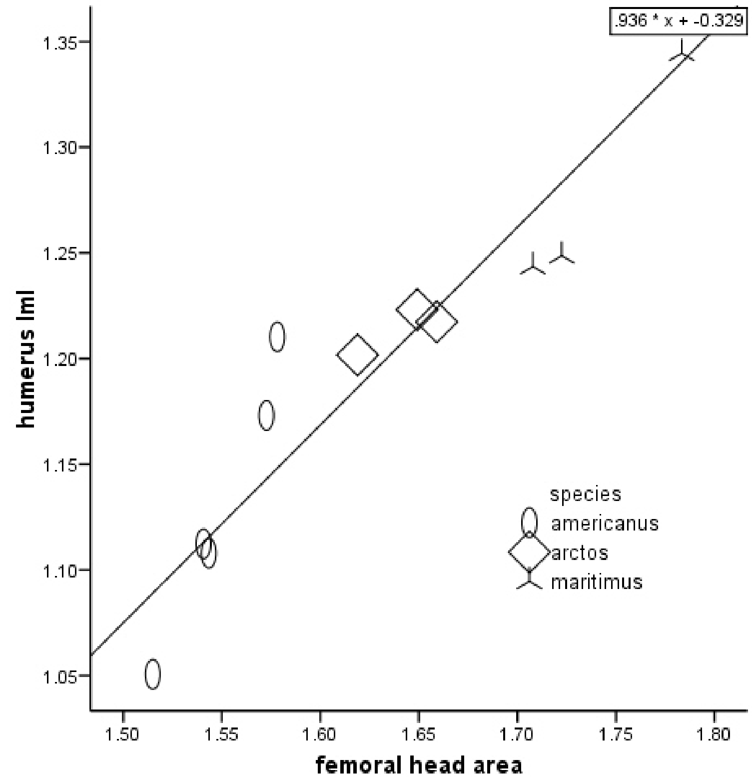


Figure 28: Humerus Iml on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

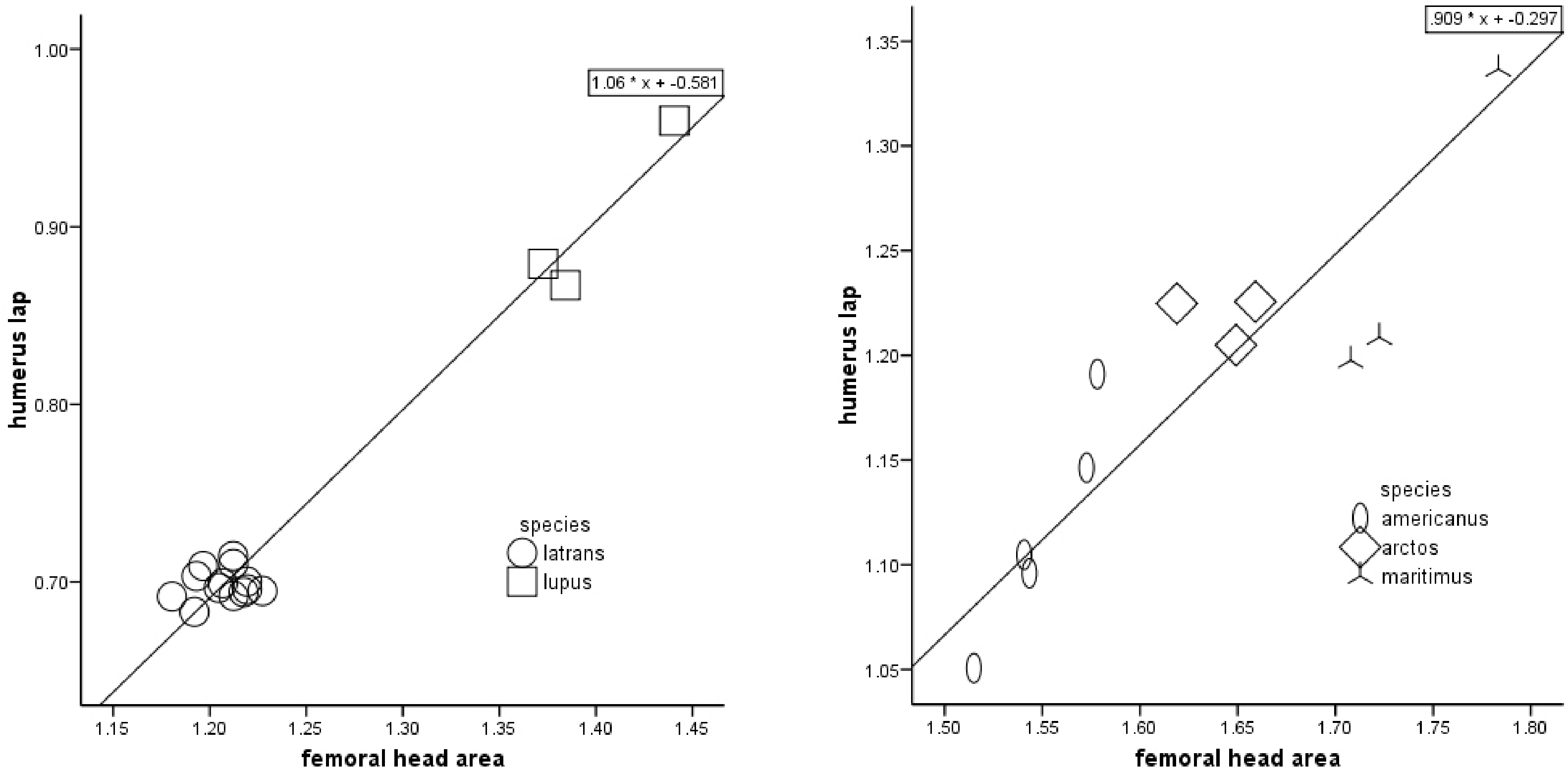


Figure 29: Humerus Iap on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

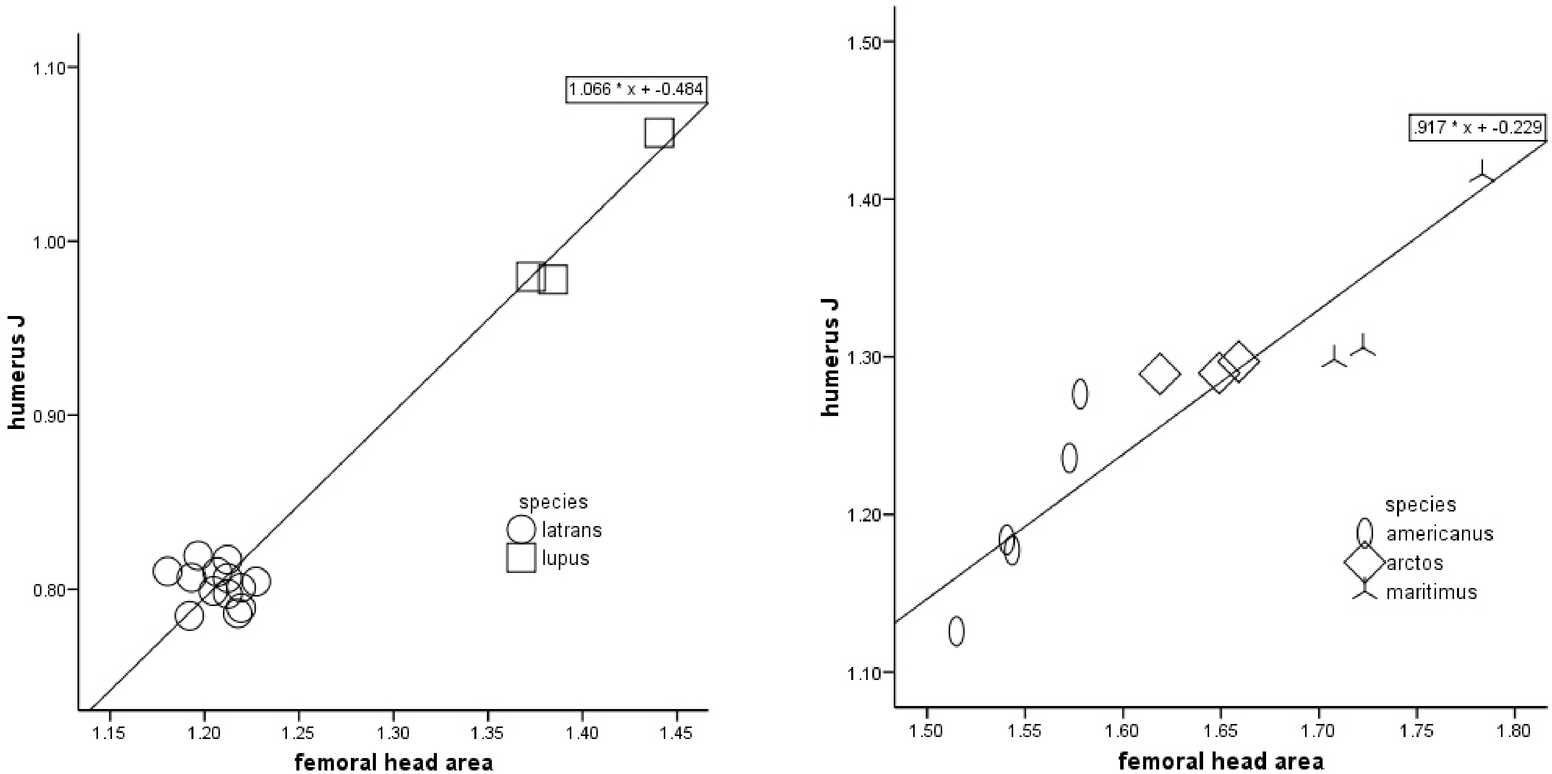


Figure 30: Humerus J (mm) on femoral head area (mm) in *Canis* and *Ursus* (units in mm; all data logged)

4.4.1.3 Tibia

Table 24: RMA regressions of tibial cross-sectional dimensions on femoral head area (body mass)

Y variable	X variable (tibia)	slope	intercept	CI slope	R^2	N
Femoral head area *Canis*	midshaft ml	0.84	0.02	0.76 – 0.93	.958	37
	midshaft ap	1.00	-0.17	0.91 – 1.08	.945	37
	Iml	0.84	0.02	0.76 – 0.93	.987	21
	Iap	0.90	-0.39	0.81 – 1.00	.990	21
	J	0.92	-0.34	0.85 – 0.99	.990	20
Femoral head area *Ursus*	midshaft ml	0.93	-0.15	0.81 – 1.05	.975	23
	midshaft ap	1.08	-0.26	0.72 – 1.43	.952	25
	Iml	0.85	-0.24	0.67 – 1.03	.998	9
	Iap	0.84	-0.29	0.56 – 1.11	.997	9
	J	0.84	-0.18	0.64 – 1.03	.998	9

Table 25 provides results of RMA regressions of tibial cross-sectional dimensions on femoral head area (body mass) for *Canis* and *Ursus*. These results are similar to the results obtained from the regressions of femoral and humeral cross-sectional dimensions on femoral head area. There is an overall pattern of isometry of scaling tending toward slight negative allometry. The only exceptions for the tibia are found in the genus *Canis* (tibial medial-lateral midshaft diameter, tibial Iml, and tibial J), all of which scale with negative allometry that does not include isometry in the 95% confidence intervals. Due to logistical problems with the x-ray equipment, there are only a limited number of *Ursus* for which there are second moments of area. This small sample size has not affected the significance of the high correlation coefficients, but it does mean that the confidence intervals for each regression are large. A larger sample size with smaller confidence intervals might show that the low scaling exponents for the second and polar moments of area of *Ursus* actually exclude isometry, but the data presented here cannot exclude isometry as a finding for these regressions.

The negative allometry of half of the cross-sectional variables on femoral head area in *Canis* reveals that the strength of the tibial cross-section is slightly less than would be expected to support the body mass of larger individuals. The tibia has an irregularly shaped cross-section that can complicate conclusions drawn about the strength of this bone relative to other, more circular shaped bones such as the femur (Daegling, 2002). Even with this odd shape, the scaling pattern of the diameters and the second and polar moments of area of the tibia scale in a pattern similar to those variables of the femur and humerus on femoral head area, the proxy measure of body mass used here.

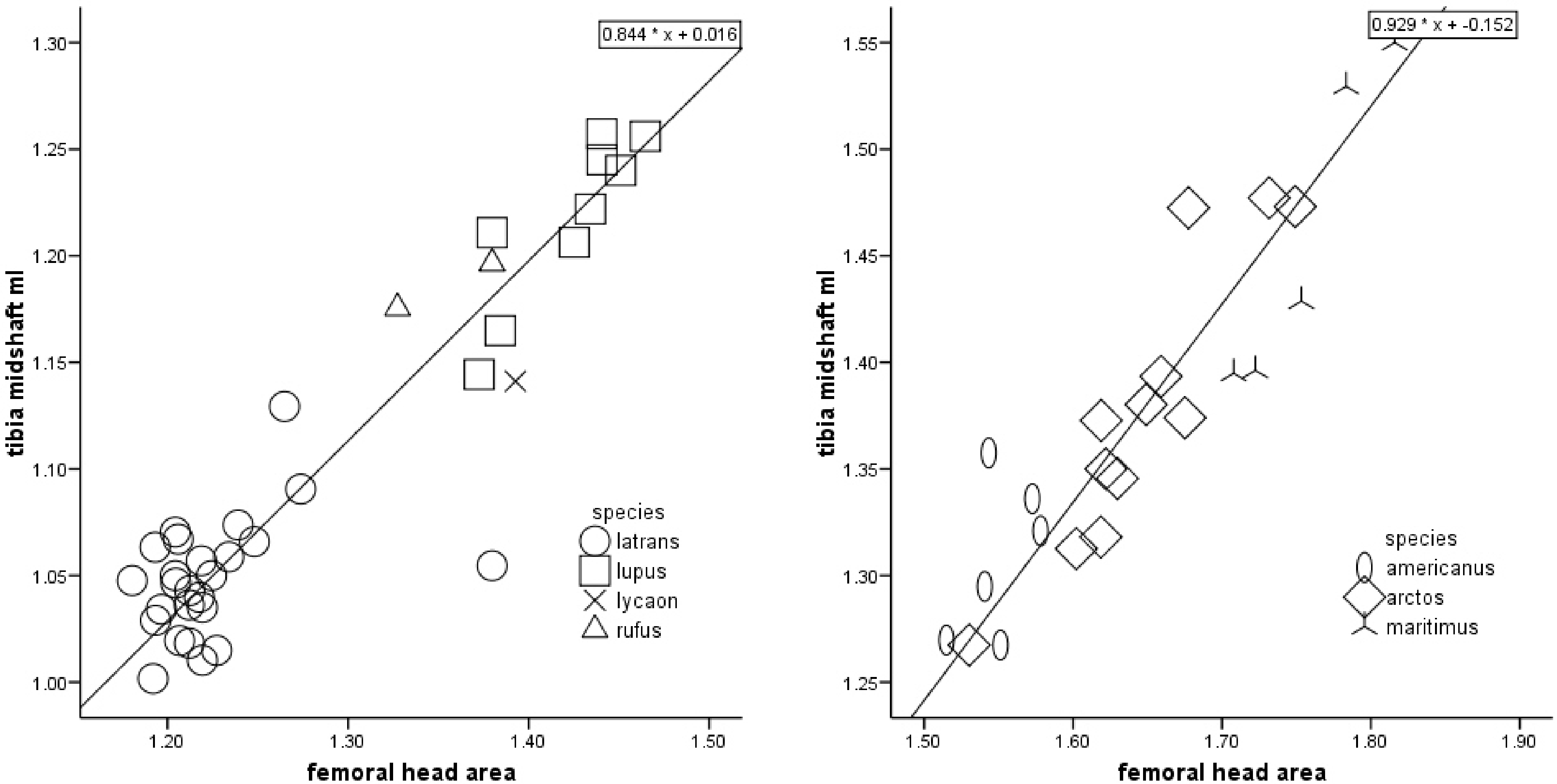


Figure 31: Tibial midshaft medial-lateral diameter on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

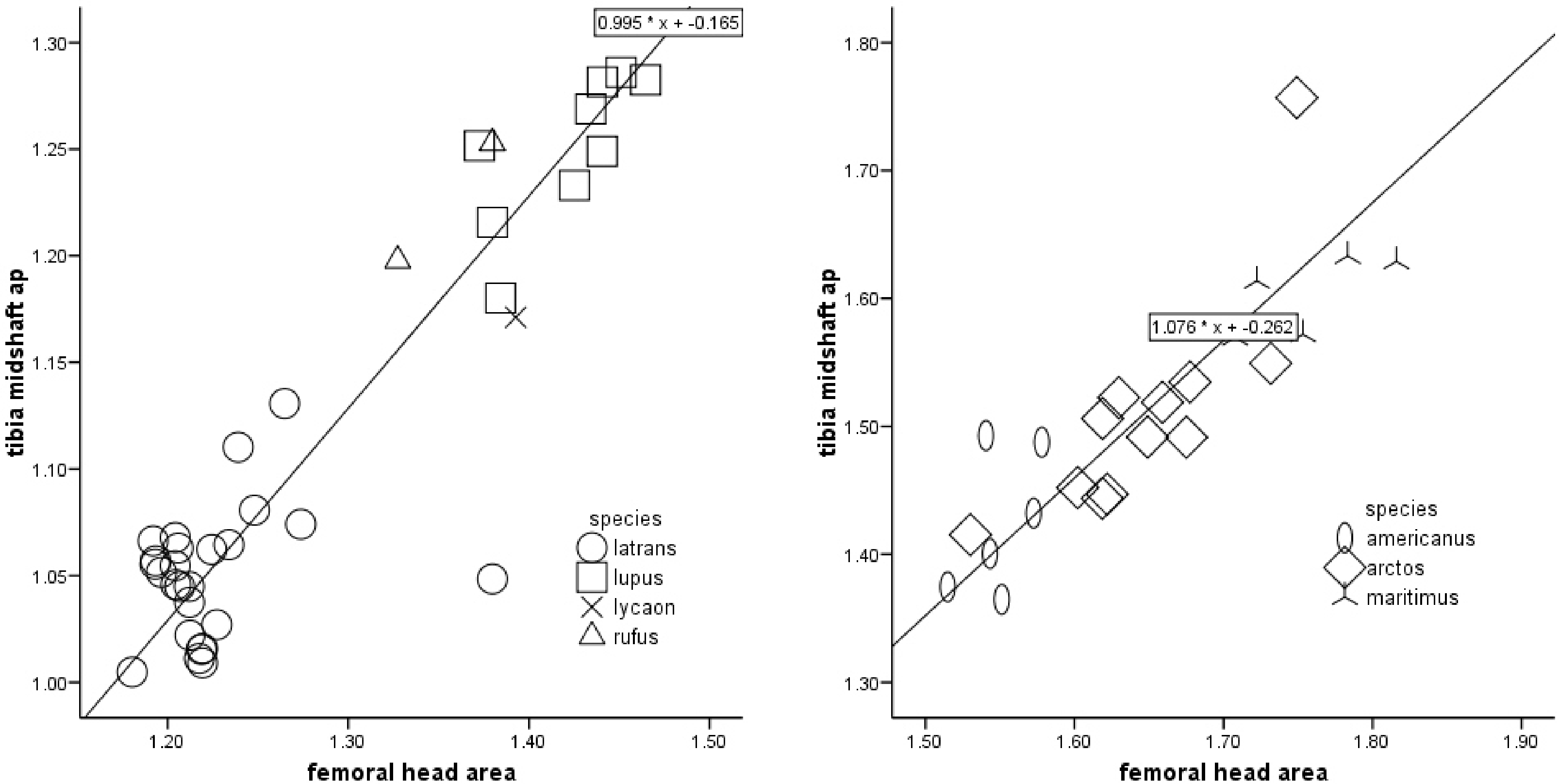


Figure 32: Tibial midshaft anterior-posterior diameter on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

