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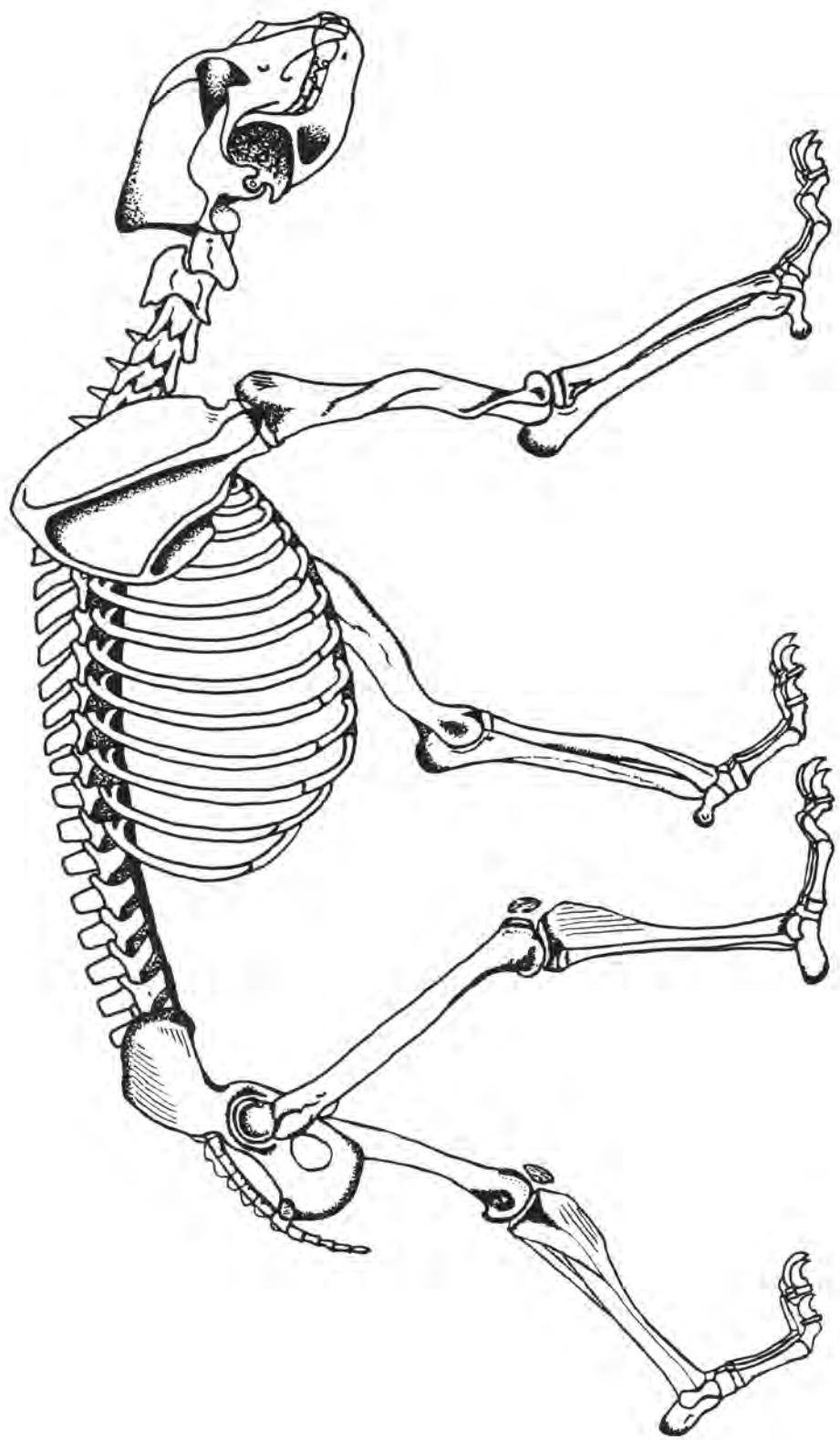


LOCOMOTOR ADAPTATIONS AND ECOMORPHOLOGY OF SHORT-FACED BEARS (*Arctodus simus*) IN EASTERN BERINGIA

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The Giant Short-Faced Bear (*Arctodus simus*) as reconstructed by author



Publication Note:

This monograph was originally written as Chapters 2, 3, and 4 of the Ph.D. dissertation entitled, "Paleoecology and Ecomorphology of the Giant Short-Faced Bear in Eastern Beringia," completed by the author in 1997 at The University of Alaska Fairbanks. The content is essentially unchanged, except for minor editing, typographic corrections, and re-formatting. The complete dissertation contained two additional papers (Chapters 1 and 5) that are cited in this monograph

as Matheus 1995 and 2001. The dissertation also contained an appendix with stable isotope data on modern and Pleistocene carnivores along with a manual for extracting and purifying collagen from bone. The present monograph may be cited directly, but if the citation is used to establish when the ideas herein were established or data herein made public, then the dissertation or Matheus (1995) take precedence.

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ABSTRACT

The giant short-faced bear (*Arctodus simus*) was a widespread Tremartine (New World) bear indigenous to North America until its extinction around 11,500 BP. *Arctodus* inhabited Pleistocene ice-free refugia in Eastern Beringia (the northwestern limit of its range) until at least 20,000 BP. *Arctodus* was the largest bear and perhaps the largest species of terrestrial Carnivora that ever lived, yet it was characterized by a gracile postcranial morphology and it was relatively long-legged. Most ecological models reconstruct this bear as a high-speed cursorial pursuit predator which preyed on the largest herbivores of Pleistocene North America. However, it also has been argued on energetic grounds that this bear was too large to be carnivorous and evolved its large size within an herbivorous/omnivorous niche. Within both models, the immigration of brown bears into North America during the late Pleistocene has been invoked as a possible cause for the extinction of *Arctodus*.

Previously (Matheus 1994, 1995) I extracted fossil bone collagen from east Beringian short-faced bears, brown bears, and other carnivores for stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in order to test competing dietary models and the competition hypothesis. Results of that study showed that *Arctodus* was highly carnivorous, that its diet was completely terrestrial (i.e., no salmon), and that it fed on herbivores which consumed C₃ vegetation. The herbivore/omnivore foraging model was thus rejected.

Given the knowledge that *Arctodus* was carnivorous, I re-examined this giant bear's postcranial morphology and locomotor abilities in order to test predictions of the predatory model. Within the predatory model there are two sub-hypotheses that can be constructed based on the types of prey which were available to *Arctodus*: 1) *Arctodus* preyed on the largest and slowest megafaunal species, or 2) *Arctodus* preyed on faster, moderate-sized megafaunal species. The first hypothesis predicts a large body and strong, robust build in *Arctodus* and must be rejected because of *Arctodus'* gracile postcranial morphology. The second hypothesis predicts that there should be certain morphological features in *Arctodus* that would enhance one or more of the following skills: top running speed, ability to accelerate, or ability to maneuver at high speeds. Data collected on running speed and bone strength in other large mammals show that a bear the size of *Arctodus* with long gracile limbs would not have been able to endure the extreme dynamic forces incurred at high speeds, during rapid acceleration, or during sharp turns, making it

unsuitable as a predator. Therefore, while the first predatory sub-hypothesis accurately predicts *Arctodus'* large size, it does not predict *Arctodus'* gracile build. The second predatory sub-hypothesis is consistent with *Arctodus'* gracile build but cannot explain its large size.

On the other hand, numerous aspects of *Arctodus'* morphology and body size indicate that it was an incipient courser that had evolved not for speed, but rather for increased locomotor efficiency during prolonged travel. *Arctodus* swung its legs in a more parasagittal plane in-line with the body compared to other bears, and it had a short, sloping back with tall front limbs and short hind limbs. This conformation indicates that *Arctodus* evolved to use a pacing gait—a highly efficient, moderate-speed gait. Its large body size and long legs also would have increased locomotor efficiency because these traits 1) increase the amount of elastic strain energy that can be stored and recovered from stretch tendons in mammalian limbs, and 2) increase stride length—one of the most effective way to increase locomotor efficiency. Considering these facts, I suggest that this carnivorous bear had evolved as a specialized scavenger adapted to cover an extremely large home range in order to seek out broadly and unevenly distributed large-mammal carcasses and to dominate this lucrative, but unpredictable carrion resource. Under such a model, there would have been additional selective pressure for increased body size so that *Arctodus* could procure and defend carcasses from other large carnivores, some of which were gregarious.

To test the energetic feasibility of the scavenging hypothesis I develop a model of carcass production on Beringian landscapes based on estimates of herbivore populations and their expected mortality rates. Results indicate that Pleistocene environments would have produced enough carcass biomass from natural mortality and predation by other carnivores to support at least twice the required minimum viable population of short-faced bears. The model helps show that *Arctodus'* extinction probably is best tied to the lack of year-round carcasses on Holocene landscapes, a condition brought on by the Holocene's less diverse herbivore fauna, which is dominated by ruminants experiencing highly seasonal mortality. The Holocene condition produces a seasonal glut of carcasses (late winter-spring) followed by a tight dietary bottleneck (summer-early winter) when few carcasses are available—conditions which led to the demise of *Arctodus*.

LOCOMOTOR ADAPTATIONS AND ECOMORPHOLOGY OF SHORT-FACED BEARS (*Arctodus simus*) IN EASTERN BERINGIA

PART I: GENERAL EFFECTS OF BODY SIZE AND LIMB MORPHOLOGY ON LOCOMOTOR PERFORMANCE IN LARGE QUADRUPEDAL MAMMALS —DESIGNS FOR SPEED, ACCELERATION, AND ENDURANCE

1. INTRODUCTION

This three-part monograph re-examines the locomotor abilities and ecomorphology of the extinct giant short-faced bear (*Arctodus simus*), a formerly widespread indigenous bear of Pleistocene North America. Part I provides a general review of relevant morphological features that influence performance aspects of locomotion in large quadrupedal mammals. Part II is a specific diagnosis of locomotor function in *Arctodus*. In Part III, I model energetic aspects of *Arctodus*' foraging ecology and present a theory for the evolutionary ecology of short-faced bears. These chapters represent a detailed discussion of arguments presented previously in Matheus 1994, 1995, 2001.

I undertake a fairly lengthy review of locomotion in Part I for a number of reasons. First, I found that existing interpretations of *Arctodus'* post-cranial morphology are fairly cursory, speculative, and draw on inaccurate concepts about locomotor dynamics. Consequently, it seemed important to synthesize information relating to the mechanics and physiology of locomotion relevant to the *Arctodus* question—namely the effects of very large body size and long gracile legs. However, in Part I I discuss *Arctodus* very little. Instead, I lay down general arguments for locomotor adaptation, which allow me to be more direct and concise in Part II; rather than cluttering the discussion of *Arctodus* in Part II with digressions and explanations of biomechanics and physiology, I can refer the reader back to concepts established here. I also feel that this elaboration is necessary because I will make conclusions about *Arctodus* which are not always intuitive and which are contrary to current beliefs about this unusual bear's behavior. Finally, the review in Part I may provide other vertebrate paleontologists with a convenient synthesis of some current concepts regarding locomotion from the perspective of physiologists and anatomists.

Current Ecological Models and the Hypotheses Being Tested

Parts II and III of this monograph contain more thorough discussions of the *Arctodus* problem, but I will briefly introduce the issues here, so the reader

understands the direction I am heading (also see Matheus 1995).

Kurtén (1967a) was the first to seriously address the functional implications of *Arctodus'* morphology, and he concluded that this bear was a fast, cursorial super-predator that had evolved as a specialized hunter of North America's Pleistocene megaherbivores. Kurtén's conclusions regarding *Arctodus'* predatory behavior and cursorialism were based on its powerful, robust cranium, which Kurtén argued was adaptive for prey capture, and long, gracile, legs, which Kurtén thought were adaptive for speed and cursorial pursuit. The premise that *Arctodus* was at least carnivorous and probably an active predator has been widely accepted with little qualification from Kurtén's original model (Harington 1973, 1977, 1996; Kurtén and Anderson 1980; Agenbroad and Mead 1986; Agenbroad 1990; Voorhies and Corner 1982, 1986; Guthrie 1988, 1990a; Gillette and Madsen 1992; Churcher *et al.* 1993; Baryshnikov *et al.* 1994; Richards and Turnbull 1995; Richards *et al.* 1996). However, it is a premise I will refute.

Emslie and Czaplewski (1985) have voiced the only dissent regarding *Arctodus'* carnivorous habits. These authors argued that short-faced bears were not cursorially adapted and must have been herbivorous because, in their estimate, such a large carnivore would have had to procure an unrealistic amount of animal biomass (meat) to achieve its energetic requirements. They formulated the latter argument based on data in Eisenberg (1981), who summarized patterns relating body size to trophic position and showed that no modern terrestrial carnivore approaches the size of *Arctodus*.

Using stable isotopes, I rejected Emslie and Czaplewski's hypothesis by showing that short-faced bears were highly, if not purely carnivorous (Matheus 1994, 1995; also see Bocherens *et al.* 1995). In those works I also laid down preliminary arguments showing that *Arctodus* was not built to be an effective predator because it most likely was incapable of accelerating rapidly and generating high speeds (or at least not maneuvering at high speeds)—all traits that are necessary to some degree for essentially all modes of prey capture. As an alternative hypothesis, I suggested that this bear showed the traits predicted for an animal that had

evolved to locomote with great economy and for sustained travel. Thus, I proposed that *Arctodus* mainly functioned as a wide-ranging scavenging specialist that had evolved to efficiently traverse a large home range in order to economically seek out, procure, and defend megafaunal carcasses from other large carnivores.

In this monograph, I follow up on this model by showing in more detail why it is unlikely that *Arctodus* was much of a predator. Baryshnikov *et al.* (1994) also have suggested that *Arctodus* may have had scavenging habits (as do most carnivores). In addition, Voorhies and Corner (1986), Guthrie (1988, 1990a), Agenbroad (1990), and Harington (1996) alluded to the possibility. However, none of these authors has suggested that scavenging was *Arctodus'* primary occupation and they assert that this bear was still an active, capable predator. Moreover, none of these authors developed significant arguments addressing mechanical aspects of short-faced bear morphology. In contrast, I will use mechanical and ecological evidence to demonstrate why *Arctodus* most likely had evolved specifically as a scavenger, and, while I do not deny that *Arctodus* was capable of killing its own prey when an easy opportunity arose, I will argue that this behavior was not the driving force that shaped *Arctodus'* morphology—but scavenging was.

Primer on Arctodus' Morphology

Knowing that *Arctodus* was carnivorous, the key to reconstructing its foraging ecology lies in diagnosing the adaptive significance of its highly derived morphology. Again, this subject will be addressed in detail in Part II; only a summary of *Arctodus'* morphology is provided here for orientation. Also, this monograph will only address specific details of post-cranial adaptations; while *Arctodus'* cranial morphology provides additional clues into its foraging behavior, I will be addressing that subject in a separate manuscript (in prep) (hypothesis regarding *Arctodus'* cranial features were presented in Matheus 1995).

Short-faced bears were extremely large, even for bears (Figs. 1 and 2), and various attempts have been made to estimate the body weight of individual specimens (Kurtén 1967a; Nelson and Madsen 1983; Agenbroad and Mead 1986; Voorhies and Corner 1986; Churcher *et al.* 1993; Richards and Turnbull 1995; Harington 1991, 1996). Most of these estimates were calculated using allometric equations relating long bone cross-sectional area to body mass, while some are best guesses based on comparisons to other bears. Generally, these authors estimated that males were around 600 - 700 kg and perhaps reached 800 kg. Voorhies and Corner (1986) even suggested that large males may have topped 1000 kg. Kurtén (1967a) showed that sexual dimorphism was pronounced, as it is in other bears, on the order of 15 - 25

%; this would place females to be around 450 - 600 kg. If Voorhies and Corner's extreme estimate (1000 kg for males) is correct, then some females may have even reached nearly 750 kg. Considering *Arctodus'* gracile build, and the mass of modern bears, I think that Voorhies and Corner's estimates are too extreme. Nonetheless, *Arctodus* was a large bear, and the bulk of this Part I will discuss the ramifications of such large size, and I will frequently reiterate that body mass and both static and dynamic forces of support increase with body size at a greater rate than the support capability of long bones. This should be a strong clue that such a large animal like *Arctodus* with gracile limbs must have been very lean. Furthermore, Voorhies and Corner do not explain how they derived their estimate of 1000 kg for large males in their 1986 paper, but based on the their 1982 article it seems that they arrived at this value simply by their impression with how big *Arctodus* long bones are compared to those of modern black bears (*Ursus americanus*).

Even if one accepts a conservative estimate of 500 kg and 600 kg for an average female and male short-faced bear, respectively, this means that an average individual was nearly as massive as a small domestic horse and two to three times the mass of a modern, non-coastal grizzly bear (*Ursus arctos horribilis*). Figure 1b compares the skeletal size of *Arctodus* (a) to three morphs of male brown bears: the largest known modern, male, brown bear (which could also represent the largest known polar bear) (b); a very large modern, male, brown bear from coastal Alaska or Kamchatka (also the size of a typical large brown bear from interior Alaska during the Pleistocene) (c), and; a large, modern, male brown bear typical of interior Alaska, the contiguous 48 United States, Europe, and interior Russia (d). Figure 2 compares the size of *Arctodus* to other carnivores that are discussed. A primary thesis throughout monograph will be that *Arctodus'* enormous size is one key to understanding its locomotor abilities and foraging behavior and that *Arctodus* was too large to be an effective predator.

Comparisons to other bears, however, can be misleading because *Arctodus* was not built like more familiar modern bears. In contrast to the stereotypical impression of a bear's morphology, *Arctodus* had a very light build, with a laterally compressed but deep thoracic cavity, and limb bones that were very long, gracile, and lacked much of the characteristic bowing and toe-in posture of ursine bears (Part II, Merriam and Stock 1925, Kurtén 1967a). I discuss these traits in detail in the Part II, where I also will show that, contrary to other portrayals (e.g., Kurtén 1967a, Baryshnikov *et al.* 1994), *Arctodus'* front legs were especially long compared to the hind legs and that it had a fairly short back. This

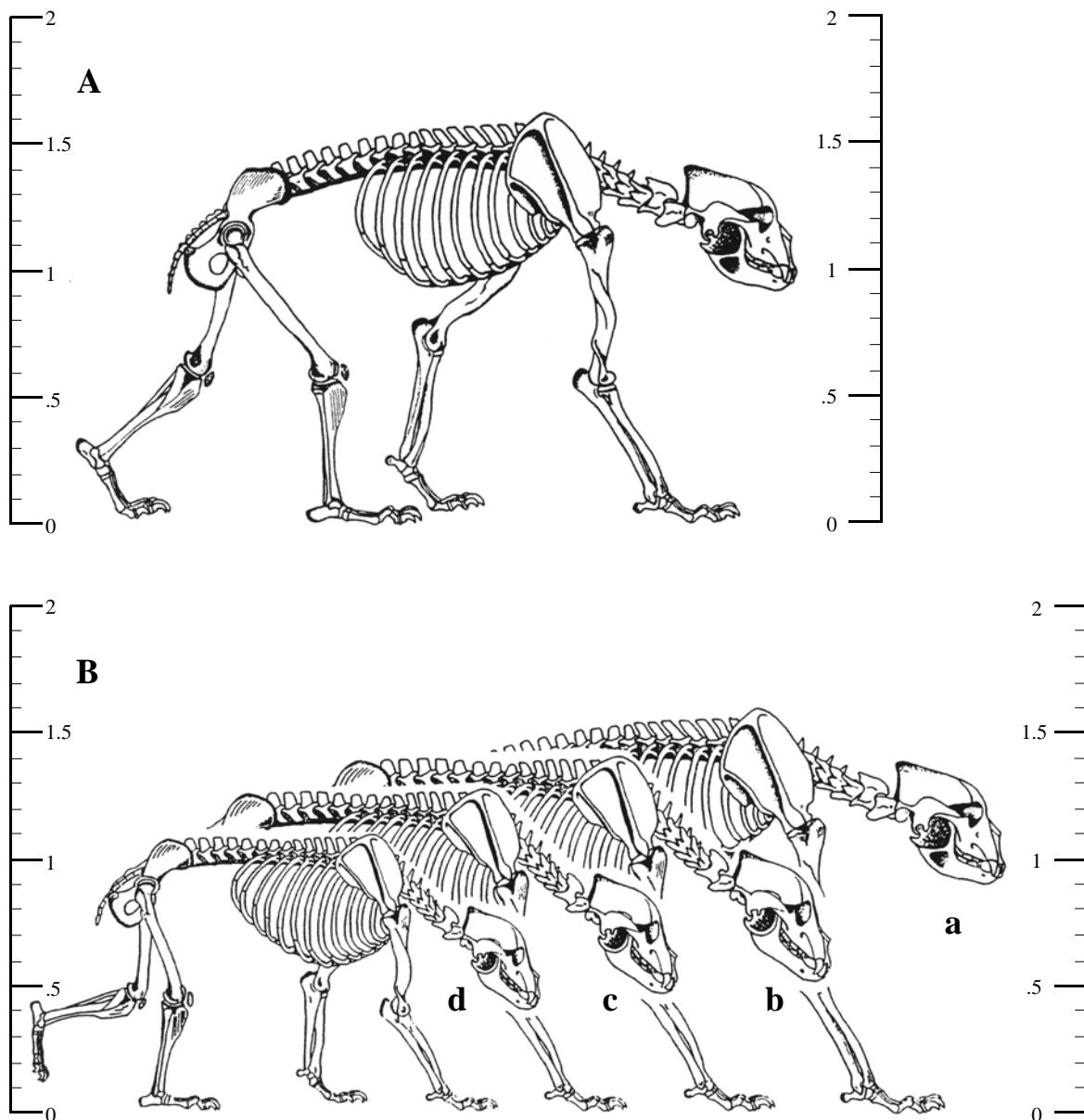


FIGURE 1. A) Reconstruction of the short-faced bear's skeletal conformation. B) Size comparison between short-faced bears and various brown bear morphs: *a* = large male short-faced bear, *b* = largest size attained by coastal brown bears today (could also represent the largest polar bear), *c* = large male brown bear typical for eastern Beringia during the Pleistocene (also approximate size of a large male modern coastal brown bear), *d* = large male grizzly from modern interior Alaska (units in meters)(original illustrations by author).

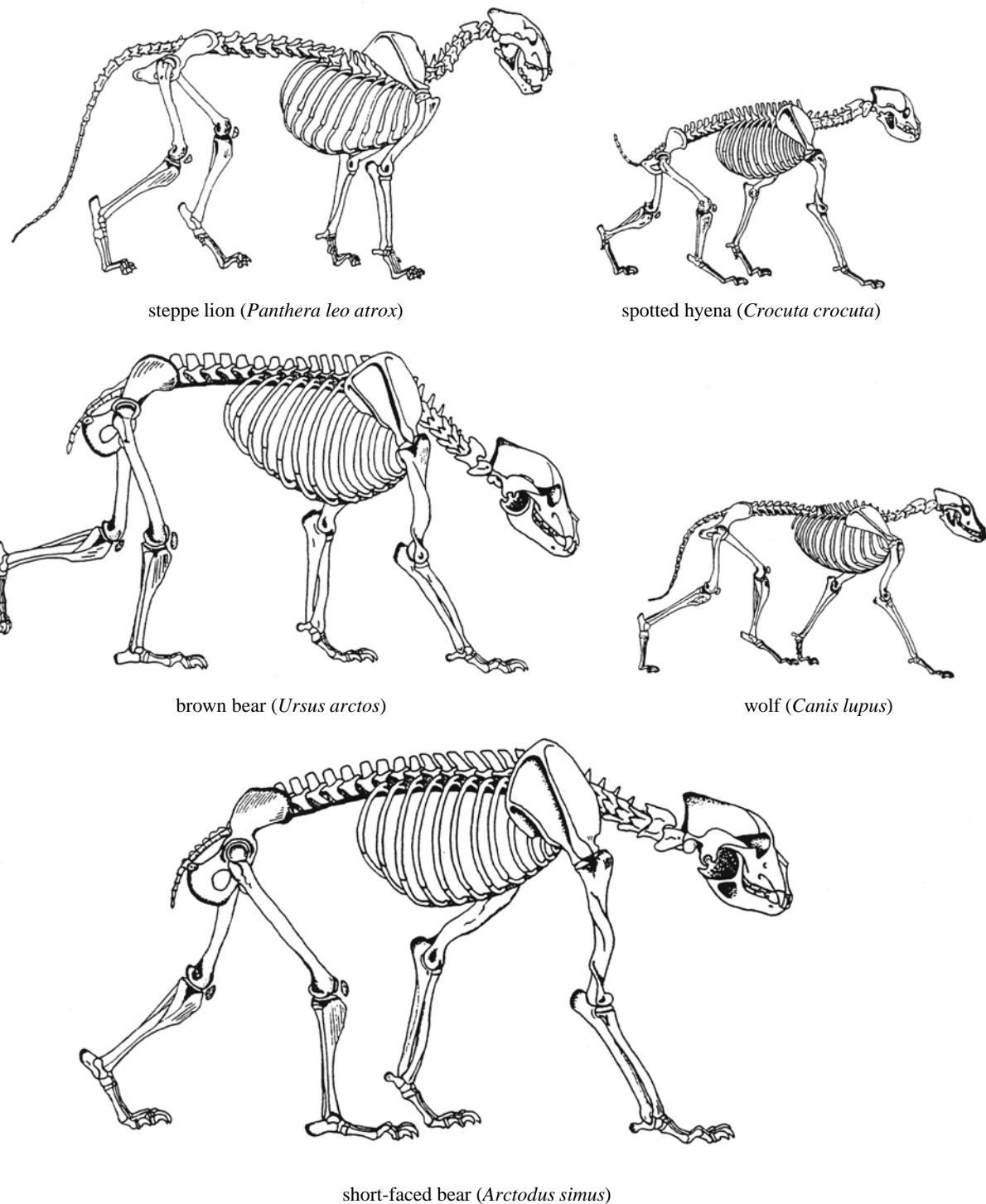


Figure 2. Body size and skeletal conformation of short-faced bears and other carnivores discussed in text. All body sizes adjusted to depict adult males in Pleistocene east Beringia, except hyena, which did not occur in Beringia. Bear illustrations by author; others adapted from Ewer (1973).

configuration gave *Arctodus* a high-shouldered, sloped-back appearance, which is significant for diagnosing its gait and locomotor adaptations. Its manus and pes (metapodials and phalanges) also were characteristically long and slender and more elongated along the central (third and forth) digits, compared to Ursine bears (Kurtén 1967a). This means that *Arctodus*' feet were more symmetrical than Ursine bears, whose feet have axes aligned with the most lateral (fifth) digit (Kurtén 1967a). Also, the first digit (hallux) of *Arctodus* was positioned more closely against and parallel to the others four digits, compared to Ursine bears (i.e., it had less lateral splaying)(Kurtén 1967a). Considering these traits, along with its large size and its gracile build, *Arctodus* must have appeared incredibly tall and lanky compared to extant bears.

More details on *Arctodus*' morphology follow in Part II, but here I want to make the point that *Arctodus*' morphology is quite derived from other bears, both modern and fossil. In this regard, I disagree with Baryshnikov *et al.* (1994:350) when they stated, "These limbs and locomotion are *satisfactory* for a scavenger," implying that there would be little, specific selective pressure on the locomotor morphology of a scavenging bear (emphasis on "satisfactory" is mine). The image of *Arctodus* as an unspecialized forager that made a living on the "leftovers" of other, more highly adapted, carnivores and the idea that scavengers are necessarily generalists, are two misnomers that I will try to dispel. Baryshnikov *et al.*'s (1994) interpretation seems especially inappropriate for a bear which had evolved a morphology so divergent from other bears.

Limbs are Compromises

Performance aspects of quadrupedal locomotion, such as top speed, acceleration, endurance, and maneuverability, depend on limb conformation in conjunction with other body proportions, as well as overall body size and metabolic limitations. Any analysis of limb design also must consider that limbs do not evolve solely for locomotion, but are employed for non-locomotor functions as well.¹ Even within the realm of locomotion, limb design is a tradeoff between competing demands: it is practically axiomatic among morphologists that limbs designed for high velocity can not simultaneously function for high power output (Hildebrand 1995:445), and sometimes it is difficult to make *a priori* determinations about the precise selective pressures driving limb morphology in an extinct species.

Phylogeny and evolutionary time also place constraints on the direction and rate of limb evolution. It is unrealistic, for instance, to expect a species with cheetah-like proportions and running abilities will arise within an ursid lineage in only one million years (yet this is almost what has been suggested for *Arctodus*). For the same reason, one should not expect animals to be perfectly adapted for a particular niche at any given time during their evolution—but this does not mean that they are not being shaped by strong selective pressures. Therefore, multiple demands on limbs, as well as phylogeny and evolutionary time frames, can confound attempts to decipher the precise locomotor habits of an extinct and unique animal such as the short-faced bear, which has left few other clues about its niche.

The Comparative Approach and Layout of Part I

The most intuitive starting point in deciphering an extinct species' locomotor abilities is to make comparisons with extant animals. However, I think that there are no good analogs for *Arctodus*. What's more, the comparisons which have been made only involve comparisons with other species of Carnivora (e.g., Kurtén 1967a, Emslie and Czaplewski 1985, Agenbroad and Mead 1986, Baryshnikov *et al.* 1994). I believe that this perspective has sent researchers down the wrong path towards understanding this bear's life, because short-faced bears were not built like other Carnivora and they were not simply scaled-up bears (discussed in detail in Part II). In fact, for some morphological features, I will show that better analogs can be found from the ranks of other very large, long-legged mammals outside of the Carnivora. It is because of this problem of analogs, a process which lends itself to oversimplified and misleading comparisons, that I am approaching the *Arctodus* problem mainly using first principles of locomotor dynamics. That also is why I will spend so much time discussing first principles for the remainder of Part I. If one analyzes *Arctodus* without any *a priori* assumptions about the way it moved, but instead dissects its parts and proportions to determine the functions they are optimized for, then a different picture of this bear emerges.

The remainder of Part I is divided into nine sections that discuss facets of locomotion relevant to the *Arctodus* problem. The first four sections (Sections 2-5) mainly define terms and introduce concepts which I refer to repeatedly, including discussions on cursorialism, gait terminology, and scaling in quadrupedal mammals. Then, I review current concepts on the energetics of locomotion (Section 6), where the importance of body size becomes apparent. Body size also is the main theme in the next two sections (7 and 8), which examine the ways that body size influences muscle performance and bone loading—

¹ throughout this thesis, the term "designed for" is used as an efficient phrase with the meaning "evolved under selective pressure for."

two critical issues for very large mammals. Finally, I discuss limb mechanics from the classic perspective of lever systems (Section 9) and kinematics (Section 10). These last two sections mainly consider concepts of mechanical advantage and the effects of limb mass on locomotor performance, and it is here that I distinguish ways that mammals are built for different types of locomotor abilities such as acceleration, endurance, and high speeds. Because of the two prominent traits in *Arctodus*—its extraordinarily large body size and long, gracile legs—the effects of body size and limb dimensions on locomotor performance will be dominant themes throughout these discussions. In Parts I and II, I will try to show that large size and long, gracile limbs would have afforded *Arctodus* certain locomotor advantages, such as increased stride length and economy of travel, while limiting it in other ways—namely the ability to accelerate and maneuver at high speeds.