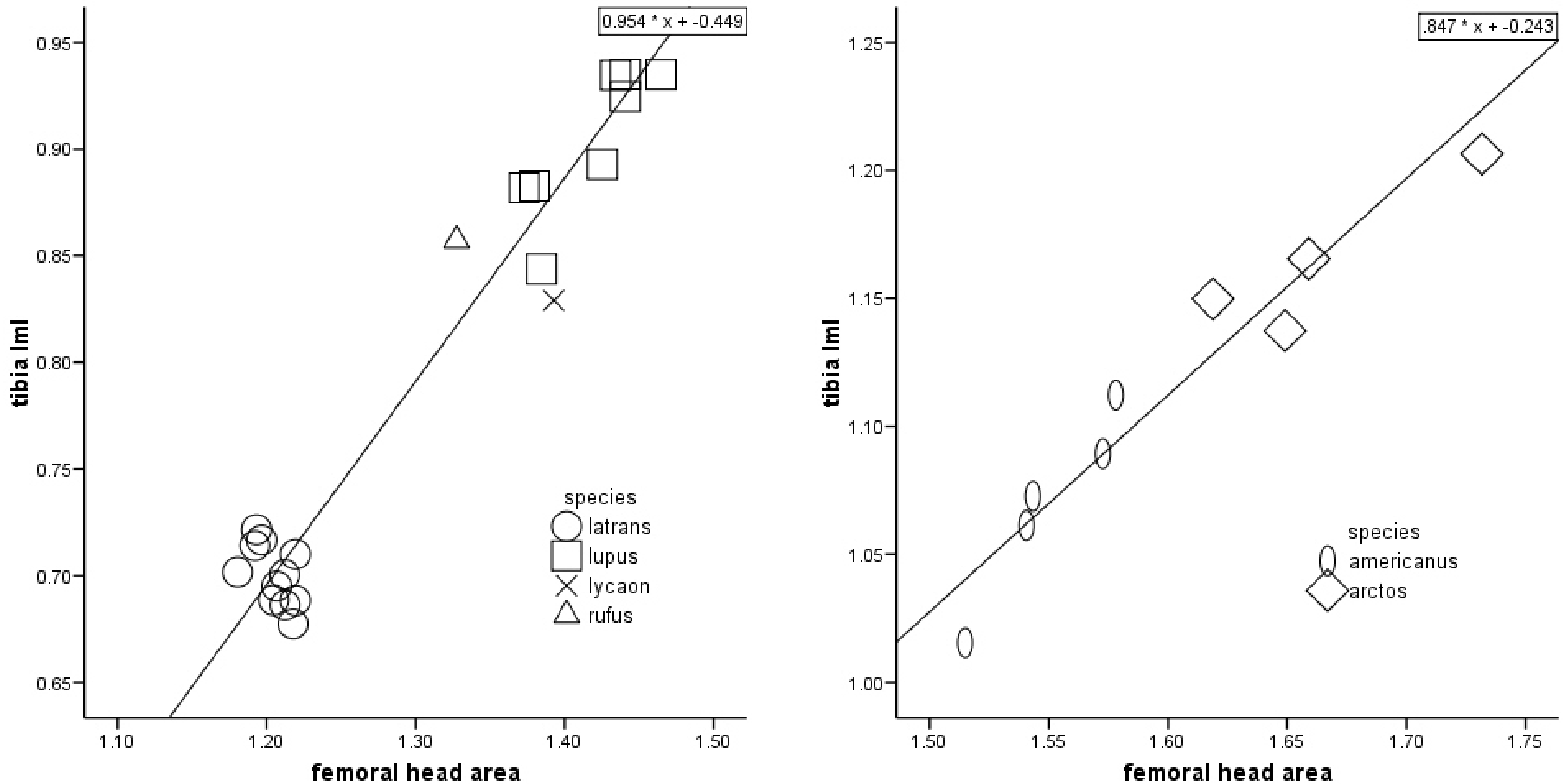


Figure 33: Tibia Iml on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

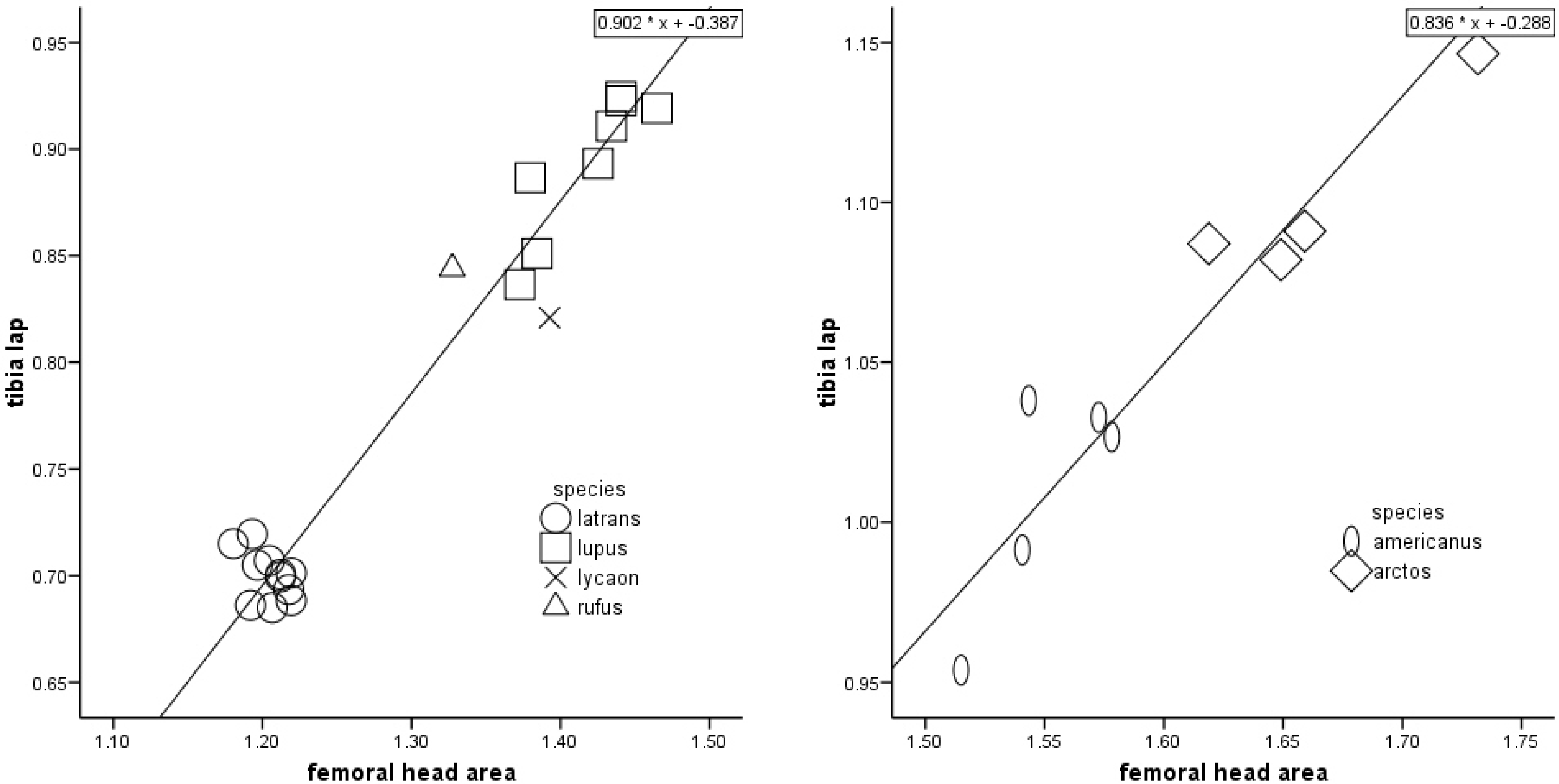


Figure 34: Tibia Iap on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

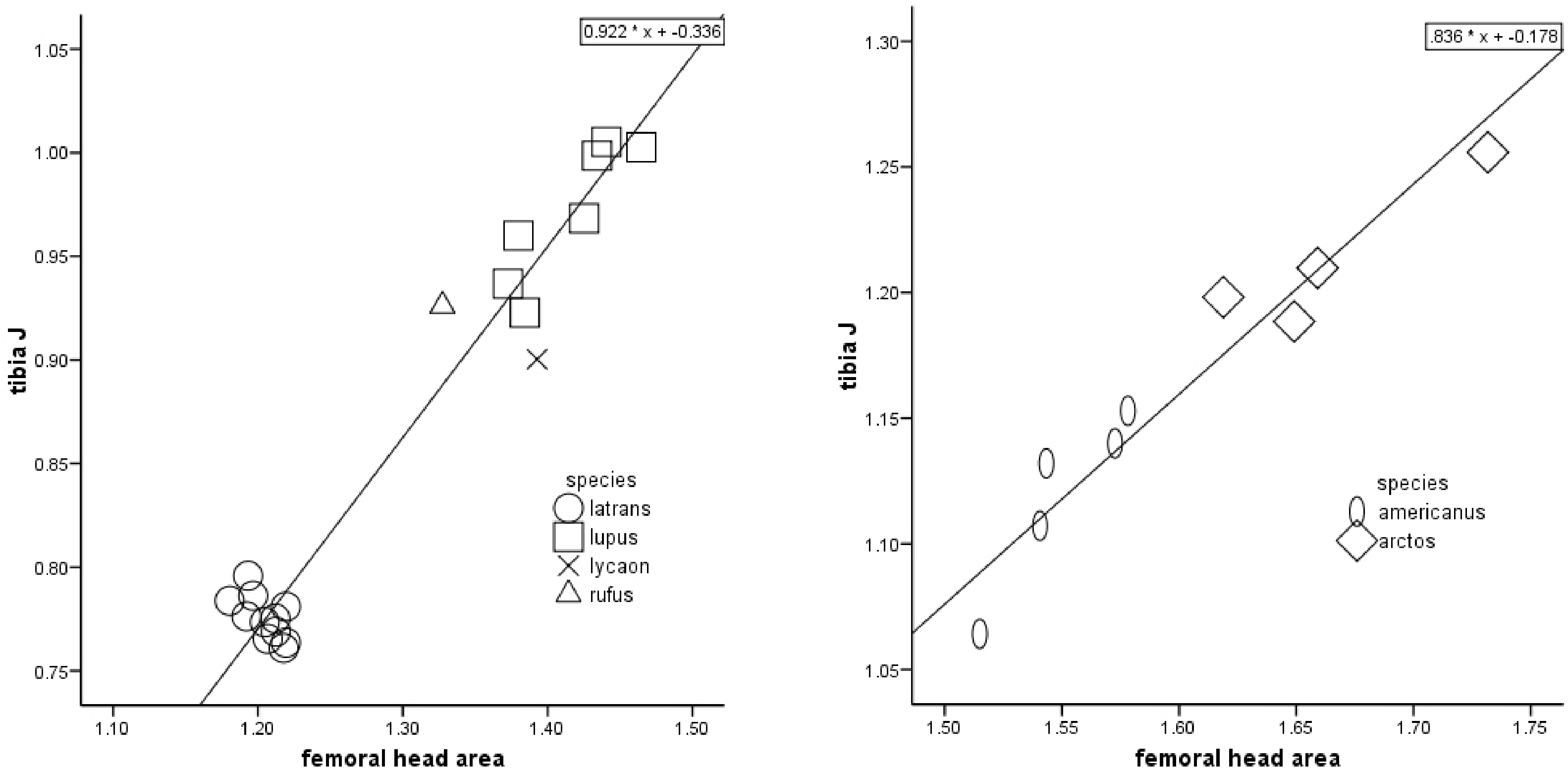


Figure 35: Tibia J on femoral head area in *Canis* and *Ursus* (units in mm; all data logged)

4.4.2 Discussion

Cross-sectional variables for the femur, humerus, and tibia were regressed onto femoral head area as a proxy for body mass to understand adaptations to loading. Both genera, *Canis* and *Ursus*, showed a nearly uniform pattern of isometry of scaling with regards to the bone midshaft diameters, second and polar moments of area on body mass (femoral head area). The isometric pattern of scaling of cross-sectional variables on body mass means that long bones increase in strength to keep pace with increasing body mass, but it does not reveal if there are relative strength differences between individuals in the sample. This question will be addressed in the next section (4.6) with a modified version of Alexander's (1989) index of athletic capability.

Table 26 provides a comparison between these data and results and the results of previously published studies (Jungers and Burr, 1994; Demes, Jungers and Selpien, 1991; Heinrich and Biknevicius, 1998). The overall pattern for these regressions is positive allometry. The only exceptions to this are from the sample group of indriids, for which four of the regressions show a pattern of negative allometry (humerus Iml, femur Iap, humerus Zml, and femur Zap). It is worth noting that there is similarity in the direction of the scaling pattern of all three groups. Differences among the groups may be attributed to differences in modes of locomotion (arboreal quadruped (monkeys), vertical clinger and leaper (indriids), scansorial (mustelids) and cursorial quadruped (canids)) among the three groups.

The indriids are the only group out of the four compared in Table 26 that have scaling exponents that are lower than expected by isometry. The humerus Iml and Zml and the femur Iap and Zap both have relatively low scaling exponents. This is not surprising for the humerus because this species has a hindlimb dominated locomotor style, but the results from the femur are rather unexpected. It is unclear why the anterior-posterior cross-sectional strength variables of the femur would scale with negative allometry in this group, and the medial-lateral strength variables with scaling exponents that are not statistically different from isometry.

The group that the *Canis* sample appears closest to in limb bone strength scaling relationships is the quadrupedal monkey group. This is not surprising because this group is probably the closest in locomotor type to *Canis*. Indriids are categorized as vertical clingers and leapers, with a hindlimb dominated style of locomotion (Demes, Jungers and Selpien, 1991). Mustelids exhibit a wide variety of different locomotor types (Simpson, 1945) and this diversity makes it hard to categorize the group and compare it to other groups with more restricted types of locomotion.

The issue of taxonomic level and scaling differences that may accompany sampling at different levels is not as relevant here as it is with the comparison to the results of Bertram and Biewener (1990). Each of the groups compared in this section are from roughly the same taxonomic level (family). This means that the groups are less likely to have phylogenetic differences that would account for differences between small and large individuals or species in the sample. The larger the group, and the more species that are included, the more inherent variability there will be in the sample, which will make it more difficult to detect size-related differences in scaling. Restricting the taxonomic group provides more information about how different loading regimes lead to differences among species.

Table 25: Cross-sectional variables (cortical area and second and polar moments of area) on body mass; comparison with other studies

Variable	Exp. slope	J&B slope	D, J, S slope	H&B slope	Canis slope	J&B R^2	D,J,S R^2	H&B R^2	Canis R^2
Humerus CA	0.67	0.75	0.692	.743	0.793	0.969	0.992	.991	0.967
Femur CA	0.67	0.812	0.696	NA	0.772	0.987	0.992	NA	0.976
Humerus IAP	1.33	1.554	1.339	1.525	1.556	0.973	0.992	.990	0.983
Humerus IML	1.33	1.458	1.292	1.392	1.576	0.975	0.994	.991	0.971
Femur IAP	1.33	1.543	1.305	NA	1.381	0.985	0.995	NA	0.971
Femur IML	1.33	1.568	1.344	NA	1.446	0.994	0.998	NA	0.981
Humerus J	1.33	1.482	NA	1.470	1.517	0.976	NA	.990	0.975
Femur J	1.33	1.554	NA	NA	1.415	0.991	NA	NA	0.978
Humerus ZAP	1	1.141	1.008	1.122	1.168	0.974	0.993	.990	0.981
Humerus ZML	1	1.102	0.981	1.064	1.201	0.976	0.994	.990	0.959
Femur ZAP	1	1.162	0.987	NA	1.032	0.987	0.996	NA	0.955
Femur ZML	1	1.189	1.009	NA	1.135	0.993	0.997	NA	0.972

Notes: J & B is Jungers and Burr (1994) and the sample group is quadrupedal monkeys; D, J and S is Demes, Jungers and Seplien (1991) and the sample group is indriids; H and B is Heinrich and Biknevicius (1998) and the sample group is mustelids

4.5 Index of bone strength, modified from Alexander's (1985) index of athletic capability

The regressions of the previous two sections describe the morphology of the postcranial skeleton and the relationship of cross-sectional dimensions to body mass, but they are structural descriptions that assume that bone is loaded in a single direction. Obviously, the bones in a living organism are loaded in many directions as the organism moves across varied terrain and faces the difficulties and unpredictability of resource acquisition. Consequently, these results are not able to answer the questions of how well these bones are adapted to the demands of daily life, including locomotion, resource acquisition, and interactions with other organisms. For example, the femur of a large bear may be equally as strong as the femur of a small bear when both are standing still on level ground and the bone is subjected to a simple compressive force. However, there may be a considerable difference between the large bear and the small bear if they are running at top speed or over varied terrain. Under these conditions, the forces on the skeleton of the large bear are likely to be relatively greater, meaning that, structurally speaking, its femur is relatively weaker than that of the small bear. For this reason, a measure of skeletal strength that takes into account body mass, limb length, and the distribution of cortical bone is necessary for fully evaluating variability in postcranial skeletal strength. The index of athletic capability (Alexander, 1985, 1989) is a ratio that takes into account all of these factors.

The index of athletic capability is a ratio that compares bone strength (Z) relative to loading environment (mass, moment arm, and acceleration) and is used to determine the amount of fast running or athletic type feats done by extinct animals and it has the added value that it can be calculated from skeletal remains (Alexander, 1985, 1989). A higher index of athletic ability indicates that a bone is stronger and can withstand higher bouts of loading than would be predicted on the basis of body mass alone. The index of athletic ability is expressed as: Z/amgx, where 'Z' is the section modulus, 'a' is the fraction of weight borne by the limb, mg is body weight (mass * gravitational acceleration on earth), and 'x' is the distance from the section to the end of the bone, the result being a measure of the amount of stress experienced by a unit of bone (measured in mm) that can be used to compare relative bone strength across very different mammalian groups. The section modulus is calculated as the second moment of area (I) in a particular plane, divided by ½ of the bone width in that plane at that section of the bone. Appendix B provides a look at the index of athletic capability as proposed by Alexander, with the units in mm, for comparison with the following derived dimensionless ratio.

The modified version of Alexander's index of athletic capability was calculated for both *Canis* and *Ursus*. The fraction of weight borne by the limb (a) and gravitational acceleration (g) were assumed to be constants that could be omitted. The third modification is the use of femoral head area (mm^2) in place of body mass (mm^3) because actual body mass was not known for most individuals. Therefore, the modified formula for the index of athletic capability, used in this dissertation is Z/x(fh), where 'fh' is femoral head area. Both the numerator and denominator are in units of mm^3, so the resulting figure is a dimensionless ratio. This is different from Alexander's index, which has units of mm, but it follows the techniques of Ruff et al., (1993), who use a dimensionless ratio to compare postcranial bone strength across individuals and species with different body mass. As such, this modified index of athletic capability can be compared across species and sizes within a genus. An illustration of this index for the two genera presented here is provided in Figures (36 and 37).

4.5.1 Results and discussion

In *Canis*, the two larger species have larger indices than the coyote (*Canis latrans*), the smallest *Canis* species included in these analyses. The Mann-Whitney U test was used to determine whether there are significant differences in the modified index of athletic capability between species, (sig. < .05). There is a significant difference between *C. latrans* (coyotes) and *C. lupus* (gray wolves), but not between either of those species and *C. rufus* (red wolf), probably due to the small sample size of red wolves. The gray wolf, largest of the three species, has a higher index of athletic capability than the coyote, but lower than the red wolf. The red wolf, close in size to the gray wolf, but considerably larger than the coyote, has a higher index of athletic capability than either species.

In *Ursus*, by contrast, the largest species has the smallest index of athletic capability. The overall strength of the femur of the polar bear, when body mass and moment arm (limb length) are taken into account, is less than the strength of this bone in the black bear. This leads to the inference that the polar bear would have to accommodate this strength decrease through a series of anatomical, postural, behavioral and locomotor changes. These changes might include changes to the angle of the joint, a more vertical orientation of the limbs, an increase in duty factor, and a relatively slower gait (Biewener, 1989, 1990). The medial-lateral femur strength at midshaft of each *Ursus* species is lower than the anterior-posterior femur strength. In addition, the range and standard deviation of the medial-lateral indices of athletic capability are not as wide as those for the anterior-posterior indices.

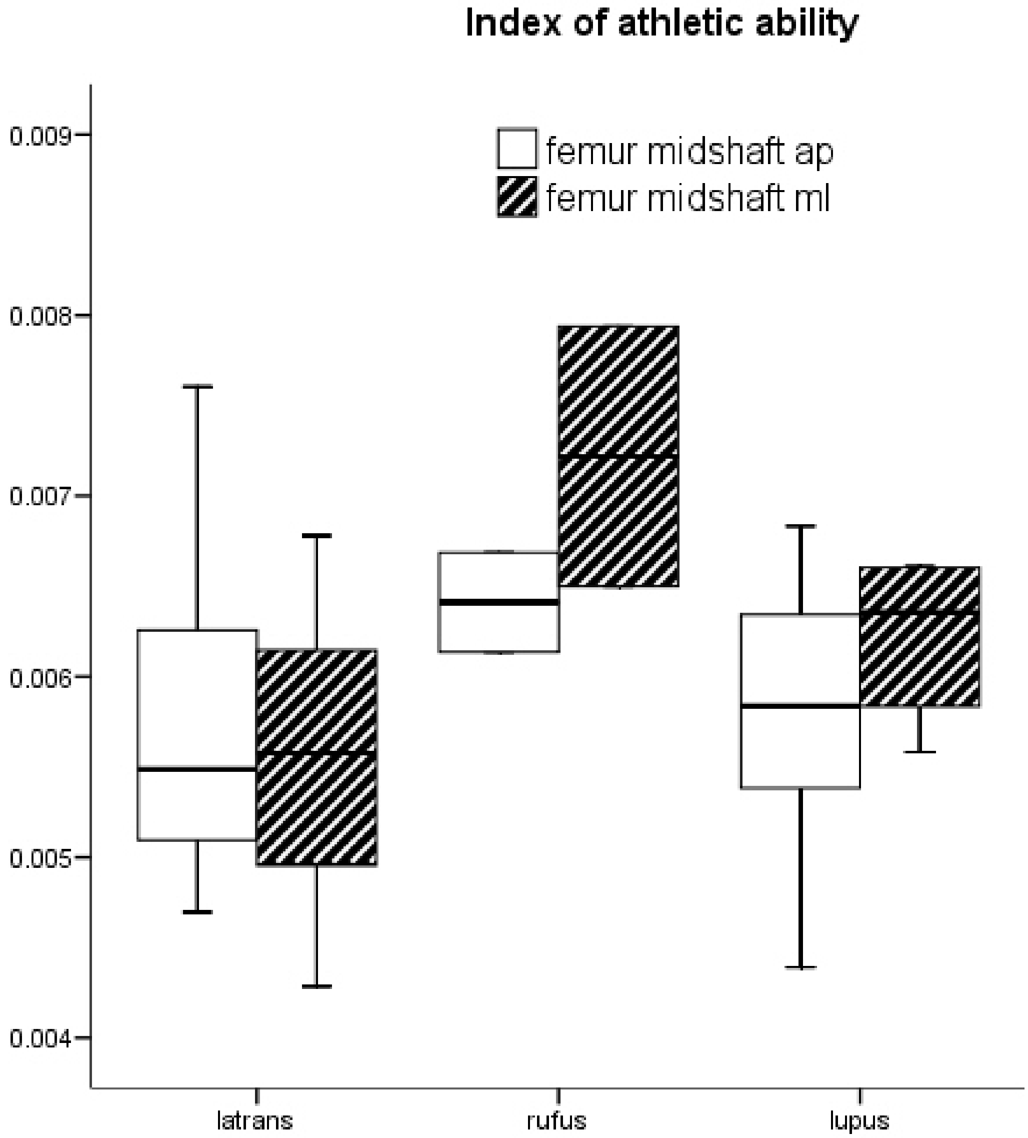


Figure 36: Indices of athletic ability for the midshaft femur among *Canis*

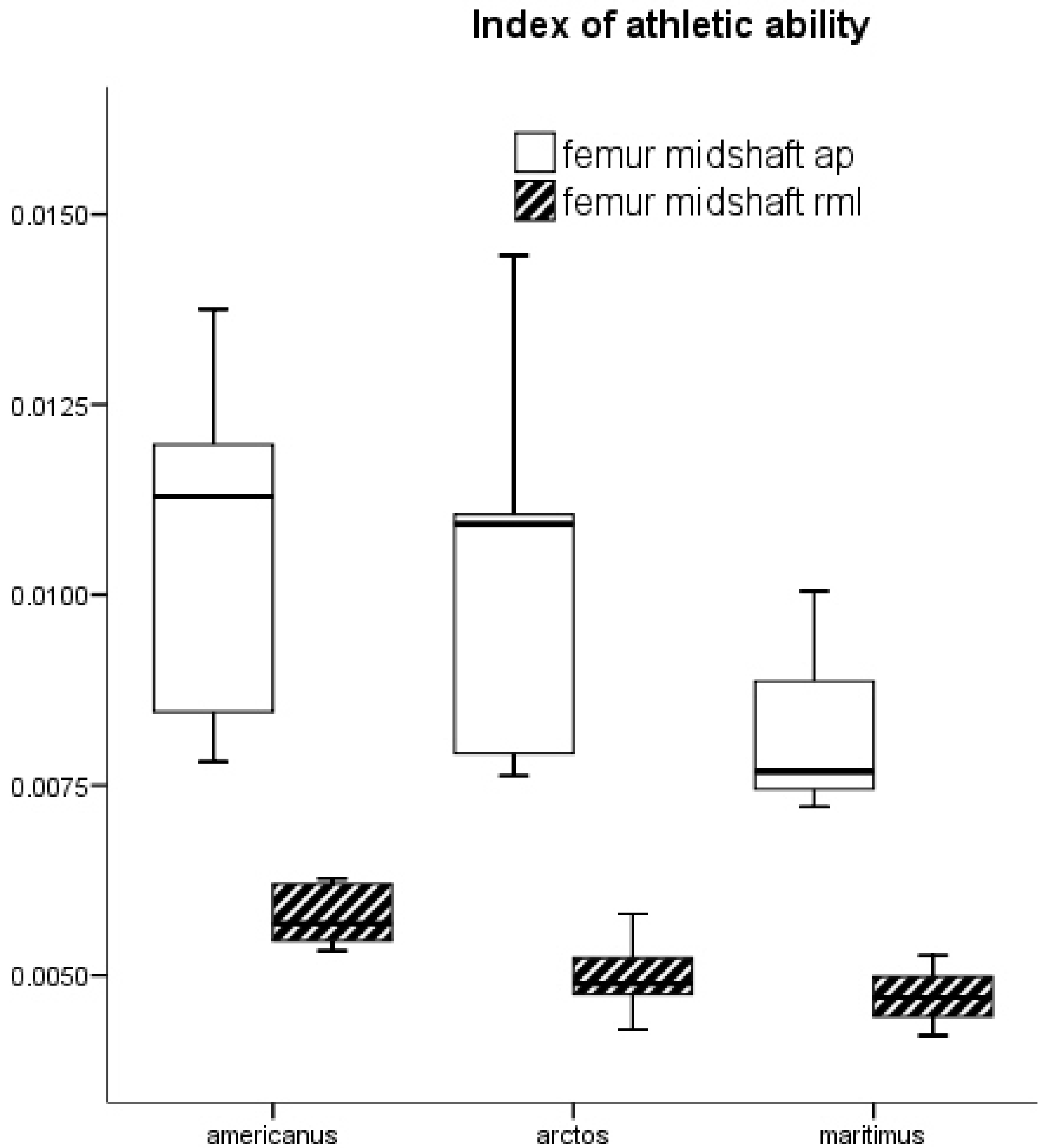


Figure 37: Indices of athletic ability for the midshaft femur among *Ursus*

The comparisons of the modified index of athletic capability for each genus highlight the differences in relative strength that are exhibited between the two genera. Within *Ursus*, larger animals have bones that are less well adapted to running fast or performing agile athletic feats than smaller bears. In notable conrast, within *Canis*, the larger animals have higher indices of athletic capability, suggesting greater agility and strength in the skeletons of larger individuals. The difference in the relationship between strength and body mass between the two genera deserves further exploration. In particular, the results for the genus *Canis* are somewhat unexpected because normally strength and agility decrease with increasing body mass. Elephants and other large animals represent ideal examples of that, although notably, rhinoceros do not follow that pattern (Bertram and Biewener, 1990). The reasons behind the increasing strength within extant members of *Canis* will be explored further in Chapter 5.

These very different patterns show that the relationship between bone strength and body mass differs between these two genera. In *Canis*, athletic capability increases with increasing body size and in *Ursus*, athletic capability decreases with increasing size. What's even more interesting is that bone strength is increasing in the genus *Canis* with increasing body mass through a relative shortening of limb length rather than an increase in deposition of bone tissue about the cross-section. This finding suggests that the variation in limb length in mammals could have a mechanical explanation. It also leads to the possibility that there is a relationship between ecological conditions and the mechanical demands placed upon the skeleton. One additional and also one of the most interesting findings of Chapter 4 is that *Canis* may be shortening limbs as a mechanism for increasing strength. If the reason for shorter limbs in larger *Canis* is related to the need for greater strength due to increased loading on the skeleton, then the next step would be to investigate the possible reasons behind this increased loading.

The ecological hypothesis, as outlined in Chapter 1, provides an explanation for the pattern of changing robusticity that is seen among hominins, and may also be applied to the pattern of robusticity seen in this sample of *Canis*. Essentially, the ecological hypothesis states that in areas of low productivity, carnivores will have relatively more robust skeletons than congenerics living in areas of high productivity due to the large body mass and dispersed distribution of their prey species. There are preliminary indications that this hypothesis has some explanatory power based on the results from this dissertation showing that larger members of *Canis* are able to strengthen their limbs through a relative shortening of limb length. This is further highlighted by recent research into felid postcranial strength found that prey body mass was a better predictor of bone strength than was locomotor type (Doube et al., 2009).

To test the ecological hypothesis, Chapter 5 will explore bone strength, limb length and latitude in extant *Canis* and include a fossil species. The fossil species that will be included is *Canis dirus*, the Pleistocene dire wolf. The inclusion of this fossil species is extremely valuable to this dissertion because it will help to explore changes over time, which will allow for comparisons to changes seen in the hominin lineage over the sample time frame. In addition, this species regularly hunted very large prey, especially compared with the size of the prey hunted by extant wolves, and will provide a good test of the relationship between prey body mass and skeletal robusticity. An evaluation of both the relative strength of the species, and the relative limb length of the dire wolve will provide a test of whether limb length is influenced more heavily by mechanical demands than by temperature related demands.

5. Ecological hypothesis

The ecological hypothesis, proposed in Chapter 2, is based on the observation that herbivores in less productive environments are larger in body mass than herbivores in more productive environments (Best, 1981; Murphy, 1985; Klein, 1986). The ecological hypothesis states that carnivores will show differences in skeletal strength such that those living in productive environments will have less strong skeletons relative to their body mass than those living in less productive environments. This hypothesis follows from the biomechanical assumption that hunting, killing, and processing a large herbivore will require the predator to produce and resist higher forces than when hunting, killing and processing the carcass of a small herbivore. In order to maintain similar bone safety factors, therefore, predators in less productive environments should have stronger bones relative to body mass than predators in more productive environments.

Primary productivity is typically defined as the amount of plant biomass (measured in grams or kilocalories) produced through photosynthesis in a given area (measured in m^2) and is calculated for the year, with the resulting unit of $g/m^2/y$. Because productivity is a complex variable to measure and is influenced by a number of factors, it is difficult to determine actual productivity for each individual in a sample group that encompasses a wide geographic area, like the groups sampled in this dissertation. However, there are many different variables that have been shown to correlate well with primary productivity, including mean annual temperature, annual rainfall (Rosenzweig, 1968b; Whittaker, 1970), and latitude (Churkina and Running, 1998), although the relative importance of each of these variables varies considerably depending on the dominant type of vegetation (Churkina and Running, 1998). Additional variables that directly affect productivity of an area are CO_2 in the atmosphere, lower levels indicating lower productivity and higher levels indicating higher productivity. Pleistocene carbon dioxide levels were much lower than those of today (Barnola et al., 1987), which means that the productivity levels of the Pleistocene were much lower than those of the Holocene. These correlations suggest that the ecological hypothesis for variation in postcranial skeletal strength can be tested in a number of different ways. These correlations also suggest that testing for the effects on bone predicted by the ecological hypothesis can be confounded by other biological processes, such as cold adaptation (i.e., Bergmann's and Allen's Rules – see below).

The results obtained for the genus *Canis* in Chapter 4 suggest that limb shortening is a mechanical adaptation to increase bone strength. The traditional explanation for relatively short limbs was the heat-conservation effects described as the reason behind Allen's Rule (Allen, 1877). The explanation through which shorter limbs arise is dependent on cold temperatures (Ashoub, 1958; Weaver and Ingram, 1969). An Allen's Rule effect has been confirmed experimentally (Serrat et al., 2008), showing that temperature does influence limb length during the growth of the individual. The ecological hypothesis will be evaluated in this chapter by comparing members of the genus *Canis*, including individuals of *C. lupus*, *C. latrans*, and *C. rufus* that live at different latitudes and are therefore expected to live in environments that differ in terms of productivity, as well as temperature. In addition, the inclusion of the Pleistocene species *Canis dirus* allows a further evaluation of the ecological hypothesis because the Pleistocene overall is reconstructed as being less productive than the Holocene (Henry, 1989; Wright, 1993; Sage, 1995). Perhaps most importantly with regard to evaluating the potential for productivity to affect human postcranial robusticity, the inclusion of *Canis dirus* provides for a contrast of temporal trends in postcranial robusticity across the a time span that includes changes in human postcranial robusticity.

The first section of this chapter looks at whether or not there is a relationship between the index of athletic ability and latitude *Canis lupus, C. latrans*, and *C. rufus*, the three extant species for which there were geographic data available for some specimens. The second section will look at whether there are differences in relative strength between the extant *Canis* species and the fossil *Canis dirus*.

5.1 Introduction to primary productivity correlates

It is proposed in this dissertation that primary productivity is an important determining factor influencing bone strength of predators, and that understanding ecology within the context of long bone scaling has the potential to provide new insights into understanding the decrease in human postcranial robusticity that occurred during the late Pleistocene and early Holocene by going beyond the standard tool technology explanation.

This section will test whether one factor that correlates with primary productivity, latitude, shows any kind of relationship with postcranial skeletal robusticity in extant *Canis*. Generally speaking, areas at higher latitudes in the northern hemisphere will be less productive than areas at lower latitudes due to the reduction in photoperiod, resulting in a reduction in sunlight available for photosynthesis (Cooper, 1975). It is recognized here that latitude is not the only factor that correlates well with productivity. It is also recognized that latitude is correlated with mean annual temperature, and thus may have additive influences on postcranial proportions due to selective pressures associated with body temperature regulation. Thus, factors such as mechanical loading, productivity, latitude, and temperature may be so inter-related that it is difficult to tease apart the primary signal affecting skeletal robusticity. However, if a relationship is found between bone strength and latitude, these data will allow for a foundation for further, more complete analysis in the future.

The index of athletic ability (Alexander, 1989), discussed in Chapter 4, is a measure of bone strength that can be compared across individuals and species. As such, it is a useful measure to test for correlations with ecological variables. In the following figures, the index of athletic ability for both the medial-lateral and anterior-posterior axes of the femora of extant *Canis* are plotted with latitude on the y-axis.

5.1.1 Results and discussion

The first step in this evaluation of the ecological hypothesis is to show that the specimens of *Canis* living at both low and high latitudes overlap in body size. There is a group of *Canis lupus* that was part of a group collected at the same latitude, and all members of this group are fairly large in body mass. Figures 47 and 48 show no discernable relationship between the index of athletic capability of the femur and latitude. A comparison of individuals from the three extant species (*C. latrans*, *C. lupus*, and *C. rufus*) indicates that there is a lot of overlap in this index across both species and latitudes. Thus, the results do not lend support to this particular test of the ecological hypothesis. There are a number of potential explanations for this finding. First, the sample size is small. Second, the range of latitudes sampled is small. Thus, this contrast might not adequately capture differences in productivity for *Canis*.

The results of Chapter 4 show that bone strength increases in *Canis* occur primarily as a result of decreases in relative bone length with increasing body mass. Variation in relative limb length has traditionally been explained through Allen's Rule, which states that animals that live in cold environments will have relatively shorter limb bones than those living in warm environments due to the heat-retention advantage offered by lowering the surface area to volume ratio of the animal. Latitude is used in here as a measure of productivity, but it also has complex and variable relationships with humidity (Lindsay, 1987) and photoperiod. This is an important distinction to keep in mind while evaluating the results of this section. A re-evaluation of the mechanism behind Allen's Rule has suggested that humidity, as it relates to evaporative cooling, may be more of a driving force behind variation in limb length than temperature (Lindsay, 1987). The lack of correlation between latitude and body mass and latitude and the index of athletic ability means that latitude is not a good predictor of morphology in this sample. The next section of this chapter will address the issue of productivity more directly by asking whether Pleistocene *Canis dirus* was more robust than Holocene *Canis*, in the same manner that Pleistocene *Homo* was more robust than Holocene *Homo*.