2. DEFINITIONS

The following terms will be used throughout this monograph, some frequently and some in passing. They are defined or summarized here for quick reference, but important conceptual terms also are discussed in the text.

acceleration (a) = v/t (general linear); $a = d v/d t$ (instantaneous); $a = \Delta v/\Delta t$ (average); change in velocity per unit time usually measured in m/s^2 ; as with velocity terms, the acceleration of limbs or individual body parts is distinct from whole body acceleration (change in ground speed).

angular acceleration (α) = ω/t (general); $\alpha = d\omega/dt$ (instantaneous); $\alpha = \Delta\omega/\Delta t$ (average); curvilinear equivalent of linear acceleration.

angular momentum (L) = $I \cdot \omega$; the curvilinear equivalent of linear momentum.

angular velocity (ω) = L/I ; $\omega = dL/dI$ (instantaneous); $\omega = \Delta L/\Delta I$ (average); curvilinear equivalent of linear velocity

cost coefficient of locomotion rate of energy consumption by each kg of body mass during steady state locomotion; does not depend on distance traveled but purely on mass-specific rate of consumption; compare to *cost of transport*.

cost of transport amount of metabolic energy consumed per kg of body mass per km traveled during locomotion; also called the *mass specific cost of transport*; not the same as the *cost coefficient of locomotion*.

cursor (*cursorial*) an animal that has evolved substantial musculoskeletal features which reduce the effort required to swing the limbs and propel the body; includes animals adapted as such for either sustained locomotion or higher sustainable speeds, but these adaptations do not necessarily increase acceleration (that is a function of power output).

economy of effort similar to efficiency, it is a term that emphasizes the amount of effort required for a given task; increased economy may be achieved by increasing energetic efficiency or by reducing the absolute amount of work necessary for a task.

endurance measure of an animal's ability to sustain a given speed or activity; endurance is increased by increasing economy of effort.

force (F) = $m \cdot a$; expressed in kg/cm^2 or Newtons, force is the quantity of push or pull that drives (accelerates) or slows (decelerates) motion in a unit of mass; forces applied to solid surfaces are called *loads*; quantity of force generated by a muscle is a function of its cross-sectional area.

gait a regular and repeated pattern of footfalls used by an animal during locomotion.

inertia (m) measured as mass; tendency of an object to remain at rest or in uniform motion (constant velocity and direction) unless acted upon by a force; weight is gravitational inertia, or $m \cdot g$.

in-lever moment arm on the side of a fulcrum (joint) receiving an in-force; see *moment arm*.

kinetic energy (E_k) = $\frac{1}{2} m \cdot v^2$ (rectilinear); $E_k = \frac{1}{2} I \cdot \omega^2$ (curvilinear); energy of motion; may be converted to potential energy (E_p) or stored as elastic strain energy in tendons; energy is used to perform work.

limb velocity velocity of a whole limb or limb part relative to the body's center of mass.

load (and loading) any force applied to a solid object such as bone, muscle, or tendon.

locomotor efficiency ratio of the energy consumed during locomotion versus an output variable such as the amount of work performed or force generated.

mechanical advantage in-lever:outlever ratio in a lever or limb; high mechanical advantage gives a limb more torque but decreases rotational velocity.

moment see torque

moment arm or lever arm lengths of the levers (*in-levers* and *out-levers*), or arms, in a lever system; the length of a moment arm times a force is called a *moment, turning force, or torque*.

moment of inertia (I) = $m \cdot D^2$; the curvilinear equivalent of inertia; I is a function of mass and the length of its rotational axis.

momentum (M) = $m \cdot v$; a moving mass' capacity to resist a change in velocity or overcome resistance.

out-lever moment arm on the side of a fulcrum (joint) delivering an out-force; see *moment arm*.

power (P) = $F \cdot v$ or $P = W/t$; the rate of force application or the time over which a unit of work is performed; in a muscle, power is a function of the force applied times the rate of contraction. Power generation is directly related to limb/muscle acceleration. Physiologists measure *metabolic power* as the rate of oxygen consumption.

radius of gyration (D) length of a rotational axis; in a pendulum it is the distance from the pivot point to the center of oscillation.

run any gait where each foot is on the ground less than half the stride cycle and there is an unsupported (aerial) phase.

safety factor (safety margin) ratio between a bone's normal strain and yield strain.

speed (ground speed) average forward velocity of an animal's center of mass relative to the environment; calculated as stride rate \times stride length or as step length \div by time of foot contact with the ground (and by other means).

step length distance the body moves forward while a single foot is on the ground during a stride.

strain physical deformation in a solid material such as bone, muscle, or tendon during the application of a force (i.e., during loading).

strength (of bone) ability to deform under stress without breakage or permanent deformation; or the ability to dissipate strain.

strength (of muscle) amount of work a muscle can perform; is not equivalent to power.

stress force transmitted within a bone due to loading.

stride cycle cycle of motion during which each foot has completed one footfall.

stride length distance the body moves forward during one complete stride cycle.

stride sequence order of individual footfalls during a stride cycle.

torque, or turning force (τ) = $I \cdot \alpha$; curvilinear equivalent of force; in a lever system a torque is called a *moment* and is the product of a force times a moment arm.

velocity (v) = d / t (general, linear); $v = d d / d t$ (instantaneous); $v = \Delta d / \Delta t$ (average); velocities are vectors so they have both magnitude and direction; as with acceleration, the velocity of a limb or body part is distinguished from the whole body velocity, or ground speed.

walk any gait where each foot is on the ground more than half the stride cycle and there is no unsupported (aerial) phase.

work (W) = $F \cdot d$; the distance over which a unit of force is applied; in a muscle, work is roughly a function of volume; work is not always an informative concept in locomotion because it is not time dependent and force can be exerted without performing work if no change in position (distance) occurs.

3. CONFUSION REGARDING CURSORYALISM

When Kurtén (1967a) assessed *Arctodus* as a fast, cursorial predator, he followed common (mis)conceptions about what cursorialism is and is not. Cursorialism is not strictly, nor principally, about adaptations for running at high speeds. That is merely one form of cursorialism. Assuming that all coursers are built for speed (a somewhat misused term, itself) gets away from the heart of what cursorial adaptations are all about: musculoskeletal and physiological modifications that increase the efficiency of energy expenditure (i.e., economy) while swinging the limbs and propelling the body through a stride sequence. This definition most closely follows Hildebrand (1985a, 1995), who considers coursers to be animals that are structurally modified to improve speed *or* endurance; they travel fast *or* far and are distinguished from non-cursorial animals, which do not show structural modification principally for increased locomotor efficiency and who rely principally on walking gaits (the latter are termed “amblers”).

Some authors (for example, Alexander and Jayes 1983) prefer Jenkins’ (1971) definition of cursorialism in mammals, which is based more on size and posture than function. According to Jenkins, cursorial mammals stand and run with their legs less bent, with the femur and humerus positioned nearly vertically, and they swing their

limbs with little deviation from the sagittal plane. By this definition, nearly all mammals greater than 10 kg are cursorial and no very small mammals would be considered cursorial. The strength of Jenkins’ definition is that it does not use speed or running ability as criteria for cursorialism, but its dependence on mass is misleading. Small mammals do not necessarily move any less “cursorially” than large mammals, but because the stresses of locomotion and support scale in their favor, small animals do not need to make such severe skeletal modifications (see later sections). Furthermore, Jenkins’ definition is too general for my purposes, since I am discussing finer-scale details of cursorialism across a relatively narrow range of taxa and body sizes.

Taylor (1989), who considered cursorialism specifically in carnivores, distinguished three types of coursers: 1) those designed for prolonged, moderate speed travel, usually using a trot, but which seldom use high speeds (e.g., hyenids and some canids), 2) those that depend on a combination of speed and stamina for higher speed pursuit (e.g., African hunting dogs, *Lycaon pictus*), and 3) those that are built for extreme acceleration and high, but unsustainable, speed (e.g., large felids). I suggest that these are more appropriately called categories of running, rather than cursorialism, but Taylor acknowledges the critical distinctions between high speed, acceleration, and endurance, and the fact that coursers make tradeoffs among these three (a point I will emphasize repeatedly).

Frequently, the distinction between coursers adapted for sustained long range locomotion versus locomotion at high speeds (running) is a matter of ecology: animals adapted for sustained travel often migrate to follow seasonally available resources and/or are constantly on the move to forage, while those adapted for acceleration or high speeds absolutely rely on running to capture food or to escape predation. The important difference between the two categories often comes down to this: while long distance coursers *can* run, they often do not depend on it, and frequently they lack good running skills. The camel, for example, is the quintessential long range courser, and while it *can* run, it accelerates and maneuvers (at high speeds) very poorly.

Cursorial adaptations are most pronounced in the appendicular skeleton and principally involve modifications that affect the relative lengths of limb segments and the distribution of weight along the limbs (see section on kinematics). Generally cursorial modifications do not directly increase top speed. *The main effect of cursorial modifications is that they allow a given speed to be maintained for a longer period*—by decreasing the energy required to swing the limbs, the muscles fatigue more slowly. Cheetahs, for example, are less cursorially modified than the gazelles they chase.

Yet, cheetahs achieve the highest speeds amongst quadrupeds and their success at hunting is based on their ability to accelerate faster than their prey (after stalking within range). Without doubt, cursorial adaptations are beneficial to sprinters, such as the cheetah, but mainly because they allow coursors to sustain their speeds for longer periods, and I will be showing that some cursorial adaptations improve acceleration, while others detract from it. Without its advanced cursorial features, a cheetah would perform no better than a diminutive lion. With cursorial modifications, the cheetah still can only sustain its extraordinary speeds for up to about $\frac{1}{2}$ km (Schaller 1969). After this distance, the cheetah is exhausted and has accrued a large lactic acid debt, whereas the “more cursorial” gazelle continues to run for many kilometers without fatigue.

These examples illustrate how cursorialism is a relative term. Some authors even go to the extreme by considering only ungulates to be fully cursorial, referring to most carnivores, including the cheetah, as “subcursorial” (for example, Coombs 1978). Ungulates truly are the most cursorially adapted quadrupeds, but cheetahs also show advanced cursorial modifications, especially compared to other felids, which are all much more cursorial than brown bears, for instance. But this type of comparison (ungulates versus large predators) shows the fallacy of defining cursorialism as a simple gradational scale. There are distinct types of coursers, ranging from high speed sprinters to long-range migrators and comparisons of degree only should be made within categories. When Kurtén (1967a) surmised that *Arctodus* was cursorially adapted, he was probably correct, but I will be showing that I think he was incorrect when he assumed this implied *Arctodus* was adapted for high speed running and sprinting.

4. QUADRUPEDAL GAITS

I provide the following review of gait terminology and classification because I will argue in Part II that *Arctodus* would have relied heavily on a very particular gait—the pace—and that this fact reveals a lot about *Arctodus*’ behavior.

Quadrupedal locomotion involves the concerted oscillation of four limbs through a repeated stride sequence, or *gait*. A gait is the regular and repeated pattern of footfalls used by an animal during locomotion. Gait selection varies with speed of travel and can differ considerably among species. Over the past few decades, Hildebrand has done the most, by far, to categorize animal gaits and provide a formalized terminology to describe gait patterns, and my definitions below mostly follow his (Hildebrand 1959, 1976, 1977, 1980, 1985a, 1995; but also see Muybridge 1899, and Gray 1968). There are deviations in the literature from Hildebrand’s

terminology, particularly in the use of the terms *walk* and *run*, but the discrepancies are not of critical importance here. Here, I am most interested in the strategies and limitations of gait selection in animals of a certain size or shape, and what this implies about their behavioral ecology.

In gait terminology, a *stride sequence* refers to the order of footfalls, and one *stride cycle* is completed after each foot has completed one stride. *Stride length* is the distance the body moves over the ground during one stride cycle. I also will refer to *step length*, which is the distance the body moves while a single foot is on the ground (Gray 1968). *Ground speed* refers to an animal’s whole body velocity and is distinct from the velocity of limbs or limb segments. Ground speed is a product of stride length times stride rate or can it be calculated as a single foot’s step length divided by the time of its contact with the ground. An animal increases ground speed by increasing either stride rate or stride (step) length, but mostly the latter (Heglund *et al.* 1974).

A *walk* is defined as a gait whereby each foot is on the ground for more than half the time of one stride cycle, and during a walk there are no unsupported (aerial) phases during which all feet are off the ground. Viewed another way, there are never fewer than two feet on the ground in a walk. When an animal *runs*, each foot contacts the ground for less than half the stride cycle, and there is at least one aerial phase. Numerous walking and running gaits have been described and some can be used either during a walk or a run, the distinction being whether or not there is an aerial phase. Because of this confusion, the terms “walking” and “running” can be imprecise and they do not describe specific footfall patterns. For this, the convention is to use terms such as “singlefoot,” “trot,” “gallop,” and “pace.”

All the animals I will discuss use a *singlefoot* when walking at slow speeds (the singlefoot is not limited to slow speeds as it is the “running” gait of elephants, and horses that “rack” (Hildebrand 1985a)). During the *walking singlefoot*, each foot is placed on the ground one at a time and consecutive footfalls are evenly spaced in time—neither front nor hind feet move in couplets. Furthermore, during slow walks most quadrupeds use a *lateral singlefoot*, whereby each fore footfall follows the hind footfall on the same side of the body. The lateral singlefoot is a very stable gait, and animals can make the transition from a lateral singlefoot to faster gaits smoothly. The *diagonal singlefoot* is even more stable, but it is used only by primates and wide-bodied quadrupeds with short legs relative to their body length, such as suids and hippopotami (Hildebrand 1976). Other quadrupeds with longer legs apparently avoid the diagonal singlefoot because diagonal pairs of front and hind feet would cause interference with each other during the stride (Hildebrand 1976, Dagg 1979). Furthermore,

wide-bodied quadrupeds would have difficulty balancing on lateral legs and perhaps they retain short legs in order to use a diagonal sequence walk without leg interference. Phylogenetically, it appears that the lateral singlefoot is a primitive gait that gave rise to many other footfall sequences (Hildebrand 1976).

The *trot* is a diagonal gait whereby two legs on opposite sides of the body swing as a pair and ipsilateral legs are considered to be “out of phase.” The trot may be used either as a fast walk or a slow run, but more commonly the latter. It is the most frequently used moderate-speed gait for medium to large quadrupeds, and it is favored by large carnivores (Hildebrand 1976). Because ipsilateral legs are out of phase in the trot (one swings forward while the other swings rearward) interference between front and hind feet must be resolved. As a result, some quadrupeds trot with their bodies “cocked” laterally a few degrees so that front and hind feet are swung either to the inside or outside of each other. Because of interference problems, small feet appear to be an asset for trotters—big-footed bears, for instance, rarely trot (but for more reasons than just foot size—see below).

A major determinant of trotting ability appears to be the relative proportions of the limbs and back. Animals with front legs considerably longer than their hind limbs and with short, sloping backs either never or seldom trot at moderate speeds. Examples include spotted hyenas, giraffes, polar bears, brown bears, and camels (personal observation; Pennycuick 1975, 1979; Hildebrand 1976; Dagg 1979). I suggest two reasons for this. First, the two in-phase legs on opposite sides of the body would have very disparate natural stride lengths, producing an uneven and inefficient trot. Second, and more important, if an animal with a short-back were to use a trot, there would be too much overlap between the paths of the front and rear legs on each side of the body, causing either excessive interference or a much reduced stride length. It has also been observed that quadrupeds specializing in long range migrations, such as blue wildebeest (*Connochaetes taurinus*), may bypass the trot and go directly from a walking singlefoot to a canter, even though they are capable of trotting (Pennycuick 1975). Later I will show specifically why short strides lead to inefficient locomotion. In Part II, I will show that short-faced bears had short, sloping backs and were tall in the shoulder, and that they probably were incapable of trotting efficiently.

Quadrupeds that cannot trot typically will use the *pace* for moderate speed travel. In contrast to the trot, the pace is a lateral gait whereby the front and hind legs on each side of the body swing in phase. Like the trot, the pace can be used as a walk or a run. Typical pacers include camellids (all species), giraffids (*Giraffa spp.*,

Okapi johnstoni), saiga antelope (*Saiga tatarica*), hyenas (*Crocuta crocuta* and *Hyena spp.*), and long legged dog breeds (*Canis familiaris*). Most large carnivores, including bears, occasionally pace, (personal observation, Hildebrand 1976, Dagg 1979), but in Part II, I will show why short-faced bears seem to have evolved specifically as pacers. Pacing eliminates the issue of foot interference encountered in trotting, so it is used by animals with legs that are long relative to the length of their back. But the greatest assets of pacing seem to be that it allows for longer strides and lets an animal use trunk muscles to assist in extending and flexing the limbs (Dagg 1979). Long strides increase locomotor efficiency, the mechanics of which will be discussed in Section 6. By using trunk muscles, pacers spread the work of locomotion over more muscle groups and each fatigues less quickly. I have observed that sled dogs that normally trot will revert to a pace when they become fatigued, or during training runs in the early season, apparently because pacing relieves tired leg muscles. The same pattern can arise in sled dogs that receive minimal rest between hard workouts or in older dogs (personal observation).

Gaits like the pace, which use laterally supported legs, are inherently less stable than diagonal gaits (Dagg 1979, Hildebrand 1985a), and to keep balanced a pacing animal must place its feet more directly under the body's mass. Wide feet, such as in camels, and giraffes, also help to maintain stability during a pace. Because of the pace's instability, it is commonly believed that only animals inhabiting open country with a smooth substrate utilize the pace (Hildebrand 1977). However, Dagg (1979) showed that there can be a phylogenetic propensity to pace, regardless of habitat. She noted that all camellids, including lamoids, have a tendency to pace even when living in rough, mountainous terrain. Although there is a phylogenetic component to gait selection, there seem to be two functional reasons why the pace has evolved in large mammals: 1) to accommodate long legs or legs with disproportionate lengths (e.g., giraffids and hyenas), or 2) to increase the efficiency of prolonged travel at moderate speeds (e.g., some camellids and saiga). Large carnivores tend to use lateral gaits to a large extent (Dagg 1979), but few other than hyenas pace for long distances. These arguments do not mean that all efficient long-range couriers will be pacers. Caribou, for instance, do not pace but are efficient long-range trotters. In caribou, trotting may be necessary because tundra ground is very broken and requires a more stable gait.

There seems to be a general belief that large bears (e.g., brown bears and polar bears (*Ursus maritimus*)) are pacers. Based on my own observations of live and videotaped bears, I believe this is a false notion. Ambling (walking) bears almost exclusively use a lateral singlefoot, like all other large carnivores. Occasionally,

a walking bear will pace, but this behavior seems to be involved with intraspecific demonstrations (body displays). Data on gait selection in Dagg (1979) and Hildebrand (1976) also indicate that bears rarely pace, and I believe the perceptions that bears pace has arisen because the lateral singlefoot has a footfall pattern superficially resembling a pace. In the lateral singlefoot, the left hind leg is placed down, followed by the left front leg; then the right hind leg is placed down, followed by the right front leg. The legs are also lifted in that order, which can give the appearance that the two legs on a side are moving as a pair, but they do not. Especially misleading is the fact that a photograph taken at the right moment during footfalls can make a bear using a lateral singlefoot appear to be pacing.

The few times I have observed brown bears pacing has been mostly when they are making the transition from a galloping gait (see below) down to a walking gate. In these cases, the pace is done at moderate speeds (slow run) and only for a brief transitional period. Bears using this running pace look quite awkward because their hind limbs are too long for the front limbs, causing them to swing their hips laterally back and forth for each stride. Therefore, this gait probably is relatively inefficient and may be one of the reasons why bears (like other amblers) rarely use intermediate speeds. I also have observed that Polar bears, which have conspicuously high hips compared to brown bears, will occasionally trot but rarely pace. This seems especially true of smaller individuals, mainly females, where the tall hind quarters are accentuated. Polar bears, with their high back ends, actually adopt a trot similar to a canid's (personal observation, but also see Hildebrand 1976). This pattern is important because it shows how tall hind limbs promote trotting over pacing in bears. The running style of bears is discussed more below, and in Part II I will explain why it seems that short-faced bears, with their tall shoulders and short hind-quarters, would have been incapable of trotting and relied heavily on pacing.

The *gallop* and the *bound* are the two fast running gaits used by the animals discussed in subsequent sections. During both of these gaits, the two front and two hind feet each travel as pairs and are called couplets. In each couplet, the feet usually are somewhat out of phase with each other, in which case the foot leading in space is called the "leading" foot, while the other is the "trailing" foot. Although trailing in its flight path, the trailing foot usually hits the ground before the leading foot (as Hildebrand (1976) pointed out, the trailing foot trails in space, not time).

In the *bound*, the spacing (in space and time) between the leading and trailing feet is so small that each couplet appears to move with both feet virtually in phase. A bounding animal essentially makes two jumps—one by

the hind feet, then one by the front feet. In small mammals with very flexible backs, like weasels, the bound resembles a slinking motion. In the *half bound*, there is no lead in the hind feet, but there can be considerable lead in the front feet. When a bear suddenly charges from a stationary position it uses a half bound. Its hind feet propel the bear as in a leap, and the front feet support it on subsequent landings, after which they add propulsion with their own leap. Because of a bear's large size, there is only one brief aerial phase after the hind leap. When the front leap occurs, the hind feet are already back on the ground, and there is no second unsupported phase. There also is considerable lead between front couplets in a half-bounding bear, and its back remains fairly stiff throughout this gait, unlike the weasel's full bound. Whereas bears charge (rapid acceleration) using a half bound, they run for longer distances at steady-state speeds using a conventional gallop. Based on mechanical modeling and theoretical calculations, Alexander *et al.* (1980) suggested that the bound is an energetically expensive gait compared to galloping, but these authors admit that their models do not account for the ability of the muscles of the back and trunk to assist in locomotion.

Except for charging bears and running proboscideans, the *gallop* is essentially the universal high speed running gait of large mammalian quadrupeds. In the gallop there is considerable lead in both the front and the hind feet, and there are one or two unsupported phases. Two types of gallops are recognized: *transverse* and *rotary*. In the transverse gallop the leading foot in each couplet is on the same side of the body. It seems to be more stable than the rotary gallop and tends to be used by larger mammals in general, and by smaller mammals while running at slow speeds. In the rotary gallop, lead feet are on opposite sides of the body, and in a footfall diagram it can be seen that there is a rotary pattern in the timing of each foot striking the ground (i.e., left rear, left front, right front, right rear, then repeated)(see Hildebrand 1977). The rotary gallop is theoretically less stable but appears to offer greater maneuverability. Probably for these reasons, it is favored at higher speeds, where increased momentum helps maintain stability, and by smaller mammals, which are inherently more stable. Large predators use the rotary gallop to chase prey, probably because it facilitates greater maneuverability (Hildebrand 1985a).

The *canter* is a special kind of slow gallop during which there is considerable distance between leading and trailing feet in each couplet (cantering animals often appear to have either a hesitation or a head bobbing motion in their stride). However, in a canter one diagonal set of fore and hind feet touches the ground at nearly the same time, like in a trot, while the other diagonal pair swings out of phase with each other. The canter can be

used at surprisingly slow speeds, and is employed mostly by ungulates that engage in sustained moderate speed travel during migrations, including blue wildebeest and plains bison (*Bison bison*) (Pennycuick 1975, Guthrie 1990a). For migrating ungulates, the canter is the functional equivalent of trotting in a carnivore. Because the canter is essentially a gallop, it can be used to modulate smoothly between fast and slow speeds without changing gait, facilitating quicker and smoother acceleration/deceleration. The only carnivore that I know regularly uses a canter is the spotted hyena (Kruuk 1972, Mills 1989), and in Part II I discuss how this relates to its back and limb proportions and the weight of its head and neck. There I will show that the pace and canter go hand-in-hand for spotted hyenas, as they may have for short-faced bears.

Duty factor, the fraction of the stride cycle that each foot is on the ground, is an important concept in running gaits because it reflects the amount of time each foot has to dissipate vertical ground forces imparted on the limbs (and thus the instantaneous velocity of these forces). Later, I will show that these forces are disproportionately greater in larger animals and at higher speeds and that the gaits of large animals traveling at high speeds are dictated in part by the need to manage these increased forces. Dangerously high duty factor is probably the reason why large mammals (< 250 kg) have only one unsupported phase per stride in their gallop, which occurs when the feet are gathered beneath the body; during the extension phase, one or more of their front feet hits the ground before the last hind foot leaves the ground. Smaller mammals tend to have two aerial phases per stride—both when the legs are gathered beneath the body and when they are extended. The number of aerial phases also seems to be correlated to back flexion. When galloping, nearly all carnivores (except bears— see below) have both gathered and extended aerial phases because the spine flexes and extends with the legs. Most ungulates do not flex the spine much and are not aerial during the extended phase (Hildebrand 1960, 1977).

Hildebrand (1977) concluded that bears use a transverse gallop. However, I have studied films of running brown bears of various sizes, and slowed the film speed down to observe footfall patterns. All the bears in these films used only a rotary gallop (unpublished data), just as other large carnivores do. However, there typically is less lead in the hind feet couplet of a galloping bear, compared to other carnivores. Also, bears only have only one aerial phase (the gathered phase) when galloping, probably because their large size prohibits them from flexing their backs and achieving a second aerial phase during extension. Smaller carnivores, such as felids and canids, use both aerial phases (gathered and extended)(Hildebrand 1960, 1977). The lack of a second

aerial phase in polar bears and brown bears suggests that large extant bears experience limitations to galloping abilities. I will argue in later sections of that this is because they approach structural limitations of their bones in relation to the very large dynamic stresses of locomotion incurred by bears due to their large size. A charging bear, as noted, usually will accelerate using a half bound—essentially a series of leaps off the hind limbs whereby the weight is supported during landing by two largely out of phase front limbs. The difference between a half-bound and gallop, however, is not great in an animal like a brown bear where there is little back flexion. Essentially, the only difference is that there is noticeable lead in the hind limbs during a gallop but not during a half-bound.

5. PRELIMINARY REMARKS ON SCALING AND ALLOMETRY

The effect of body size (scaling) on function is a particularly critical factor impacting an animal's locomotor abilities. Practically every aspect of locomotion is directly affected by body size. Large size especially is a double-edged sword: it affords an animal certain energetic and spatial benefits, but very large animals also face a host of structural thresholds which limit high force locomotor activities. Scaling effects and references to body size allometries will arise throughout the remainder of Parts I and II, so a review of allometry and remarks on scaling principles seem in order.

Allometric Functions

Consider two related metrics (x and y) of an animal's shape, physiology, or performance, such as a the length and width of a long bone. The relationship by which these metrics co-vary over a range of sizes can be described by the allometric (power) equation:

$$y = b \cdot x^{\alpha} \quad (1)$$

This equation yields a curvilinear relationship between x and y where α is the power function, or allometric constant, and b is the y -intercept. Untransformed (i.e., not logarithmically transformed) data also can be fitted to a linear equation:

$$y = ax + b \quad (2)$$

but this line often has a poorer statistical fit to the data because body shape does not change in a linear fashion over a large size range. That is, the slope (a) does not remain constant, and the slope of Equation 2 functions as an average slope. Using Equation 2 to describe untransformed data is equivalent to forcing a rectilinear

fit to curvilinear data.

Typically in allometric studies one is testing the hypothesis that the data fit a particular equation, or line, such that the values of y and x are driven by a conserved allometry over a range of sizes. That is, the following proportion remains constant:

$$\frac{(y_2/y_1)}{(x_2/x_1)} \quad (3)$$

In scaling discussions biologists often are not concerned with the precise values of x , y , or the y -intercept (but see Gould 1971 for why these can be important). Instead biologists apply the most biological meaning to the slope (of log-transformed data) because it indicates the proportionality of x and y , as per Equation 3. Statistically, and visually, this sometimes is easier if Equation 1 (a power function) is logarithmically transformed into the linear equation:

$$\log y = \alpha \log x + \log b \quad (4)$$

where α is the slope of the line and b is its y intercept. Log-transforming the data also can help to normalize their variance (Lasiewski and Dawson 1969). This allows one to perform parametric statistical tests on the data, commonly a least squares regression, to test their fit to a specified line or slope (the hypothesis). Some authors have rightly questioned whether the data should always be log-transformed (see discussions in Lasiewski and Dawson 1969, Smith 1980, Harvey 1982, and Calder 1984). I think this is an important issue, and will be discussing it more at the end of this section. As a general procedure, both linear and power functions should be derived for the untransformed data; if the correlation coefficient (r^2) and p -value are substantially better for the power function, then the data should be log-transformed for linear statistical analyses. (Alternatively, non-linear statistical tests can be applied directly to the power function.)

Similarity Hypotheses and Scaling Theory

Biologists from diverse fields have invested considerable effort into the theory of allometry, proportionality, dimensional analyses, and similarity hypotheses—that is, the regular manner in which animal shape and function change with body size (see summaries in Thompson 1942; Huxley 1932; Gould 1966, 1971; Gunther 1975; Economos 1982, 1983; Calder 1984; Schmidt-Nielsen 1984; and papers listed below by McMahon and Alexander). Similarity hypotheses, in general, predict that animal proportions will change with size in systematic, or “similar” ways.

Early in their training, biologists are indoctrinated

to the concept of geometric similarity and its predictions about animal shapes at different sizes. This concept states that, according to geometric principles, as an animal is scaled up or down, its structural surface areas (s) should vary with linear dimensions (l) as $s \propto l^2$, and its structural volumes (and masses) (m) should vary as $m \propto l^3$. Accordingly, structural surface areas and masses/volumes (of the whole body or specific structures) should scale to each other as $s \propto m^{2/3}$ — the famous two-thirds rule.² It follows that geometrically similar animals will have different sizes but similar shapes, and thus are termed isometric (*iso* = same, *metric* = measure). The slope (α) of a plot comparing two linear dimensions in isometric animals will be 1, because changes in the proportions of y are equal to changes in the proportion of x (Equation 3). The slope of a line relating a surface area dimension to a linear dimension in two such animals will be 2, and a line relating a volume (mass) dimension to a linear dimension will have a slope of 3 (on a logarithmic scale).

The two-thirds rule of geometric similarity predicts that as animals are scaled up in size, functions which are dependent on surface areas (e.g., gas and fluid absorption rates, bone strength) will not keep pace with increases in functions that scale proportional to volume or mass (e.g., cellular respiration rates or the forces exerted by the body’s weight). For these very reasons, one might predict that animals generally should not be proportioned geometrically (i.e., isometrically) over a large size range—rather, they should be proportioned allometrically (*allos* = different). Allometric scaling implies that related animals of different size also will have different shapes, or proportions. Changes in shape and proportion (i.e., deviations from geometric proportions) may be interpreted as ways that morphologically similar animals try to maintain adequate levels of performance at dissimilar sizes to compensate for problems that arise from geometric scaling, such as inadequate bone strength, gas absorption rates, etc.. This has led biologists to wonder if animals perhaps scale according to some other principle of similarity—in other words, is animal shape responding to changes in body size in a systematic way other than geometric similarity?

The theory of *static stress similarity* (originally proposed by Galileo) predicts that surface areas should increase as l^3 to keep pace with increases in mass, but this theory has been shown to be a poor predictor of animal shape (Gunther 1975, McMahon 1975a, Schmidt-Nielsen 1984). Today, the leading alternatives to geometric

² Traditionally, theoretical scaling exponents are expressed as fractions and empirically-derived exponents are expressed as decimal values. This convention will be followed throughout the text.

similarity are the theories of *elastic similarity* (Rashevsky 1962, McMahon 1973, 1975a) and *dynamic similarity* (Gunther 1975, Alexander and Jayes 1983, Economos 1983). The most rigorous tests of these competing similarity hypotheses have been conducted on limb bone dimensions in mammals, but their implications have been extended to most other aspects of scaling and allometry (Gunther 1975).

Elastic similarity borrows from engineering principles which state that solid support structures should be proportioned with the ability to dissipate static bending stresses and resist buckling (Rashevsky 1962). Biological elastic similarity theory predicts that animal structures should be scaled to experience similar degrees of elastic deformation during support and locomotion. In plants, the lengths and diameters of trunks and limbs seem to scale well according to properties of elastic similarity (McMahon 1973), and McMahon extends the logic to animal design (McMahon 1975a, 1975b). An important prediction of elastic similarity is that lengths and diameters (such as in a bone) should scale as $l \propto d^{2/3}$ (geometric similarity predicts $l \propto d$), meaning limbs will get proportionately wider as animals are scaled up. Since m must be proportional to $l \cdot d^2$, elastic similarity predicts that $l \propto m^{1/4}$.³

Alexander's and his colleagues have demonstrated a number of inadequacies of the elastic similarity model and they question the premise that animal structures will respond to elastic strain forces in ways similar to plants and I-beams. They also contend that elastic similarity primarily addresses static stresses, and does not adequately account for dynamic forces incurred during locomotion (Alexander 1977, 1985; Maloiy *et al.* 1979). However, McMahon (1975b, 1977) has developed a spring model that extends elastic principles to dynamic systems. Alexander argues that animals should be scaled so that homologous parts on different sized animals experience equivalent net forces (strains) during locomotion and support—that is, they should scale to be “dynamically similar.” Alexander and Jayes (1983) specifically state that under the laws of dynamic similarity the motions of two different sized animals could be made identical by multiplying all linear dimensions by one constant, all time intervals by another constant, and all forces by a third constant. Later I will show how animals which run in dynamically similar ways do so by modifying their range of motion more than their morphology.