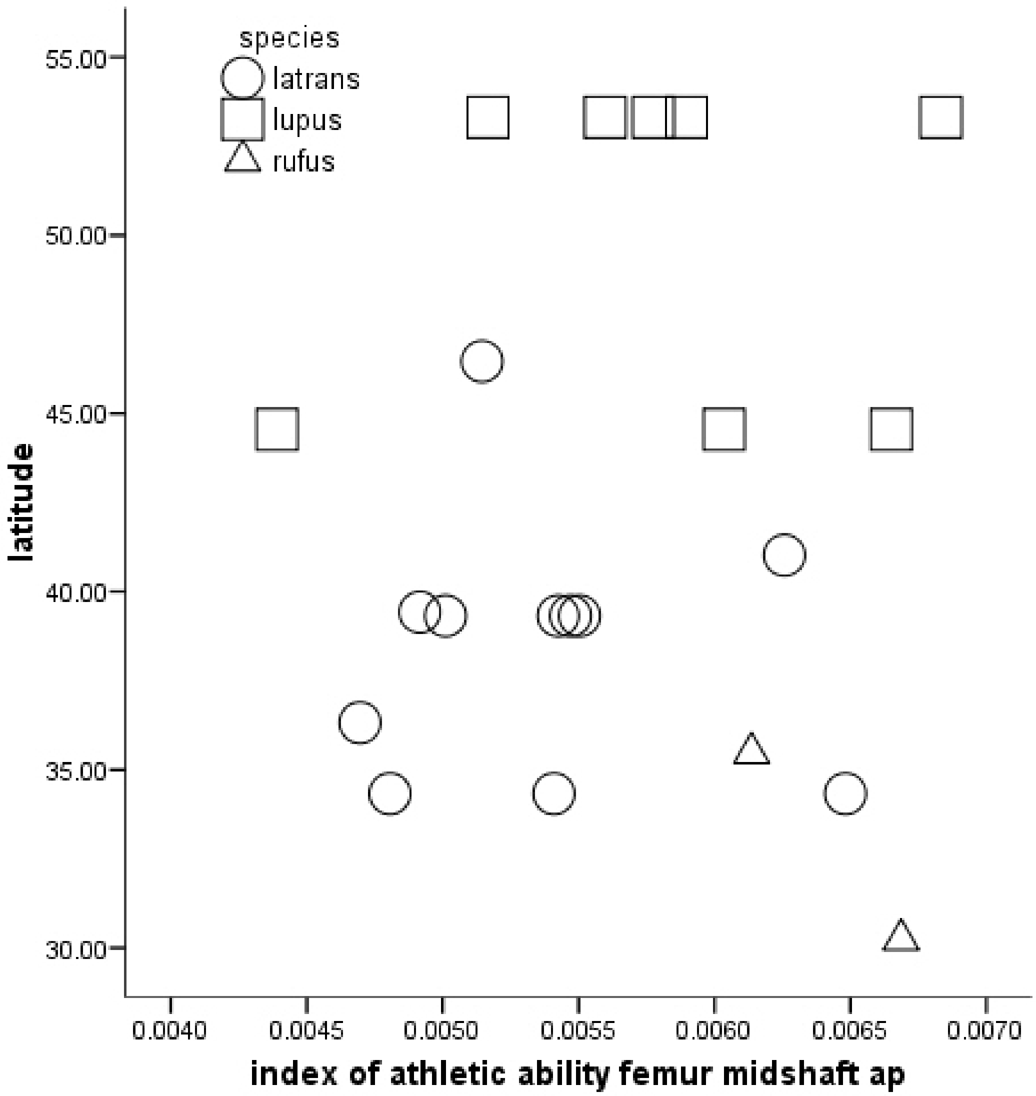


Figure 32: Index of athletic ability femur midshaft ap on latitude for *Canis*

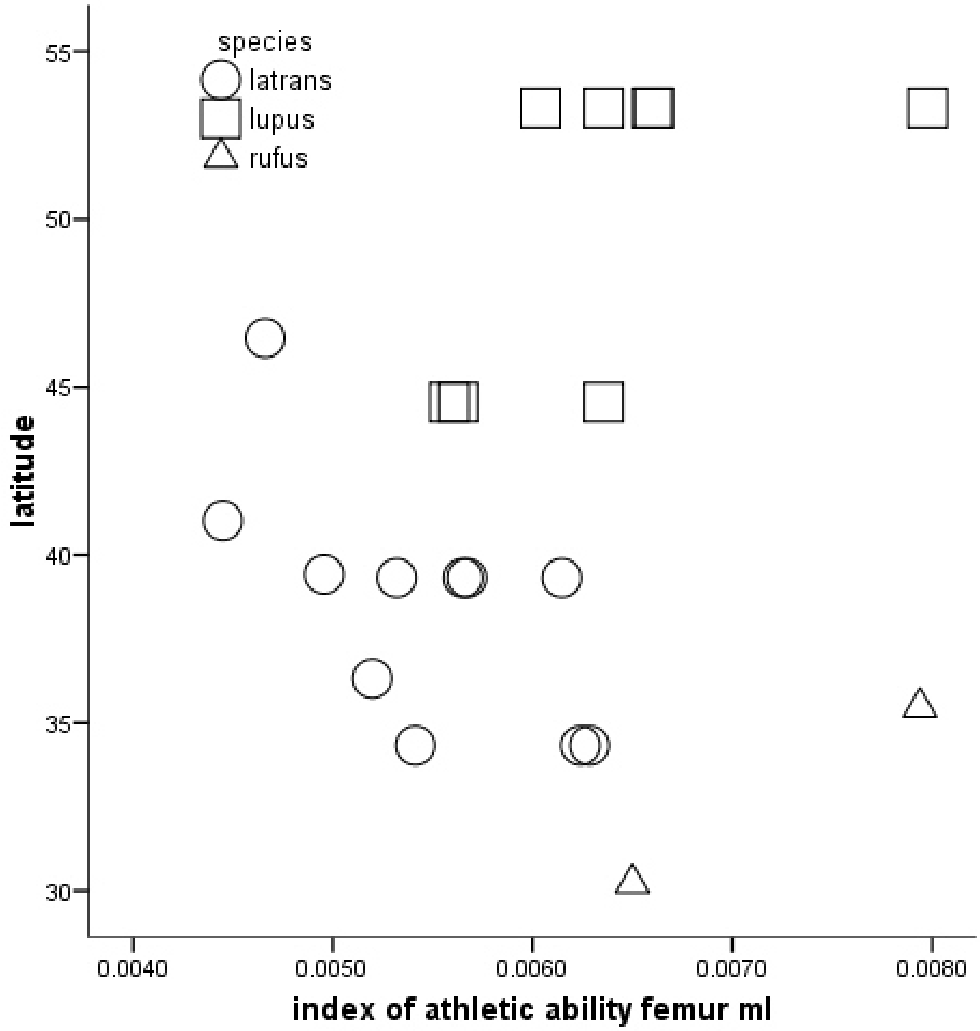


Figure 34: Index of athletic ability femur midshaft ml on latitude for *Canis*

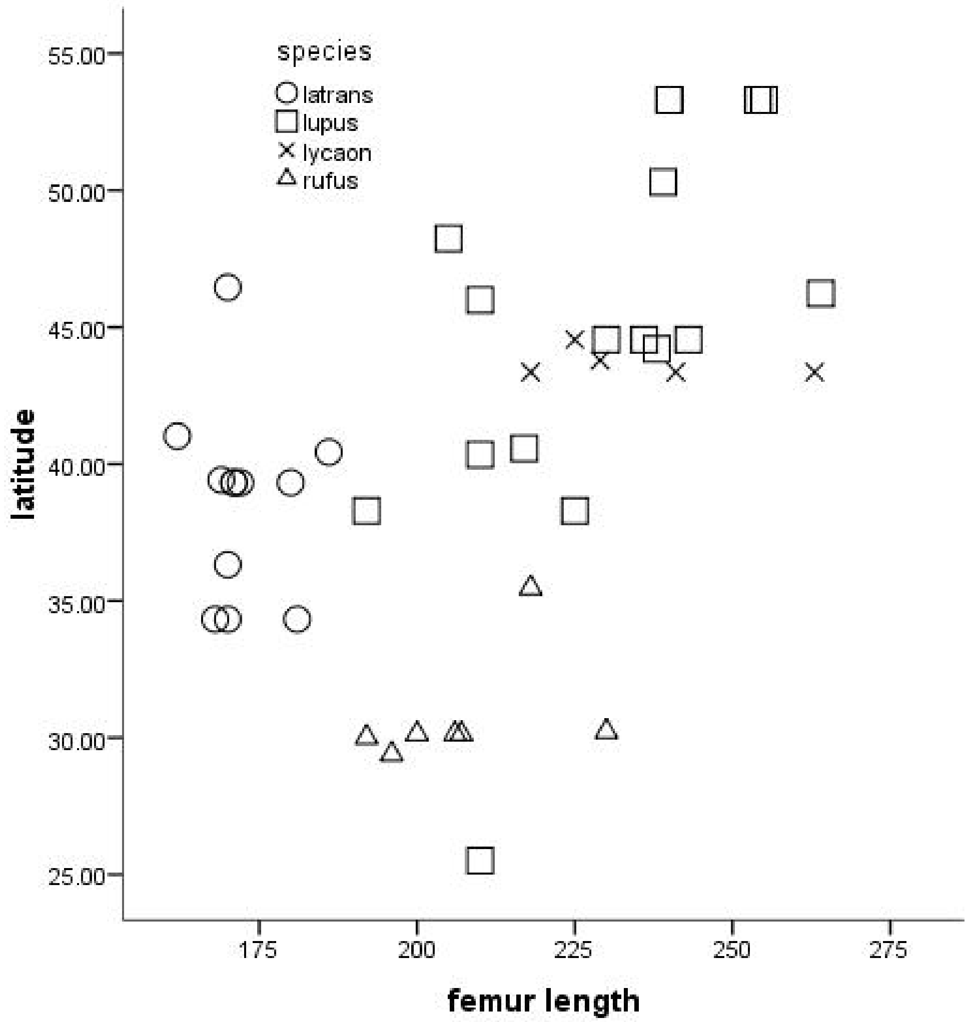


Figure 35: Relationship of latitude and femur length for extant *Canis*

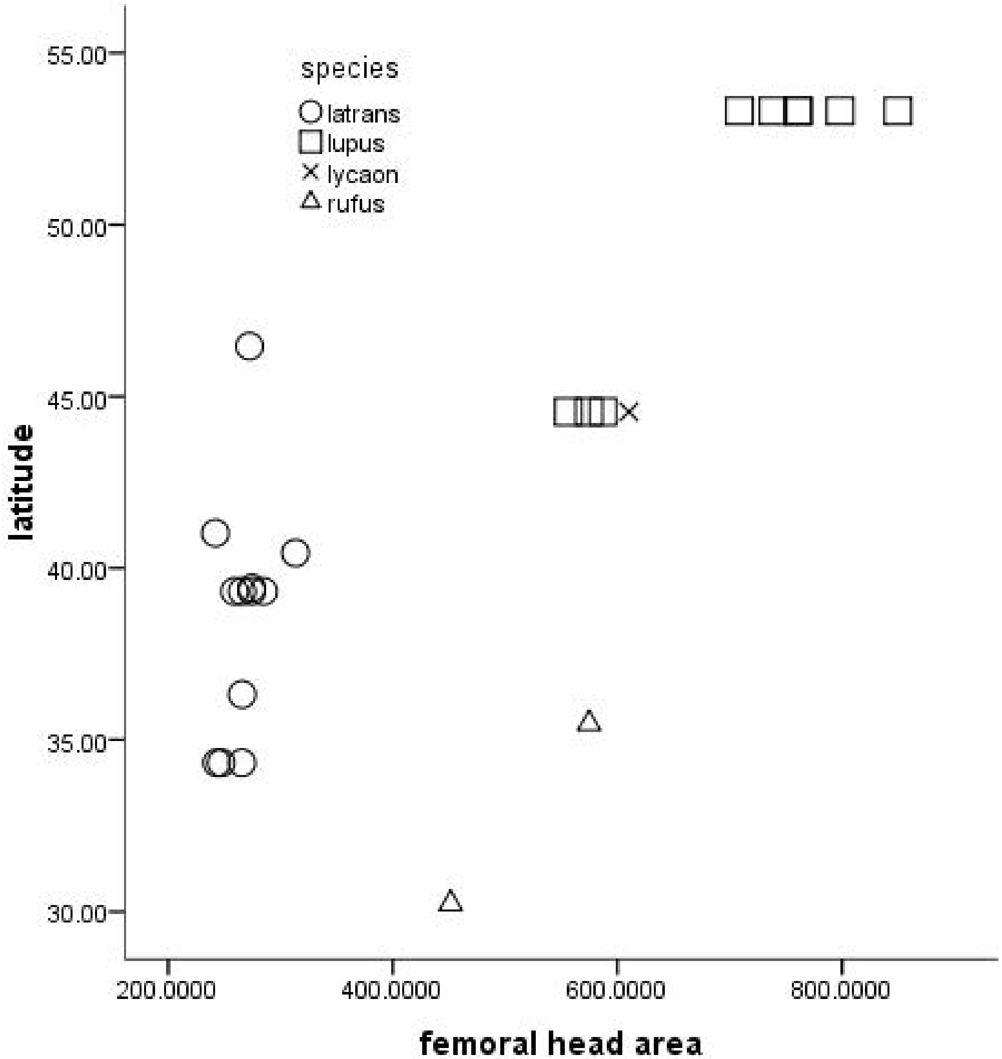


Figure 36: Relationship of femoral head area and latitude for extant *Canis*

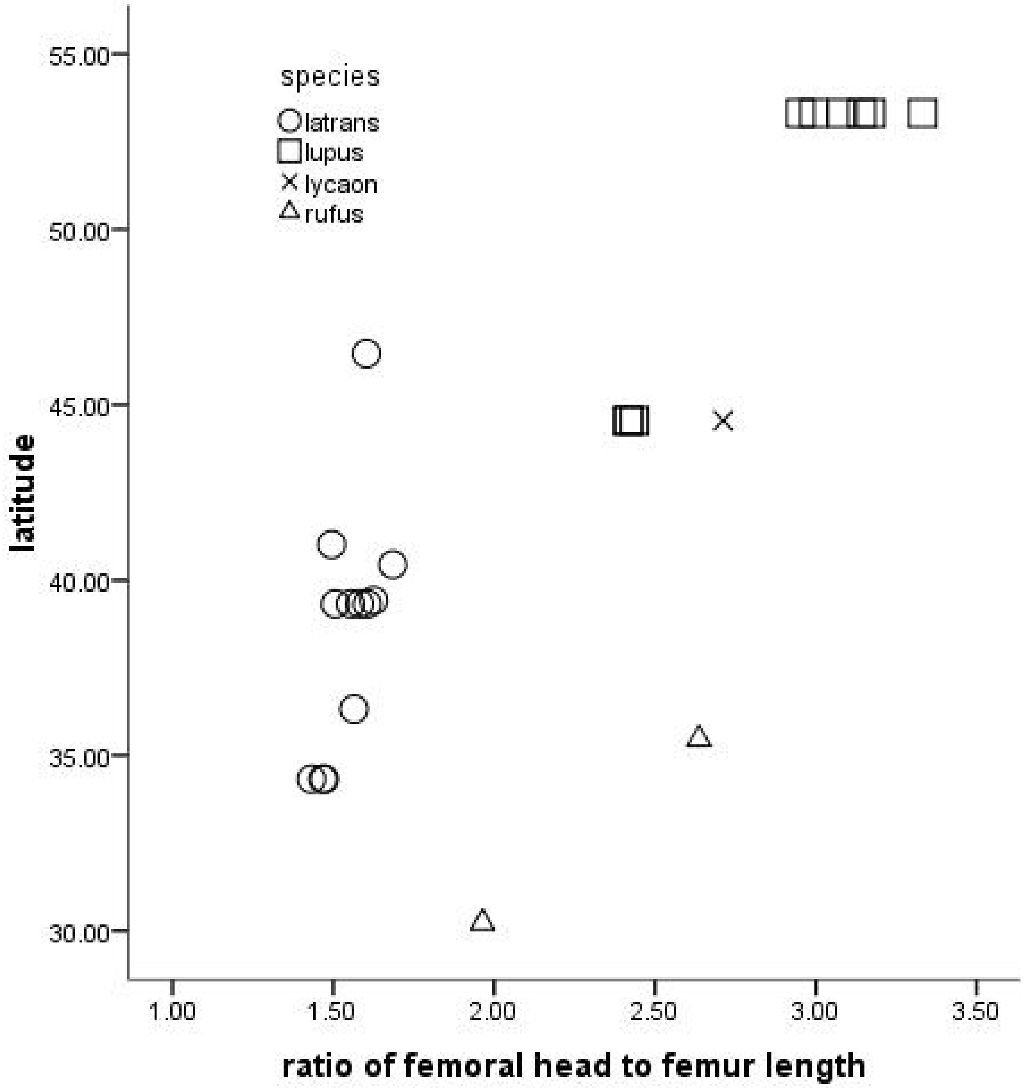


Figure 37: Relationship of latitude and the ratio of femoral head area to femur length

5.2 Is Pleistocene Canis more robust than recent Canis?

Postcranial skeletal robusticity in Pleistocene and Holocene mammals has been compared in only two other non-primate mammalian genera, *Bos bison* and *Connochaetes gnu*. Both genera trend towards gracilization during the Holocene (Churchill et al., 2000; Lewis, 2004). This trend is mirrored in *Homo* (Ruff et al., 1993). The Pleistocene was on average much cooler than the Holocene. The warming of the Holocene is associated with the extinction of large-bodied mammals (Kurten, 1965), as well as a reduction in body mass in many mammalian lineages (Davis, 1981; Avery, 1982; Guthrie, 2003). These examples provide a potential link between climate, productivity, and morphology, which is at the heart of the ecological hypothesis (and at the heart of Bergmann's and Allen's Rules).

The ecological hypothesis predicts that carnivores living in less productive environments will have postcranial skeletons that are relatively more robust than carnivores living in more productive environments. Thus, we can predict that *Canis dirus*, living during a time of lowered primary productivity and temperatures that were 5°-10° colder than today (Ward et al., 2004), will have a relatively more robust limb skeleton than the extant species of *Canis*. The faunal composition of the Pleistocene was dominated by large-bodied prey species (Kurtén, 1968), a key element for predicting increased levels of bone strength in the animals that were hunting these larger forms. The climatic conditions of Pleistocene California were characterized by drought and low productivity (Johnson, 1977) and the faunal composition was similar to other geographic regions that typified the Pleistocene, populated by large-bodied mammalian species (Kurtén and Anderson, 1980). These conditions mean that dire wolves lived in an environment in which the herbivorous prey species were much larger than the wolves themselves, and also much larger than the prey that is hunted by extant species of wolves. Therefore, the dire wolf, similar in size to the gray wolf, was regularly hunting larger prey relative to its body mass.