Reservations about Scaling Applications

It is not my intention to review or refute the various scaling hypotheses. I bring them up to raise the point that biologists still debate the principles by which size affects shape and function, and because I am skeptical of the *a priori* assumption that animals will follow scaling laws, especially above the species level. Indeed, allometric constants have been measured for numerous morphometric features across a great diversity of animals, yet the data do not unequivocally support one similarity hypothesis over the others. For instance, Alexander (1977), Alexander *et al.* (1979), and Biewener (1982, 1983a) have shown that limb bone length and diameter generally scale geometrically. However, the limb bones of artiodactyls, especially bovids, are an exception and scale better according to predictions of elastic similarity, and some specific bones, especially metapodials and femurs, can be completely aberrant (McMahon 1975b, Alexander 1977a, Alexander *et al.* 1979, Garland 1983). Kinematic parameters related to gait, such as stride frequency and limb excursion angles, also tend to scale according to elastic similarity (Biewener 1983a). However, maximum running speeds in mammals scale to body mass in closest agreement with dynamic similarity (Garland 1983), suggesting that animals do, in fact, run in ways such that homologous parts experience equivalent forces and strains. This will be an important consideration when comparing *Arctodus* to other smaller carnivores because as animals get larger, dynamic forces increase faster than the strength of support structures (bones). I will show that *Arctodus* did not evolve the bone strength necessary to handle the dynamic stresses of high force activities such as acceleration, maneuvering, or running at very high top speeds, all of which are implied directly or indirectly by predatory models for *Arctodus*. This is an important point that I will return to frequently.

Throughout Parts I and II, I will need to refer to theoretical and empirical scaling relationships and the consequences of large size. However, I have a number of reservations about the use of scaling functions and allometry. First, there is a tendency to seek linear equations or simple exponential functions to describe relationships that are complex and which may better fit a polynomial equation (if any equation at all). This has been the case, for example, for the relationship between body size and maximum running speed in mammals (Garland 1983). To some extent, there is a tendency for larger mammals to have higher top speeds, but after attempts by previous authors (e.g., Bakker 1975) to derive a linear allometric relationship between maximum speed and body size, Garland showed what should have been obvious—that maximum running speed is not a simple (single order) linear function of size. Otherwise, the largest animals would also be the fastest. Garland's data show that maximum speed fits a second order

³ If $l \propto d^{2/3}$, then $d \propto l^{3/2}$. Substituting l for d in the equation $m \propto l \cdot d^2$ yields $m \propto l \cdot (l^{3/2})^2$ which is equivalent to $m \propto l^4$. l then becomes proportional to m as $l \propto m^{1/4}$.

polynomial (quadratic) equation and tends to increase with size up to about 119 kg, after which it declines. I will be examining this pattern in detail in subsequent sections because it suggests that there is an upper limit to body size in predators (Garland's data is discussed in more detail later Part I).

Furthermore, using logarithmically transformed data, while necessary for some statistical analyses, can be misleading. This is because the magnitude of residuals is not as apparent in plots of log-transformed data. In such plots, large and biologically significant deviations from a regression line become masked, especially when data are plotted over a large range of body sizes (the effect is seen most in the small-bodied animals in these plots). In fact, that is why a log-log regression often looks like such a good fit to a data set.

Moreover, allometric constants derived for multiple taxa represent *average* slopes, and indicate the way that body proportions or functions *generally* change with body size. They reflect, but they do not indicate, actual values, and averaging values over a wide range of taxa washes individual species allometries. Stated another way, an averaged interspecific allometry may not resemble any of the actual individual allometries it supposedly represents (interspecific allometries are epiphenomena— see Fig. 3f and further discussion below). Still, biologists frequently seek universal principles from interspecific allometric slopes rather than looking for ways that species deviate from these slopes. Yet, this often is where the real biological information lies. For example, allometry has been used to investigate the manner in which muscle mass scales to body mass. In mammals, muscle mass is $\propto m^{1.0}$ (Calder 1984). Emphasis is placed on the meaning of the exponent, 1, and the idea that perhaps a single relationship between muscle mass and body mass can be found among mammals. Yet, this general allometric equation for muscle mass in mammals predicts muscle mass in any given species very poorly. Lions, for instance, have the greatest percentage of muscle mass measured in any mammal— about 62 % (Davis 1962). These types of patterns either are not apparent from allometric data or they are not emphasized as much as the scaling exponent, yet they are very important biologically.

Arguing along these lines, Davis himself (1962:511) remarked, “To me it seems unrealistic to assume a universal growth constant (α) for organs, such as the heart, whose size is directly related to performance. It is possible, of course, to determine a mean value ... but it does not follow that the mean value has any biological significance.” Even Alexander (1985:37) commented, “It seems unprofitable in any case to persist in looking for similarity principles. There is no reason to expect evolution to seek similarity as such. Rather it seeks some

kind of optimality.”

Because of the above reservations, I will be using scaling principles conservatively, and I prefer a loose meaning of the term scaling, whereby I refer to the fact that there are natural dimensional consequences of changes in body size— namely that linear dimensions, surface areas, and volumes (masses) will increase at differing rates, with real functional consequences. As alluded to above, it is the predictive and axiomatic side of scaling that I am dubious about— the notion that animals across broad taxa will respond to body size changes in systematic and predictable ways, and that their evolution is somehow bounded by scaling laws. It seems more reasonable to assume that an animal’s individual shape and proportions evolve not as functions of similarity laws, but as function of selective forces acting on the realities of the animal’s size, in conjunction with its phylogeny and niche.

There is little reason to suspect that scaling rules and similarity laws will supercede selection or that an animal is tied to its allometry. Rather, allometry (or more accurately, proportionality) is like any other character that changes in response to selective pressures, and I believe that the most appropriate use of allometry and scaling are in the *a-posteriori* study of these changes. One may think of it this way: *scaling principles predict some physical ramifications of body size changes, while the study of allometry reveals how animals have or have not dealt with those realities through their evolution.* For instance, Kurtén used allometry in many studies (including Kurtén 1954, 1955, 1967b, 1970; Kurtén and Rausch 1959) to show that certain mammalian lineages have retained similar proportions as body size evolved over short periods of time, but that after long periods of time or in response to large changes in size, proportions changed as species diverged. Kurtén held no preconceived notions about scaling laws, but instead looked at the direct functional reasons for why animals have evolved certain proportions in consideration of body size (he also used allometry to test phylogenetic hypotheses in the fossil record).

Functional Interpretations Using Allometry

With the preceding caveats in mind, I next want to offer some functional interpretations that can be made by comparing allometries between species or subspecies. The ideas in this discussion will not be applied until Part II, where *Arctodus*' limb proportions are compared to other bears using allometric techniques. But since the discussion is theoretical and provides a general review, it is included in Part I.

In any allometric comparison among taxa, one must be clear in distinguishing between two confounding forces acting on the allometry— phylogeny and function.

Both phylogenetic and functional hypotheses can be tested using allometry, but when functional hypotheses are being tested one needs to be clear about the taxa's phylogenetic relationships so their influence can be gauged. However, if the phylogenetic relationships among the taxa in question are unclear, interpretations of function may be dubious. For instance, if two taxa are closely related or of direct ancestry, it is likely that one allometry descended from the other, and any differences in proportions for the structure in question may signify either a functional change or compensatory growth (growth in larger individuals that yields different proportions—usually structures that are more robust—in order to retain function similar to smaller individuals). Alternatively, the allometry and/or proportions of the descendent taxa simply may be an extension of the ancestral allometry without change, in which case it is probable that not enough time has elapsed since speciation for selection to significantly impact body proportions—only body size has changed. If two more distantly related taxa are being compared, then one allometry is not assumed to be descended directly from the other and it can be concluded that any differences are functional and that any similarities in proportions may represent functional convergences.

My concern here is principally about function, not phylogeny. Therefore, I will be comparing not just the slope of allometric lines, but also their implications to actual structural shape and performance (i.e., real proportions). It is important to reiterate that a straight line of allometry on a logarithmic scale does not imply that a structure's shape is held constant over a range of sizes (unless $\alpha = 1$), but rather that its shape is changing with size in a regular fashion, and that this probably has functional implications. In the case of a long bone, if $\alpha > 1$ then the bone grows relatively wider as size increases, if $\alpha < 1$ it grows relatively narrower. Recall from Equation 3 that the slope of log-transformed data also can be conceptualized in terms of the non-transformed data as the conserved ratio of the proportionality of one variable (y) versus the proportionality of the other (x) (Smith 1980) (also note for subsequent discussions that by definition α is both the slope of the log-transformed data and the exponent of the power function derived from untransformed data).

Smith (1980) and Harvey (1982) both have shown that linearity is not always improved by log-transforming data nor does it necessarily produce a better fit to the data. Furthermore, relationships which are linear before log-transformation will remain linear when plotted on a log-log scale. In Part II, I will present allometric data for various bears and depict them on a linear (non-log) scale because their trends are nearly linear without transformation. Correlation coefficients for bone length

vs. width in those data are essentially identical when either linear or power functions are derived. So, while non-transformed data in presented, I will discuss them in terms of α because α is a constant function of proportionality which is independent of scale or units. This is a requisite to test certain biomechanical and evolutionary hypotheses based on proportionality when comparisons are being made between animals of varying size and between different bones. The slopes of untransformed data could not be used for these comparison in most cases because they represent absolute, not relative, proportions and thus are not comparable over wide ranges in size.

Five modes of allometric comparisons are shown in Fig. 3 for the hypothetical relationship between length and width of a structure such as a long bone in two taxa (*a* and *b*), which may be species or subspecies. Figure 3a depicts a simple example of two taxa that differ in body size but have identical α and y -intercepts. This pattern is commonly seen in closely related taxa of recent descent where the change in body size is not great or where the divergence occurred very recently (Kurtén 1967b). As long as $\alpha \neq 1$ then the shape of the bone in taxon *b* will be different than in taxon *a*. Functionally, this means that taxon *b* has made no change to the allometry of this structure in order to compensate for its larger size. Over time, one would expect that natural selection would lead to a compensatory change in allometry which would give taxon *b* similar performance but different shape, as long as the structure's function remained the same. Since this has not occurred in the taxa depicted in 3a, one may conclude that selection has been for a new function or performance level in the structure (especially when the difference in body size is large or when the two taxa are distantly related), or more likely that the two taxa only recently diverged. When the latter can be ruled out by other evidence, then a change in function or performance can be inferred.

Figure 3b depicts two *equal-sized* taxa which have the same α but different y -intercepts. The structure in an individual of taxon *b* will be absolutely wider than in a similar-sized individual of taxon *a*. From a performance standpoint, if the structure is a long bone then it will be stronger but also relatively heavier in *b* than in *a*. The allometries of *a* and *b* are different in this case, but the difference does not compensate for a change in body size, since both taxa are the same size. In other words, the allometry of taxon *b* cannot be explained as a means of retaining similar function and performance as taxon *a*. Instead, one would conclude that selection has favored a more robust limb in *a* vs. *b* for functional reasons. A common form of compensatory growth is shown in Fig 3c. Here two taxa of *different size* have similar α , but different y -intercepts. This strategy has been interpreted

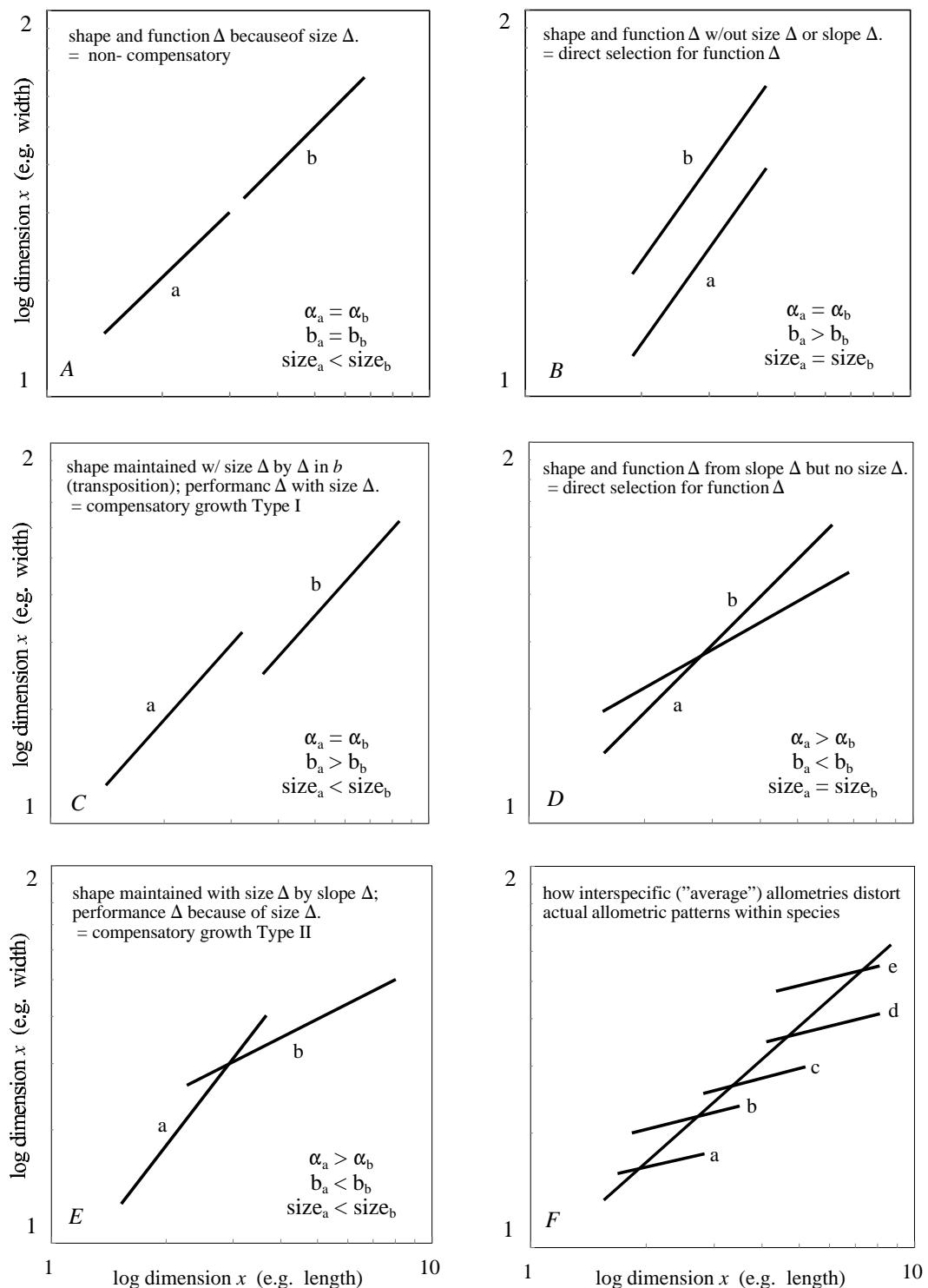


FIGURE 3. Six modes of allometric comparisons for two or more taxa, usually species or subspecies. *F* shows how interspecific, or average, lines of allometry usually yield slopes and y-intercepts that do not reflect the actual values for any given species because interspecific lines simply connect the average allometries for each of the individual species. See text for discussion. (*F* modified from Gould (1971)).

as a means by which large animals retain proportions similar to smaller relatives (Kurtén 1954, Gould 1971). Consider the allometry of taxon *a*. Its α is > 1 , which is typical for long bones, meaning that the structure being measured gets relatively wider (more robust) in larger individuals of taxon *a*. If taxon *a*'s line of allometry were extended to the size range of taxon *b*, the structure's proportions would become increasingly divergent from the norm. Presuming that the shape of the structure is adaptive, this simple extension of line *a* would change the performance of the structure, as discussed for the example in 6*a*. In order for a larger version of taxon *b* to retain a similar (geometric) shape, its allometry needs to be "transposed," as this type of compensation has been termed by Meunier (1959a, 1959b in Gould 1971). Kurtén (1954) also noted this pattern of allometry and its compensatory effect on the dentition of two closely related bears, cave bears and brown bears. However, in subsequent sections I will be reiterating an important point: that *similarity in performance does not arise from similarity in shape, especially over very large ranges of body size*. This is why α values of 1 are uncommon for linear dimensions and why lines of allometry can only be conserved over a narrow range of body sizes—the larger α is, the narrower the size range. Furthermore, even compensatory growth, which maintains similar proportions between taxa, will lead to a change in functional performance because, as will be shown, a geometrically scaled structure does not perform the same in large and small animals.

Figure 3*d* presents a case of two *similar-sized* taxa with *different* α . Because there is no size disparity, the differences in allometry can not be interpreted as compensatory but must reflect a difference in performance or function for the structure. A change in α which may be interpreted as compensatory (for size differences) is depicted in 6*e*. In this case, the structure in taxon *a* may become too wide for practical use if extended to the size range of taxon *b*. As many authors have pointed out (e.g., Kurtén 1967b; Gould 1966, 1971, Schmidt-Nielsen 1984; Calder 1984), this leads to monstrosities. In these cases, compensation is perhaps more a matter of accommodation, rather than a strategy to achieve similar performance. If both taxa are fast running coursers, for instance, and α of taxon *a* > 1 , then the bone is getting relatively heavier with increasing size. Perhaps when reaching the size of taxon *b*, the additional weight becomes considerable, and a change in allometry has evolved to keep the limbs light. This may help taxon *b* to remain swift, but in later sections I will discuss how this implies compromises to other features of the limb, including its strength. So while taxon *b* compensates to retain certain kinematic advantages, it will need to curtail other activities relative to taxon *a*, such as making sharp

turns, accelerating rapidly, or even running at slower speeds (see Sections 7 - 10).

All of the above conclusions apply strictly to allometries constructed for individual species or subspecies, not those constructed for multiple species. Such interspecific lines of allometry, or "average" allometry, do not accurately quantify the way that shape changes with size in any of the taxa or individuals involved. Rather, interspecific allometries are epiphenomena, even when closely related taxa are involved, such as within a single genus. This is because allometries are inherited, therefore are shared only at the level of species and below (Gould 1971). Figure 3*f* demonstrates why this is so. There it can be seen how interspecific slopes essentially connect the median points of individual species allometries. So within a species or subspecies, one may calculate the genetically-determined ratio of proportionality (allometry), but, as Fig. 3*f* shows, even if a straight line of regression can be drawn through multiple species, this line does not accurately match the ratio of proportionality in any of the individual species. As discussed above, this is because animals evolve differences in allometry (i.e., transpositions, changes in α) which reflect the way that functional needs change with size.

The discussions in this section were intended to provide a sense for the way that scaling principles and allometry are used to investigate the functional effects of changes in body size and body proportions. What follows is a review of some specific body size-dependent factors of locomotion, including the effects of scaling on energetics, the ability of muscles to generate force, and the structural limitations of bones.

6. ENERGETICS, METABOLISM, AND THE COST OF LOCOMOTION

There are various ways to look at energy expenditures during locomotion and to account for the costs of transport. On one level, biologists speak of the amount of energy consumed (total, rate, or instantaneous) during locomotion, which physiologists often measure as the amount of oxygen consumed by an animal. At another level, biologists speak of the mechanics of locomotion, that is, the exchange of metabolic energy for mechanical work as performed by an animal's muscles. The ratio of these two—metabolic energy input versus work output>equals muscular efficiency. In this section I will be discussing whole body energetics, both in terms of metabolic inputs and work outputs, and I will review the mechanics of this energy conversion. I will show that the efficiency by which animals convert energy to work varies regularly with size. In the subsequent two sections I look specifically at the way muscles generate force for

locomotion and how the skeletal system deals with these forces, especially as animals get larger.

Setting the Stage

Hill (1950) set down a series of classic hypotheses regarding locomotor costs and body size based on dimensional analyses (scaling). Many of Hill's ideas still form the premises being tested in modern experiments on animal locomotion, so they are worth repeating. Starting with the assumption that the properties of individual muscle fibers do not vary among taxa or animals of different size, Hill used geometric scaling principles to predict that all animals, regardless of size, should be capable of achieving the same absolute levels of performance for certain locomotor skills. Specifically, Hill predicted that all animals should theoretically be able to achieve the same absolute top speeds and jump to the same absolute heights, but the muscles of small animals should consume energy faster and perform work at higher rates than large animals. This latter prediction indicates that smaller animals should fatigue more quickly and after covering shorter distances. Taylor *et al.* (1982 pp. 2) summarized Hill's logic as follows: "each gram of muscle performs the same amount of work and uses the same amount of energy during a step, but the small animals have to take many more steps to cover the same distance because of their shorter legs. Therefore, when running at the same speed small animals should have higher stride frequencies and consume energy at higher rates." I will

discuss how modern analyses have shown Hill to be wrong on a few of these points and correct on others, but often for the wrong reasons.

The Cost of Transport

Locomotor physiologists have established that the mass-specific rate of energy consumption increases with speed but that the rate of increase is inversely proportional to body size (Fig. 4)(Schmidt-Nielsen 1972; Taylor *et al.* 1970, 1982; Taylor 1977; Kram and Taylor 1990). Data from those studies also show that the "incremental cost of transport"—the amount of energy consumed while moving a unit of body mass a given distance—decreases as body size increases. The incremental cost of transport scales $\propto m^{-0.40}$ according to Taylor *et al.* (1970), $\propto m^{-0.316}$ according to Taylor *et al* (1982), and $\propto m^{-0.25}$ according to Kram and Taylor (1990) (Fig. 4a).

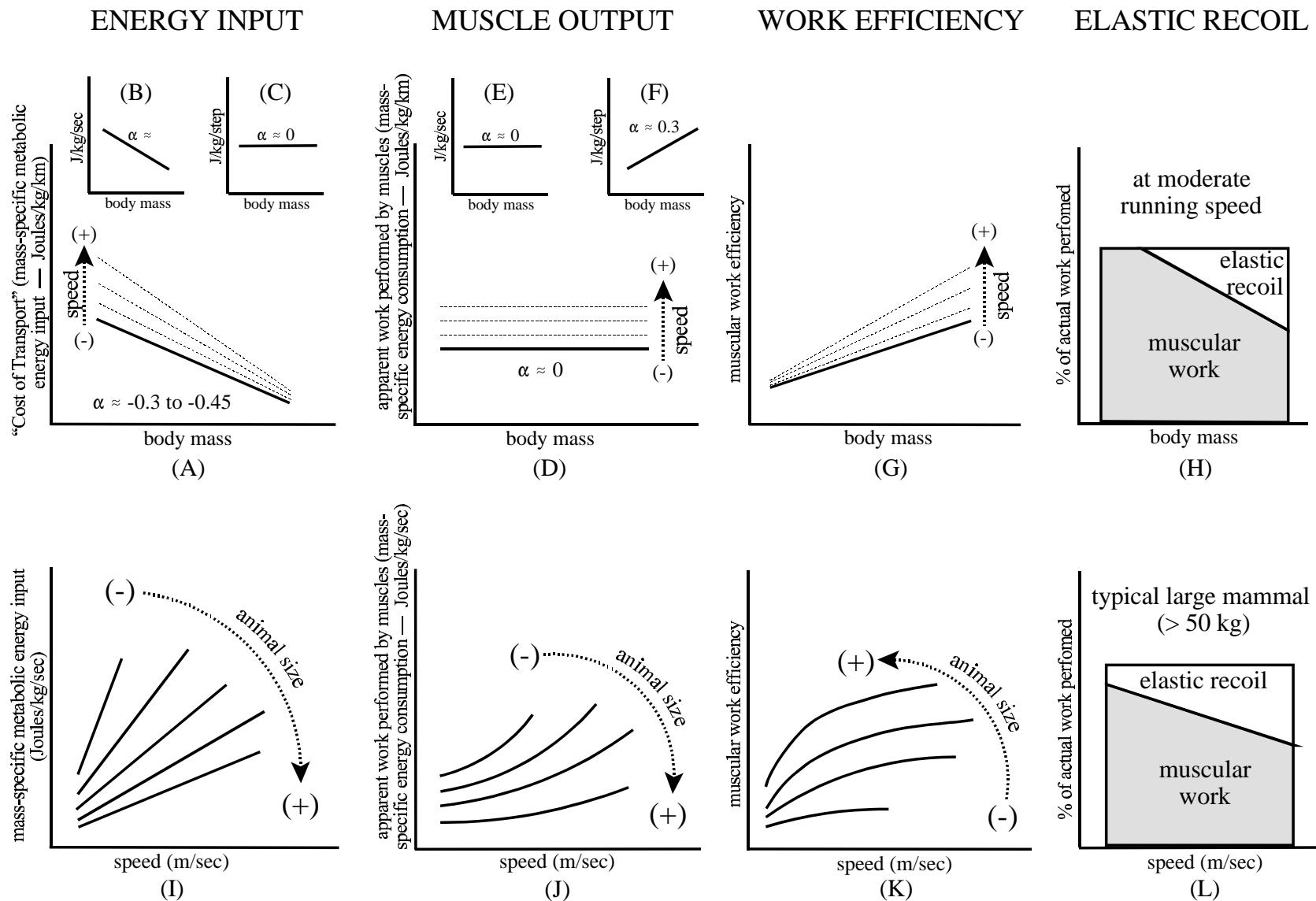
The incremental cost of transport must be distinguished from the "cost coefficient" of locomotion, which is a constant and equals the rate of energy consumption by each kilogram of body mass during steady state locomotion, independent of distance traveled. This value is mass independent ($\propto m^0$) so it is the same for animals of all size (Fig. 4c) (Taylor *et al.* 1982, Kram and Taylor 1990). Therefore, while animals expend about the same amount of energy per kilogram per step at physiologically equivalent speeds, small animals take more steps to cover a given distance. Physiologically

Figure 4. Patterns of energy input and work output during locomotion showing how energetic efficiency increases with body size and with speed in larger mammals, due to their increased ability to recoil elastic strain energy stored in leg tendons.

Body Mass (top row): The energy expended to move one kg of body mass over 1 km (cost of transport) decreases in larger animals (A). While smaller animals spend energy at a faster rate (per kg) (B), all animals spend about the same amount of energy per kg per step (C)—smaller animals simply need to take more steps to move 1 km, and thus spend more energy doing so. However, the mass-specific work performed by the muscles to move 1 km does not increase with size (D), meaning that work efficiency (work performed : energy input) increases with body size (Values in G are per km efficiency derived as the ratio of D : A. Similar patterns arise from comparing E : B and F : C for work performed per second and per step respectively). But actual performance of muscle fibers does not vary among mammals and the increased efficiency of larger mammals arises because they are able to store and recoil more elastic strain energy. H shows how the smallest mammals recover almost no elastic energy even when running, while this energy may account for nearly 50 % of the work performed in very large animals.

Speed (bottom row): Mass-specific rates of total metabolic energy consumption increase linearly with speed, but at slower rates in larger mammals (I), but the energy used by the muscles to perform work increases curvilinearly and at slower overall rates in larger mammals (J). Thus, work efficiency also increases with speed (K) because the amount of kinetic energy stored and recovered as elastic strain energy increases with speed. This effect is amplified as animals get larger, as depicted in L for a typical large cursor (this pattern also is apparent from the dotted lines in upper graphs). (Data compiled mostly from Taylor *et al.* (1970, 1982) and Heglund *et al.* (1982b). α = slope; scales are logarithmic)

Large size and speed increase locomotor efficiency because both increase vertical ground forces imparted to the limbs—these are the forces that stretch leg tendons and become available as stored elastic strain energy. Large size (or long legs) also increases the potential use of elastic strain energy because a tendon's ability to stretch is dependent on its length, which generally increases with body size. These patterns of energetic efficiency mean that *Arctodus*' large size and elongated legs allowed it to recover considerable elastic strain energy during locomotion, even at low speeds. For reasons discussed in the text, *Arctodus* probably rarely ran at high speeds, so its limb morphology strongly suggests that it had evolved for super-efficient moderate speed travel.



equivalent speeds are speeds at which equivalent locomotor events occur in different animals, such as changing from a trot to a gallop or running at top speed—these do not occur at the same absolute speeds for all animals, but the events are considered to be a physiologically equivalent (Heglund *et al.* 1974). Often it is most meaningful to compare the energetics and stride traits of different sized animals at physiologically equivalent speeds, rather than absolute speed.

Kleiber's (1961) well-known comparison of basal metabolic rate (M_b) and body size also shows a negative scaling relationship (mass specific $M_b \propto m^{-0.25}$; whole body $M_b \propto m^{0.75}$), so it is not surprising that a similar relationship holds for locomotor metabolism. This relationship should not be taken to mean that large animals are metabolically more efficient than small animals. First of all, as Calder (1984) pointed out, efficiency is a dimensionless term that implies a ratio of input versus output; comparing just mass-specific energy inputs (which is what metabolic measurements do) says nothing about outputs. But probably more important, comparing energy consumption between large and small animals potentially leads to the pitfall of doing so without regard for the way that physiological time, space, and rates scale to body size (Calder 1984, Lindstedt and Swain 1988). For instance, while larger animals consume less energy *per kilogram* per kilometer during a given activity, they invariably perform that activity for a longer time, over a greater distance, and over a longer lifetime—and they have more kilograms to move.

It turns out that over the course of their lives, large and small animals spend about the same amount of energy to support a unit of body mass, regardless of size (Calder 1984). This does not mean that large animals do not incur certain benefits for their size. Indeed, they are able to take advantage of a larger home range and its greater spatial diversity, and large animals can more readily make large scale migrations (Lindstedt and Swain 1988). Reciprocal arguments can be made for the advantages/disadvantages of being small. It is important to emphasize that these statements only hold true for metabolic input, not work output. Later I will discuss how large and small animals differ considerably in their inherent abilities to engage in certain locomotor activities simply due to their size, and that large animals are more efficient locomotors because they are better able to utilize elastic strain energy.

Mechanics of Walking and Running

Next, I turn to the mechanisms by which metabolic energy is converted into work during locomotion. As an animal walks or runs, energy is expended to accelerate and decelerate different parts of the body relative to each other and relative to the ground. In this regard, energy is used primarily for two tasks: 1) lifting and accelerating

the body's mass against the vertical forces of gravity (since the body's mass rises and falls with each stride), and 2) accelerating/decelerating the limbs relative to the body's center of mass (Manter 1938; Cavagna *et al.* 1964, 1977a, 1977b; Alexander 1977b; Heglund *et al.* 1982a). The energy expended to lift the body's mass seems to account for most of the energy expended during locomotion, although there is some disagreement in the literature regarding the relative importance of these two expenditures (Taylor *et al.* 1980). For instance, Manter (1938) trained cats to run over force plates and found that the energetic component of moving the limbs varied from almost 0 to > 25 % of total energy expended, the most important factor being the animal's speed and rate of acceleration. Using similar apparatus but more species, Cavagna's group and others have concluded that the cost of lifting the body's mass can be over 10 times the cost of swinging the limbs (Cavagna 1977a, Taylor *et al.* 1980, Farley and Taylor 1991). In a four-part study, Heglund, Taylor, Cavagna, Fedak, and Maloiy attempted to account for the costs of locomotion in 15 homeotherms by simultaneously measuring the metabolic energy consumed during locomotion, the work performed to lift the body's mass, and the work performed to swing the limbs (Taylor *et al.* 1982; Fedak *et al.* 1982; Heglund *et al.* 1982a, 1982b). They found that swinging the limbs may account for as little as 3 % or as much as 30 % of the applied forces, and like Manter's data, the most important determinant was speed (they did not test acceleration). Theoretical calculations by Alexander *et al.* (1980) also show that the cost of moving the limbs can be fairly high. Anatomists (e.g., Smith and Savage 1956, Hildebrand 1985a, 1985b, 1995) tend to emphasize the cost of accelerating/decelerating the limbs, not necessarily to discount other costs, but more to show the relative costs of limb oscillation between animals of different builds. I will return to these points in the section on kinematics, where it will be shown why the cost of swinging the limbs increases with speed.

Walking: When an animal uses a walking gait, its center of mass rises and falls, during which kinetic energy (E_k) is exchanged for gravitational potential energy (E_p). As the animal lifts its mass, E_p increases and E_k decreases, by which they are said to be out of phase. When the body mass falls again, E_p decreases and E_k increases. The process of walking depends on capturing this E_k as forward momentum by leaning the body's mass forward. Up to 70% of the E_p may be recovered in this way (Manter 1938; Cavagna *et al.* 1964, 1977a; Heglund *et al.* 1982a). These mechanics are analogous to the exchange of E_k and E_p in a pendulum or rolling an egg end over end; when an animal walks it only performs work to “keep the egg rolling” (analogy of Cavagna *et al.* 1977a, pp. 260). Later I will show that there is an optimal

walking speed for this energy exchange and that it increases with leg length, which partially explains why long-legged animals naturally walk at higher speeds but with slower stride rates.

Trotting and Pacing: Running is energetically and mechanically quite different than walking. When an animal runs using a *trot* or a *pace* there is almost no transfer between E_k and E_p because both rise and fall in phase. That is, when the body mass is lifted, E_p rises but so does E_k . This occurs because E_k is converted to elastic strain energy in tendons of the leg during each footfall and is recovered again at the end of each footfall when the body mass is lifted. Both E_p and E_k are highest at the body mass's highest point, and both fall as the body falls (E_k falls because all of the elastic strain energy has been consumed). Because of this stored elastic energy, the running trot and pace are analogous to a spring or a bouncing ball, not a pendulum (Cavagna *et al.* 1977a, 1977b).

Galloping: The running trot and pace rely heavily on a spring-like mechanism and recovery of elastic strain energy, but when a running animal changes from a trot or pace to a gallop it utilizes both pendulum and spring mechanisms. The shift in energy phases at the trot-gallop transition is a result of the acceleration process when an animal changes from a steady state trot or pace to higher galloping speeds. The exchange between E_p and E_k during this transition is used to elevate the animal's body mass even higher and to increase forward velocity—therefore, there is a bounce and a lift. As the animal increases speed, E_k and E_p become more in phase (they rise and fall together) and purely spring dynamics take over again, whereby elastic strain energy is used to perform much of the work. But whereas the steady state running trot and pace are analogous to a single spring, the steady state gallop works like two springs because the front and hind limbs function as independent pairs with two bounces (energetic cycles) per stride.

Locomotor Efficiency and the Role of Stored Elastic Strain Energy—Advantages of Being Big

I now have examined some of the metabolic requirements of locomotion in regards to mass and speed, as well as the general way that energy is used by animals to propel their mass. Next, I want to look at the efficiency by which muscles convert energy into work. Throughout this and subsequent sections I will rely on the well established fact that individual mammalian muscle fibers have essentially identical performance properties in all species (Hill 1950; Alexander 1973, 1977b; Cavagna *et al.* 1964, 1977b; Heglund and Cavagna 1985).

Typical striated muscle fibers are capable of converting metabolic energy into usable work at about 25% efficiency; the balance is lost as heat (Heglund and

Cavagna 1985). But when energy consumption and amount of work performed are measured in running animals, muscular efficiency appears to increase as body size and speed increase, and exceeds 25% (Fig. 4) (Taylor *et al.* 1982, Heglund *et al.* 1982b). Those authors show that the mass-specific energy consumption *per kilometer* decreases with size for animals running at equivalent speeds, whereas the mass specific rate of work performed *per kilometer* is independent of body size (Fig. 4*a* and *b*). Looking at these relationships on a *per step* basis, rather than per kilometer, it is apparent that mass-specific energy consumption is independent of body size and that mass-specific work performed increases with body size (Fig. 4*c* and *d*). The resulting ratio of work:energy can be as high as 73 % in larger animals and as low as 7 % in smaller animals. Energy input also increases linearly with speed, but at a faster rate in larger animals, while work output increases curvilinearly with speed, but at a slower rate in small animals (Fig. 4*e*, *f*) (Taylor *et al.* 1982, Heglund *et al.* 1982b). Therefore, animals seem to use energy more efficiently at higher speeds and when they are bigger (Fig. 4*g* and *h*). If all muscles perform the same, how can this be so?

The explanation lies in the differing abilities of animals to store and recover elastic strain energy using tendons of the limbs—there is no intrinsic difference in muscle performance. The importance of elastic strain energy in the energetics of locomotion is becoming increasingly apparent, but evidently it only can be effectively used by large animals and/or at higher speeds, thus explaining the body size patterns observed in Fig. 4 (elastic energy also is important for hopping animals) (Cavagna *et al.* 1964, 1977a; Biewener *et al.* 1981; Alexander *et al.* 1982; Alexander and Bennet-Clark 1977; Alexander 1988, 1989; Heglund *et al.* 1982b; Heglund and Cavagna 1985; Bennett and Taylor 1995). The amount of energy stored in a tendon is a function of the distance stretched, and since tendons stretch as a percentage

of their length, long tendons store more energy. It takes fairly high forces to stretch a tendon, such as the forces generated at high speeds. But higher force also can be generated by increasing mechanical advantage to the tendon or by increasing the applied mass.

For these reasons, elastic storage can be used by large animals even at modest speeds, whereas medium-size mammals only store elastic energy while running at high speeds. The camel stores a considerable amount of elastic energy even at moderate speeds because it has super-long tendons with high mechanical advantage, which are stretched simply by the animal's weight and minimal dynamic forces (conclusion extrapolated from data in Alexander *et al.* 1982). This is an important point, because it shows how very large mammals with long legs

are optimized to store elastic strain energy even at lower speeds. Apparently, the tendons of small animals are too stiff and too short to store significant amounts of elastic strain energy and small animals generate less absolute force during locomotion. Also, in order to store elastic energy, tendons must comprise a considerable percentage of the muscle/tendon length (Alexander 1992). In small mammals, most of this length is comprised of muscle (Alexander *et al.* 1981, 1982; Biewener *et al.* 1981).

Tests on *in vitro* tendons show they can return up to 93% of stored energy as elastic recoil, while only 7% is lost as heat (Ker 1981). In running animals of moderate size, up to ~ 50% of the work performed during each stride can be derived from elastic recoil of energy stored in tendons, but average recovery is more like 35% (Cavagna 1964, 1977a; Alexander and Bennet-Clark 1977; Ker 1981; Alexander *et al.* 1982; Heglund *et al.* 1982b; Taylor 1985). Thus, it is likely that the disparity between work efficiencies in large and small animals described earlier (Fig. 4) can be largely attributed to their differing abilities to store elastic strain energy. However, Heglund *et al.* (1982b) suggest another compelling reason for the difference: because small animals take more steps at a given speed, they must generate forces for locomotion at higher rates and consequently they have a higher percentage of fast-twitch muscle fibers. Fast-contracting muscles generate force at reduced efficiency, perhaps explaining some of the reduced work efficiency of small animals.

McMahon (1975b, 1977, 1985) developed a theory to describe animal locomotion based on the mechanics of spring models and stored elastic energy. He proposed that most of the actual energy consumed by muscles at steady state running speeds does not result in muscle shortening (technically, no work is performed), but rather is used isometrically to keep the springs (tendons) under tension. Under this theory, a high percentage of the energy exchanged during steady state locomotion is mediated through spring oscillations. Furthermore, the theory

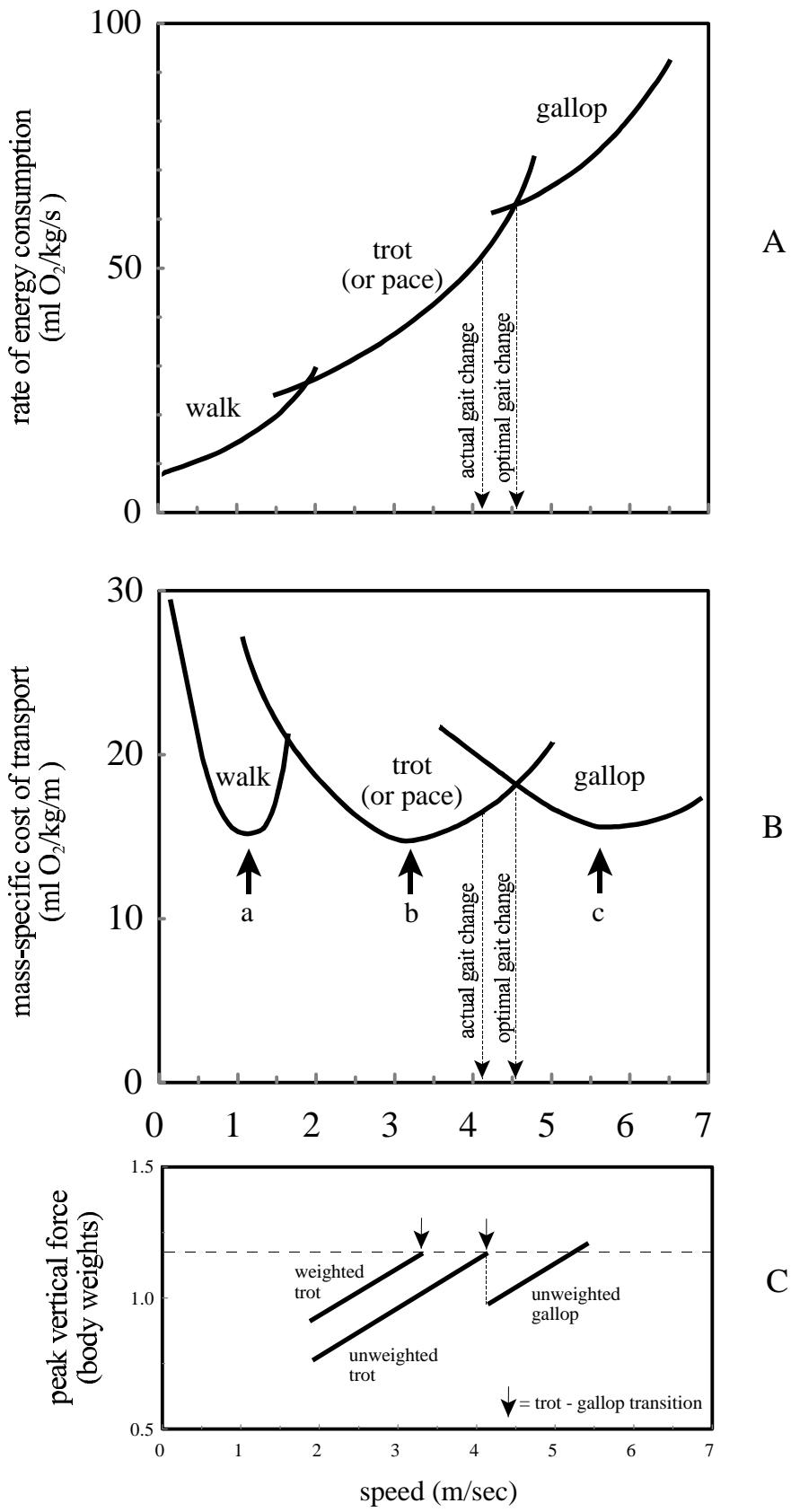
predicts that animal limbs, like springs, should oscillate at natural harmonic frequencies that depend on size, which will dictate optimal steady state speeds for each gait (natural speeds, not maximum speeds). In fact, Taylor (1985) showed that for any given gait, there is an optimal speed (limb frequency) that maximizes the amount of recovered elastic strain energy. If an animal runs below that frequency (too slow), the strain dissipates as heat; if it travels above that frequency (too fast) there is not enough time for the tendon to stretch or for the foot to apply the tendon's force. This is another reason why small animals are not able to utilize much elastic strain energy—because they naturally have greater stride rates and thus swing their limbs at higher frequencies. McMahon's spring model is consistent with the findings of Taylor *et al.* (1980), who showed that a great deal of energy consumed by muscles is used isometrically and during muscle stretch to control motion at the joints and to maintain posture.

Optimal Speeds Within a Gait and the Effect of Limb Length—Reconsidering the Cost of Transport

Hoyt and Taylor (1981) measured oxygen consumption in horses that were trained to extend their gaits (walk, trot, gallop) to speeds above and below those normally used within each gait (Fig. 5). Through this manipulation they were able to show that energy consumption increases curvilinearly with speed for each gait, and that horses change gait where these lines intersect (Fig. 5a). Furthermore, there is an optimal speed for each gait which minimizes the energy expended to move a given distance. When allowed to move at natural speeds, the animals chose these optimal speeds with little variance (Fig. 5b). Pennycuick (1975) also observed that wild African bovids choose a very narrow range of speeds within a gait. Hoyt and Taylor's data further show that the minimum cost to move a given distance is the same for a walk, trot, or gallop—that is, cost of travel (per km) is independent of speed. Later, Kram and Taylor (1990)

Figure 5. Patterns of energy use and force application across gait transitions in large mammals. A and B are modified from Hoyt and Taylor (1981) who measured energy consumption in small horses (\bar{x} mass = 140 kg) that were trained to extend their gaits beyond normal speeds. Rates of energy expenditure increase curvilinearly with speed within each gait (A), but when animals are allowed to choose their own steady state speeds they use speeds that are energetically optimal for each gait (points *a*, *b*, and *c* for walking, trotting, and galloping in B). Also note from B that the cost of moving a given distance (the mass-specific cost of transport) is essentially independent of speed or gait at these optimal points (only rate of energy consumption varies). Since gait transitions occur below optimal speeds (where lines cross) they must not be triggered directly by energetics. C depicts Farley and Taylor's (1991) data on horses that ran carrying extra weights, showing that gait transitions seem to be triggered when critical levels of vertical ground force (limb stress) are reached, since animals carrying extra weight changed gaits at lower speeds.

Curves in A and B shift to the right with increasing body size, so larger animals will naturally walk, trot (or pace), or gallop at higher speeds. However, top galloping speeds appear to be limited by critical levels of limb stress, as in C. The dynamic forces of locomotion increase with body size at a faster rate than animals can increase skeletal strength, so critical force levels are reached at lower speeds in very large animals (also see Fig. 7).



reasoned that this is because the cost of transport is inversely proportional to step length, and while an animal may expend energy faster at higher speeds, the increased efficiency of longer strides at higher speeds balances this out, yielding no net change in the cost of transport.

Kram and Taylor (1990) revealed another important pattern relating limb length to the cost of transport. Consider the fact that as running animals increase speed, their feet contact the ground for a shorter percentage of the stride (i.e., there is a longer aerial phase), yet the magnitude of vertical ground forces increases. Since the feet have less time to distribute these forces at higher speeds, the mass-specific rate and magnitude of force application to the limbs naturally increases with speed (Cavagna *et al.* 1977a, 1977b). Kram and Taylor (1990) showed that the mass-specific rate of energy consumption is inversely proportional to the mass-specific rate of force application, i.e., energy is saved by applying force more slowly. This means that animals which spread the forces of locomotion over a greater time spend less energy on locomotion. Now consider the following relationship:

$$V_g = L_c / t_c \quad (5)$$

where V_g is ground speed, L_c is step length, and t_c is the time each foot spends on the ground. Since step length is directly related to leg length, it is apparent that, at any given speed, long legs will be in contact with the ground for longer periods than short legs. As step length (i.e., leg length) increases, the time course of force application increases and the cost of transport goes down proportionately. (Later I will show that this pattern arises because muscles use energy more efficiently when they contract more slowly—that is, when their force is applied over a longer period of time.) Larger animals have relatively longer legs and take longer strides, and their step length increases like other linear dimensions, roughly proportional to $m^{0.3}$ (Kram and Taylor 1990). Because larger animals have longer legs, this helps explain why they have a lower cost of transport (per kg) and why this cost can be reduced in any animal just by increasing leg length. Furthermore, since smaller animals run at higher stride rates and take more steps per kilometer, they consume energy faster at all speeds. These are important relationships that I will return to repeatedly, as they clearly have implication for locomotor adaptations for short-faced bears.

As I move into the next sections, I will be discussing locomotion less from the viewpoint of physiologists and more from the viewpoint of morphologists. There are a couple of reasons for this. First, most physiological studies measure locomotor energetics on animals in steady state locomotion—that is, animals traveling at constant speeds (no acceleration

or deceleration), constant direction (no turning), and for short periods (no fatigue). These conditions are not typical for wild animals, especially carnivores, so the data is not always relevant in terms of evaluating real-world performance limits. In particular, these studies reveal little about the mechanics of acceleration and anaerobic contributions to locomotion—two important issues for an animal suspected of being a predator.

Furthermore, data from locomotor physiologists explain some of the energetic advantages and disadvantageous of animal size, but they have done a poor job explaining the finer details of limb design, and in particular, how animals built for long distance running differ from those built for sprinting (for instance, see Taylor *et al.* (1974), whose data show that the cost of running is the same in a cheetah, gazelle, and goat). The next three sections address these types of questions. First I examine the way muscles generate force and bones dissipate these forces, and how such variables depend on body size and limb configuration. Then I evaluate limbs as lever systems and discuss the concepts of mechanical advantage and high gear/low gear muscles. The final section is a discussion of kinematics and the way that mass distribution affects the performance of limbs.

7. SCALING OF MUSCLE FORCE

The performance of individual muscle fibers remains essentially constant across mammalian taxa. However, in order to understand the specific ways that locomotor performance is impacted by relative body size and limb morphology, it is important to consider how size influences a muscle's capacity to generate *force*, *power*, and *work*.

Force: The force generated by a whole muscle is a function of the number of fibers contracting, which is proportional to a muscle's cross-sectional area (Hill 1950; Alexander 1977a, 1992). Regardless of the scaling scheme, area functions are predicted to increase with body size at a slower rate than mass or volume functions (e.g., area $\propto m^{2/3}$ under geometric scaling). Therefore, one might expect that, as animals get larger, they will have increasing difficulty generating the forces necessary to move their own masses. It turns out that cross-sectional area and force generation in limb muscles scale around $m^{0.8}$, not $m^{2/3}$ (Alexander *et al.* 1981), and for reasons I discuss later, locomotion in large animals is not limited by their ability to generate adequate force.

Work: The work ($W = F \cdot d$) performed by a muscle equals its force output (cross-sectional area) times its shortening distance, which is about one third of its total length (Hill 1950). This calculation (cross-sectional area \times length) makes work output a function of muscle volume, and thus isometric with body mass (work $\propto m^{1.0}$)

(Alexander 1977a). Therefore, work output is predicted to keep pace with changes in body size. Previously I mentioned that muscle fibers generally convert metabolic energy into mechanical work at about 25% efficiency, but that recorded efficiencies are much higher in larger animals and running animals. I also showed that this “extra work” is performed by elastic strain energy stored in tendons, which can theoretically return up to 93% of stored strain energy to perform work (Ker 1981). While total work performed indicates something about energetics and metabolic efficiencies, it is not always a very useful way to judge locomotor performance because it is not time specific—that is, when an animal moves a given mass over a given distance the amount of work performed is the same, whether it takes a minute or a day.

Power: To evaluate features such as speed and acceleration, it is more useful to think in terms of the rate that work is performed or the velocity of force application—this is *power* (P):

$$P = W/t = F \cdot v \quad (6)$$

where W is work, t is time, F is force, and v is velocity. Power is a function of the velocity that a muscle contracts in relation to the amount of work being done. For comparison, a muscle’s strength is measured by its capacity for work, but power is a measure of how fast it does that work—strength does not equal power. Powerful muscles are energetically inefficient because muscles consume energy at a rate that is directly proportional to the forces they exert (Taylor *et al.* 1980) and because fast muscles use energy at disproportionately high rates (i.e., they are less economical) (Alexander 1973, 1992). But fast muscles also produce less force and empirical data show that muscle economy is almost doubled by cutting the speed of contraction in half (Huxley 1974, Heglund and Cavagna 1985, Alexander 1992).

Histologically, fast muscles are less efficient because actin-myosin crossbridges dissociate more rapidly, before each has completed a full shortening cycle. Also, crossbridges form and dissociate so quickly that they do not always pull in unison—some may be shortening the filament while others have not released, and so are resisting shortening (Close 1972, Heglund *et al.* 1982b, Alexander 1992). This also explains why fast-contracting muscles generate less force, and why slower, longer muscles are more energy-efficient and generate higher forces (but more slowly—i.e., with less power). The rate of muscle contraction also is inversely proportional to muscle length, so long muscles inherently contract more slowly, generating more force but less power than short muscles. This is because long muscles have more filaments shortening simultaneously, and

crossbridges do not need to form and dissociate as frequently as in short muscles while generating equivalent forces. There also is evidence that pumping Ca^+ across cell membranes (the trigger for a muscle twitch) may consume up to 30% of the energy used by muscles (Homsher *et al.* 1972). Since this trigger fires more frequently in fast muscles, it increases their rate of energy consumption. Therefore, powerful muscles must be both fast (short) and strong (large cross-sectional area). Later, I will show that the power imparted to a limb by a muscle also depends on the limb’s mechanical advantage.

The power output of a muscle depends on muscle size and speed of contraction, but ultimately it depends on muscle loading, which varies considerably among animals of different builds. Muscle loading is equivalent in magnitude to the tensile forces resisting a muscle during contraction. Therefore, it is a function of the mass being moved relative to the force exerted and the muscle’s mechanical advantage (mechanical advantage is explained in the next section). Heavily loaded muscles require more force to contract, but in order to generate these forces they naturally contract more slowly, which reduces power. Later I will discuss how this is the type of muscle found in the limbs of animals such as tortoises and fossorial mammals (diggers). Those animals have heavily loaded limbs that do a lot of work, but slowly. Thus, they are strong—but not powerful—animals. Animals that rely on acceleration have powerful limb muscles, because they need to bring their limbs up to maximum velocity as quickly as possible. Therefore, the muscles of a good accelerator should have reduced loading, while muscle force, size, and mechanical advantage should be maximized. This formula predicts a certain build in good accelerators: muscle mass should scale positively with body mass, and muscles should be wide (to generate high force) but short (for quick contractions). The remainder of this section on muscles uses published data to test each of these predictions.

Muscle Mass: If mammalian muscles scale geometrically, one would expect muscle mass to increase $\propto m^{1.0}$. In fact, the empirical value is very near this when all mammalian taxa are averaged (Alexander *et al.* 1981, Calder 1984). Using the information above, we would predict that powerfully-built mammals should deviate from this average. Alexander *et al.* (1981) measured the mass, length, and cross-sectional area of limb muscles in relation to body mass in numerous mammals. Unfortunately these authors pooled their data into a few broad groups based on taxa, not locomotor style. For instance, they combined data for all Carnivora, including diverse forms ranging from ferrets and mongooses to lions and hyenas. However, their data still show that muscle mass in carnivores scales higher than other mammals for almost all muscles measured (Table 1). The

TABLE 1. Scaling dimensions in mammalian limb muscles. All values are scaling exponents (α) derived from the allometric equation $y = bm^\alpha$, where m is body mass. Mass and length data (first two columns) from Alexander *et al.* (1981), last two columns calculated using those authors' data.¹

muscle group	exponent of muscle mass	exponent of muscle fiber length	exponent of muscle cross-sectional area (mass ÷ length)	bulkiness index (S.A. ÷ length)
Adductor & Hamstrings				
primates	1.06	0.26	0.80	0.54
carnivores	1.18	0.37	0.81	0.44
bovids	0.97	0.19	0.78	0.59
others	1.10	0.27	0.83	0.56
Quadriceps				
primates	0.99	0.39	0.60	0.21
carnivores	1.16	0.42	0.74	0.32
bovids	0.94	0.25	0.69	0.44
others	1.08	0.32	0.76	0.44
Ankle Extensors				
primates	1.12	0.30	0.82	0.52
carnivores	1.02	0.16	0.86	0.70
bovids	0.97	0.23	0.74	0.51
others	0.97	0.14	0.83	0.69
Deep Hind Flexors				
primates	0.76	0.16	0.60	0.44
carnivores	1.03	0.24	0.79	0.55
bovids	1.03	0.18	0.85	0.67
others	1.01	0.20	0.81	0.61
Triceps				
primates	1.27	0.36	0.91	0.55
carnivores	1.23	0.33	0.90	0.57
bovids	1.10	0.30	0.80	0.50
others	1.11	0.33	0.78	0.45
Fore Flexors				
primates	1.19	0.38	0.81	0.43
carnivores	1.11	0.24	0.87	0.63
bovids	1.09	0.33	0.76	0.43
others	1.04	0.18	0.86	0.68

¹ All values are exponents so division is by subtraction

scaling factor for carnivores varies by muscle and is between $m^{1.02}$ and $m^{1.23}$, with an average of $m^{1.12}$. Averages for bovids and primates are $m^{1.02}$ and $m^{1.07}$, respectively. Calder (1984) compared actual muscle mass in mammals versus values predicted by general allometric equations. He showed that in dogs (the only carnivore he analyzed) actual muscle mass is 1.24 times greater than the predicted value. Values for horse (*Equus caballus*), deer (*Odocoileus virginianus*), and wapiti (*Cervus elaphus*) are 1.14, 1.00, and 0.98 respectively. Davis (1962) measured muscle mass in lions and found it to constitute up to 62.5% of body mass—the highest amongst mammals. The average range for mammals is about 44 - 50% (Pitts and Bullard 1968, Munro 1969, Calder 1984). Values for other felids are between 56 - 59% (Munro 1969, Calder 1984). Thus, we can conclude that powerfully-built mammals have above-average muscle mass.

Muscle Force: Under predictions of geometric scaling, muscle force should increase with body size as a function of muscle cross-sectional area, or $m^{2/3}$. However, Alexander's (Alexander *et al.* 1981, Alexander 1985) empirical data on muscle cross-sectional area indicate that muscle forces scale more like $m^{0.8}$. Alexander arrived at this value for cross-sectional area by measuring muscle mass ($m^{1.1}$) and fiber length ($m^{0.3}$) in numerous mammals, and dividing the former by the latter ($m^{0.11} \div m^{0.3} = m^{0.8}$). These values are for proximal limb muscles, but values for distal muscles are similar. The authors also suggest that the actual scaling of muscle may be closer to $m^{0.9}$. This value, although higher than predicted by geometric scaling theory, is not surprising, since 2/3 scaling would cause muscle force to lag well behind the mass it must move. One might conclude that even $m^{0.8}$ (or $m^{0.9}$) scaling means that muscle force is not keeping pace with body mass, but consider the following: Alexander *et al.* (1981) calculated that if limb muscles generate maximum forces proportional to $m^{0.8}$, but their moment arms scale as $m^{0.4}$ (moment arms are discussed in section 7), then the maximum bending forces generated by these muscles will be $m^{0.8} \times m^{0.4} = m^{1.2}$. In other words, bending forces increase faster than body mass. It will be shown below that leg bones can withstand bending moments that are related to the cube of their diameter.⁴ Bone diameter scales as $m^{0.36}$, so withstandable bending moments scale as $m^{1.08}$ (the result of cubing $m^{0.36}$). These calculations show that the force generated by limb muscles ($m^{1.2}$) is theoretically greater than the bending strength of limbs they move ($m^{1.08}$), and that large animals should not be

fundamentally limited by the forces generated in their muscles. Indeed, we will see that the bending strength of bone becomes the limiting factor in large animals.

With those principles in mind, I still want to test the prediction that powerful animals and good accelerators will have limb muscles with relatively greater cross-sectional areas (forces). Table 1 contains Alexander *et al.*'s (1981) scaling exponents for muscle mass and fiber length for six limb muscles in primates, fissiped carnivores, and bovids. I have divided the masses of these muscles by their lengths in order to calculate their cross-sectional areas. Cross-sectional area estimates the force generated by a muscle. Results of these calculations (Table 1, column 4) show that fissiped carnivores have the highest force values for nearly all muscle groups. The higher value for triceps in primates is to be expected because of their specialized locomotion (the group includes brachiators). Values for cross-sectional areas of the deep hind flexors are highest in bovids, but these are a minor group of muscles that mainly flex the digits and are expected to be larger in bovids because they have greatly elongated metapodials.

Muscle Length: The comparison gets more difficult when one considers relative muscle lengths in mammals (which I predicted would be relatively shorter in good accelerators). This is because most ungulates reduce (shorten) the muscle portion of a muscle-tendon unit, effectively increasing the tendon portion so that more elastic strain energy can be recovered (Alexander 1977a, 1984; Alexander *et al.* 1981, 1982). So, in comparison, the muscles fibers of large carnivores and other powerfully built animals seem long, apparently contradicting my prediction. To address this problem, I have calculated a "bulkiness index" by dividing cross-sectional area by fiber length (Table 1, column 5). This index gives an indication of a muscle's relative width versus length (i.e., its bulkiness). Muscles with long stretch tendons in bovids have higher bulkiness indices because these muscles have reduced lengths, not greater widths. These include the hamstrings, deep hind flexors, and the quadriceps (the quadriceps both extend the knee and flex the thigh; the extensor portions can store elastic strain energy and have longer ligamentous portions). For all other muscles, the more powerfully built carnivores and primates have bulkier muscles—that is, shorter for quickness, and wider for high force generation.

Powerful Limbs vs. Efficient Limbs: So far, I only have discussed muscles designed for high power output. However, mammals vary considerably in muscle configuration, balancing needs for power and efficiency; some emphasize sustained work, while others emphasize sustained high speeds. I showed that powerful muscles fatigue quickly because they contract rapidly and are short. Muscles built for economy have the opposite traits.

⁴ the bending moment of a bone is equal to its cross-sectional area times its length. Since $SA = l^2$, the bending moment is equivalent to $SA \times l$, or l^3 .

They are long and narrow to provide slower, more efficient contractions. Animals with these types of muscle that also develop high top speeds do so by decreasing the mechanical advantage of their limbs, which effectively increases their turning velocities but reduces their strength. In the next section on lever systems, it will become apparent that this separates runners with high top speeds from those that simply accelerate well. And in fact, this is what drives the differences in muscle proportions among the carnivores and bovids in Table 1.

With *Arctodus'* long legs, it stands to reason that either its muscles were longer and/or it had long stretch tendons. Considering the muscle anatomy of bears, it seems unlikely that *Arctodus* had evolved elaborate stretch tendons like ungulates. But even in running humans, not known for their stretch tendons, about one third of the work performed during running comes from recovered elastic strain energy, and any large, long-legged mammal will use a good deal of recoiled elastic energy during locomotion (Alexander 1988, 1992; Alexander and Bennet-Clark 1977; Alexander *et al.* 1982). Another important implication of *Arctodus'* long legs is that the accompanying elongated muscles would have been optimal for slow, repeated contractions, and/or high force (but not power) generation; in a very large animal, this would be most adaptive for efficient and sustained locomotion, not for power or acceleration. I also have been alluding to the idea that the long, slender legs of such a large animal could not have withstood the strains of sudden turns, rapid speed changes, or high speeds that characterize essentially all modes of predation. To understand why this is so, one needs to consider how bone strength scales with body size and how this affects a bone's ability to incur the forces of locomotion. I address those issues next.

8. BONES AND SKELETAL STRESSES

As the primary elements of rigid support, bones incur the static forces of supporting an animal's mass, but also the greater dynamic forces of locomotion. In this section, I will discuss how *both the static and dynamic forces of support increase with body size at rates faster than skeletal strength, and that this scaling effect ultimately limits animal locomotion*.

Forces, or loads, incurred by bone are transmitted internally as stresses (see definitions section) and are dissipated as deformational strains, usually as bending, compressive, torsional, shear, and tensile strains (tensile strains are not significant in bones, but they are the main strains incurred by muscles and tendons). A bone's strength is a measure of its ability to deform under stress without breakage or permanent deformation, and a bone will break when stresses exceed its deformational

capacity—i.e., its strain limits. For almost all limb bones (with exceptions such as metapodials in ungulates) bending forces are by far the most important stress threatening a bone's integrity—typically 80 - 90 % of the stress in a bone is from bending; the balance is usually compressive stress (Rubin and Lanyon 1982, Biewener *et al.* 1988). When a bone yields to bending stresses it is said to *buckle*. A bone's safety factor, or safety margin, is the ratio between its normal strain and its yield strain. Typically, bones which incur mainly compressive stresses are straight, while those incurring mainly bending stresses are curved. Curved bones are less resistant to bending stresses, so this pattern seems odd at first. However, the axis of curvature is invariably in line with the normal direction of bending, and it has been suggested that this curvature is "predictive," focusing bone strain in a single direction, which then can be countered by strategic remodeling (Rubin and Lanyon 1985, Biewener *et al.* 1988). This strategy conserves materials since the bone does not need to be built to resist bending in other directions or along its entire length.