5.2.1 Results

The following figures show least-squares regressions of extant *Canis* with *Canis dirus* plotted to show where it falls relative to predictions based on the living groups. The regression formula and regression line on each figure is calculated from the extant sample. All data in this section are logged. The first set of regressions in each group is of bone diameter (dependent variable) on bone length (independent variable). The second set of regressions is of bone diameter (dependent variable) on joint surface area or joint surface breadth (independent variable) of the bone from which the diameters are measured. This differs from Chapter 4, which used femoral head area as a substitute for body mass. Because the *Canis dirus* sample consisted of isolated individual bones that were not associated with other remains from the same individual, the only measure that was appropriate to approximate body mass was a measure of joint surface. Therefore, the humeral diameters are regressed onto a measure of distal humeral breadth and the tibial diameters are regressed onto a measure of proximal tibial breadth. The expectation in this section, based on the ecological hypothesis, is that *C. dirus* will be relatively more robust than Holocene *Canis*, and will lie above the regression line of the extant group in these regressions of midshaft diameters on bone length and joint surface area or diameter.

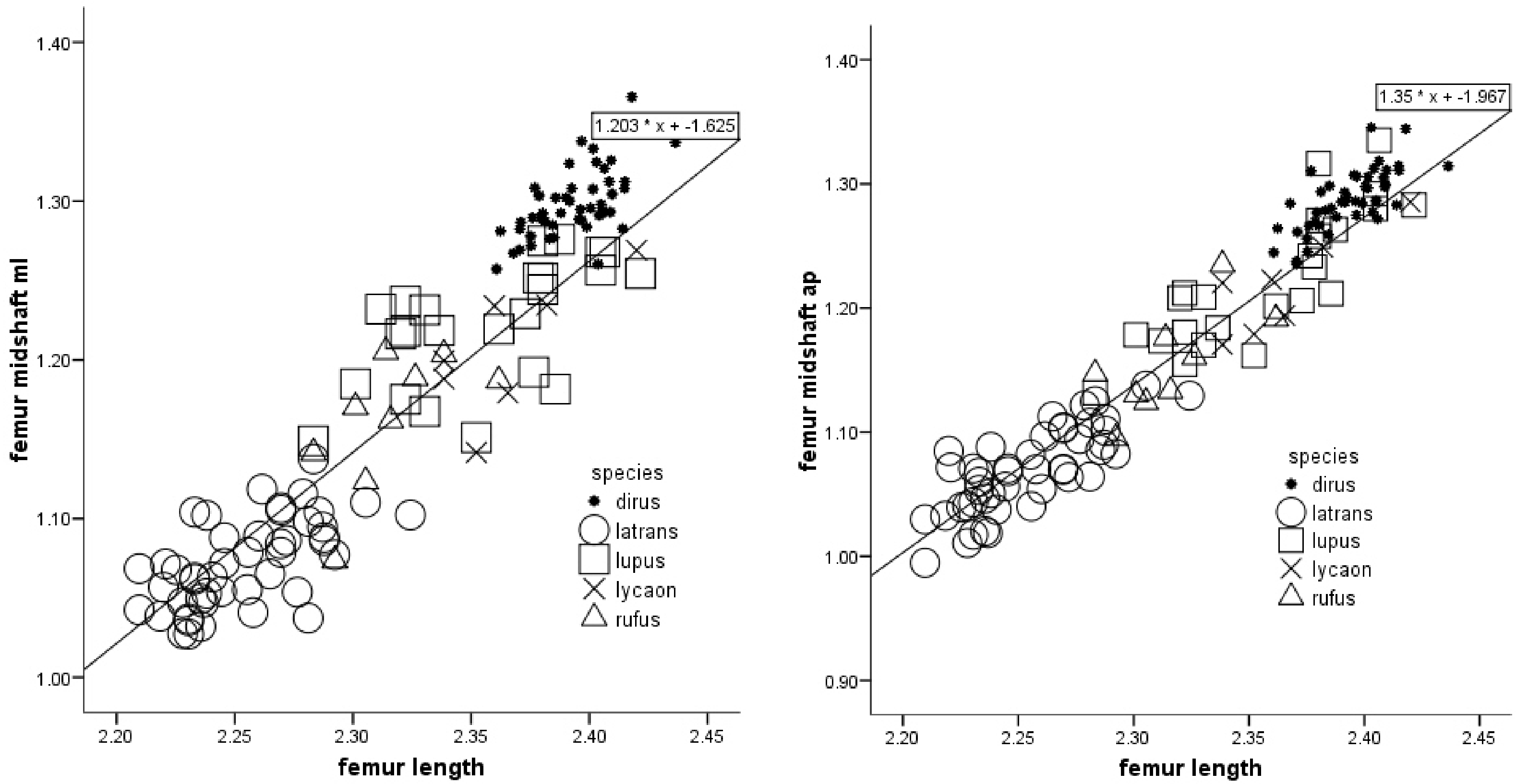


Figure 38: Femoral midshaft diameters on femur length of extinct dire wolf relative to extant wolves; regression line is for extant species

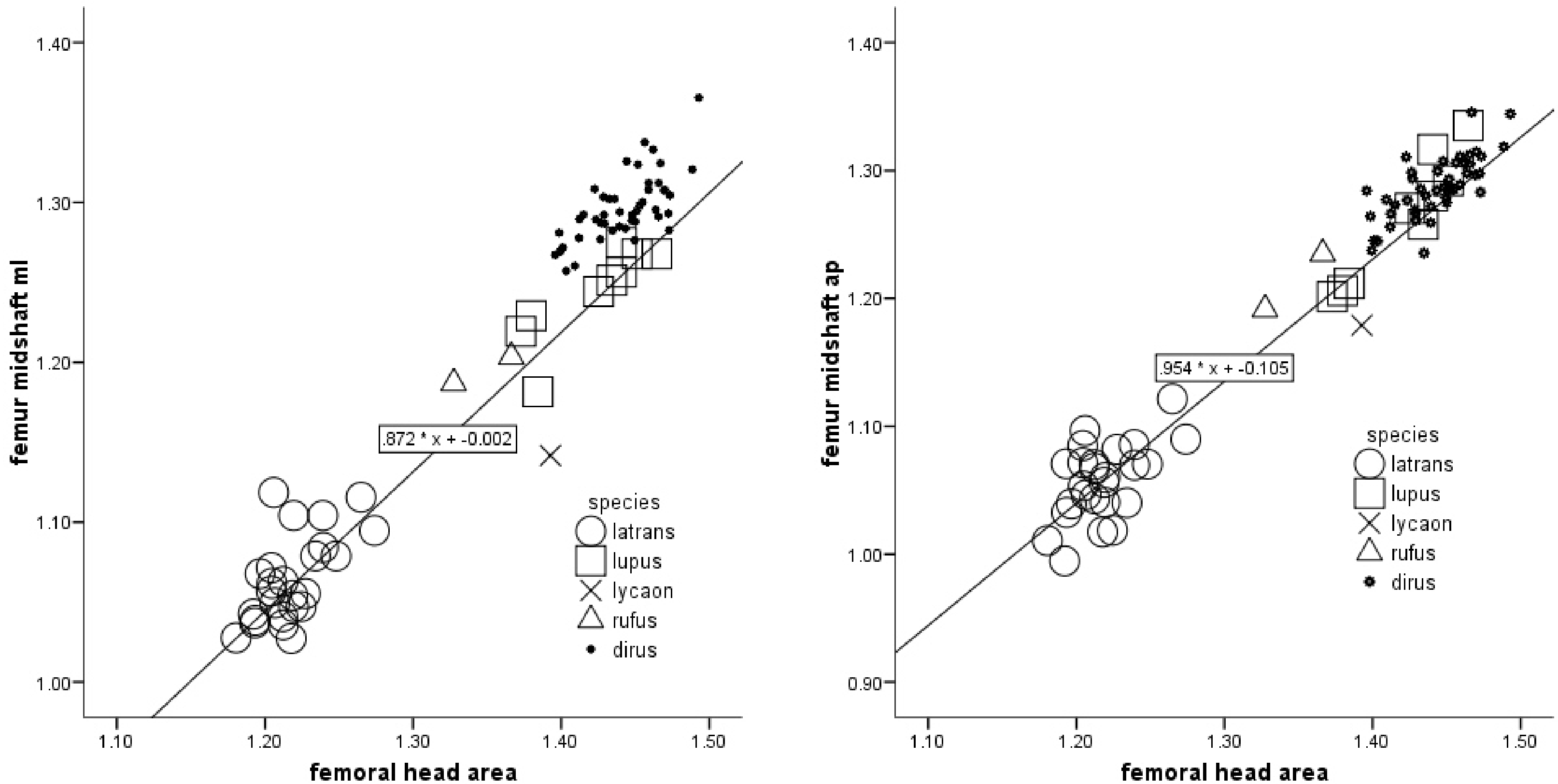


Figure 39: Femoral midshaft diameters on femoral head area of extinct dire wolves relative to extant wolves; regression line is for extant species

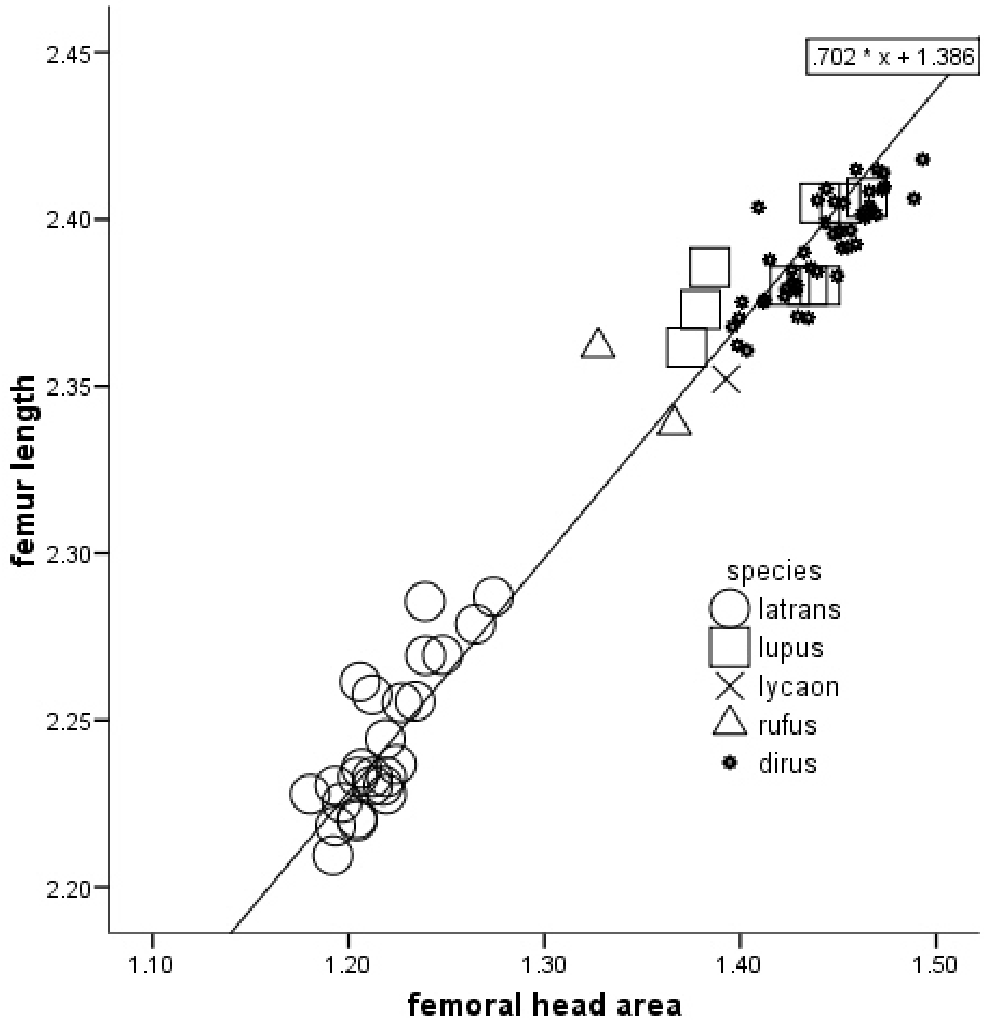


Figure 38: Femur length on femoral head area for *Canis*

5.2.1.1 femur

Figure 39 shows the scaling relationship of femur length on femoral head area. The dire wolves overlap the gray wolves in both femoral head area and femur length. The similarity in femoral head area suggests that dire wolves are similar to extant gray wolves in body mass. The dire wolves tend to have shorter femora relative to femoral head area than the gray wolves, suggesting somewhat greater amounts of negative allometry of femur length relative to femoral head area in dire wolves.

Against this background of similarity in body mass and negative allometry of femur length, dire wolves have more robust femoral mid-shaft medial-lateral diameters relative to both femur length (Figures 38) and femoral head area (Figure 39). This pattern may reflect functional loading differences between the extinct and extant groups. This comparison is in line with the prediction of the ecological hypothesis that *Canis dirus* will be more robust in measures of postcranial bone strength than extant *Canis*. The femur is particularly reinforced in the medial-lateral dimension.

One explanation for this pattern is that the megafauna of the Pleistocene roamed the landscape with the dire wolves, creating a hunting environment in which the skeletons of predators would need to have relatively stronger skeletons in order to capture and process these large prey species. There may be clues in the mechanics of how these animals were hunting that would explain why the femur is more reinforced in the medial-lateral dimension than in the anterior-posterior dimension. This is a possible area of future research.

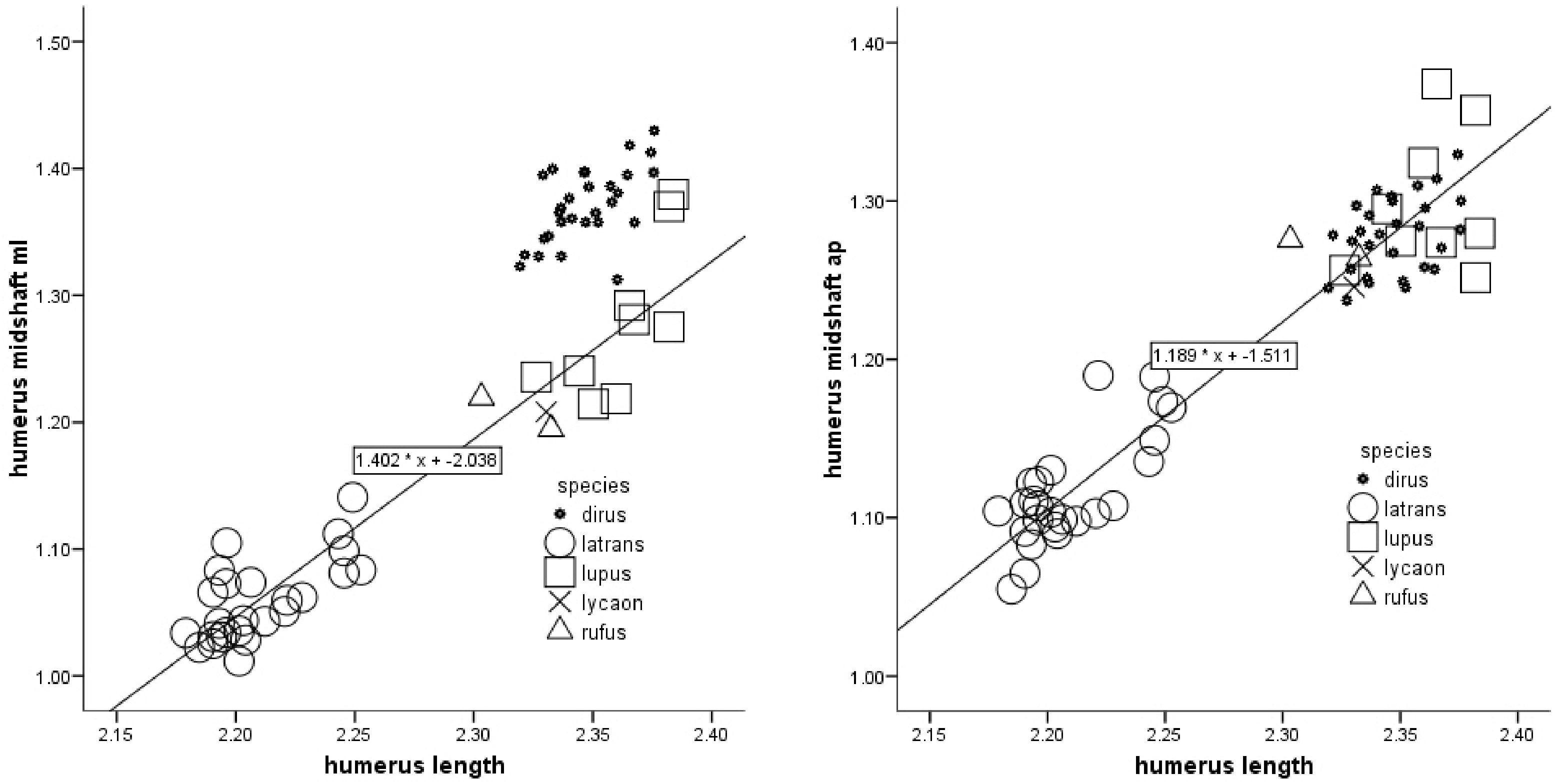


Figure 39: Humeral midshaft diameters on humerus length of extinct dire wolves relative to extant wolves; regression line is for extant species

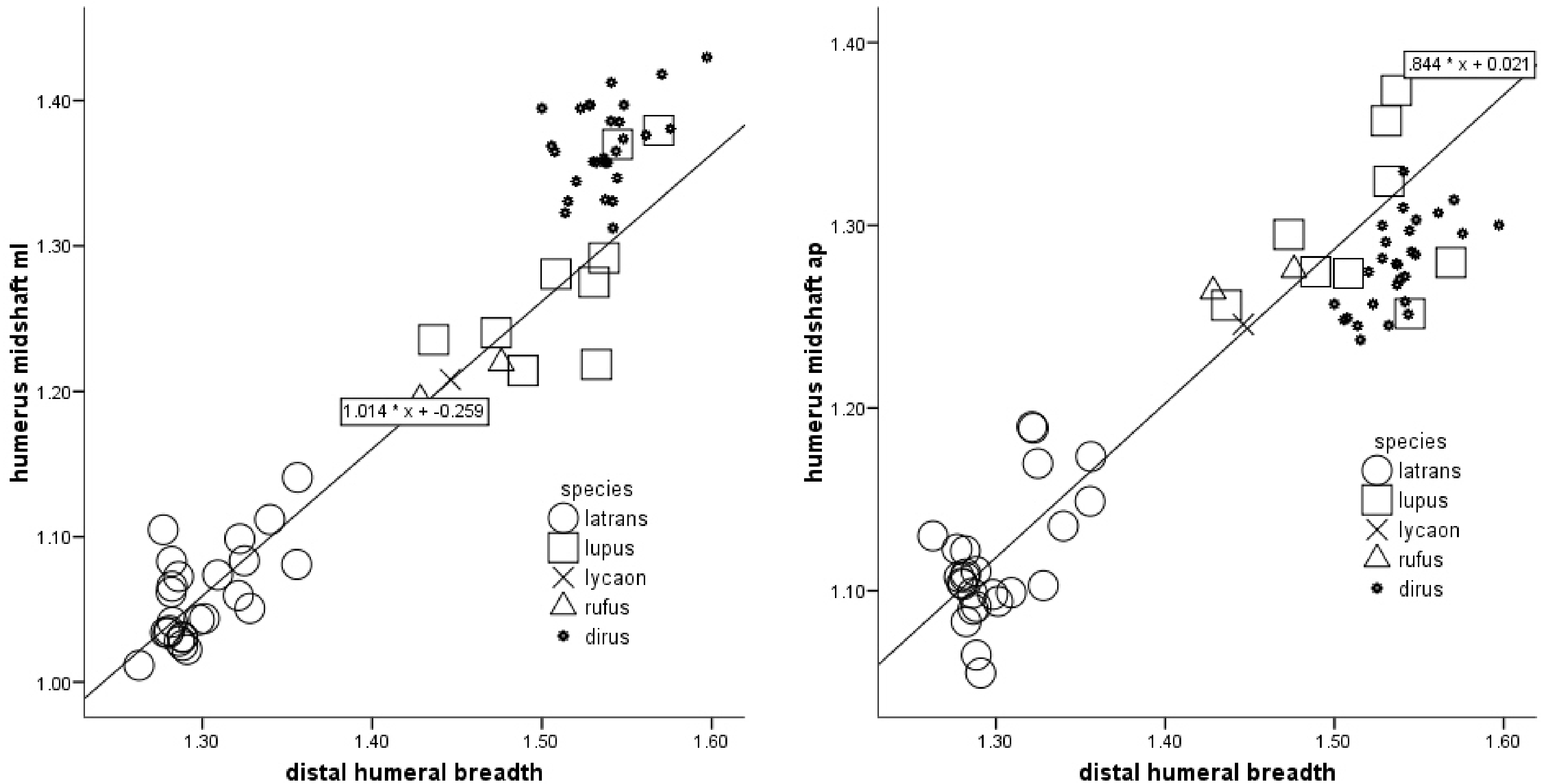


Figure 40: Humeral midshaft diameters on distal humeral breadth of extinct dire wolves relative to extant wolves; regression line is for extant species

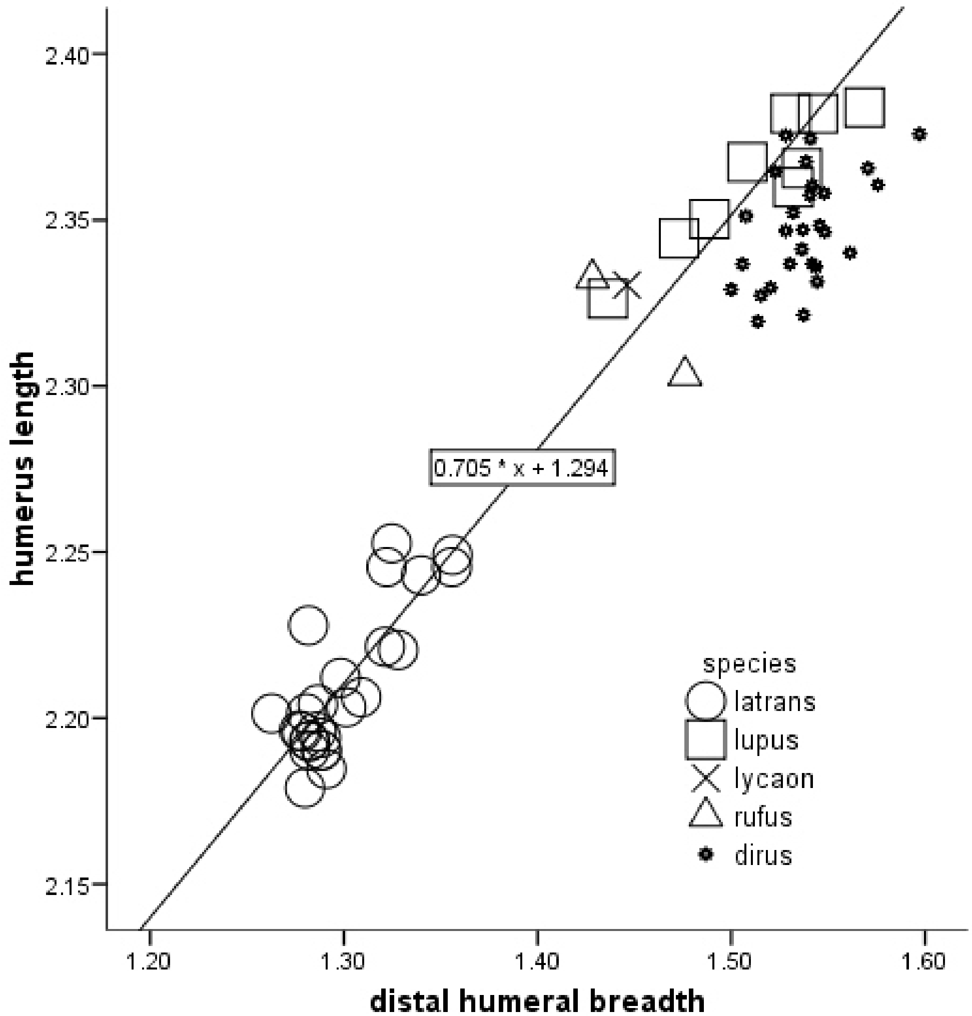


Figure 41: Humerus length on distal humeral breadth for *Canis*

5.2.1.2 humerus

Distal humeral breadth is used as an estimate of body mass in this regression of humeral length relative to distal humeral breadth. Humeral length in *Canis dirus* falls well below the regression line for extant *Canis*, suggesting that at similar body sizes, the dire wolf had a much shorter humerus than extant gray wolves. The pattern seen when the humeral diameters of *Canis dirus* were plotted on the regression with the extant *Canis* contrast with the pattern for the femur. The first thing to note is that, like the femur, the anterior-posterior diameter of the humerus of *Canis dirus* falls on the regression line for humerus length of the extant group, but well below the regression line for distal humeral breadth. These results suggest that dire wolves may have an anterior-posterior diameter that is *reduced* in strength relative to its modern counterparts (Figure 43 and 44).

As with the femur, the medial-lateral diameter of the humerus on humerus length of *Canis dirus* falls well above the regression line of the extant sample (Figure 43). Note also that the slope of the line for the extant sample is strongly positively allometric (1.467). This pattern suggests different loading patterns in the skeleton of the dire wolf. There may be differences in hunting technique and carcass-processing that are necessary when dealing with very large animals that would affect the relative strength of the humerus in the dire wolves.

5.2.1.3 tibia

The pattern for the tibial length relative to proximal tibial breadth is almost identical to that seen in the humerus. Proximal tibial breadth is used as a proxy for body mass. The dire wolves have very short tibiae relative to proximal tibial breadth in contrast to gray wolves. As with the other long bone comparisons, both medial-lateral and anterior-posterior tibial diameters are relatively large in dire wolves when compared to tibial length. Medial-lateral tibial diameter is also large relative to proximal tibial breadth. However, anterior-posterior tibial diameter does not show a relative increase in dire wolves as compared to gray wolves, except for two outliers that lie well above the line.

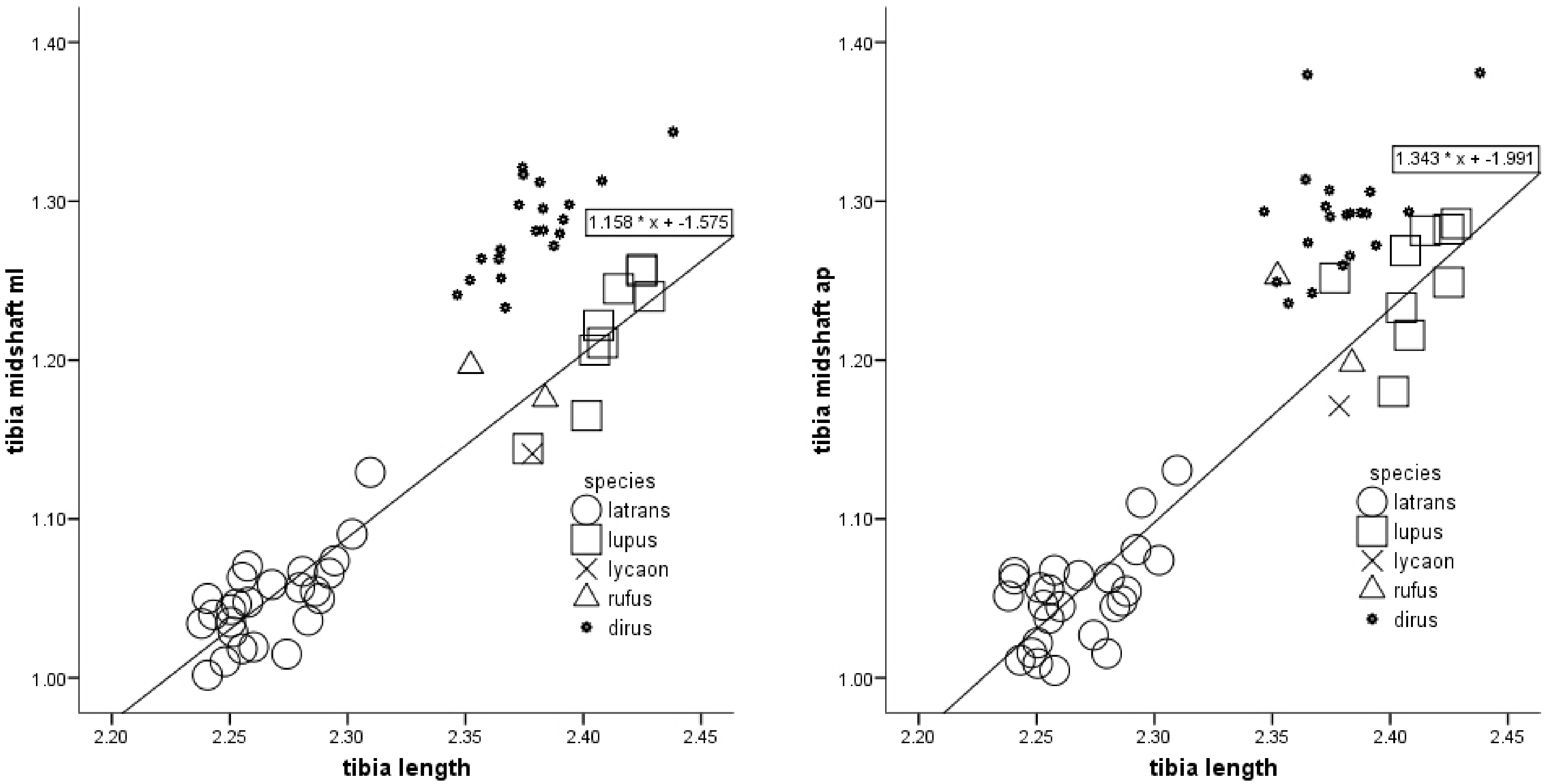


Figure 42: Tibial midshaft diameters on tibia length of extinct dire wolves relative to extant wolves; regression line is for extant species

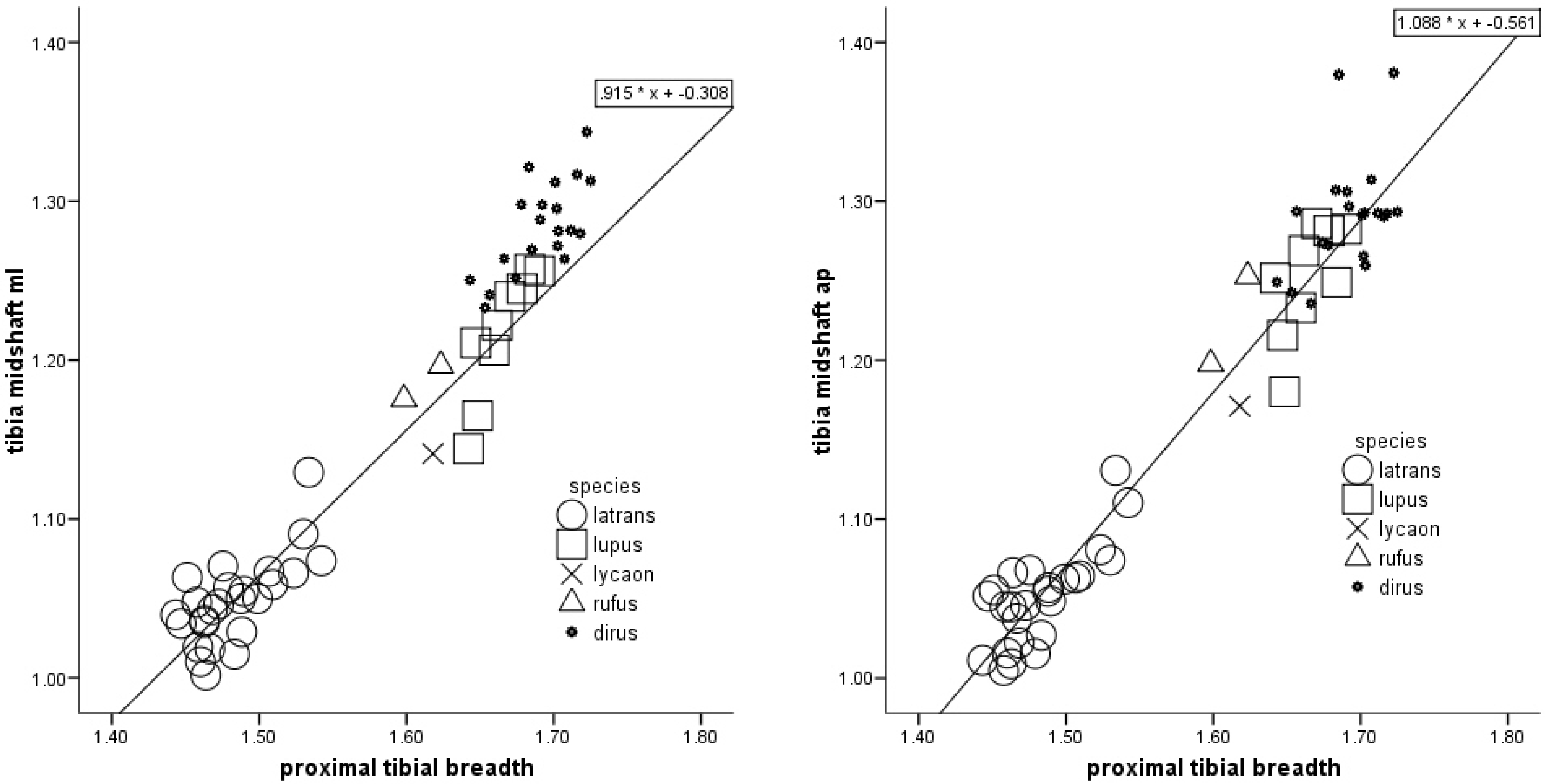


Figure 43: Tibial midshaft diameters on proximal tibial breadth of extinct dire wolves relative to extant wolves; regression line is for extant species

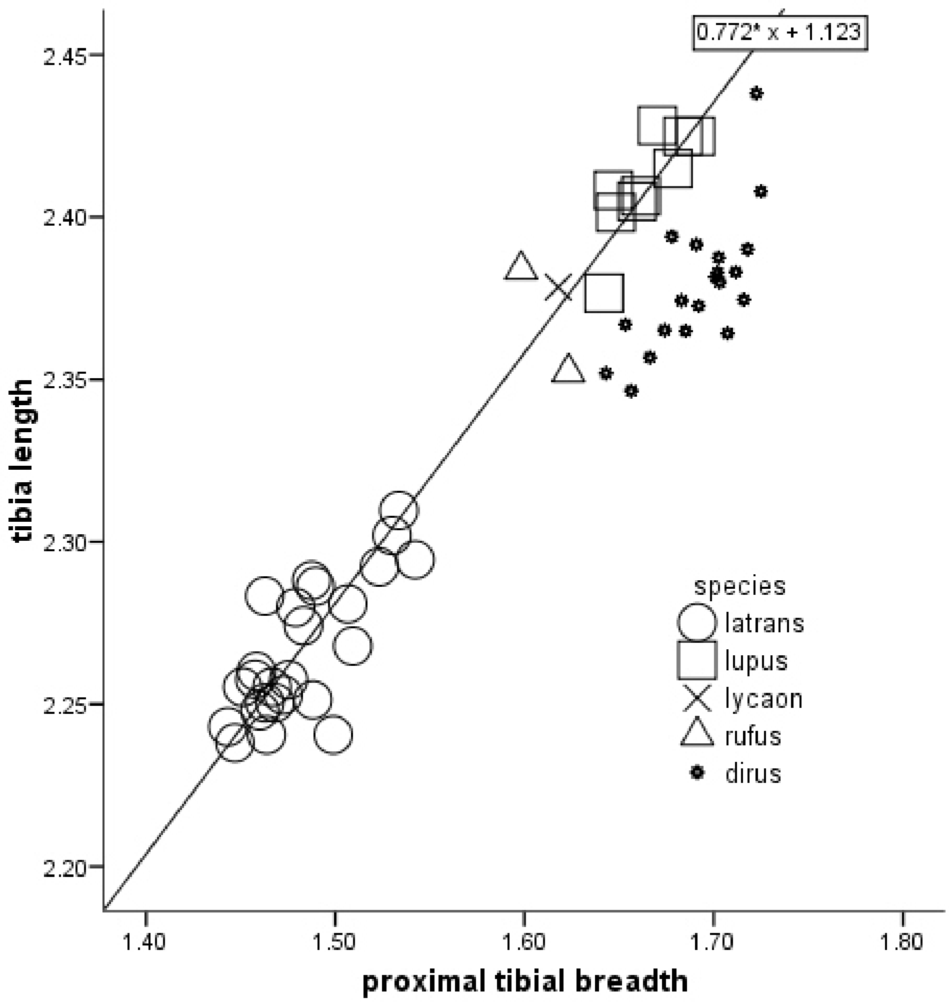


Figure 44: Tibial length on proximal tibial breadth for *Canis*

5.2.2 Discussion

The inclusion of the fossil *Canis dirus* shows some interesting patterns that may be relevant for the ecological hypothesis. First, the over-lapping joint diameters of dire wolves and gray wolves suggest that they were of similar body mass with some indication that dire wolves may have been slightly larger. Second, dire wolves have very short long bones relative to joint diameters in comparison to extant canids. Furthermore, most contrasts indicate an increase in mid-shaft diameter relative to joint dimensions and bone length in dire wolves as compared to the similarly sized gray wolf. This relationship is particularly consistent and strong for medial-lateral diameters in relation to bone length. These results suggest that, like modern canids, dire wolves achieve greater relative bone strength in large part by shortening their limbs thereby reducing the load arm. These results also suggest that, over and above their short limbs, dire wolves have enlarged particularly the medial-lateral diameters of their long bones. These results suggest that the dire wolf may have had a different loading pattern on the skeleton than modern wolves and coyotes, perhaps related to the difficulty of hunting large fauna.

There is provisional support of the ecological hypothesis based on this temporal comparison of a species from the less productive Pleistocene compared to a sample of extant wolves from the more productive Holocene. The support for this hypothesis comes mainly from the buttressing of the medial-lateral diameter of all bones and from the relative shortening of the long bones, which is most marked for the humerus and the tibia (and may also reflect Allen's Rule). Further research will need to be done to learn more about the functional implications of these various patterns.