Predicted vs. Actual Bone Stress

Here I want to briefly describe how dimensional analyses of limb bones predict that larger animals will incur greater dynamic forces in their bones, whereas the actual data on bone stress show that they do not.

A bone's strength is a function of its dimensions and thus is subject to scaling influences. Compressive, torsional, and shear strength are primarily related to a bone's cross-sectional area, which would be proportional to l^2 and $m^{2/3}$ if animals were built in a geometrically similar fashion (recall l is any linear dimension, including bone diameter, and $l \propto m^{1/3}$ in geometrically similar animals). On the other hand, the magnitude of compressional, torsional, and shear forces acting on bone should be a function of body size (i.e., m^1 or l^3), in geometrically similar animals. Therefore, it would be surprising if large mammals actually scale geometrically; otherwise, how could they withstand the forces of running? Alexander *et al.* (1979) measured limb bone dimensions and found that most mammalian limb bones do in fact scale close to geometric proportions (except in bovids). Specifically, those authors found that long bone diameters (d) are generally proportional to $m^{0.36}$ —slightly, but not significantly, higher than $m^{1/3}$ (they also found that $l \propto d^{0.97}$, in accordance with geometric proportions, except in bovids). Using Alexander *et al.*'s data, cross-sectional area (d^2) thus scales empirically as $m^{0.72}$ (the square of $m^{0.36}$), which is statistically indistinguishable from geometric prediction of $d^2 \propto m^{2/3}$ (statistical analysis performed by Alexander *et al.* 1977). This implies that the compressional, torsional, and shear strength of bone should increase with body size only as

$m^{0.72}$, meaning that stresses will still increase as $m^{0.28}$ (i.e., as $m^{1.0} - m^{0.72}$) (the same value was predicted by Biewener 1982). In other words, larger animals incur relatively greater compressional, shear, and torsional stresses in their limb bones than smaller animals.

Similarly, bending strength, the most critical factor determining dynamic bone strength, is a function of a bone's cross-sectional area times its length. Under rules of geometric similarity, bending strength is predicted to scale as $d^2(l) = l^3 = m^{1.0}$. Using Alexander *et al.*'s empirical data for bone diameter (see above), actual limb bone bending strength would appear to scale closer to $(d^{0.36})^3$, or $m^{1.08}$. However, Alexander *et al.* (1981) subsequently calculated the theoretical maximum bending moments generated in limb muscles by multiplying their cross-sectional area ($\propto m^{0.8}$) times their moment arm ($\propto m^{0.4}$), yielding bending forces $\propto m^{1.2}$ (see previous section on muscle scaling). If maximum bending moments of limb muscles increase with body size $\propto m^{1.2}$, but bending strength of limb bones increases only $\propto m^{1.08}$, then one would predict that bending stresses also will increase disproportionately with body size at a rate of increase $\propto m^{0.12}$ (derived from $m^{1.2} - m^{1.08}$). Biewener (1982) predicted this value to be $m^{0.28}$, identical to the prediction above for increases in compressional and shear stresses.⁵

When dynamic stresses are actually measured in bones, it is apparent that the mass-specific magnitude of these stresses is fairly independent of body size (proportional to m^0) in animals running at physiologically equivalent speeds, such as at gait transitions or at maximum speeds. In fact, this is just what Alexander (1977a) initially predicted when formulating his theory of dynamic similarity (also see Alexander and Jayes 1983). Not only are dynamic stresses independent of mass (i.e., not $\propto m^{0.28}$ or $m^{0.12}$), but all mammals locomote within about the same safety factor in their bones — around 2.1 - 3.1 (Alexander 1977c, Alexander *et al.* 1981, Alexander and Jayes 1983, Rubin and Lanyon 1982, Biewener 1983b, Biewener and Taylor 1986, Biewener *et al.* 1988, Kram and Taylor 1990). Figure 6 (modified from

Biewener 1982) depicts the absolute bending strength of bone measured in a variety of sizes of mammals and shows how this value does not change significantly with body size. Figure 6 also shows the way that absolute bone strength would need to increase with body size in mammals if dynamic stresses increased with body size $\propto m^{0.28}$ — the value predicted by strictly dimensional analyses.

How do Large Animals Reduce Realized Bone Stress?

The reason why actual stresses in bone scale as m^0 is important: *the physical dimensions of large and small mammals may scale roughly according to geometric predictions, but large and small animals do not run in geometrically similar ways*. Large animals decrease the realized stresses of locomotion and maintain similar safety margins as do small animals by running much more conservatively (but not necessarily slower) and through modified limb architecture. By running more conservatively, I mean that large animals accelerate and decelerate at slower rates, and they avoid other sudden changes in velocity, such as those incurred during rapid turns. These are key principles that I will return to, but first I want to discuss the ways that large animals modify body architecture.

Architecturally, large animals reduce bone stress using three strategies: 1) reducing bone curvature, which scales as $m^{-0.09}$, 2) reducing angles of bone alignment, which scale as $m^{-0.07}$, and 3) reducing excursion angles, which scale as $m^{-0.1}$ (McMahon 1975a, Biewener 1983b). All of these strategies maximize axial loading (compressive forces) and reduce transverse loading (bending forces). Bone is more resistant to compressive forces than bending forces, and these three strategies reduce bending strains by keeping stresses more in line with vertical ground forces (Biewener 1983b, Biewener and Taylor 1986, Biewener *et al.* 1988). Thus, since curved limb bones generate greater bending moments, large mammals reduce bone curvature. Reducing the angle of alignment between bones keeps the limbs less bent at the joints. Reducing excursion angles makes the limbs swing through a smaller radius during locomotion.

While large animals stand and run with their legs less bent than small animals to reduce dynamic stresses, reducing joint angles has the additional effect of decreasing the mechanical advantage of muscles operating their limbs (levers and mechanical advantage are discussed in the next section). As a result, the straight-leg stance of larger animals generates less torque and imparts less stress to the bones than the bent-leg stance of smaller animals (Biewener 1983b). In the next section, I will discuss how reduced mechanical advantage is one reason why larger animals are less adept at acceleration. It is interesting to note, however, that the less curved limb

⁵ These calculations, based purely on dimensional analyses, argue that mammalian limb bones scale geometrically and predict that larger animals should experience disproportionately greater static and dynamic stresses in their limb bones. I would qualify Alexander's conclusions, however, by pointing out that Biewener's (1983b) data on limb bone diameter and length across a broad range of taxa show that they scale as $l \propto d^{0.89}$, which Biewener reports as being significantly different from $l \propto d^{1.0}$. His data are combined for bovids and non-bovids, but his results can be taken to mean that mammals probably do increase bone diameter at a faster rate than bone length as body size increases in response to increased stresses.

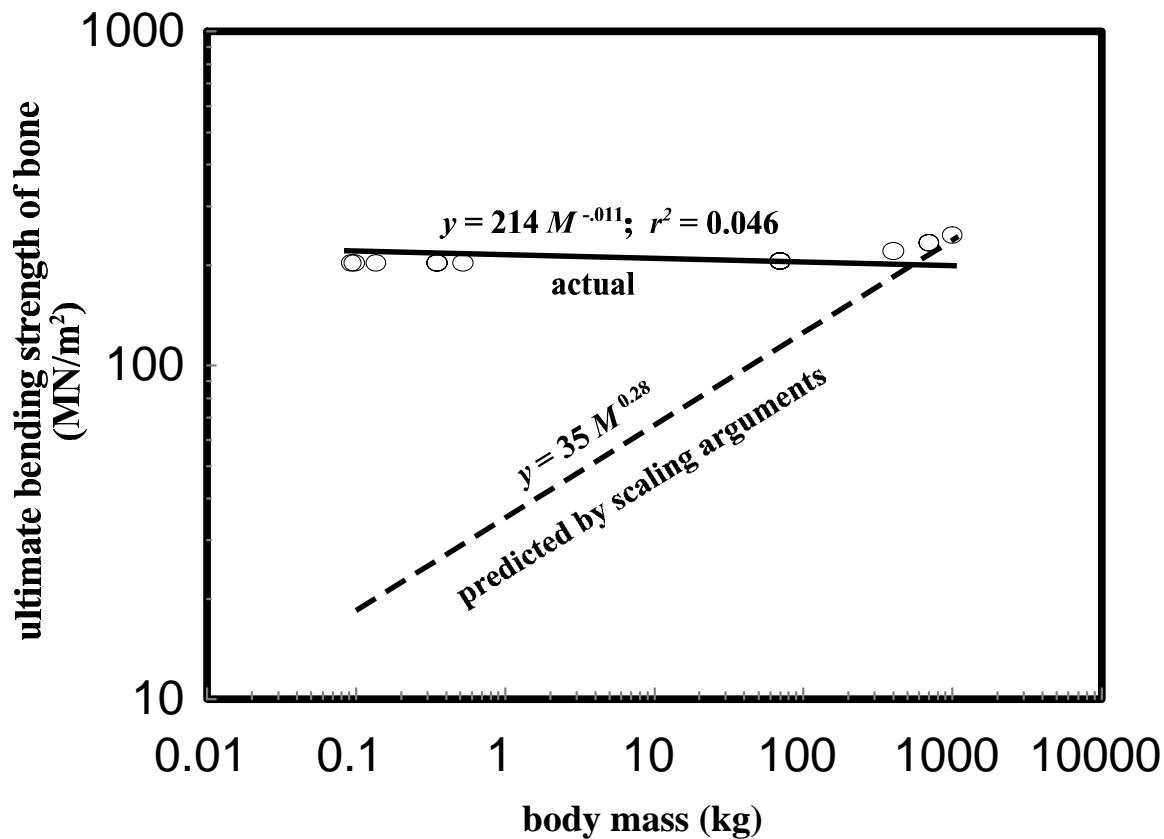


FIGURE 6. Actual bone strength in mammals (solid line) and the predicted bone strength that would be required if all mammals ran in geometrically similar ways and still maintained the same safety factor in their bones (dashed line). The slope of the line for actual bone strength is not significantly different from 0. The line for predicted bone strength was drawn using the actual bone strength in a 1000 kg animal and extrapolating backwards using a slope of 0.28 to derive a *y*-intercept value of 35. See text for derivation of slope. Adapted from Biewener (1982).

bones of *Arctodus* have been interpreted as an indication of its cursorialism and running ability. Later, I will argue that *Arctodus* did in fact make many modifications to its limbs that were cursorial adaptations, but its straightened limb bones most likely reflect the greater stresses incurred by its large size and should not be strictly interpreted as a cursorial adaptation.

Previously, some authors (e.g., Pennycuick 1975, Alexander 1977b, 1977c) have suggested that large animals may be reducing bone strain by increasing duty factor. These authors reasoned that an animal can reduce the absolute magnitude of vertical ground forces and stress in the limbs by increasing the percentage of time that each foot contacts the ground during a stride, thereby spreading these forces over a longer period. For similar reasons, these authors predicted that duty factor also should increase with speed, since ground forces increase with speed (within a given gait). Pennycuick (1975) even suggested that ungulates change gaits for the purpose of increasing duty factor. Early data of Alexander's (1977b) seemed to support these hypotheses. He showed that duty factor is $\propto m^{0.11}$ for the front limbs of mammals and $m^{0.14}$ for their hind limbs. However, the hypothesis that duty factor increases with size or speed has largely been refuted. The data of McMahon (1977) and Biewener (1983b), for instance, show no increase in duty factor with either size or speed in quadrupedal mammals. Biewener's results even indicate that duty factor decreases curvilinearly with speed, and scales to body size with a slope not significantly different from zero (i.e., m^0). Later, Jayes and Alexander (1978) found that there is a drop in duty factor at the walk-trot transition, and that this increases leg loading. Subsequent studies have failed to show much change in duty factor at the transition from a trot to a gallop (McMahon 1977, Biewener 1983b, Rubin and Lanyon 1982, Kram and Taylor 1990).

Recent work has clarified the issue of force application by the feet, and shows that it is not a simple matter of changing duty factor. The pattern of force application depends on many complex and interdependent factors such as speed, gait, limb compliance, and leg length. Recall from the discussion of energetics that the magnitude (and rate) of vertical ground force application increases with speed within a gait, but that it decreases again after a gait transition (for example, after switching from a trot to a gallop). The same pattern holds true for the rate of energy consumption (Hoyt and Taylor 1981)(Fig. 5a). This applies to animals of all sizes, but the rate of increase should be greater in small animals (recall Fig. 4). Next I want to return to Figure 4 and discuss these patterns in more detail.

When Hoyt and Taylor's (1981) data is plotted as the mass specific cost of transport (Fig. 4b), it can be seen

that once an animal reaches a higher gait and is allowed to choose its own speed, it quickly settles on one that is the most economical for that gait, after which it consumes energy at about the same rate as it did during the previous gait. In Fig. 5b I showed that this steady state cost of transport is nearly the same for each gait, meaning that an animal expends about the same amount of energy to move a given distance regardless of its speed (only *rate* of energy consumption changes with speed— Fig. 5a). Furthermore, since the rate of energy consumption initially declines after a gait change, Hoyt and Taylor and others (Alexander *et al.* 1980, Alexander 1992, Hildebrand 1985a) have concluded that animals change gaits in order to save energy. This would be a correct conclusion if animals changed gaits at speeds where the lines in Fig. 5a and 5b cross. But this is not the case. Taylor's group (Farley and Taylor 1991) later measured energy expenditures in horses carrying various amounts of extra weight and showed that these animals change gaits at speeds below those which would optimize energy costs (speeds *a*, *b*, and *c* indicated on Fig. 5b). In other words, animals switch from a trot to a gallop at speeds where galloping actually requires more energy than trotting.

What Triggers Gait Changes?—More Clues Into the Role of Body Size

If gait changes do not occur at speeds that optimize energy expenditure, then they must be triggered by some other demand. There is good evidence from Taylor (1985), Biewener and Taylor (1986), and Farley and Taylor (1991) that animals change gait in response to threshold levels of musculoskeletal stress—that is, they change gaits when a critical level of stress is reached, regardless of speed. Almost universally, this point is reached when the bone safety margin (ratio of yield strain: applied strain) approaches 3 (Rubin and Lanyon 1982, Biewener and Taylor 1986, Biewener *et al.* 1988, Farley and Taylor 1991). This process is exemplified by Farley and Taylor's experiments with weighted-down horses. The weights increased limb loading and caused the animals to change gaits at subnormal speeds. However, while their speeds varied, the horses uniformly changed gait when the same critical vertical ground forces were reached. Biewener and Taylor (1986) used this and other data to argue that *maximum speeds in animals are defined by the strain limits of limb bones, not by an animal's ability to generate enough force or power* (also see Taylor 1985 and next subsection).

But how is the rate of force application reduced by switching from a trot to a gallop? I indicated that some earlier researchers hypothesized that animals reduce these forces by increasing duty factor, but this has been largely disproved. McMahon (1985) presented a compelling

argument showing that galloping reduces leg strain by increasing leg compliance (a measure of leg stiffness). Stiff-legged (non-compliant) gaits like the trot and walk use less energy to flex and maintain bent limbs, whereby more of the work performed against the ground is converted to propulsion. For these reasons stiff-legged gaits use energy more efficiently than compliant gaits like the gallop. The tradeoff is that stiff legs transmit greater vertical ground forces, and because these forces increase with speed there is a rather low speed limit for stiff legged gaits (if safety margins are to be maintained).

Therefore, to dissipate increasing forces the legs need to become more compliant at faster speeds. The compliant legs of a gallop “absorb” the increased ground forces by flexing and then rebounding this energy as the feet are placed on the ground in rapid, non-overlapping succession. This also distributes the forces more evenly throughout the stride. The net effect is that peak vertical forces in the feet are reduced, step length increases, and the animal gets a smoother ride. McMahon’s study shows that *compliant running consumes energy at a faster rate than stiff-legged running, but it is the only way to achieve higher speeds without exceeding the safety margins of limb bones*. Recall, too, the important conclusions of Kram and Taylor (1990), who show that longer legs decrease energy costs and decrease the magnitude of peak vertical forces (but not total force) imparted to the limbs because long legs afford an animal longer strides, longer individual foot contact, and thus more time to distribute these forces. Therefore, increasing leg compliance and leg length achieves all the hypothesized goals of increasing duty factor (and more), but without necessarily increasing the total period of foot contact with the ground (each foot spends a longer time on the ground in a gallop, but because there is a prolonged aerial phase, total foot contact as a percentage of the stride—i.e., duty factor—does not increase).

McMahon’s data on compliant gaits provide critical insight into the *Arctodus* question in terms of gait selection. Recall that an animal uses the same amount of energy to move a given distance regardless of speed of travel—all that changes is the rate of energy consumption. But an animal cannot sustain maximum galloping speeds indefinitely because it is limited by the rate that it can provide energy to its muscles (Margaria *et al.* 1963, 1964). Combining this information with McMahon’s data on rates of energy consumption during compliant and non-compliant gaits, one would predict that animals which can maintain non-compliant gaits at high speeds will have the fastest speeds of sustainable travel; they will use energy at a slower rate and get to far off destinations quicker, because they do not need to rest as often.

The inherently smoother ride of a compliant gait is

not insignificant, as it reduces vertical displacement of the body’s center of mass. Rubin and Lanyon (1982) showed that less displacement in a gallop (versus a trot) reduces limb loading when the body mass comes down on the feet. These authors also showed that the rate of strain change in a bone—not the magnitude of peak strain—often is the most relevant factor determining bone strength. The stiff legs of a trot impart a much more rapid rate of strain change when the feet hit the ground than would the compliant legs of a gallop, which absorb vertical forces more gradually. Indeed, it was shown that this is probably why animals change gait (Taylor 1985, Biewener and Taylor 1986, Farley and Taylor 1991).

Not only are bones subject to failure from rapid strain change, but they also are prone to damage by rapidly repeated strain, or repetitive loading. This type of “fatigue damage” occurs because the bone is not allowed to recoil, or “de-strain.” The accumulation of strain means that even low levels of stress can cause failure when applied constantly or in rapid succession (Rubin and Lanyon 1982). The pattern of bone breakage in mammals indicates that both fatigue strain and the rate of strain change can be more important than the magnitude of strain in causing bone failure. For example, The vast majority of fractures in steeplechase horses occur during jumps, both at takeoffs and landings (Currey 1981, Biewener *et al.* 1988). Those are times when limbs experience the most intense rate of strain change and their greatest rate of acceleration and deceleration; but the fractures probably occur in part because of fatigue strain accumulated during the course of the race.

Biewener (1983a) and Biewener *et al.* (1988) measured bending and compressive strain at different points along limb bones of running mammals (horses, dogs, chipmunks) and found that distal bones generally experience strains 1.5 to 2.0 times greater than proximal bones. This would suggest a strong evolutionary incentive to keep distal bones stout, yet these bones are highly reduced in many coursers (for reasons discussed in the section on kinematics).

A closer look at patterns in Biewener’s strain data for the limbs of running horses shows that the tibia and radius receive the highest bending strain values, followed by both metapodials (receiving predominantly compressive strains). But data on bone breakage in horses show that metatarsals are fractured much more frequently than tibias (Currey 1981). Biewener (1983a) argued that this apparent discrepancy arises because strain is typically measured in animals running at a steady state, while bone breakage occurs during brief periods of extreme stress, concurring with Rubin and Lanyon’s (1982) data. When Biewener (1983b) measured bone strain in a small mammal (chipmunk, *Tamias striatus*), he found that its metatarsals incur greater strains than its tibias. Small

animals normally run with relatively greater acceleration, greater rates of force application, and greater stride rates compared to large animals, so small animals routinely experience more rapid changes in strains, more accumulated fatigue strain, as well as greater peak strains than large animals. Therefore, Biewener argues that these data on a small mammals more accurately assess bone strain during strenuous locomotion such as during rapid acceleration/deceleration and that these are the critical tests of bone strength. Hence, during rigorous running, a horse's metatarsal, not its tibia, probably experiences the most strain, which the studies of steady state locomotion could not demonstrate.

An Upper Size Limit For Predators

Throughout this discussion, I have been alluding to the notion that the scaling of locomotor forces sets an upper body size limit for conventional predators—somewhere in the neighborhood 250 kg. At this point I want to examine this hypothesis more closely and present what may be an important new empirical relationship between maximum running speeds (MRS) and body size. This discussion closely follows Fig. 7.

Figure 7a reconstructs Garland's (1983, Fig. 1) data relating MRS to body size across a wide range of mammalian taxa, from shrews to elephants (Garland's data for the smallest mammals has been cropped out of Fig. 10a). The polynomial fit to these data ($\log MRS = 1.47832 + .025892 (\log Mass) - 0.06237 (\log Mass)^2$; $r^2 = 0.574$) shows how MRS increases with size but plateaus around 119 kg, after which it clearly drops off with increasing body size. The physical and biological forces driving this pattern have been discussed throughout Part I, but only in a qualitative sense. In Fig. 7b, I propose a quantitative reason for it. This plot shows empirical data for two physical parameters: 1) the ultimate bending strength of bone, represented by the solid horizontal line (modified from Biewener 1982; same plot as my Fig. 6), and 2) the cross-sectional area of the humerus and femur midshafts in 27 mammal species (data from Biewener 1983b), which I have divided by body mass to show how their relative cross-sectional area (and strength) decreases with body size. Data for the tibia, radius, and ulna are not shown because they frequently are part of a two-bone system, i.e., the combined support of the ulna-radius and tibia-fibula would need to be considered.

The phenomenon I want to emphasize in Fig. 7 is that the lines for bone strength and mass-specific cross-sectional area (averaged for both bones) cross at nearly the exact same body mass at which MRS begins to decline—around 119 kg. This pattern probably is not just an epiphenomenal artefact, since these three parameters are functionally so tightly linked. Indeed, in the simplest sense body support in mammals is a factor of the inherent

strength of boney material and the fact that the cross-sectional surface area of bone decreases relative to mass increases (two thirds rule). I have been discussing at length why this limits MRS and other facets of locomotion, but what I am proposing in Fig. 7 is a precise, functional relationship that predicts 119 kg as the natural limit to MRS, based on the physical properties of boney material and the geometry of vertebrates. This relationship supports the conclusion that speed in small mammals is limited by their absolute size and limited power output, not the strength of their bones. In progressively larger mammals speed increases in conjunction with their ability to generate absolutely more power. At the same time, relative bone strength decreases with size until the crossing point in Fig. 7 is reached, where skeletal safety margins can no longer be maintained without reducing speeds. Garland's polynomial equation relating top speed to body mass could be used theoretically to predict MRS in an unfamiliar or extinct mammal, such as *Arctodus*. However, while this equation accurately describes the general relationship between speed and body mass, it does not predict MRS very precisely for any given species, as evidenced by the broad scatter in the data in Fig. 7a. Deviations from the trend line are considerable and reflect morphological adaptations for divergent locomotor and ecological strategies. For instance, cheetahs are around 55 kg, but not all 55 kg mammals would gain selective advantage if they too could sprint at 100 km/h. As with most exercises where an equation is fitted to empirical data, one often gains the most insight about a species by examining the way it diverges from the average trend.

Along similar lines, consider the comparison between goats and large breeds of dogs: both are about the same size (~25 kg), but their skeletal builds are quite different. Dogs run at much higher MRS and engage in higher force activities, and their more massive limb bones reflect this. Biewener and Taylor (1986) showed that these two mammals experience similar peak strains in their bones at physiologically equivalent speeds, including top speeds, but dogs do not reach critical levels of strains until higher speeds because their bones are larger (stronger). Using arguments summarized throughout Part I, one also may conclude that dogs will fatigue more quickly and use energy at a faster rate than goats running at identical speeds. There is an important conclusion to be drawn from this pattern in pertaining to animals built like *Arctodus*: *couriers built both to run at high top speeds and to maneuver have heavier limbs than similar sized couriers which are adapted for straight-line running or for endurance. Furthermore, as body size increases couriers in the former category must make even greater skeletal compensations because the forces*

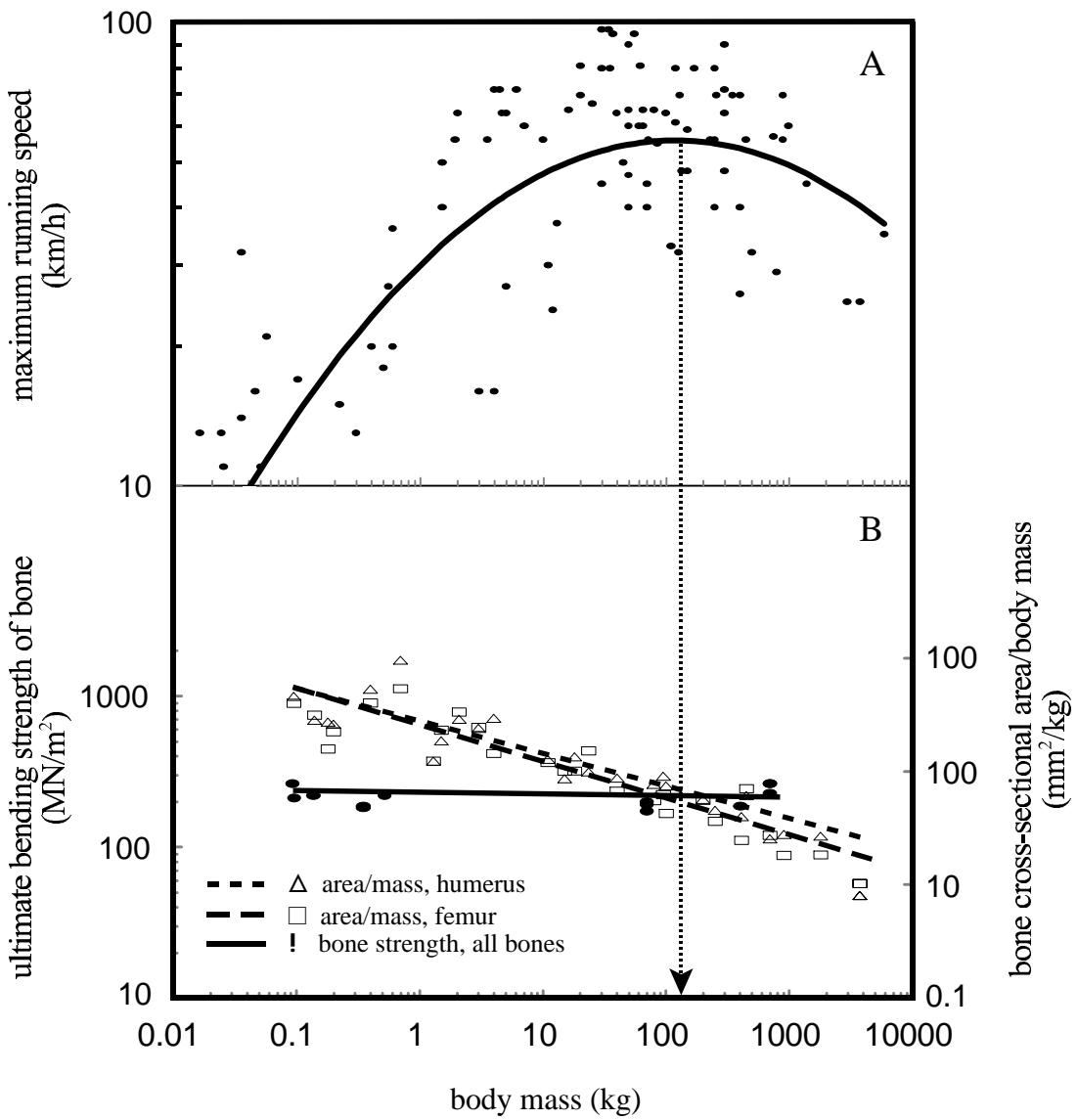


FIGURE 7. The relationship between body mass and maximum running speed (MRS). *A*: Garland's (1983) data for MRS and body mass in a wide variety of mammals. The second order polynomial which best predicts MRS as a function of mass is:

$$\log MRS = 1.47832 + 0.25892 (\log M) - 0.06237 (\log M)^2$$

This function shows how MRS increases with speed until around 119 kg, after which it declines again. *B*: Plots of bone's material strength (solid line) and the relative cross-sectional area of limb bones in mammals (dashed lines; only humerus and femur plotted). The solid line has a slope of zero because the properties and strength of bone do not change with body size. However, the realized strength of a long bone is a function of its cross-sectional area and this decreases (relatively) with size. These two lines intersect around 119 kg, and I am proposing that this relationship between bone property and scaling realities in mammals is functionally significant and ultimately explains why MRS also declines at 119 kg.

of locomotion increases disproportionately with size. On the other hand, coursers with lighter limbs typically are adapted for straight line running and/or increased endurance; this is especially true in larger mammals.

Other equations besides Garland's have been developed for calculating speeds in animals— either maximum speeds or speeds at gait transitions (e.g., Bakker 1975 , Heglund *et al.* 1974, Thulborn 1982)— but these mostly tend to be reliable only over a narrow range of body sizes and shapes. They are especially inaccurate when applied to very large or unusually-shaped animals. Furthermore, even though Garland has produced a fairly accurate, if not precise, equation predicting MRS, I believe it is dubious to rely strictly on body mass to predict speed, especially in an animal like *Arctodus* that has an unusual morphology. Alexander and Jayes (1983) have developed a technique for estimating speeds using principles of dynamic similarity and Froude numbers, which are non-dimensional constants that scale quantities of motion to linear dimensions in dynamic systems. Alexander and Jayes' technique is valuable in that it uses readily measurable linear dimensions like leg length or stride length instead of body mass, which can be difficult to estimate accurately. But even this technique has pitfalls, as two animals with similar leg lengths do not always locomote in similar ways or at similar speeds. In Part II, I will specifically address and estimate speed capabilities in *Arctodus* with an approach that combines both Garland's polynomial function based on body mass and Alexander and Jayes' technique based on scaled linear dimensions.

Summarizing the Relationships Between Force Generation, Bone Stress, and Body Size

At this point I want to briefly summarize how limitations to locomotion differ in small versus large animals both in terms of their ability to handle dynamic stresses and the ability of their muscles to generate forces. At the beginning of this section I discussed how dimensional analyses predict that smaller animals should have stronger limb bones and experience less bone stress than larger animals. Then I presented evidence which showed that realized stresses in bone do not vary much between animals of different size because large and small animals run in different ways and have different limb architectures. That is, small animals are able to move in ways that, if scaled up, would break bones in larger animals— squirrels can safely jump out of a tree ten times their own height, whereas a large bear or elephant could not. To reiterate, this is because the force of the fall is proportional to the weight of the animal, which increases faster with body size than the strength of its bones.

Relative to their body size, the muscles of smaller

animals are proportionately stronger too; they generate relatively more force and work than larger animals (even though their muscles are not relatively much larger). But this is not primarily why a squirrel can leap many times its own height, whereas a bear cannot. The main reason for this is twofold. First, if large animals jumped that high, they could not handle the impact of landing. But more important, very small animals are able to take advantage of their ability to use sharp joint angles and bent limb postures to increase their locomotive power output. They can do this, because the bones of small animals can handle higher bending forces. I showed that muscles which have more time to contract can generate more power and can reach top velocities more quickly, and a crouched stance, often used by smaller mammals, has the effect of increasing the time course of force application because the greater angle of rotation at the joints increases the effective limb length. As Biewener (1983b) points out, this is why a human can jump higher if he/she starts out in a crouched stance. Large animals with straighter legs (necessary so that bending stresses are reduced) have shorter angles of flexion over which their muscles must develop forces of locomotion. To reiterate, this does not mean they generate less force (that is a function of cross-sectional area), but rather less power (the time course of force application). The result is that smaller animals generate relatively more power, and it is primarily for this reason that they are better leapers and accelerators. This also is why small animals can reach top speeds often on the first or second stride, whereas large animals need numerous strides in order to accelerate to top speeds. However, large animals with their longer legs can often reach higher top speeds, and more important, they are able to sustain any given speed for a longer period and over a greater distance.