6. Conclusions

The research presented in this dissertation tested hypotheses about variation in bone strength in two mammalian genera through an exploration of scaling patterns. In addition, I began an examination of how ecological variables may correlate with skeletal robusticity in extant and extinct species. This research was aimed at learning more about the determinants of skeletal robusticity in mammals generally, in order to interpret patterns seen in human evolution specifically, especially the gracilization of the skeleton during the Holocene. The research presented in the previous chapters will be summarized here and discussed in the context of human evolution. A summary of the results of each hypothesis, and the different questions posed to address that hypothesis appears in table form at the end of each section (Table 25 and 26).

6.1 Scaling hypothesis

In order to interpret changes in postcranial skeletal robusticity in a broader ecological and evolutionary context, it is necessary to understand how bone strength scales across mammalian groups at different taxonomic levels. Early research in this field was aimed at understanding scaling across a broad taxonomic spectrum, often combining samples ranging in size from mice to elephants in the same analyses (Alexander et al., 1979). Subsequent research has explored scaling relationships on a somewhat finer scale, such as the level of the family (Bertram and Biewener, 1990; Demes et al., 1991; Heinrich and Biknevicius, 1998; Christiansen, 1999a, b). Studies in human evolution have focused on the genus *Homo*, though they often include both extant and extinct representatives (Trinkaus et al., 1994; Ruff et al., 1993). The research presented in this dissertation follows a similar pattern by combining a study of two mammalian genera and including extinct representatives of one genus with the goal understanding the scaling patterns associated with ecology and to test specific hypotheses about changes in human anatomy and the range of variability in postcranial robusticity over time.

The research presented in this dissertation focused on the similarities and differences of the scaling patterns of the postcranial skeleton in two different mammalian genera: *Canis* and *Ursus*. There are several theoretical predictions for how mammalian postcrania should scale with body mass. Two of these predictions were tested in this dissertation, geometric similarity and elastic similarity. The first expectation to be tested was that *Canis*, smaller in body mass than *Ursus*, would scale with geometric similarity (isometry) of long bone cross-sectional dimensions on bone length and body mass (McMahon, 1975). In contrast, it was predicted that *Ursus*, larger in body mass than *Canis*, would scale with elastic similarity (positive allometry) of long bone cross-sectional dimensions on bone length and body mass (Alexander, 1977; Bertram and Biewener, 1990). On the basis of these scaling predictions (Christiansen, 1999a), hominins should scale similarly to wolves, that is, with isometry. This prediction relies on the hypothesis of differential scaling for large and small mammals.

Larger individuals within the genus *Homo* should have postcranial skeletons that are equivalent in strength relative to body mass to smaller individuals. Extensive research on humans shows that the pattern is much more complex, however. The larger Pleistocene hominins were also relatively more robust, leading to an observation of positive allometry of cross-sectional dimensions on body mass in hominins. This observation relies strictly on body mass and cross-sectional dimensions in order to determine scaling within this genus, and does not account for the different time periods in which these two species lived. Larger members of the genus *Homo* lived during the Pleistocene. These Pleistocene *Homo* were also relatively more robust than living *Homo*. Therefore, there is a pattern of positive allometry of postcranial cross-sectional variables on body mass within the genus *Homo*.

The results of analyses of extant species of *Canis* and *Ursus* did confirm that there were two different scaling patterns for these genera, but there were no consistent patterns that held throughout all regressions for either genus. Some postcranial elements of *Canis* scaled with elastic similarity of long bone midshaft diameters on bone length, and some postcranial elements of *Ursus* scaled with geometric similarity of long bone midshaft diameters on bone length. The primary mechanical reason that larger wolves have relatively stronger bones was through a relative shortening of the bone length rather than through a thickening of the cross-section. Larger *Canis* have relatively shorter limb bones than smaller *Canis*. It has been proposed that the variation in skeletal robusticity among hominins is also simply a function of differentiation in limb length (Pearson, 2000). This is interesting and consistent with the wolves who, like hominins, may be seen as social carnivores. However, this seemingly straightforward similarity may be more complex if we look more deeply at the data. The observation for hominins was made for both living and extinct hominins, living in different environments. This latter factor may have a profound influence on interpretation as my own data on carnivores summarized in Chapters 4 and 5 as well as below indicates. Although there is variation in limb proportions among modern humans (Roberts and Bainbridge, 1963; Trinkaus, 1981; Holliday, 1997; Holliday and Ruff, 2001), there is no evidence among this extant species that limb length is the driving force behind variation in skeletal robusticity.

Another way to look at strength, an approach which attempts to account for body mass and limb length, is through Alexander's index of athletic capability. The index of athletic ability as modified here is a dimensionless ratio, referred to as the modified index of athletic capability. The original formulation of the index of athletic capability by Alexander (1985) measures the relative degree of strength and agility of an organism on the basis of cross-sectional dimensions. A similar ratio was used in Table 1 (Chapter 1) to calculate overall bone strength for the specimens of *Homo* that were listed there. This is 'J standardized' (Ruff et al., 1993), which divides the polar moment of area (J) by femur length raised to the third power (as an approximation of body mass) times femur length. J standardized was not used for the *Canis* and *Ursus* sample for two reasons. The first is that limb length did not scale isometrically with body mass, and so this measurement would overestimate limb length in larger individuals, and underestimate bone strength in larger individuals. This problem is also evident in the genus *Homo*, and was accounted for through the use of the constant 1.28 being multiplied by limb length in Neandertals (Ruff et al., 1993). The second reason is that the modified index of athletic capability is a ratio that uses a reliable measure of body mass (in this case, femoral head area), which will yield more accurate results than using limb length as an estimator for body mass. For purposes of comparison, both the modified index of athletic capability and J standardized will be referred to in the following paragraphs as 'standardized strength'.

Among *Homo*, there is a tendency for larger individuals (here represented primarily by Pleistocene specimens) to have a greater amount of standardized strength (J standardized) than smaller individuals. Figures 31 and 32 (Chapter 4) demonstrate the standardized strength of three *Canis* species for comparison to the *Homo* pattern. There is a statistically significant increase in standardized strength from the coyote (*C. latrans*) to gray wolf (*C. lupus*). Figure 31 shows that the gray wolf, which is slightly larger in body mass than the red wolf, also has a lower average (but not statistically significant) standardized strength than the red wolf. The red wolf, despite the fact that its average index is larger than both species, is not significantly different from either.

This may be attributed to small sample size of the red wolf, and it is also worth noting that these two species (red wolf and gray wolf) overlap in body mass and there is no overlap between either of those species and the coyote. *Homo* and *Canis* stand in contrast to *Ursus*, which instead of showing an increase in standardized strength with body size, there is instead a statistically significant decrease in standardized strength in the larger species (Figure 32).

In seeking to understand why these two genera differ in this relationship from the genus *Ursus*, it is worth briefly discussing the manner of resource procurement and size of preferred prey for each of the species within these genera. There is a direct correlation between predator body mass and prey body mass that has been observed in *Canis*, as well as in other carnivorous mammals. The largest living wolves, the gray wolves, are capable of, and regularly observed hunting prey that is considerably larger than they are (Mech, 1970). Even in a group hunting situation, capturing a 482kg bison (Rutberg, 1983) is going to result in greater loading on the skeleton than capturing a 2 kg rabbit (Pfeiffer, 1887). There is evidence from felids that this group also strengthens its bones through limb shortening at large body masses in order to hunt larger prey (Meachen-Samuels and Van Valkenburgh, 2009). It is worth noting here that there is strong archaeological evidence that Neandertals were actively hunting large game at closer range during the Pleistocene (Shea, 1997). Many of the Pleistocene mammals that were known to be hunted by Neanderthals were larger in body mass, on average, than their Holocene descendents that provided game for more gracile modern humans (Richards et al., 2001). Therefore, it may be argued that larger species of both *Canis* and *Homo* hunt or hunted game that was a) much larger than themselves and b) much larger than game hunted by their smaller congenerics. I propose based on the patterns revealed in this dissertation that prey body mass relative to predator body mass affects the standardized strength of the postcrania of the predator. This deserves further study and analysis with additional sources in the future.

When the standardized strength of *Ursus* is taken into account, there is further support for this proposal. The largest bears are polar bears (*Ursus maritimus*). This species, while entirely carnivorous, subsists mainly on marine mammals such as the ringed seal that are smaller in overall body mass than the polar bear (Stirling and McEwan, 1975; Stirling and Archibald, 1977). The other two bear species studied in this dissertation are smaller than the polar bear. These two species are, unlike the polar bear, omnivorous, so their hunting bouts will be fewer than those of the polar bear. But when they do hunt, the largest brown bears are capable of hunting very large mammals such as moose (Ballard et al., 1981; Larsen et al., 1989). Thus the predator to prey body mass ratio is larger in the polar bears than it is in the brown bears or the black bears. The pattern of standardized strength among *Homo*, *Canis*, and *Ursus* appears to show a relationship to the ratio of predator body mass to prey body mass. When this ratio is low, standardized strength is high. When this ratio is high, standardized strength is low. The relationship just outlined provides further evidence in support of the ecological hypothesis, although it does not test it directly. These new data do provide a strong foundation for future explorations and suggest an interesting non-technological explanation for scaling patterns. By focusing on the relationship between the predator and its prey, a causal mechanism emerges for how cold, dry, less productive environments can produce predator postcrania that are relatively more robust than the postcrania of predators in other, more hospitable environments. A simple ratio of predator to prey body mass will allow closely related species that are separated geographically or temporally to be compared in order to test how ecological variables influence postcranial skeletal strength. This ratio fits with the available data for the hominin fossil record, as well as the living and fossil *Canis* discussed in this study.

Table 26: Summary of results of differential scaling hypotheses

hypothesis	Questions	tests	sample	expectation	results
Mammals over 100kg in body mass will scale differently than mammals under 100kg. Geometric/elastic similarity	Are there shape changes in limb bones across body sizes in *Canis* and *Ursus*?	RMA regressions of cross-sectional variables on bone length	*Canis* (under 100kg) and *Ursus* (over 100kg)	*Canis* will scale with geometric similarity, *Ursus* with elastic similarity	No consistent pattern, but overall, *Canis* scaled with elastic similarity; *Ursus* with geometric similarity
	How does bone strength scale with body mass in *Canis* and *Ursus*?	RMA of x-sec variables on body mass	*Canis and Ursus*	Both genera will scale with isometry.	isometry
	Are there differences in the scaling of relative strength (index of athletic ability) between *Canis* and *Ursus*?	Mann-Whitney U test for differences in modified index of athletic capability	*1. C. lupus, C. latrans, C. rufus* *2. U. americanus, U. arctos, U. maritimus*	Larger *Canis* and *Ursus* will have larger indices than smaller *Canis* and *Ursus*	Larger *Canis* had larger indices; larger *Ursus* had smaller indices

6.2 Ecological hypothesis

On the basis of previous studies of postcranial skeletal robusticity in both hominins and non-primate mammals, it was proposed here that ecological variables may correlate well with measures of postcranial strength. In order to test this hypothesis, latitude was used as a correlate of primary productivity in order to see whether there was a relationship between latitude and a dimensionless measure of strength that was based on Alexander's (1989) index of athletic capability. In addition, a fossil *Canis* from the Pleistocene was plotted on regressions of extant *Canis* in order to see where this species fell relative to its living congenerics.

The previous section outlined some evidence for a relationship between prey body size and predator bone strength. That model relied only on body mass as an indicator for prey body mass. It has been shown that prey body mass does correlate with predator body mass, and there is a point at which pack hunting allows for the hunting of animals much larger than the predator species (Gittleman, 1985) There are additional ways to look at this as well. This includes, but is not limited, to the way temperature influences both prey size and the number of prey items available. The latter issue points indirectly to models of productivity that have been invoked to explain Neanderthal strength measures but which have never been examined in a broader mammalian context.

In short, the ecological hypothesis states that predators such as humans and wolves, living in areas of low productivity will have more robust skeletons than predators living in areas of high productivity. This is based on the observation that prey species in areas of low productivity are relatively larger due to lower quality foods. This hypothesis would help explain why Neandertals, and other Pleistocene *Homo*, are relatively more robust than modern humans from the Holocene and would not require an explanation invoking technological changes as the sole driver of strength change, although the latter may still have some influence. Pleistocene Europe was colder, drier and contained a very different faunal composition than Holocene Europe.

The prediction of the ecological hypothesis tested here is that Pleistocene predators will be relatively more robust than their Holocene congenerics, mirroring the pattern of Neandertals and modern humans. Neandertals, although not ancestral to modern humans, occupy the same range in Europe, and are postcranially more robust than modern humans. The relationship of the dire wolf to modern wolves is similar to that of the Neandertal to modern humans. The dire wolf is a large, hypercarnivorous Pleistocene member of the same genus, but is not ancestral to modern wolves. For these reasons, it was chosen to test whether another genus exhibits the same pattern of Pleistocene-Holocene differences in skeletal robusticity that *Homo* does.

This prediction was tested by plotting cross-sectional dimensions of the dire wolf along a regression of all of the extant individuals in this study. The results showed that overall, the dire wolf was more robust in its cross-sections than a modern wolf of a comparable size. The medial-lateral dimensions of the femur, humerus, and tibia of the dire wolf are relatively larger than those of the extant wolves. In the humerus and tibia, it is likely that this increased strength is due to a relative shortening of the limb bones. The femur of the dire wolf, however, is comparable in length to modern wolves of the same body mass. The placement of the dire wolf above the regression line for modern wolves indicates that this species was more skeletally robust than its extant congenerics. Because the dire wolf preyed upon the megafauna characteristic of Pleistocene landscapes (Kurtén and Anderson, 1980; Dundas, 1999), the prey to predator body mass ratio of this species was likely very high, meaning that the postcrania of the dire wolves would have to be relatively more robust than the postcrania of similarly sized gray wolves that were hunting much smaller prey in the Holocene. This pattern of Pleistocene robusticity compared to Holocene gracility is mirrored in human evolution as well. Neandertals are relatively more robust than modern humans, and their limbs are relatively shorter. Neandertals, like the dire wolves, were also hunting the Pleistocene megafauna, thus raising the prey to predator body mass ratio for this species as well. This is a preliminary finding that will need to be independently tested to confirm if the prey to predator body mass ratio can predict measures of skeletal robusticity.

One way to further examine the ecological hypothesis uses latitude as a substitute measure for temperature, with temperature representing an important component of productivity. The expectation of this test is that, at higher latitudes animals will be relatively more robust than animals at lower latitudes. The index of athletic ability (a dimensionless ratio) was plotted against latitude in order to test the hypothesis that there will be a significant association between relative strength and latitude. The results show that there is no apparent relationship between the index of athletic ability of the individual *Canis* in this sample and the latitude at which they lived.

Because it is impossible to control for every possible ecological variable that might predict skeletal robusticity in a single test, the failure of latitude to reliably make predictions about the skeleton should not be the end-point for such analyses. Although these data do not support the ecological hypotheses as stated here, more detailed analysis should be pursued in the future. Direct measures of temperature and productivity should be examined. It is also worth noting that the sample of modern wolves may not accurately reflect geographic variation due to the recent decimation of populations due to human hunting. Wolves once had a much more extensive home range in North America, and the areas where they are found today may not be their preferred habitat. Much more research can be done and data collected in order to further investigate the ecological hypothesis.

Table 27: Summary of results of ecological hypothesis

hypothesis	Questions	Tests	sample	expectation	results
Ecological factors will influence levels of bone strength in mammals.	Are Pleistocene *Canis* more robust than Holocene *Canis*?	Ratios of x-sec. dimensions relative to body mass and bone length	*C. latrans, C. lupus, C. dirus*	*C. dirus* will be relatively more robust	*C. dirus* are more robust; also have relatively shorter limbs
	Does latitude correlate with bone strength in extant *Canis*?	Plots of the index of athletic ability on latitude	*C. lupus, C. latrans, C. rufus*	Individuals at higher latitudes will be more robust than those at lower latitudes	No correlation between latitude and robusticity

6.3 Discussion

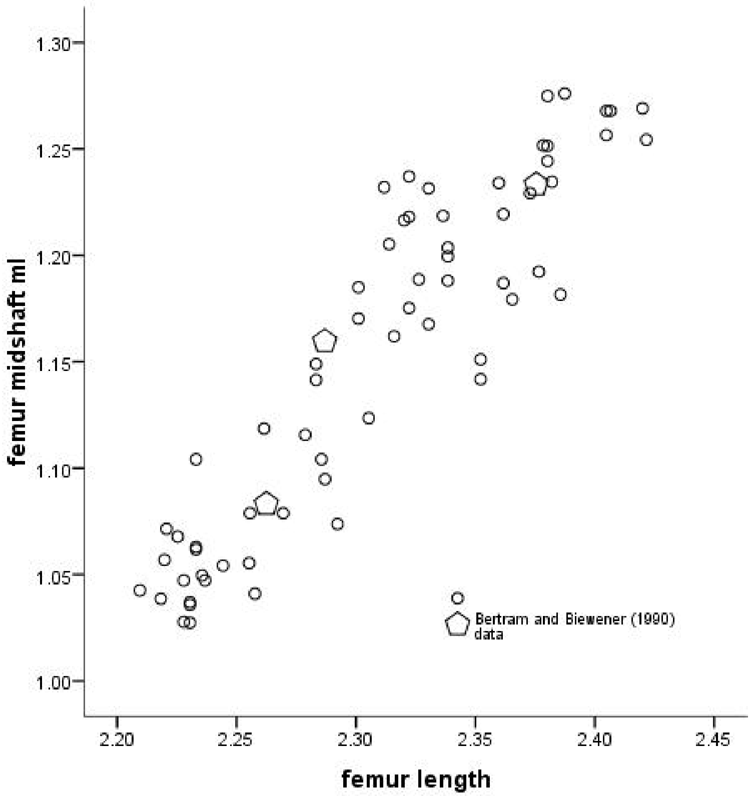
There are differential scaling patterns in the two extant mammalian groups sampled in this dissertation. The wolves, which have a smaller body mass than the bears, scale with elastic similarity of bone cross-sectional diameters on bone length, and isometry of cross-sectional diameters on body mass. Similarly, wolves scale with positive allometry of second moments of area on bone length and isometry on body mass. The bone length results are contrary to the expectations of geometric similarity (Bertram and Biewener, 1990) for species under 100kg. The primary way in which *Canis* are increasing bone strength is through a relative shortening of the limb bones in larger individuals. The main difference between the two mammalian genera is the relationship of long bone cross-sectional dimensions and measurements of bone strength on bone lengths.

There is an increase in the modified index of athletic capability with increasing body mass in *Canis*, and a decrease in the modified index of athletic capability with increasing body mass in *Ursus*, demonstrating that these genera either have different mechanical demands on their skeletons, or they adapt to these demands in different ways. This study was undertaken in order to more fully understand the forces that shaped changes in skeletal robusticity throughout human evolution. Understanding the scaling patterns of mammalian genera was the first step in accomplishing this goal. The second step was to evaluate strength differences of closely related species, including a comparison with a fossil species.

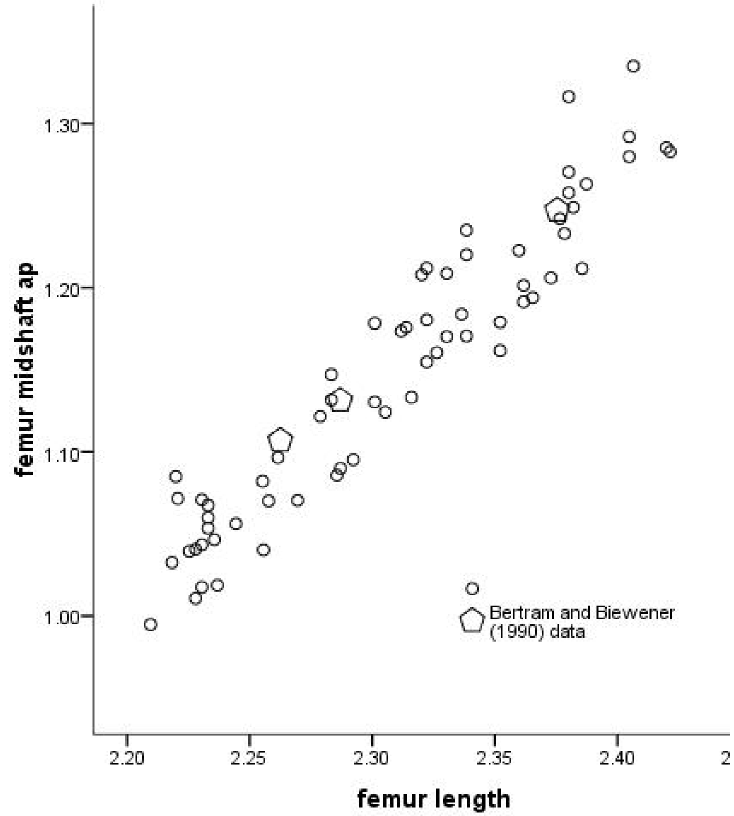
When the fossil *C. dirus* is included in the plotting of cross-sectional dimensions on limb length and body mass, it becomes clear that there are some fundamental differences between this species and the extant species. The most interesting pattern that emerges in this section is that there is an emerging relationship between the ratio of prey body mass to predator body mass and standardized strength of the predator postcrania. Species that hunt animals that are much larger in body mass than themselves have higher levels of standardized strength than those that hunt smaller animals. This explanation fits with the patterns of robusticity seen in fossil hominins, which are relatively stronger than living hominins, and also with the patterns of robusticity revealed in this dissertation in the fossil *Canis*, which is relatively stronger than the living species of *Canis*. The Pleistocene was home to herbivorous mammals that were much larger than the Holocene mammals encountered by living wolves and humans. Since body mass is heavily influenced by productivity, the ecological hypothesis should be further investigated. Productivity itself is extremely complex, and so the failure of a single component of productivity (latitude) to correlate with bone strength doesn't necessarily invalidate the hypothesis. The finding of a relationship between the prey to predator body mass ratio and bone strength suggests that a further exploration of this hypothesis is warranted.

Appendix A

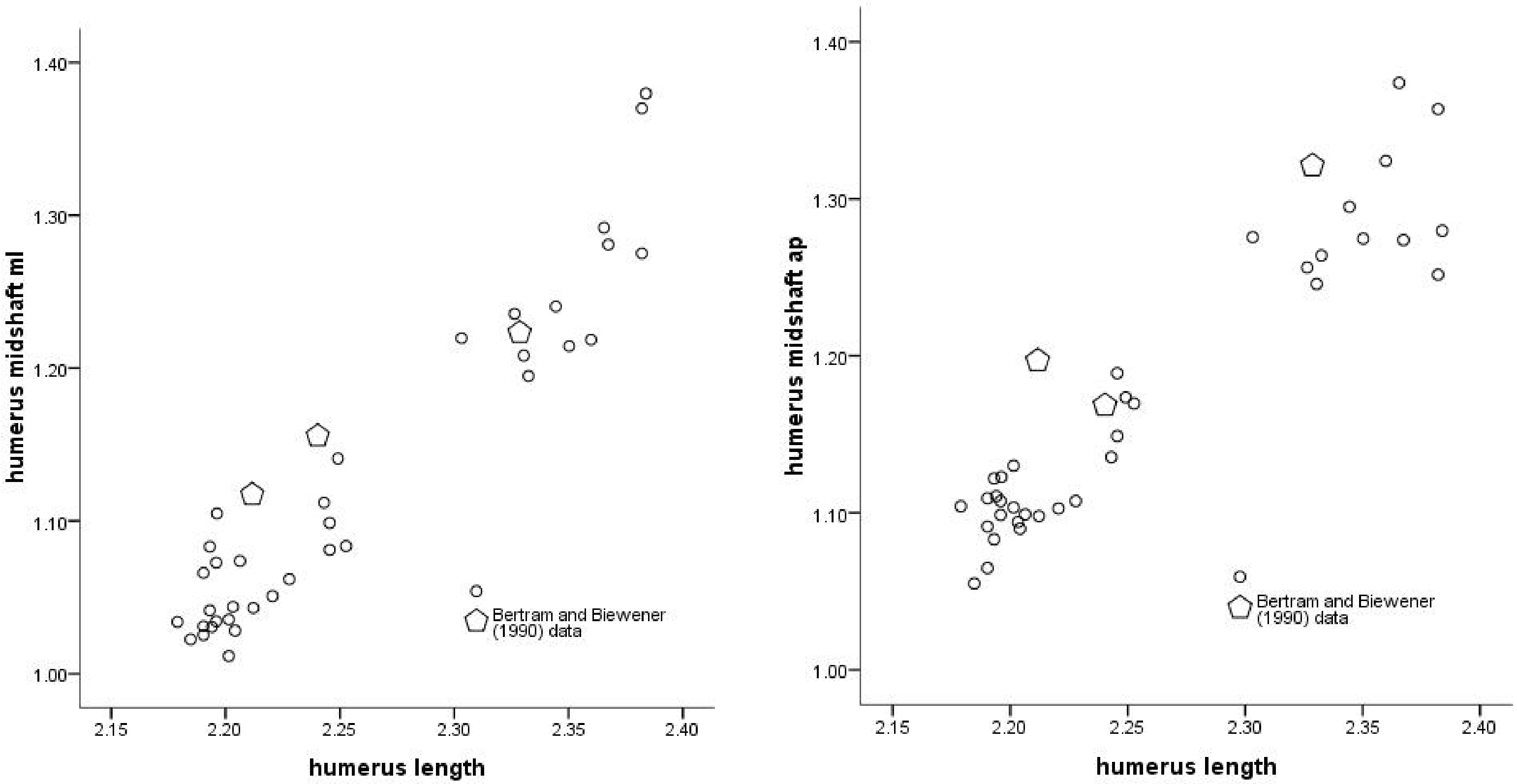
The following charts show the position of the data gathered by Bertram and Biewener (1990) relative to the data collected for this dissertation.

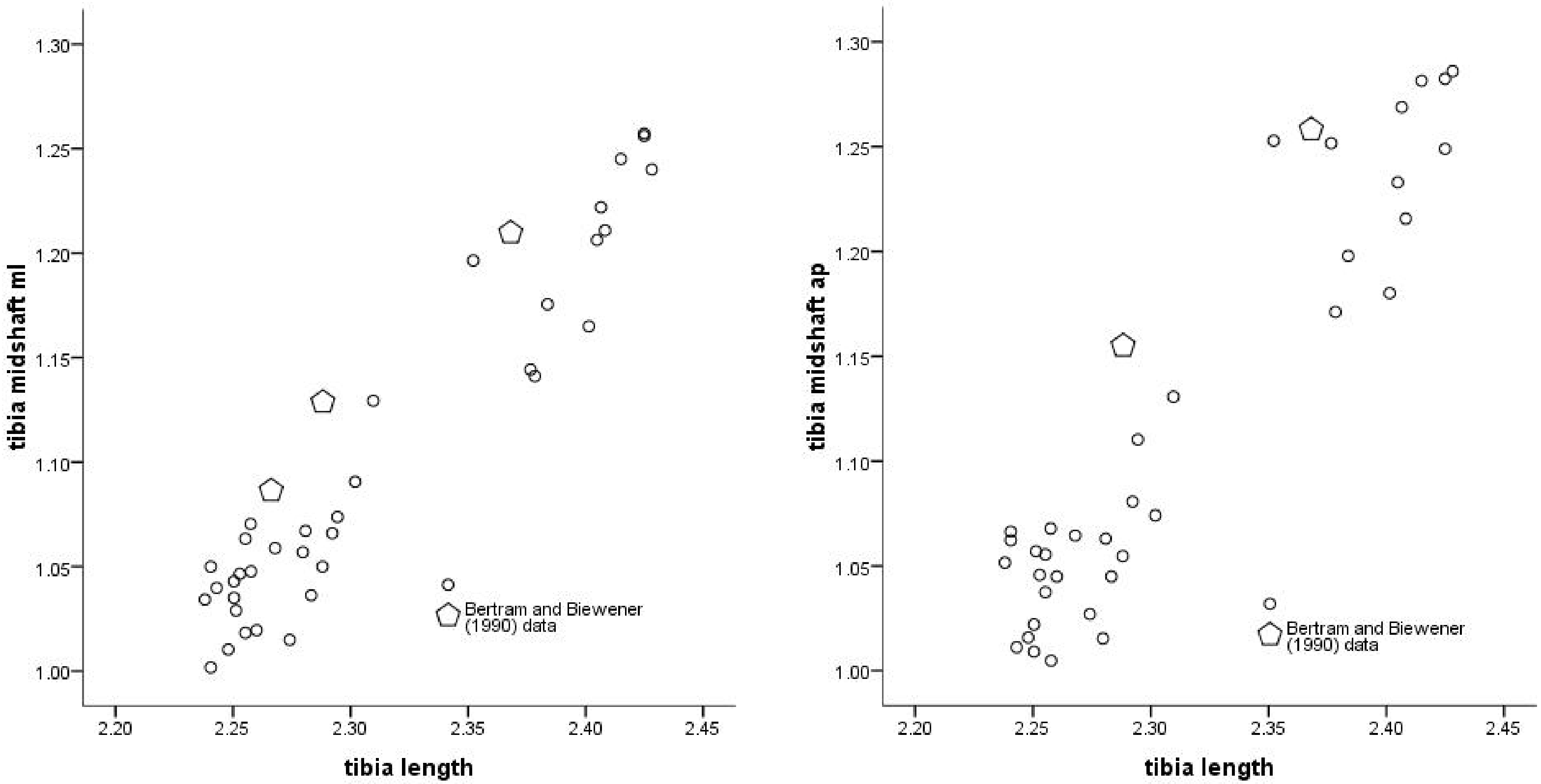


femur midshaft ml
femur length
Bertram and Biewener (1990) data
1.30
1.25
1.20
1.15
1.10
1.05
1.00
2.20
2.25
2.30
2.35
2.40
2.45



femur midshaft ap
femur length
Bertram and Biewener (1990) data
1.30
1.20
1.10
1.00
2.20
2.25
2.30
2.35
2.40

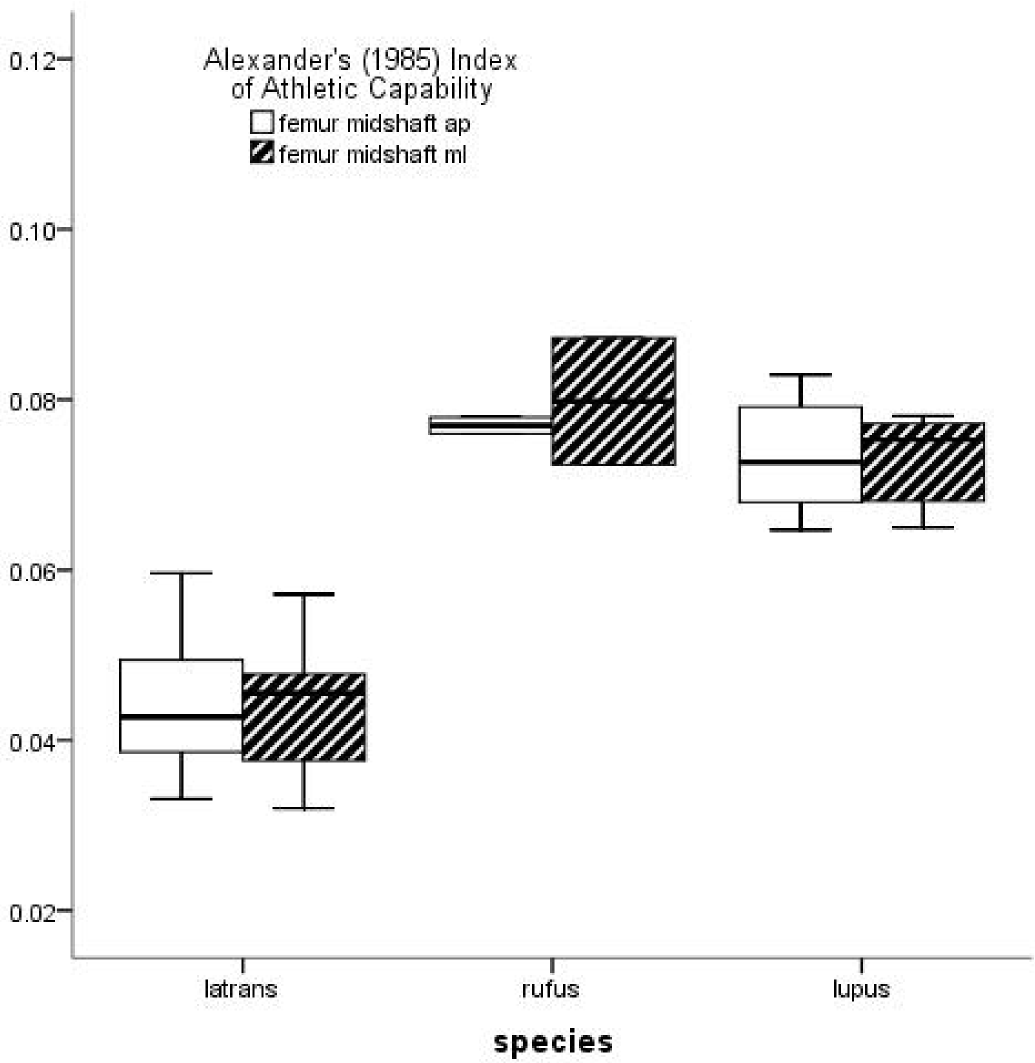

humerus midshaft ml
1.40
1.30
1.20
1.10
1.00
2.15
2.20
2.25
2.30
2.35
2.40
humerus length
Bertram and Biewener (1990) data
humerus midshaft ap
1.40
1.30
1.20
1.10
1.00
2.15
2.20
2.25
2.30
2.35
2.40
humerus length
Bertram and Biewener (1990) data

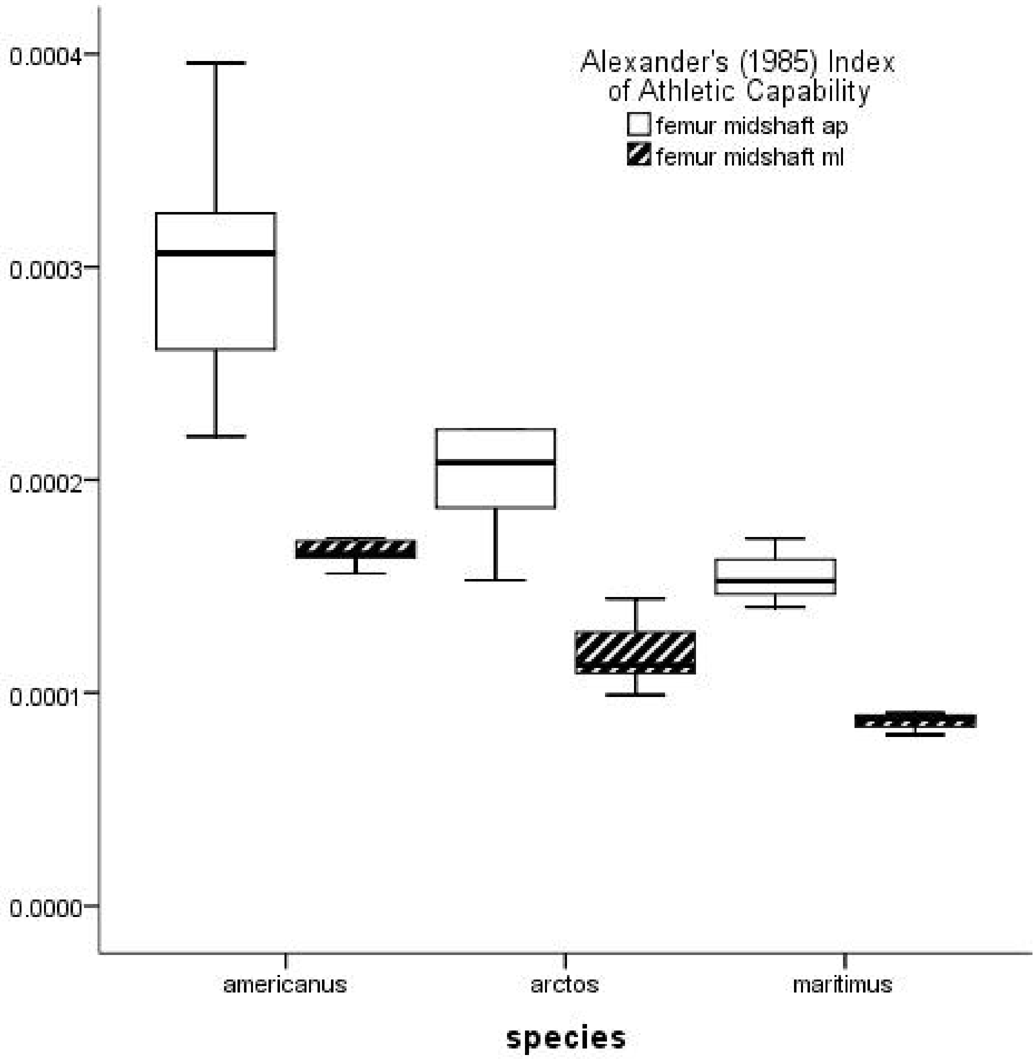


1.30
1.25
1.20
1.15
1.10
1.05
1.00
tibia midshaft ml
2.20
2.25
2.30
2.35
2.40
2.45
tibia length
Bertram and Biewener (1990) data
1.30
1.25
1.20
1.15
1.10
1.05
1.00
tibia midshaft ap
2.20
2.25
2.30
2.35
2.40
2.45
tibia length
Bertram and Biewener (1990) data

Appendix B

The following figures show the unaltered index of athletic ability, as originally described by Alexander (1985). These are shown for comparison to the figures in Chapter 4, from which they do not differ much. The units for these figures are in millimeters.


0.12
0.10
0.08
0.06
0.04
0.02
Alexander's (1985) Index
of Athletic Capability
femur midshaft ap
femur midshaft ml
latrans
rufus
lupus
species



Alexander's (1985) Index of Athletic Capability
femur midshaft ap
femur midshaft ml
0.0004
0.0003
0.0002
0.0001
0.0000
americanus
arctos
maritimus
species

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Biography

Sara Doyle was raised in Franklin, Massachusetts and has always been interested in science. She earned her BA from the University of Massachusetts, Boston, in the department of Anthropology. In the fall of 2009, she received a Ph.D from Duke University. She lives in Durham, NC with her wonderful daughter.