So, large and small animals have inherently disparate capabilities and thus exploit different regions of the locomotor spectrum (Fig. 8). Of course, this spectrum is complex and multidimensional, as continuous variables such size and morphology interact with diverse locomotor needs. It also is a gradational scale— animals are not accelerators or non-accelerators *per se*, rather there is a continuum between the best and worst accelerators. However, it is realistic to draw certain lines on such a spectrum on one side of which, for example, one would not find a mammal with good enough acceleration, maneuverability, or top speeds to be a viable predator. As I have indicated, the largest terrestrial carnivores that are adept predators today (tigers and very large male lions) rarely exceed 250 kg.

Indeed, bears in general seem to be over the line demarcating reliance on strict predation . No brown bears today rely solely on carnivory, much less predation. Polar bears are strictly carnivorous and can reach almost 700

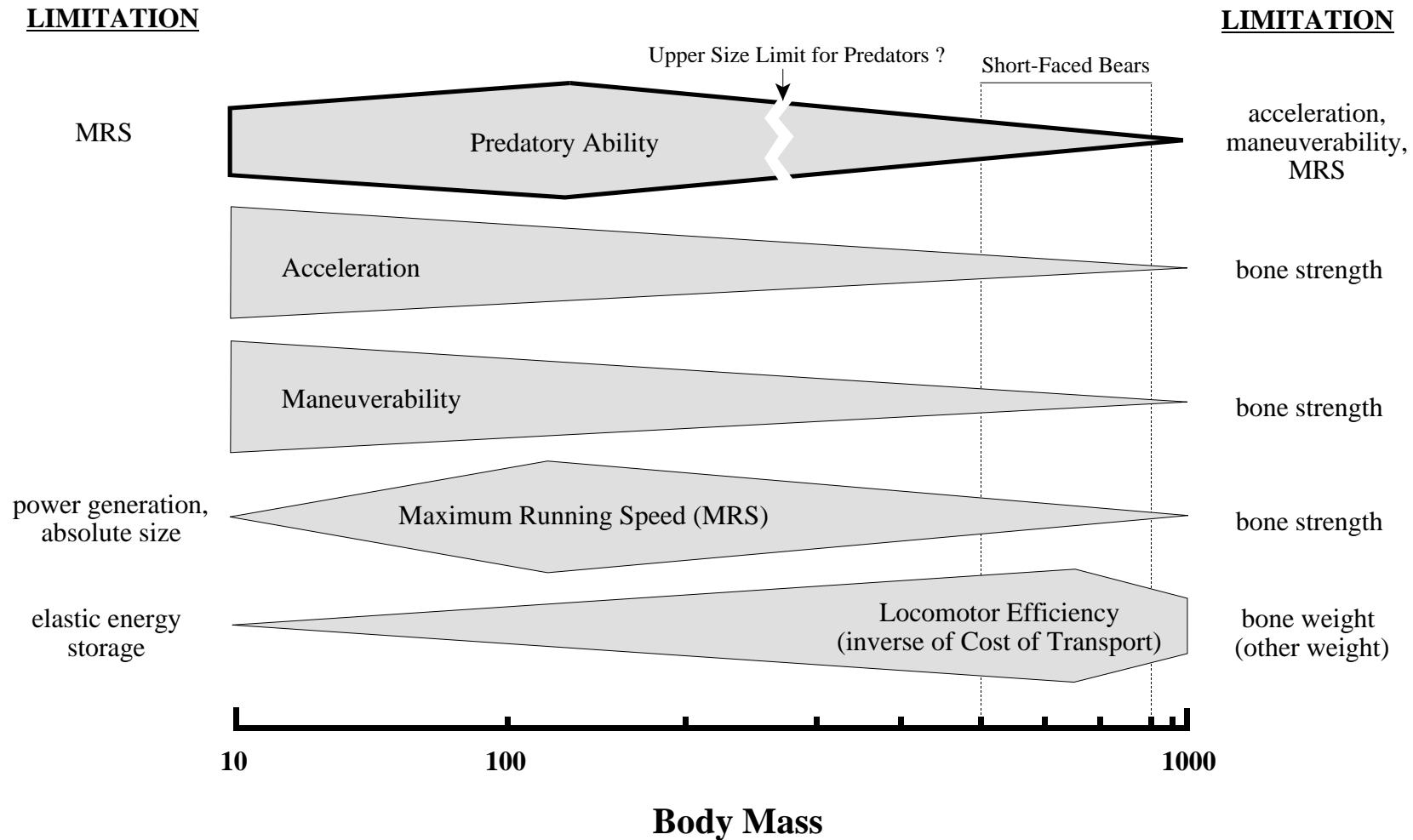


FIGURE 8. Spectrum of locomotor skills in mammals as they relate to body mass. See discussion in text.

kg, but their form of predation is extremely specialized as it primarily involves waiting to ambush seals at breathing holes and liars. Polar bears also are adept scavengers. Therefore, in order to make the argument that short-faced bears were predatory, one would have to identify a very specific and specialized predatory niche which it exploited. As I follow up on this argument in the Part II, I will emphasize that this is a tenuous argument that would require strong evidence to support it. Such evidence does not exist. My argument, therefore, will be that short-faced bears, based on their size and build, resided on the locomotor spectrum beyond the line demarcating conventional predatory skills. I think this conclusion has not been reached before because short-faced bears have been perceived as just a sort of super-huge, lean brown bear. Even if this were a morphologically correct statement, the point of my arguments presented thus far is that such a scaled-up bear would not experience scaled-up performance.

9. LIMBS AS LEVERS

Lever Systems

Machines convert energy into mechanical work. As such, limb muscles are biological machines that use metabolic energy (and stored elastic energy) to generate forces that move the limbs. A limb element rotating around a joint transmits forces from one end to the other and thus constitutes a machine whose mechanics can be described in terms of a lever system and its constituent parts (Fig. 9a). A *fulcrum* is the pivot point of a lever about which turning forces, or *torques*, are generated. Simple levers have two *moment-arms* or lever-arms—an *in-lever* (L_{in}) and an *out-lever* (L_{out}) — which represent the lengths (“arms”) of the lever on either side of the fulcrum. *Mechanical advantage* equals the ratio of the two lever-arms ($L_{in} : L_{out}$). Forces are imparted to the in-lever (F_{in}) and generated on the out-lever (F_{out}). For purposes of this discussion, levers have two turning forces or torques, referred to as *moments*. The *moment-in* (τ_{in}) is equivalent to the force imparted at a point along the in-lever times the length of that point down the in-lever. The *moment-out* (τ_{out}) equals the force generated at a point along the out-lever times the length of that point down the out-lever:

$$\tau_{in} = F_{in} \cdot L_{in} \quad (7)$$

$$\tau_{out} = F_{out} \cdot L_{out} \quad (8)$$

and when

$$\tau_{out} = \tau_{in} \quad (9)$$

then

$$F_{out} \cdot L_{out} = F_{in} \cdot L_{in} \quad (10)$$

When describing or analyzing a bone-muscle system as a lever system, one frequently is interested in assessing the effect of changing an input value in Equation 10, such as changing the amount of force applied by a muscle (F_{in}) or changing the length of a lever arm (L_{in} or L_{out}). For instance, the influence of these three values on out-force generation can be stated as:

$$F_{out} = F_{in} \cdot L_{in} / L_{out} \quad (11)$$

It is important to note that in addition to generating torques, moment-arms also have characteristic turning velocities, which respond to their lengths in the opposite way as forces. For example,

$$V_{out} = V_{in} \cdot L_{out} / L_{in} \quad (12)$$

Limbs essentially move as biomechanical levers. Consider the example of a forearm rotating at the elbow in a running or digging bear (Fig 9b). The fulcrum is at the semilunar notch, the olecranon process acts as the in-lever, and the ulna shaft distal to the semilunar notch acts as the out-lever. When the propodium is extended, such as during the propulsive phase of a stride, the torque delivered to the distal phalanges equals the force of the extensor muscles (long arm of the triceps illustrated in Fig. 9b) times the length of the olecranon process (L_{in}) divided by the combined length of the ulna shaft and hand (L_{out}). In this example, the ulna acts as a first order lever, and Fig. 9 contrasts it to second and third order levers, which also are important in biomechanical lever systems.

The Effects of Mechanical Advantage on Locomotor Performance

In Part II, I will show that the olecranon process and a number of other inlevers of short-faced bear limbs were shortened compared to other bears, reducing their mechanical advantage. The remainder of this discussion considers the functional ramifications of lever lengths and mechanical advantage on locomotor performance.

Compare the mechanical advantage and muscle configuration in a limb built for high rotational velocity versus one built for high torque or high power (at this point it is not appropriate to compare energetic efficiency or economy of effort). From Equation 12 it is apparent that rotational velocity is increased by a long outlever, short in-lever (high $L_{out}:L_{in}$), and by fast contracting muscles. Recall that fast contracting muscles generate less force and they use energy more quickly. Also, speed of contraction is inversely proportional to muscle length, so fast muscles tend to be short. If they also are not large, they will perform less work because work \propto volume. So, limbs modified for increased rotational velocity will sacrifice strength and will fatigue quickly, although I have

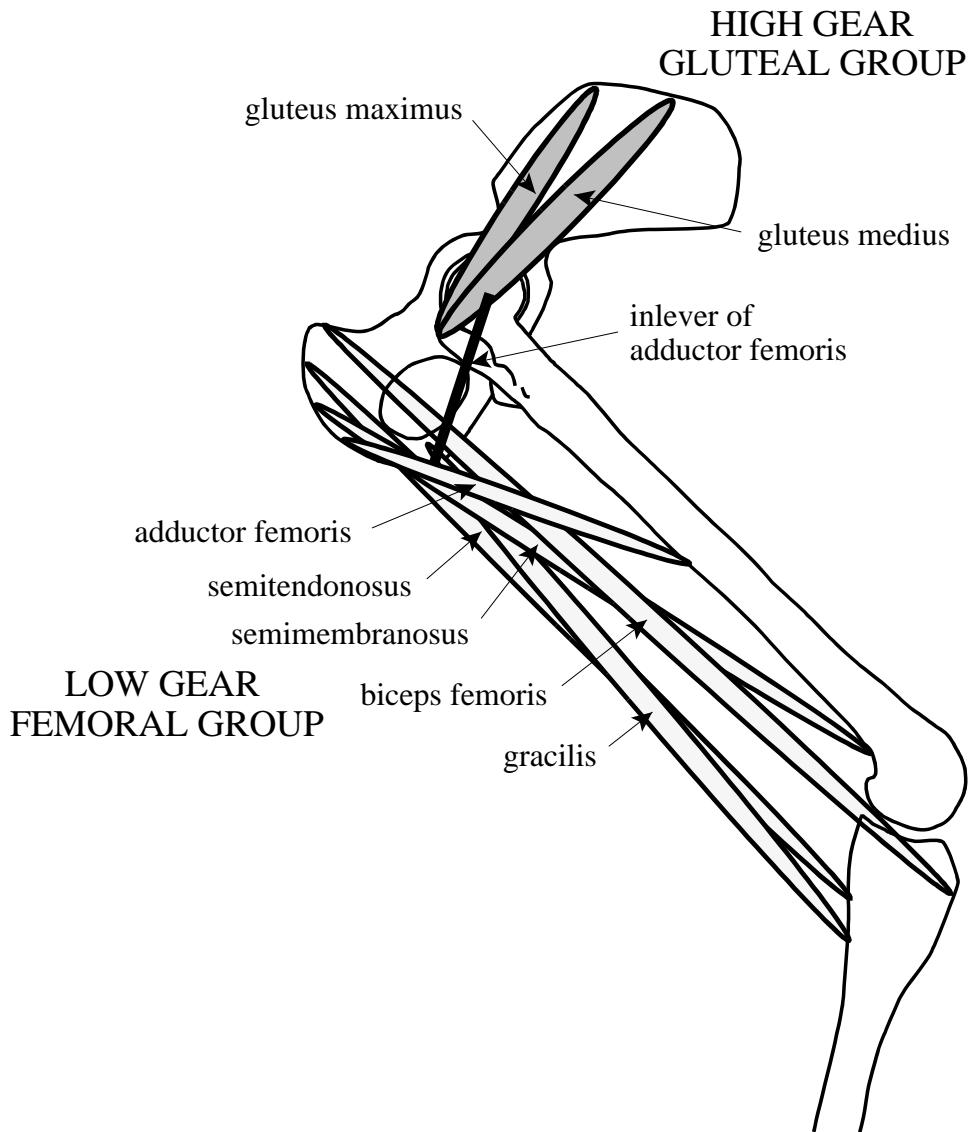


FIGURE 10. High and low gear muscle groups used by a bear to extend its femur. “Gearing” relates to the relative length of each muscle’s inlever (moment arm), drawn as a perpendicular line from the acetabulum to the muscle (inlever shown for adductor femoris only). Short inlevers, such as those for the gluteal group, have reduced mechanical advantage, so they provide little power. However, they require very little energy to extend the femur at high speeds compared to low gear muscles. Thus, they are used mainly to sustain steady state speeds. The femoral muscles have long inlevers (greater mechanical advantage) and provide power for acceleration. They are less efficient than the gluteal muscles and fatigue more quickly. Position of insertion points and leg length also affect mechanical advantage. For example, configuring femoral muscles with more proximal insertion points will reduce their mechanical advantage and thus will decrease power output, but increase efficiency, meaning they will fatigue less quickly. Long legs have a similar effect because they increase outlever lengths, and their longer muscles fatigue less quickly. Short-faced bears had longer limbs and more insertion points compared to other bears, which increased their locomotor efficiency but reduced their ability to accelerate. (Concept for drawing adapted from Smith and Savage 1956.)

shown that running specialists make other modifications to increase endurance.

A limb designed for high torque will have increased mechanical advantage (low $L_{out}:L_{in}$) and muscles that generate high forces and perform greater work. I showed that muscles with these traits typically are large and contract slowly. If the limb also is to be moved with high power output (recall power equals the rate that work is done or the velocity of force application), then the muscles also must contract rapidly. In doing so, they fatigue quickly. Therefore, one can distinguish between a limb built strictly for high torque versus one built for power. The muscles of the high torque limb will contract slowly and fatigue slowly. This is what one finds, for example, in fossorial mammals that must dig continuously but not rapidly (Hildebrand 1985c), or as I showed earlier, in turtles which move a lot of weight, but slowly. The muscles of a high power limb, on the other hand, generate forces at a high velocity, such as when a brown bear excavates a ground squirrel hole or when a lion accelerates after prey. Both high power and high torque limbs will have relatively high mechanical advantage.

What are the performance ramifications of limbs that evolve for high rotational velocity, versus limbs that evolve for high torque or high power? In the case of the fossorial mammal, I showed that high-torque limbs perform a lot of work, but slowly. These animals conduct strenuous locomotor activities for long periods, but not quickly. Limbs that evolve to rotate at high velocity are obviously adaptive for high speed locomotion, however, *a strictly fast rotating limb is not optimally designed for acceleration because acceleration requires power to get the limbs up to speeds quickly*. Therein lies the need for powerful limbs in accelerators. While both fast and powerful limbs may reach the same ultimate velocity, animals with powerful limbs will get up to speeds more quickly, while animals with “fast” (but not powerful) limbs will fatigue less quickly, and thus will be able to run longer and farther.

Runners evolve morphologies that balance their needs for power, speed, and endurance. But if one thinks of limbs only as simple levers then an obvious paradox arises: why don’t “fast-limbed” animals also increase power and acceleration by increasing muscular input? This question arises because my comparison of limbs, so far, has assumed that all limbs are identical, except for their mechanical advantage and muscle input. This assumption is wrong. It ignores the fact that limbs have mass and the fact that changes to parameters such as L_{in} , L_{out} , and muscle volume impact the quantity and distribution of limb mass. This mass costs energy to move, and this cost varies based on the muscle’s position on the limb and its rate of acceleration. These are matters of kinematics and are discussed in the next section. After

that discussion, I will bring together all of the previous issues and present an overview of locomotor adaptations for speed, acceleration, and endurance.

Low Gear and High Gear Muscle Systems

Before moving on to kinematics, I want to briefly discuss “low gear” and “high gear” muscles, since this concept relates principally to lever dynamics and mechanical advantage. In a classic paper, Smith and Savage (1956) elaborated on the ways that muscle configuration and the placement of muscles on a limb will enhance either the speed or power of their action. Hildebrand (1995) calls these high gear and low gear muscles, respectively, as the former are used for maintaining high speeds with the least effort and the latter are used for acceleration.

Figure 10 (modified from Smith and Savage 1956) shows the hind limb of a bear illustrating this concept. The gluteal group and the femoral group are the two main muscle groups that extend the femur about the acetabulum.⁶ A perpendicular line (L_{in}) drawn from the acetabulum to each muscle’s line of action represents its in-lever length. A vertical line (L_{out}) from the acetabulum to the ground represents the system’s out-lever length (the same for both muscles). The ratio $L_{in}:L_{out}$ is clearly different for these two muscle groups when the femur is in the position shown (note that each muscles’ mechanical advantage changes with the angle of flexion). Assuming that the length of contraction in a given unit of time is equal for each muscle, then the gluteal group will swing the femur through a greater arc than the femoral group during that period of contraction. However, the femoral group imparts more force because of its greater mechanical advantage.

From this example, it can be seen how the gluteal muscles are considered to be high gear muscles that maintain steady state locomotion at a minimal cost, whereas the muscles on the posterior surface of the hind limb provide most of the power and acceleration for locomotion (and other activities). When it comes to fossils, one cannot always identify the precise attachment points of individual muscles on bones, but often it is possible make some qualitative assessments about the relative importance of high gear and low gear muscles by

⁶ The gluteal group is comprised of the *g. minimus* and *g. medius* which originate primarily on the dorsal-lateral surface of the ilium (and partially on the lumbar vertebrae) and insert on the greater trochanter of the femur. The femoral group is comprised of the *biceps femoris*, *adductor femoris*, *gracilis*, *semitendinosus*, and the *semimembranosus*, which originate on the posterior and dorsal surfaces of the ischium and insert at various points along the posterior edge of the femur and the proximal tibia.

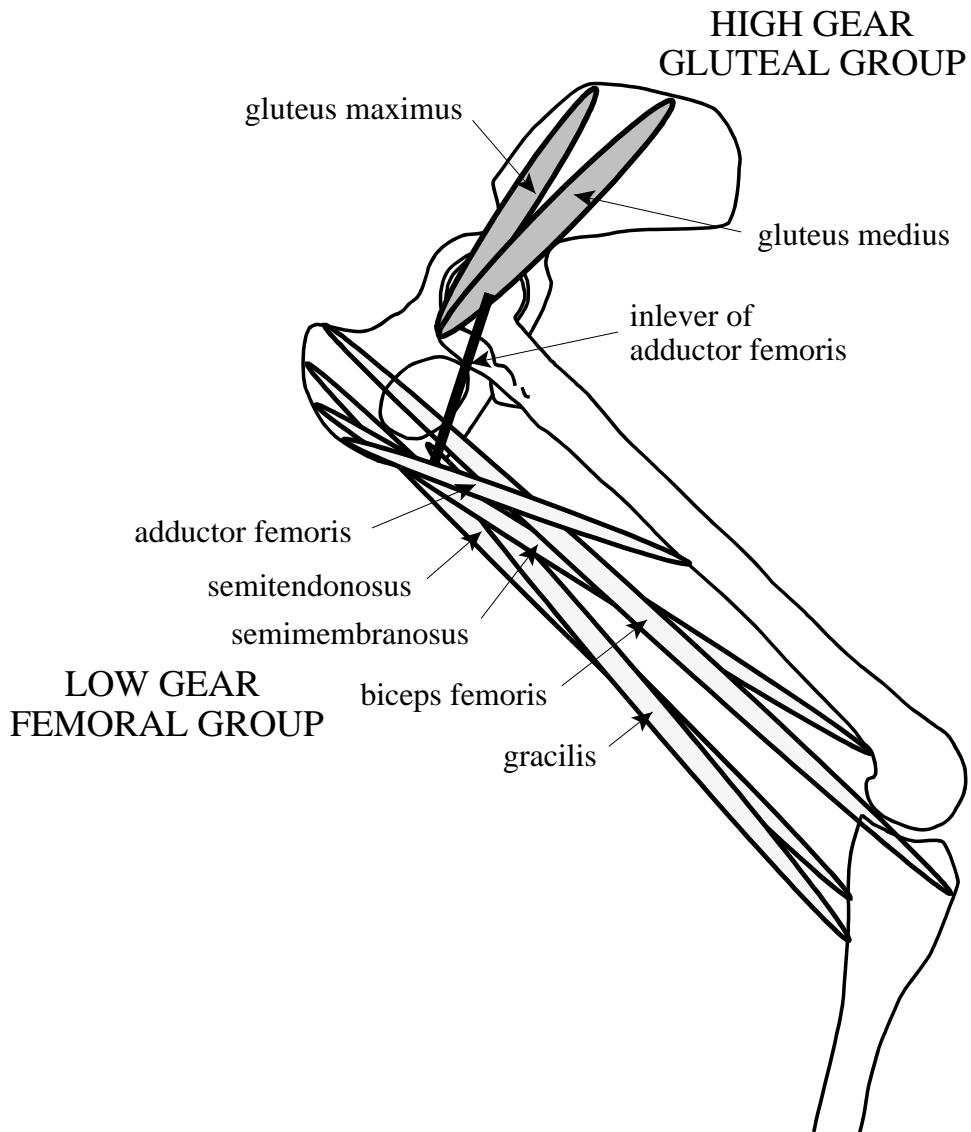


FIGURE 10. High and low gear muscle groups used by a bear to extend its femur. “Gearing” relates to the relative length of each muscle’s inlever (moment arm), drawn as a perpendicular line from the acetabulum to the muscle (inlever shown for adductor femoris only). Short inlevers, such as those for the gluteal group, have reduced mechanical advantage, so they provide little power. However, they require very little energy to extend the femur at high speeds compared to low gear muscles. Thus, they are used mainly to sustain steady state speeds. The femoral muscles have long inlevers (greater mechanical advantage) and provide power for acceleration. They are less efficient than the gluteal muscles and fatigue more quickly. Position of insertion points and leg length also affect mechanical advantage. For example, configuring femoral muscles with more proximal insertion points will reduce their mechanical advantage and thus will decrease power output, but increase efficiency, meaning they will fatigue less quickly. Long legs have a similar effect because they increase outlever lengths, and their longer muscles fatigue less quickly. Short-faced bears had longer limbs and more insertion points compared to other bears, which increased their locomotor efficiency but reduced their ability to accelerate. (Concept for drawing adapted from Smith and Savage 1956.)

analyzing dimensions of limb bones (such as the femur) and girdles (such as the pelvis). In Part II, I will make these assessments on *Arctodus* and show that it primarily had evolved a musculoskeletal configuration of the high-gear sort.

10. KINEMATICS OF LIMBS

So far, I have considered the whole body metabolic costs of locomotion, the effects of scaling on musculoskeletal performance, and the configuration of limb levers. For the most part, these were discussions about factors limiting energetic *input* in animals. Next I want to consider the *output* side of the equation—the amount of energy required to move a given mass. This is something paleobiologists can assess more easily on a fossil, even if just in relative or qualitative terms.

Physiologists assert that most of the energy spent on locomotion is used to elevate the body's mass, and that only a small percentage goes to limb oscillation. Yet anatomists have always emphasized the energetics of swinging the limbs and kinematics as central themes in interpreting limb morphology. *Kinematics* addresses the mechanics of objects (masses) in motion (*dynamics* address the *forces* associated with motion), and as stated in the previous section, any consideration of design principles and performance features in limbs is incomplete without accounting for the quantity and position of the mass being moved.

If one thinks of limbs as oscillating masses swinging back and forth during the course of a stride sequence (Fig. 11), it can be seen that each limb passes through four energetic phases relative to the rest of the body (two acceleration phases and two deceleration phases): 1) when the limb is swung forward, energy is expended to overcome inertia and for acceleration, 2) at the end of its forward motion, energy is expended to decelerate the limb's momentum to zero, 3) next, energy is expended to overcome the limb's resting inertia and accelerate it rearward, 4) to end the cycle, energy is expended to decelerate the limb's rearward motion, setting it up for phase 1 again (Hill 1950; Alexander *et al.* 1979; Fedak *et al.* 1982; Hildebrand 1985a, 1995). Certain mechanical aspects of these four phases can be described using principles of oscillating masses and pendulums, with a few qualifications (Fig. 11). First, the energy expended during each phase is unequal (Manter 1938, Fedak *et al.* 1982). Also, the rearward acceleration phase must lift and propel the animal's body mass, which requires more energy than the forward (recovery) phase. Energy expended for the two deceleration phases are unequal, too, since contact with the ground on the forward phase helps brake the limb's momentum.

The energetic cost of each oscillation phase is

dependent on two factors: the limb's inertia, which is directly proportional to its mass, and the limb's momentum, which is proportional to its mass times velocity. It takes more energy to move and stop a greater mass, but in terms of energy expenditures, the distribution of mass along the limb can be more important than total mass. Distal mass is more expensive to move than proximal mass for the following reasons. Consider a limb traveling through an arc, similar to a swinging pendulum (Fig. 11). Distal masses on the limb oscillate at higher velocities than proximal masses, and the energy required to move a given mass increases as the square of its velocity:

$$E = \frac{1}{2} m \cdot v^2 \quad (13)$$

where E is the kinetic energy of motion, m is mass, and v is velocity. The motion of limbs usually is more accurately quantified by curvilinear equations, but rectilinear equations are more intuitive so I usually will refer to both. The rectilinear equivalent of Equation 13 is:

$$E = \frac{1}{2} I \cdot \omega^2 \quad (14)$$

Where I is the moment of inertia, and ω is angular velocity.

The energetic relationship between mass and velocity explains why distal masses, which travel at greater velocities, are more expensive to propel in an oscillating system. However, it is perhaps more germane for this discussion to think in terms of the force required to accelerate a limb, and the effect of mass on acceleration, as opposed to simple velocity. Here, I draw from Newton's Second Law:

$$F = m \cdot a \quad (15)$$

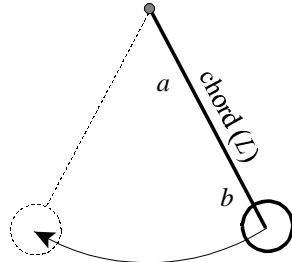
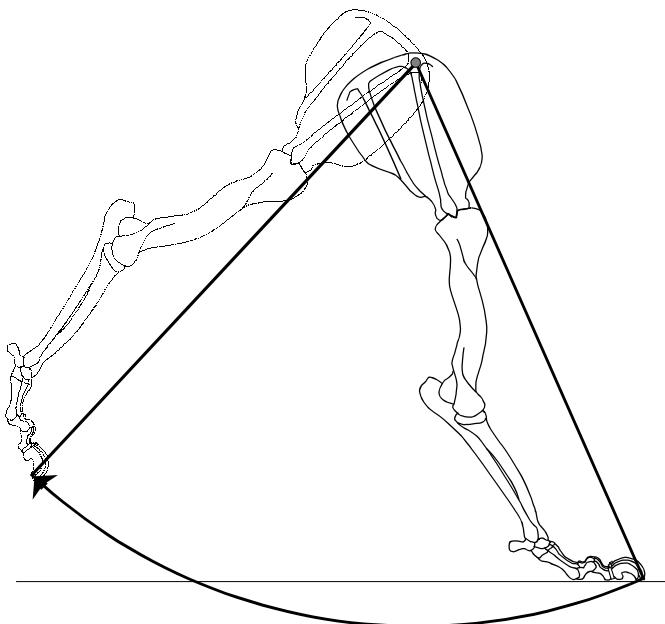
where F is force and a is acceleration. Its curvilinear equivalent is:

$$\tau = I \cdot \alpha \quad (16)$$

where τ is turning force (torque) and α is angular acceleration. The moment of inertia (I), is a measure of an object's resistance to acceleration/deceleration and, in a curvilinear system, equates to mass times the square of the radius of gyration (D):

$$I = m \cdot D^2 \quad (17)$$

Conceptually, D is the distance from a pendulum's pivot point (e.g., hip, shoulder) to its center of oscillation, which is essentially the limb's center of mass (Hildebrand 1985a). If legs were simple pendulums, which assume



Pendulum Analogy

A

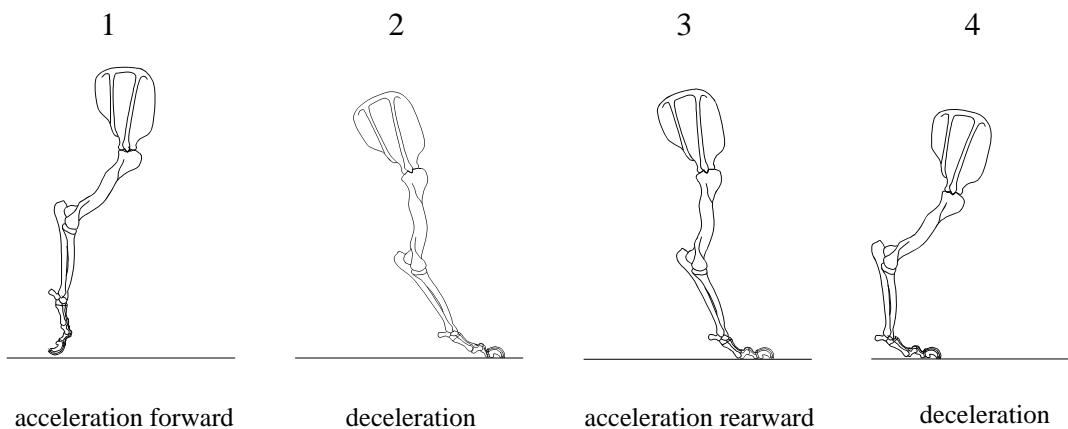
- mass at point *b* moves faster and takes more energy to propel than mass at point *a*
- periodicity depends solely on length of chord, not mass

$$\text{Force of Acceleration} \quad = I \cdot \ddot{\theta} \quad (F = m \cdot a)$$

where I is moment of inertia $I = m \cdot D^2$
and D is the distance from the pendulum's pivot point to its center of mass (equivalent to L in a simple pendulum)

$$\text{Energy of Oscillation} \quad E = \frac{1}{2} I \cdot \dot{\theta}^2 \quad (E = \frac{1}{2} m \cdot v^2)$$

$$\text{Periodicity} \quad T = 2\pi \sqrt{\frac{L}{g}}$$



B

FIGURE 11. Kinematics of oscillation in the front limb of a bear. A) An oscillating pendulum provides a useful analogy for understanding kinematic ramifications of mass distribution and leg length in terms of energy costs associated with acceleration and maintaining limb velocities. B) The four energetic phases of oscillation in a limb — see text for discussion. (Curvilinear and rectilinear formulae shown, with the latter in parentheses)

that a concentrated mass is suspended from a weightless chord, then the length of the limb would suffice for D . Since legs are unevenly shaped and have masses that vary along their lengths, D is difficult to measure but can be assessed qualitatively. From Equations 15 and 16 it is apparent that limbs which are heavy distally are disproportionately costly to accelerate/decelerate because their moment of inertia increases by mass times the square of that mass's distance down the limb (Equation 17).

Given that $a = v / t$, Equation 15 can be rewritten as:

$$F = m \cdot v / t \quad (18)$$

This relationship between mass, velocity, and time of force application has critical implications for the evolution of limbs. First, it means that heavy limbs, especially those that are heavy distally, require forces to be applied for a longer period in order for the limb to reach a given velocity. In other words, it will take a distally heavy limb more time to reach a maximum velocity for a given level of force application compared to a limb of similar mass but with its weight more proximally distributed. Equation 18 also dictates that a long limb will take more time to reach a given velocity than a short limb (for the same force application) because its distal segments must be accelerated to greater velocities (as per the pendulum discussion above). This equates directly to poorer acceleration, unless more force can be applied, which is a principle reason why long legs are generally counterproductive for acceleration. However, Equation 18 dictates that long-legged animals potentially can achieve higher overall velocities because they have a longer period of force application (i.e., longer strides), even though it will take them more time to reach those velocities.

Looking at these relationships from the opposite point of view, Equation 18 also dictates that *less force is required to swing a limb at given velocity if more time is available to apply that force*. That is just what long legged animals accomplish through longer strides. Long-legged animals take longer strides because, like a pendulum, their limbs swing with an inherent periodicity (T , the time taken to complete an oscillation) that is based solely on their length (L):

$$T = 2\pi \sqrt{L/g} \quad (19)$$

where g is the constant of gravity (Hildebrand 1985a). Note that mass plays no role in determining this rate, and that longer legs will have a longer natural periodicity. The principle of natural periodicity in oscillating limbs explains why long-legged animals will have inherently

slower stride rates compared to short-legged animals traveling at similar speeds, and if fewer but larger strides are taken to cover a given distance at a given velocity, then the animal expends less energy. This deduction agrees with the pattern found by physiologists described in earlier sections (e.g., Kram and Taylor's (1990) results). Recall too that longer muscles contract more slowly, and in doing so generate greater overall forces and use energy more efficiently.

It is a common axiom that coursers increase the lengths of their distal limb segments over the course of their evolution, and that many coursers (including fast runners) have long legs. This is not contradictory to the kinematic arguments presented here because coursers evolve limbs that are light distally so that increasing limb length does not add significant distal mass or inertia to the limb compared to the advantages gained by increasing stride length. The result is increased efficiency and often increased top speed (if the animal is not very large).

So although long-legged animals need to oscillate limbs that by definition have longer distal portions, they can do so more efficiently and without bulky muscles as long as acceleration is sacrificed. Their long strides mean that a given distance can be covered more efficiently because the time of force application can be long and slow, and thus less total force needs to be applied. And I showed how, from a kinematic standpoint, long-legged animals do not necessarily need to sacrifice speed, either. Garland's (1983) data on top speeds in mammals, however, seem to indicate that there is a limit to this strategy, which I argued is determined by limits to bone strength—once a leg gets very long or body mass gets very high, bending moments become too great, especially from the forces generated at high speeds and during rapid acceleration. This effect begins to limit speed, and especially acceleration, in animals that get much over 150 kg (Garland's value is 119 kg, but it is an averaged value and I think the real weight limit is probably somewhat higher). Another way to look at this phenomenon is that increasing leg length helps increase top speeds—to a point. That point is reached if legs get too long, or if the mass supported by the limbs becomes too great. Of course, in most cases, both factors come into play but to differing degrees depending on an animal's individual morphology.

In the previous section on levers, I poised the following question: why could not an animal built for sustained running at high speeds also be built for increased power, thereby also making it a good accelerator? For example, why haven't ungulates done this in order to both out-accelerate and out-distance a predator? By now the answer should be apparent: by adding the muscles needed for increased power, animals add weight and hence decrease endurance. Also, powerful

animals increase the mechanical advantage of their limbs and this, too, decreases endurance and potentially decreases limb velocity. Plus, an animal that has evolved powerful muscles with high mechanical advantage in addition to long, light limbs would most likely break those limbs if it tried to run fast, accelerate rapidly, or make any sharp turns. If in response to this dilemma the limb bones are made stronger, they would be more expensive (kinematically) to swing and this hypothetical ungulate would look more like a carnivore, not an ungulate. It would neither be able to out-distance a predator, nor would it be as efficient at foraging as its competitors.

11. SUMMARY OF RELATIONSHIPS BETWEEN MORPHOLOGY AND LOCOMOTOR PERFORMANCE

Throughout this discussion I have been explaining the effects of specific morphological traits on performance aspects of locomotion, such as top speed, acceleration, or endurance. In this summary section, I want to turn the question around and describe the morphological patterns one would predict to find in a large courser built either for acceleration, high top speed, or endurance. I will show that there is much overlap in the latter two categories, but that good accelerators stand out because of their powerful builds and high mechanical advantage, but minimal kinematic improvements.

Good Accelerators

Good accelerators should have muscles that generate high forces, but are not too heavily loaded, so they can also contract quickly (recall that speed of contraction is a primary determinant of power). One key to this formula is leg length. Short limbs normally will have shorter outlevers (L_{out}/L_{in}), increasing mechanical advantage and thus power. Shorter legs also have shorter muscles, which inherently contract more quickly; as long as these muscles have large volume, this becomes a formula for generating high power. Kinematically, short legs have less distal mass, which makes them less costly to accelerate. But short legs necessitate increasing stride rate to achieve a given speed (since stride length is reduced), and this is energetically costly. But animals with long legs and long stride rates take longer to reach top speeds, and that short legs taking rapid strides are able to reach these velocities quicker. Therefore, one would expect the best accelerators to have short legs with short, massive muscles.

Good accelerators sacrifice traits which would make them more efficient for the sake of increasing power output. In order for their bones to be stronger, they are necessarily heavier. Moreover, configuring muscles for

high mechanical advantage decreases their rotational velocities. To make up for this and still achieve high speeds, good accelerators have short legs to eliminate distal mass. This is equivalent to running a car at very high speeds in a low gear, or with very small tires. Such a car, or animal, accelerates well, but is very inefficient and its top speed is limited.

Efficient Runners

Couriers that have evolved to run efficiently and reduce the cost of transport share a host of diagnostic traits that contrast sharply with those found in good accelerators. Universally, efficient couriers reduce overall body weight, which decreases the energy expended lifting the body's mass during each stride. Efficient couriers also evolve legs that are light and long. Long legs increase stride length, reducing the rate of force application and giving the legs more time to reach a given velocity during each stride. This reduces the cost of transport because the muscles can contract more slowly and thus more efficiently. Light limbs, especially those that are light distally, are important for couriers with long legs because distal mass in an oscillating system is expensive to move, and with long legs there is a larger distal region. However, when high speeds are not the goal, distal mass is less of an issue since its mechanical burden is felt most at high speeds. Couriers built for efficiency also tend to evolve larger body size because the cost of transport is inversely proportional to body size. This is mainly because larger animals have relatively longer legs, but also because larger animals are better able to store and release elastic strain energy in stretch tendons.

Features that improve acceleration are not common in efficient runners, and in fact, acceleration is directly compromised by long, light limbs and a large body. Long limbs are especially damning to accelerators for at least four reasons: 1) long limbs reduce mechanical advantage, 2) long limbs typically have long, slender muscles which do not generate high power output, 3) in oscillating systems, longer chords (limbs) take longer to reach maximum oscillating velocities because portions that are more distally located ultimately have to be accelerated to a greater velocity, and 4) long limbs generate larger bending moments and greater bending strains in their bones. In addition, light limbs are not strong enough in large mammals to handle the sudden changes in velocity incurred during acceleration, deceleration, and quick turns because dynamic stresses of these high force activities increase disproportionately with size relative to bone strength. So, whereas a good accelerator can leap to top speeds in a couple of strides, often from a crouched stance, efficient runners can not generate enough power for such feats or handle the stresses, so they take more

strides to get up to maximum speed. Efficient runners often can reach high speeds, but such coursers do not have the bone strength necessary to handle sharp maneuvers at high speeds, and I showed that very large size limits speed. Indeed, it was shown that maximum running speeds in all mammals are limited by the strain limits of bone, not the ability to generate force or power.

Because small and moderate-sized animals experience relatively less dynamic stress than very large animals during equivalent locomotion, they are better suited to exploit niches that depend on acceleration, speed, and agility. In fact, if an animal has evolved such skills, one would predict selection to favor a modest body size, and perhaps even a reduction in body size if its ancestral stock was large-bodied. For instance, a bear evolving into a predatory niche would almost certainly evolve a body size smaller than an average bear. On the other hand, very small animals are limited in their ability to generate enough absolute power and speed to be good predators, and there can be some incentive for them to increase body size, depending on the size of their prey.⁷

But this logic does not hold for very large mammals for all the reasons discussed in thus far, and once a mammal exceeds around 150 kg, it must reduce top speeds and curtail other activities which a smaller mammal can perform safely. Taken together, these axioms of body size mean that small and medium-sized mammals could reach greater absolute top speeds and accelerate to them more quickly by increasing body size. But this strategy works only up to a point (up to a certain body size), after which both top speed and acceleration, but especially the latter, decrease (recall Fig. 7). It is these two competing factors that act to constrain body size in predators.

In Part II, I discuss specific locomotor adaptations in *Arctodus* and why this bear seems to clearly fall in the category of a courser that had evolved to decrease the cost of transport and not for increased speed or accelerating abilities. These conclusions and others discussed in Part III on ecological energetics portray a bear which did not evolve as a powerful super-predator, but rather as a lanky, far-roaming bear, which I propose was a unique scavenging specialist on Pleistocene landscapes.

⁷ Because very small predators are relatively limited in performance, they most commonly hunt prey much smaller than themselves. In that case, predators truly are much larger than their prey in order to outperform them.

LOCOMOTOR ADAPTATIONS AND ECOMORPHOLOGY OF SHORT-FACED BEARS (*Arctodus simus*) IN EASTERN BERINGIA

PART II: SPECIFIC MORPHOLOGICAL FEATURES OF *ARCTODUS*

1. INTRODUCTION

In Part I, I reviewed general features of locomotor dynamics in large quadrupedal mammals. In particular, I examined the ways that body size and limb configuration relate to an animal's ability to accelerate, maneuver, and run at high speeds, and I discussed how scaling factors limit these activities. I showed how all mammals undertake locomotor activities within uniform and predictable safety margins, but that the dynamic forces of locomotion increase with body size faster than the skeletal system's ability to dissipate these forces. This means that high force activities such as rapid acceleration, rapid maneuvering, and running at high speeds, which are critical for predators, become increasingly stressful in larger animals. Therefore, larger animals curtail such activities, which is the primary reason why modern terrestrial predators do not typically exceed 250 kg.

Accordingly, one can phrase the competing foraging models for *Arctodus* (predatory versus scavenging) in terms of their implicit predictions about this bear's locomotor capabilities and post-cranial morphology. These predictions then can be tested using the principles laid down in the previous chapter and morphometric data from *Arctodus*. Part II examines and tests these predictions.

Paleontologists have suggested a wide range of potential prey species for *Arctodus*, including proboscideans (*Mammuthus* and *Mammut*), giant ground sloths (*Megalonyx*), giant beaver (*Castoroides*), bison (*Bison*), musk oxen (*Ovibos* and *Bootherium*), horses (*Equus*), camels (*Camelops*), peccaries (*Platygonus* and *Mylohyus*), caribou (*Rangifer*), moose (*Cervales*), wapiti (*Cervus*), and deer (*Odocoileus*) (Kurtén 1967a; Harrington 1977, 1996; Richards and Turnbull 1995). Given the diversity of body sizes and running speeds found in these potential prey, I think it is best to subdivide the predatory model into two sub-hypotheses: those suggesting *Arctodus* had evolved as a fast cursorial predator specializing on faster, moderate-sized prey, and those suggesting *Arctodus* had evolved to overpower larger, but slower, Pleistocene megaherbivores.

The first hypothesis predicts *Arctodus* to have had features adaptive for either high acceleration (if it was an ambush predator) or high top speeds (if it was a pursuit

predator). In either case, this hypothesis predicts that *Arctodus* should be fairly maneuverable at high speeds. As a cursorial predator then, *Arctodus* should have evolved limb muscles which could generate high power, and limb bones which were strong enough to handle the high stresses of these activities. It also follows (from the Part I) that one would expect a predatory bear using either ambush tactics or cursorial pursuit to evolve a relatively smaller body size, because modern bears tend to push the limits of body size and running abilities (data in the previous chapter showed that in order to handle the stresses of these activities it would be necessary for a very fast bear, or one that accelerated rapidly, to evolve a smaller body size).

The second predatory hypothesis—that *Arctodus* had evolved to overpower very large megafauna—carries certain morphological predictions that differ from the cursorial pursuit hypothesis. First, it does predict large body size, because this would be advantageous for capturing and killing very large prey. But for the same reason, this hypothesis predicts that such a predator would evolve a strong robust build so that it could overpower animals the size of proboscideans and ground sloths, for example. Such prey species are not fast, and it would not require much speed, acceleration, or maneuvering at high speeds to catch them, so one would not expect to find many cursorial features, especially limb-lightening, in this type of predator.

Contrasting with these two predatory hypotheses is my (Mattheus 1994, 1995) proposal that *Arctodus* functioned as a specialized scavenger, a model which also carries a series of morphological predictions. First, based on the assumption that large mammal carcasses would be dispersed far apart and found at unpredictable frequencies (see Part III), it predicts selection for increased locomotor efficiency because *Arctodus* would have had to search very large home ranges while foraging. I showed in the previous chapter that locomotor efficiency is gained by increasing body size, reducing relative body weight (i.e., a bigger but more gracile body), and increasing leg length. Thus, these are the main post-cranial features predicted by the scavenging model. Since such a scavenger would not need to pursue and catch prey at fast speeds, or accelerate rapidly, it could sacrifice limb strength and power for muscular and kinematic efficiency. This model predicts that *Arctodus* would

experience additional selective pressure to increase body size because a larger body would make it a better competitor against other carnivores that challenged it for control over carcasses. In Part III, I discuss how a larger animal also is better suited metabolically for dealing with an unpredictable boom-and-bust resource such as carrion.

There are two main sections to Part II. In the first, I address the fundamental question of whether *Arctodus* was cursorially adapted. To do so, I examine the proportions of its limbs both in absolute terms and using allometric analyses whereby I compare *Arctodus* with other bears and other Carnivora. This provides insight into the direction of *Arctodus'* divergence away from its relatives. Then I evaluate important conformational features of its appendicular and axial skeleton, examining how *Arctodus* swung its limbs for more clues into the cursorialism debate. In the second section, I reconstruct the gait, speed, and locomotor style of short-faced bears by taking a new look at the relationship between *Arctodus'* leg length and back length, and by drawing upon some formulae discussed in the previous chapter. The multitude of morphological evidence presented throughout this chapter most strongly supports the hypothesis that this carnivore was cursorially adapted and optimized for sustainable long range locomotion at moderate speeds—traits which are more adaptive for a scavenging specialist than an active predator. In the next chapter I examine the ecological implications of this niche and propose a model for how it evolved in Pleistocene environments.

2. WAS ARCTODUS CURSORIALLY ADAPTED?

To many paleontologists, the degree of cursorial adaptations in *Arctodus* is the primary unresolved issue preventing us from reconstructing specific aspects of this bear's foraging ecology and life history. In his predatory model, Kurtén (1967a) used relative limb length to argue that *Arctodus* was highly cursorial, and capable of achieving high speeds, but Emslie and Czaplewski (1985) interpreted the data on limb length differently and argued that *Arctodus* was non-cursorial (discussed more below). Even though stable isotope data reveal that *Arctodus* was carnivorous (Mattheus 1994, 1995; Bocherens *et al.* 1995), there still are a number of different ways that *Arctodus* could have locomoted and foraged for meat, as outlined above, meaning the cursorial question is still of prime importance. Indeed, questions about *Arctodus'* predatory skills (i.e., was it a high speed pursuit predator, an ambush predator that relied on rapid acceleration, or a scavenging specialist built for locomotor efficiency) seem mute if one can not first establish whether or not it had cursorial advancements over other bears. Traditionally, this debate has focused on discussions

regarding the relative lengths of proximal and distal limb segments. I will review this evidence and explain why proximal-distal limb length is a poor indicator of cursorialism in bears, followed by a look at other indicators that provide better clues into *Arctodus'* cursorial abilities.

Proximal-Distal Limb Proportions

The ratio of proximal:distal segment lengths in limbs is often used as an indicator of cursorialism for kinematic reasons discussed in the previous chapter. To reiterate, as cursors evolve longer legs the distal segments almost always become preferentially elongated because they are lighter. The problem with applying this principle to *Arctodus* is that it does not work very well in bears, which have very heavy distal limb segments due to their large unspecialized feet. It would not be of any kinematic advantage for a bear to evolve relatively longer distal limb segments without concomitantly making them lighter. This would include reducing the size of the feet and the robustness of the propodia. In fact, elongation of distal limb segments may be a poor indicator of cursorialism in animals that are in the early stages of cursorial evolution, especially in an incipient cursor whose ancestors possessed large feet. With these qualifications in mind, I will briefly review the patterns of elongation found in *Arctodus* and other bears.

Humeroradial (R/H) and Femurotibial (T/F) indices for short-faced bears as well as other bears and other Carnivora are shown in Table 2. These indices demonstrate how the distal two bones (radius and tibia) are relatively unmodified in bears, including short-faced bears, compared to traditional cursorial species. Often, R/H and T/F values exceed 90 - 100 in lions, cheetahs, other felids, canids and cursorial ungulates (Gonyea 1976), but they are much lower in bears and the index values for *Arctodus* are not appreciably different than for other ursids. The greatest difference between bears and other more specialized carnivores appears in the proportions of the hind limb. Table 3 shows the relative contribution of each bone (including metapodials) to limb length in a variety of bear species. These values also reveal that the relative composition of the limbs is similar among bears, and that the distal bones of *Arctodus* are even somewhat shortened.

Values for limb segment lengths in the single *Arctodus* specimen measured by Emslie and Czaplewski (1985) are shown in Table 2. This bear had unusually low R/H and T/F index values, which these authors used as evidence against cursorialism. Moreover, they chose to compare this specimen to modern brown bear samples which included some individuals with unusually high indices (values in Table 2). Still, these authors argue that their value for *Arctodus* is more accurate than Kurtén's

TABLE 2. Humeroradial (R/H) and Femurotibial (T/F) indices in *Arctodus* compared to other carnivores. (R/H index = radius length / humerus length X 100; T/F index = tibia length / femur length X 100).^{1,2}

Species (location)	(R/H index)	(T/F index)	Sample Size		Source
			R/H, T/F		
<i>Arctodus</i> (various)	85.6	74.5	6/8, 7/8 ³		Kurtén (1967a)
<i>Arctodus</i> (various)	86.1	74.9	13/13, 11/13		calculated from data in Richards <i>et al.</i> (1996)
<i>Arctodus</i> (Nevada)	78.2	71.4	1, 1		Emslie and Czaplewski (1985)
<i>Arctodus</i> (Indiana)	80.8	73.4	1, 1		Richards and Turnbull (1995)
<i>Arctodus</i> (Beringia)	84.2	78.9 ⁴	4/4, 3/3		this study
Spectacled bear	83.4	73.9	4/4, 4/4		Kurtén (1966b)
brown bear	86.0	76.5	1, 1		Kurtén (1966b)
brown bear	88.4 (83.0 - 95.0) ⁴	73.5 (70.4 - 75.1) ⁵	9, 9		Emslie and Czaplewski (1985)
brown bear	87.7 (83.6 - 91.0) ⁴	73.7 (71.1 - 77.0) ⁵	5/5, 5/5		this study
polar bear	87.7 (87.0 - 88.8) ⁴	74.6 (72.2 - 76.3) ⁵	4/4, 4/4		this study
black bear	88.4 (82.8 - 90.2) ⁴	78.2 (75.2 - 82.7) ⁵	6/6, 6/6		this study
wolf	100.0	106.0	6, 6		this study
cheetah	103.3	105.0	6, 6		Gonyea (1976)
lion	98.3	90.6	6, 6		Gonyea (1976)
leopard	90.5	94.8	6, 6		Gonyea (1976)
tiger	89.8	90.1	7, 7		Gonyea (1976)
puma	89.5	99.6	6, 6		Gonyea (1976)

¹ Preferably, values should be calculated on limb elements from the same animal rather than composites of isolated bones. Since few paired elements exist for fossils, *Arctodus* values are calculated using average lengths for each bone. Index ranges are given when calculated on multiples of single individuals. Ranges do not exist for others because indices are calculated from composite averages or were not listed by authors.

² bone length = the greatest length parallel to the shaft

³ Kurtén's sample size is presumably based on the number of samples listed in his various tables

⁴ this value is probably too high because one of the three femurs was unusually small

⁵ variation in ratios seems to be most associated with specimen age, as juveniles tend to have relatively longer distal segments (see text)

TABLE 3. Relative lengths of limb bones as a percentage of whole limb length in *Arctodus* versus other bears.¹

limb element	short-faced bear ²	short-faced bear (Kurtén) ³	brown bear ⁴	brown bear (Kurtén) ⁵	polar bear ⁶	black bear ⁷	black bear (Kurtén) ⁸	spectacled bear ⁹	Florida cave bear ¹⁰
humerus	47.6	48.2	46.2 (46.0-46.5)	47.5	46.8 (46.8, 46.8)	46.9 (46.4, 47.4)	46.4	48.5	48.9
radius	41.0	40.0	41.0 (40.3-41.6)	40.8	40.8 (40.7, 40.9)	41.7 (41.4, 41.9)	41.5	40.2	40.8
longest metacarpal ¹¹	11.5	11.8	12.8 (12.2-13.3)	11.7	12.4 (12.3, 12.5)	11.5 (11.3, 11.6)	12.0	11.4	10.3
femur	51.1	51.3	49.9 (49.7-50.2)	49.8	50.6 (50.3, 50.9)	50.2 (50.1, 50.2)	49.9	49.2	51.5
tibia	38.3	38.3	37.4 (36.8-38.3)	38.1	37.2 (36.7, 37.7)	38.8 (38.7, 38.9)	38.5	39.9	38.0
longest metatarsal ¹²	10.6	10.5	12.6 (12.0-13.0)	12.1	12.2 (12.0, 12.3)	11.1 (11.0, 11.1)	11.7	10.9	10.5

¹ Ideally, values should be calculated from complete skeletons rather than composites of isolated bones. However, very few complete skeletons are available for most of these species. It is noted below whether values are from complete skeletons or composites.

² composite values calculated from averages of multiple single elements in Richards *et al.* (1996, appendix 2)

³ composite values calculated from averages of multiple single elements in Kurtén (1967, Table 27)

⁴ calculated individually on 3 complete brown bear limbs in the University of Alaska Museum (UAM 14784, 16559, 19765); average listed with range in parenthesis

⁵ calculated from measurements in Kurtén (1966, Table 36) from a single, complete European brown bear

⁶ calculated individually on 2 complete polar bear limbs in the University of Alaska Museum (UAM 16545, 16546); average listed with range in parentheses

⁷ calculated individually on 2 complete black bears limbs in the University of Alaska Museum (UAM 3144, 14783); average listed with range in parentheses

⁸ calculated from measurements in Kurtén (1966, Table 36) made on 5 separate individuals; Kurtén listed the resultant average but no other statistics

⁹ calculated from measurements in Kurtén (1966, Table 36) made on a single spectacled bear

¹⁰ composite values calculated from averages of multiple single elements in Kurtén (1967, Table 27)

¹¹ MC III in *Arctodus*; MC IV in other Tremarctines and all Ursines

¹² MT IV in Tremarctines; MT V in Ursines

because their's was derived from a single individual whereas Kurtén's value was calculated from composite measurements (e.g., femurs and tibias which came from different individuals). However, data from a single specimen from Indiana, measured by Richards and Turnbull (1995), and composite values from Beringia (this study), seem to confirm that Emslie and Czaplewski's value for *Arctodus* is lower than average and that their values for brown bears are somewhat high (Table 2). I believe these discrepancies have arisen because there can be a wide range in proximal-distal indices within a given species, and it is my experience that the variation seems to be most influenced by the specimen's age, as young mammals have relatively longer distal segments (unpublished data). I have observed, for instance, that the occasional R/H values over 90 in bears are found only in individuals less than a few years old, so Emslie and Czaplewski's (1985) value of 95 most likely comes from a very young, and thus atypical, specimen. This phenomenon, along with individual variation in index values has muddled the question of whether *Arctodus* had relatively long distal limb segments, and thus whether or not it was cursorial.

The above data indicate that *Arctodus* did not evolve significantly longer distal leg segments relative to Ursine bears or even its closer Tremarctine relatives. However, because such a strategy is unlikely to impart any significant energetic benefits to an animal with limbs that are distally heavy, this fact does not refute the notion that *Arctodus* had cursorial tendencies. Therefore, the next logical step is to look for ways that *Arctodus* may have been reducing distal limb weight—a feature one might see in a courser early in its evolution.

Limb Mass and Allometry

a. Podials

Kurtén (1967a) suggests that, in general, the podials of *Arctodus* (e.g., scapholunar, navicular, calcaneum, pisiform) were built somewhat lighter compared to other Tremarctine and Ursine bears. This assertion and its implications for locomotion are difficult to quantify in a meaningful way. Nonetheless, even slight reduction in the weight of the feet may impart significant kinematic advantages because the feet's distal position amplifies the effect of their mass (Part I). Thus, in terms of the cursorial debate, podial morphology (as summarized by Kurtén 1967a) weakly falls in favor of cursorialism.

b. Metapodials

In contrast, the metapodials of *Arctodus* do display a clear trend towards weight reduction: while they are absolutely longer than in other bears, they are relatively both shorter and more slender (shown by Kurtén 1966a,

1967a). Kurtén's (1967a) Table 16 and his Figs. 24 and 27 reveal how the allometry of *Arctodus'* metapodials is indeed transposed, indicating a Type II form of compensatory growth (see Part I allometry section). My calculations of width/length percentages from Kurtén's data indicate that this transposition reduces the relative width (thus density) of the metapodials. This value for width/length is 13.5 % for *Arctodus*, 17 % for brown bears, 20 % for cave bears, and 18 % for *T. floridanus*.

While *Arctodus'* metapodials are absolutely the longest among bears, they are not relatively longer for *Arctodus'* size or relative to its other limb bones (Table 3). Therefore, the slenderness of these bones is most logically interpreted as a weight-reducing measure, not an elongation of distal segments. Kurtén apparently thought that their absolute length alone was evidence for cursorialism, but data in Table 3 show that the metapodials were not lengthened compared to relative lengths in other bears. Furthermore, the fact that all other long bones in *Arctodus'* limbs increased in relative length indicates that the metapodials may have been selectively shortened. This is consistent with my argument that *Arctodus* was in the initial stages of cursorial evolution in that it reduced limb weight, but not to the point where increasing distal limb length brought it any kinematic advantage. However, it should be pointed out that short metapodials seem to be the general trend for Tremarctine bears, as indicated by values in Table 3 for the spectacled bear (*Tremarctos ornatus*) and the extinct Florida cave bear (*Tremarctos floridanus*) — two bears which are justifiably considered to be non-cursorial (Kurtén 1966a, 1967a, Kurtén and Anderson 1980).

c. Long Bones

I have quantified the gracilenss of the limbs in *Arctodus* and other bears using the width:length ratio (W/L) of the five major limb bones (Table 3). Assuming equal densities and cortical thickness, this index of gracilenss functions as an indicator of relative limb weight. The results show that all four elements in *Arctodus* were significantly more gracile, and thus relatively lighter, than in all species of *Ursus*— both when compared to each species individually or to the genus as a whole. This is even more significant considering the larger size of *Arctodus*; as per discussions in Part I, larger animals that engage in similar activities as smaller animals must evolve thicker bones in order to handle the increased stress. *Arctodus* did not do this; so, considering its size, it must have been incurring relatively lower stresses than modern bears.

Next I want to take a closer look at the allometries of the humerus, radius, ulna, femur and tibia in *Arctodus* compared to other bears of differing phylogenetic distance from *Arctodus*. This approach will help quantify

the direction and extent of morphological divergence in *Arctodus*' limbs. For instance, was *Arctodus* simply a scaled up Tremarctine bear, or was it convergent on the Ursine body plan? Only in the latter case will it be justifiable to draw analogies about locomotion, ecology, and behavior between *Arctodus* and these more familiar bears. Furthermore, since it has been suggested that short-faced bears and brown bears became competitors in North America (Kurtén and Anderson 1974, 1980; Harington 1977, 1980; Richards *et al.* 1996), one might predict certain convergences in body shape. Kurtén's (1967a) work left many of these questions about long bones unanswered or at least ambiguous, even though he made conclusions that are dependent on their answers.

In discussing these patterns of limb bone allometries, I will be referring directly to the data presented in Tables 4 and 5 and Figs. 12 - 16, and to concepts and terms discussed in the scaling and allometry sections of Part I. Note in particular that I only will be comparing lines of allometry for individual species, not higher taxa, as it is misleading for the considerations at hand to compare combined allometries—such as a comparison between the allometry of short-faced bears versus the combined allometry for all other Ursids (see reasons in Part I). Also, I will wait to discuss the overall implications to locomotion until after summarizing the specific patterns in each bone. It was not always possible to obtain large sample sizes for every bone in every species, so some of the following conclusion could be challenged by larger data sets. For similar reasons, some tests of significance indicated in Tables 4 and 5 may be spurious, and I indicate where the data are ambiguous. Finally, I would point out that the following discussion exemplifies how difficult it is to reveal true functional meaning in bone proportionality by comparing just simple proportions (e.g., length vs. width) or just lines of allometry. Both need to be used together to examine the functional effects of the way bone proportionality changes with size, and that is what I attempt to do.

HUMERUS (Fig. 12): Compared to its Tremarctine relatives, the humerus of *Arctodus* displays a classic form of Type I compensatory growth (recall that compensatory growth typically compensates for size, not function). Slopes for all three Tremarctines are over 1.0, and without some form of relative compensation, *Arctodus*' humerus would be hugely robust. The transposition in its allometry effectively gives it a somewhat similar proportionality (W/L ration of 9.0) compared to the other two Tremarctines, despite its size. But in order for *Arctodus* to withstand similar (scaled up) dynamic forces of locomotion as a smaller bear, it should be built relatively more robustly. Since it had a relatively weaker humerus for its mass, *Arctodus* must not have been

experiencing equivalent levels of force or running in a similar fashion as *T. ornatus* or *T. floridanus*.

The same sort of pattern holds true when the humerus of *Arctodus* is compared to Ursine bears. In fact, Ursine and Tremarctine humeri vary little in proportions or allometry, with the exception of short-faced bears and perhaps polar bears. Short-faced bears show the most reduction in relative strength and weight of all bears, while polar bears seem to have unusually robust humeri, although the sample size for polar bears is small in this study.

RADIUS/ULNA (Figs. 13, 14): *Arctodus'* radius allometry departs strongly from the Tremarctine plan. It is both transposed and has a very low α (< 1); both reduce W/L, making it a more gracile bone in *Arctodus*. Because $\alpha < 1$, the radius in *Arctodus* actually gets progressively more gracile with increasing size. The relationship between the radii of *T. floridanus* and *T. ornatus* displays a good example of size enlargement without a compensatory change in growth. The α of the radius in these two species are not significantly different from each other (Student's *t*-test_{2-tailed} $P = 0.280$), but their absolute W/L ratios are different (Student's *t*-test_{2-tailed} $P = 0.036$). Effectively, extending *T. ornatus'* line of allometry into the size range of *T. floridanus* gives the latter bear a very robust radius—the widest of all bears tested. The compensatory allometry of *Arctodus* (both Type I and II) produces proportions of the radius (mean W/L = 5.4) more in line with the diminutive spectacled bear. For a bear the size of *Arctodus*, this extreme gracilenss would make for a relatively much lighter and weaker radius.

In order to make a definitive functional assertion about the radius, data are needed for the ulna, since it is possible that any reduction in the radius is compensated for by strengthening the ulna. Data on Tremarctine ulnae show that this bone does indeed get absolutely more robust with size; mean W/L is 4.6 in *T. ornatus* but reaches 5.3 in *T. floridanus* and 5.5 in *Arctodus*. However, the radius and ulna both are robust in *T. floridanus*, and the two bones have parallel proportions in *T. ornatus*, meaning these two species probably had forearms with comparable strength, weight, and performance relative to their size. In *Arctodus*, however, only the ulna remains proportionally stout, but in my estimate, not enough so to completely compensate for the light radius; the forearm of *Arctodus* thus appears to have been more gracile and differed functionally from other Tremarctines.

The allometry of *Arctodus'* radius also deviates strongly from Ursine bears, and in a way similar to its deviation from Tremarctines. In fact, with the exception of *Arctodus*, Ursine and Tremarctine allometries are quite

TABLE 4. Gracilens Index in long bones of Ursids measured as *least shaft diameter* \div *length* \times 100

species	humerus ¹			radius ²			ulna ³			femur ⁴			tibia ⁵		
	mean	n	SEE	mean	n	SEE	mean	n	SEE	mean	n	SEE	mean	n	SEE
<i>A. simus</i>	9.0	10	.1694	5.4	8	.1071	5.5	11	.1385	8.8	15	.1250	10.1	13	.1524
<i>T. ornatus</i>	7.4*	4	.9569	5.3	4	.2245	4.6*	4	.1190	7.6*	4	.5233	7.5*	3	.0800
<i>T. floridanus</i>	9.0	7	.3795	6.1*	7	.1795	5.2	6	.1340	9.3*	9	.0970	9.0*	10	.2188
<i>U. arctos</i>	8.5*	11	.2937	5.3	6	.3570	5.2	4	.0510	8.1*	15	.2179	8.1*	5	.2846
<i>U. maritimus</i>	9.1	5	.2380	5.8	4	.2260	5.8	4	.0712	8.4	6	.2233	8.2*	4	.0997
<i>U. americanus</i>	8.5*	7	.1906	5.4	6	.1742	5.0*	7	.1599	8.0*	7	.1532	8.1*	6	.0959
Tremarctines ⁶	8.7*	21	.2192	5.6	19	.1240	5.3	21	.1117	8.8	28	.1427	9.4*	26	.2001
Ursines	8.7*	23	.1543	5.5	16	.1585	5.3	15	.1204	8.2*	28	.1250	8.1*	15	.0984
combined Ursid ⁷	8.7*	44	.1324	5.6	35	.0983	5.3	36	.0814	8.5*	56	.1024	8.9*	28	.1619
test of significance (<i>P</i>) in Tremarctinae vs. Ursinae				<i>P</i> _{1-tailed} = .000			<i>P</i> _{1-tailed} = .000			<i>P</i> _{1-tailed} = .000			<i>P</i> _{1-tailed} = .001		<i>P</i> _{1-tailed} = .038

* index significantly different than *Arctodus* at *P*_{1-tailed} \leq .05, using t-test and assuming equal variance

¹ minimum transverse diameter of shaft

² minimum anterior-posterior diameter of shaft

³ minimum transverse diameter of shaft above capitulum

⁴ minimum shaft diameter in transverse plane

⁵ minimum shaft diameter; can be in any plane

⁶ values shown include *Arctodus*, but test of significance calculated as *Arctodus* versus the other two Tremarctines

⁷ values shown include *Arctodus*, but test of significance calculated as *Arctodus* versus all other bears

TABLE 5. Linear ($y = ax + b$) and power ($y = bx^\alpha$) functions for length (x) versus width (y) in long bones of Ursids. Power functions indicate lines of allometry where α equals the allometric constant. W/L ratio from Table 4 provided to indicate when a change of allometry may represents compensatory growth (see text and Fig. 3, Part I). Lines are plotted in Figs. 12 - 16. (Testing of H_0 is by Analysis of Variation for linear equations, and by Student's t -test for power equations.)

HUMERUS species (n)	W/L (Table 4)	Linear Equation				Power Equation			
		equation	r^2	SEE (of y estimate)	$P_{H_0: \alpha = 0}$	equation	r^2	SEE (of slope)	$P_{1\text{-tailed}}_{H_0: \alpha = 0}$
<i>A. simus</i> (10)	9.0	$y = .1196x - 13.9724$.95	2.1483	.0000	$y = .0169x^{1.27}$.93	.1232	.0000
<i>T. ornatus</i> (4)	7.4	$y = .1200x - 11.0569$.65	2.3295	.1949	$y = .0009x^{1.80}$.68	.8832	.0892
<i>T. floridanus</i> (7)	9.0	$y = .1056x - 6.0006$.60	4.3914	.0417	$y = .0283x^{1.19}$.67	.3756	.0124
<i>U. arctos</i> (11)	8.5	$y = .1286x - 12.5093$.91	2.5315	.0001	$y = .0082x^{1.40}$.91	.1624	.0000
<i>U. maritimus</i> (5)	9.1	$y = .1451x - 18.9985$.92	1.3167	.0091	$y = .0023x^{1.59}$.92	.2663	.0952
<i>U. americanus</i> (7)	8.5	$y = .0679x + 4.9906$.66	1.5416	.0272	$y = 3.9039x^{0.81}$.68	.2450	.2316

TABLE 5 (continued)

RADIUS species (<i>n</i>)	W/L (Table 4)	Linear Equation					Power Equation				
		equation	r ²	SEE (of y estimate)	P H ₀ : <i>a</i> = 0	equation	r ²	SEE (of slope)	P _{1-tailed} H ₀ : <i>a</i> = 0	P _{1-tailed} H ₀ : <i>a</i> ≠ 0	
<i>A. simus</i> (8)	5.4	y = .0452 <i>x</i> + 3.4752	.72	1.3869	.0074	y = .1369 <i>x</i> ^{.84}	.73	.2079	.0034	.2354	
<i>T. ornatus</i> (4)	5.3	y = .0731 <i>x</i> - 4.0135	.63	1.0768	.2070	y = .0091 <i>x</i> ^{.33}	.62	.7426	.1076	.3501	
<i>T. floridanus</i> (7)	6.1	y = .0860 <i>x</i> - 7.6395	.89	1.1781	.0013	y = .0054 <i>x</i> ^{.42}	.87	.2511	.0012	.0776	
<i>U. arctos</i> (6)	5.3	y = .1046 <i>x</i> - 14.6531	.98	0.8189	.0001	y = .0004 <i>x</i> ^{.87}	.98	.1331	.0001	.0014	
<i>U. maritimus</i> (4)	5.8	y = .0933 <i>x</i> - 10.6089	.83	1.3200	.0897	y = .0017 <i>x</i> ^{.62}	.85	.4766	.0392	.1615	
<i>U. americanus</i> (6)	5.4	y = .0823 <i>x</i> - 7.0943	.79	1.0274	.0170	y = .0030 <i>x</i> ^{.52}	.84	.3372	.0054	.0989	

ULNA	W/L (Table 4)	Linear Equation					Power Equation				
		equation	r ²	SEE (of y estimate)	P H ₀ : $\alpha = 0$	equation	r ²	SEE (of slope)	P _{1-tailed} H ₀ : $\alpha = 0$	P _{1-tailed} H ₀ : $\alpha = 1$	
<i>A. simus</i> (11)	5.5	y = .0807 x - 11.5234	.87	1.7900	.0000	y = .0043 x ^{1.42}	.83	.2175	.0001	.0428	
<i>T. ornatus</i> (4)	4.6	y = .0304 x + 3.8135	.54	.5709	.2667	y = .3119 x ^{0.65}	.51	.4502	.1423	.2591	
<i>T. floridanus</i> (6)	5.2	y = .0927 x - 13.2913	.43	1.1396	.1542	y = .0006 x ^{1.78}	.44	1.0007	.0748	.2396	
<i>U. arctos</i> (4)	5.2	y = .0542 x - .7731	.96	3525	.0212	y = .0355 x ^{1.07}	.96	.1583	.0107	.3591	
<i>U. maritimus</i> (4)	5.8	y = .0571 x + .4054	.91	.5920	.0480	y = .0625 x ^{0.99}	.90	.2361	.0263	.4850	
<i>U. americanus</i> (6)	5.0	y = .391 x + 3.0932	.47	1.2518	.1340	y = .1885 x ^{0.76}	.48	.3960	.0628	.2886	

TABLE 5 (continued)

FEMUR		Linear Equation					Power Equation				
species (<i>n</i>)	W/L (Table 4)	equation	r ²	SEE (of y estimate)	P H ₀ : <i>a</i> = 0	equation	r ²	SEE (of slope)	P _{1-tailed} H ₀ : α = 0	P _{1-tailed} H ₀ : α = 1	
<i>A. simus</i> (15)	8.8	y = .1054 <i>x</i> - 9.4423	.90	2.5168	.0000	y = .0293 <i>x</i> ^{1.17}	.89	.1156	.0000	.0826	
<i>T. ornatus</i> (4)	7.6	y = .1519 <i>x</i> - 20.4205	.57	2.9531	.2482	y = .0003 <i>x</i> ^{2.02}	.54	1.3068	.1314	.2584	
<i>T. floridanus</i> (9)	9.3	y = .1078 <i>x</i> - 6.0827	.95	1.1324	.0000	y = .0361 <i>x</i> ^{1.16}	.96	.0947	.0000	.0675	
<i>U. arctos</i> (15)	8.1	y = .1048 <i>x</i> - 9.6964	.82	3.1664	.0000	y = .0160 <i>x</i> ^{1.27}	.80	.1759	.0000	.0744	
<i>U. maritimus</i> (6)	8.4	y = .1030 <i>x</i> - 8.1830	.81	2.5452	.0135	y = .0190 <i>x</i> ^{1.24}	.83	.2766	.0054	.2173	
<i>U. americanus</i> (7)	8.0	y = .1061 <i>x</i> - 8.340	.87	1.2658	.0020	y = .0133 <i>x</i> ^{1.31}	.90	.2000	.0006	.0909	

TIBIA		Linear Equation					Power Equation				
species (<i>n</i>)	W/L (Table 4)	equation	r ²	SEE (of y estimate)	P H ₀ : <i>a</i> = 0	equation	r ²	SEE (of slope)	P _{1-tailed} H ₀ : α = 0	P _{1-tailed} H ₀ : α = 1	
<i>A. simus</i> (13)	10.1	y = .1331 <i>x</i> - 13.5728	.94	1.7445	.0000	y = .0140 <i>x</i> ^{1.33}	.93	.1117	.0000	.0066	
<i>T. ornatus</i> (3)	7.5	y = .0452 <i>x</i> + 6.2817	.87	.2053	.2339	y = .6398 <i>x</i> ^{.60}	.86	.2377	.1202	.1672	
<i>T. floridanus</i> (10)	9.0	y = .1600 <i>x</i> - 20.0259	.93	1.1632	.0000	y = .0015 <i>x</i> ^{1.72}	.92	.1811	.0000	.0020	
<i>U. arctos</i> (5)	8.1	y = .1315 <i>x</i> - 13.3426	.83	1.5289	.0320	y = .0031 <i>x</i> ^{1.58}	.81	.4373	.0182	.1383	
<i>U. maritimus</i> (4)	8.2	y = .0677 <i>x</i> + 4.3681	.95	1.2964	.0276	y = .2156 <i>x</i> ^{0.83}	.94	.1523	.0160	.1902	
<i>U. americanus</i> (6)	8.1	y = .0926 <i>x</i> - 3.0291	.86	.6255	.0072	y = .0307 <i>x</i> ^{1.17}	.87	.2225	.0031	.0101	

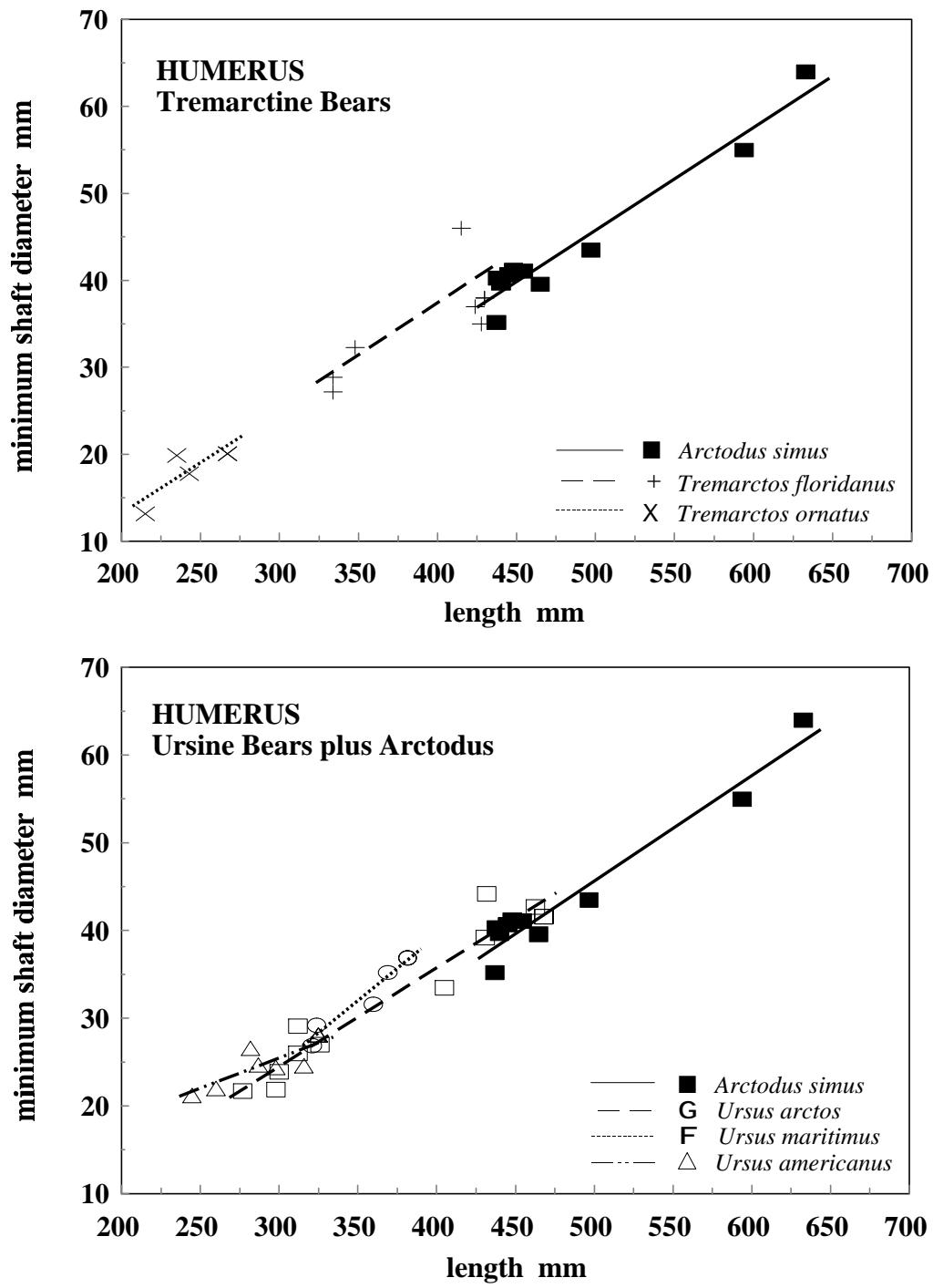


FIGURE 12. Humerus allometry in bears. Line formulas located in Table 5. Minimum diameter is in transverse plane. *Discussion in text.*

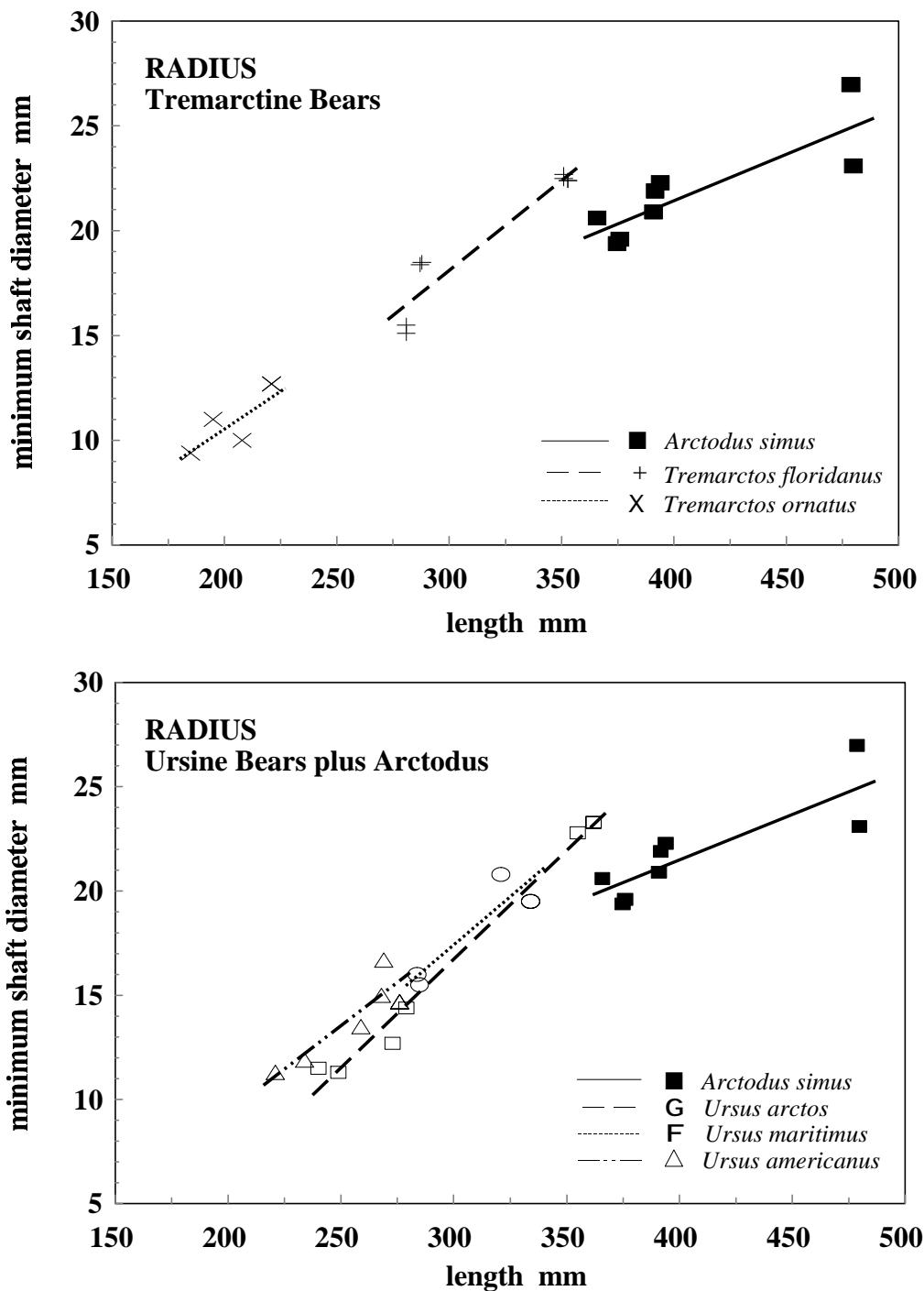


FIGURE 13. Radius allometry in bears. Line formulas located in Table 5. Minimum diameter is in anterior-posterior plane. *Discussion in text*.

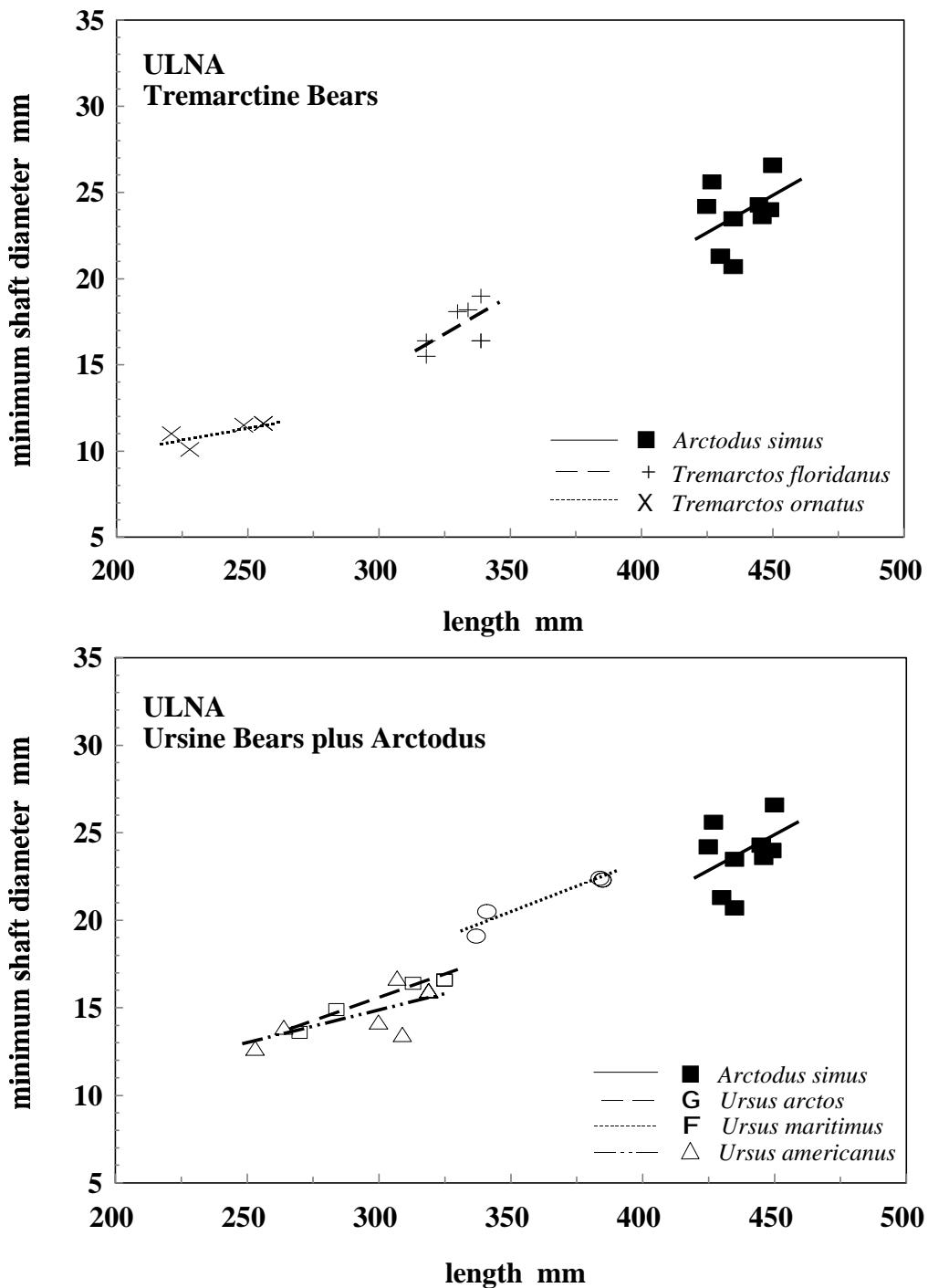


FIGURE 14. Ulna allometry in bears. Line formulas located in Table 5. Minimum shaft diameter is least transverse diameter above the capitulum. *Discussion in text.*

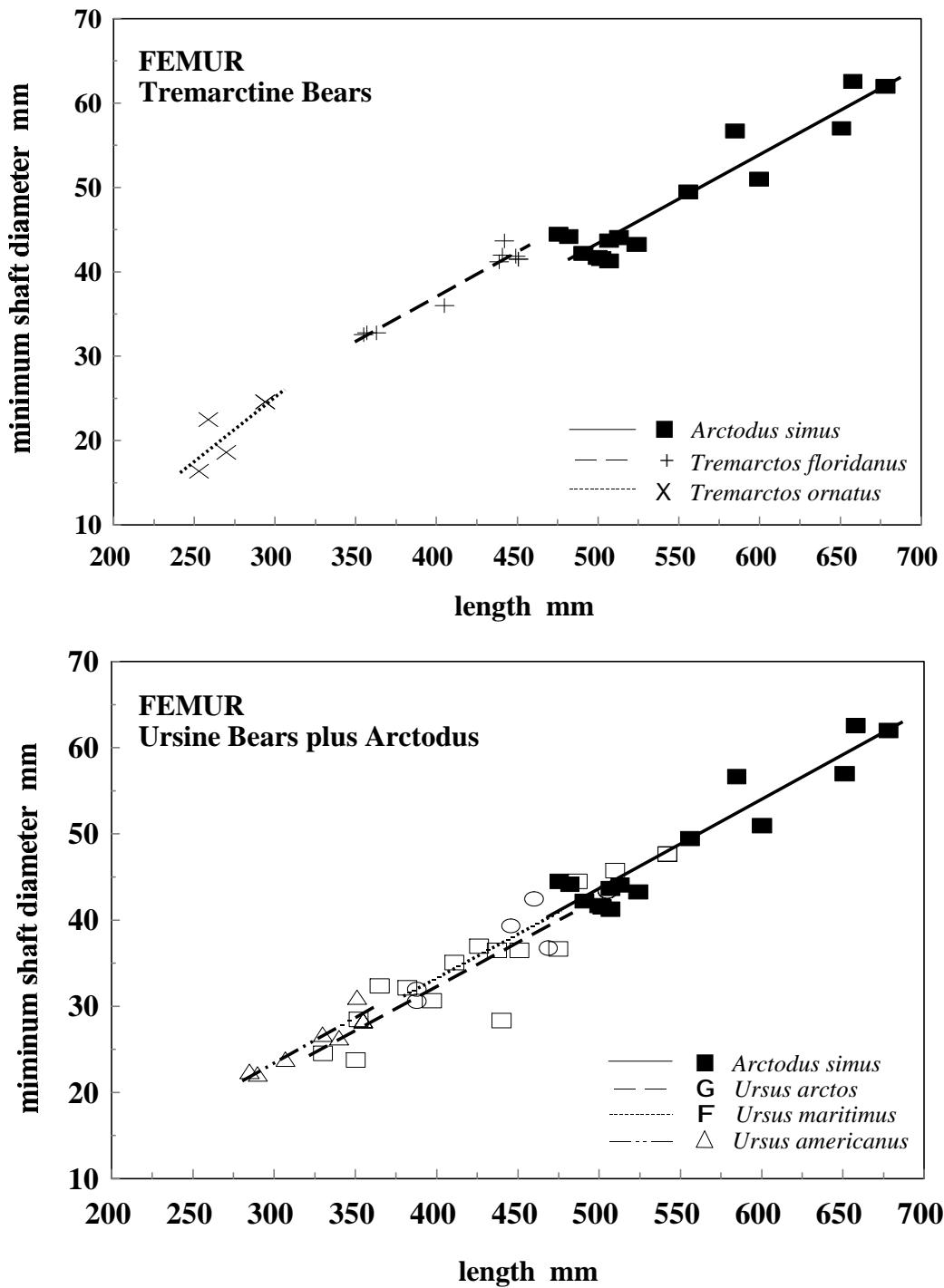


FIGURE 15. Femur allometry in bears. Line formulas located in Table 5. Minimum diameter is in transverse plane. *Discussion in text.*

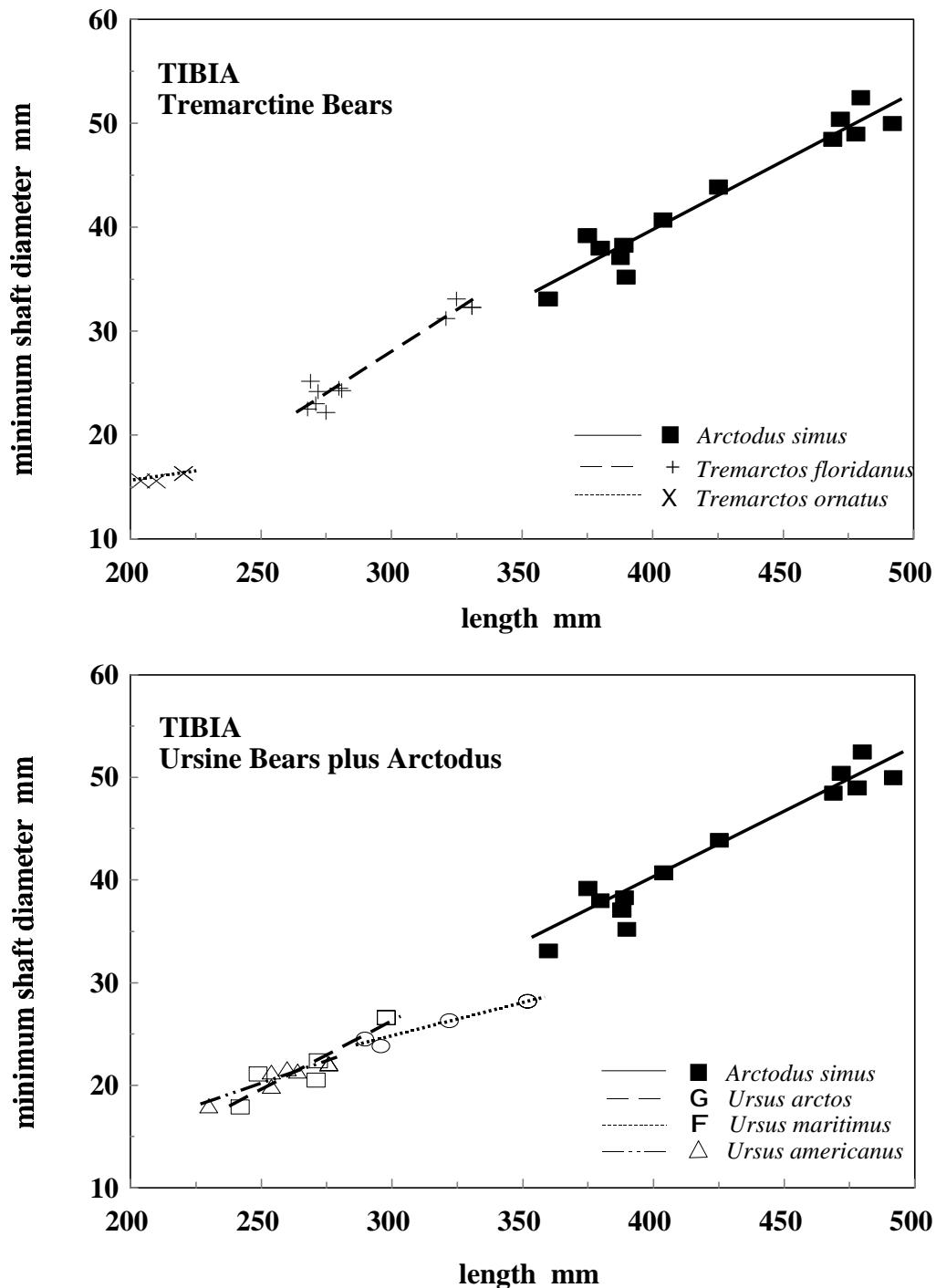


FIGURE 16. Tibia allometry in bears. Line formulas located in Table 5. Minimum diameter along shaft can be in any plane. *Discussion in text.*

similar for the radius. Values for α tend to be higher in Ursines, so their radii get somewhat stronger and heavier in larger individuals of a given species compared to Tremarctines, but *T. floridanus* stands out because of its high absolute W/L ratio. The relative transposition of *Arctodus*' allometry and its extremely low α give this largest of bears nearly the lowest mean W/L for its radius. Considering the increased static and dynamic forces imparted by its large size, *Arctodus*' radius was substantially lighter and weaker than that of all other bears.

The ulna of *Arctodus* did not increase proportionately with size to compensate for a lighter radii, whereas it did in other Tremarctines. The same pattern essentially holds true when *Arctodus* is compared to Ursines. Bear ulnae in general have low α values compared to other long bones, and while it seems that this bone increases in robustness with size at a fast rate in *Arctodus* (i.e., high α) this trend probably is not as strong as it appears. I make this statement because the data in Fig. 14 (and the statistics in Table 5) show that there is considerable variation in ulnae proportions within a species, especially *Arctodus*, and the apparently high α (1.42) in *Arctodus* is just barely statistically distinct from 1 ($P = 0.0428$).

Overall, the forearm of *Arctodus* was not a scaled up version of any bear in consideration, nor does its allometry compensate (functionally) for its large size—both the radius and ulna of *Arctodus* were relatively weak and light.

FEMUR (Fig. 15): Like the humerus, the femur allometry of *Arctodus* exhibits a clear transposition compared to the other two Tremarctines. And since the absolute proportion (W/L) of *Arctodus*' femur is significantly less than that of the other two, the arguments presented for the humerus also apply here, but even more so—the femur of *Arctodus* was relatively lighter and weaker than that of its closest relatives.

Functionally, one gains better insight into the proportions of *Arctodus*' femur by comparing it to that of the more familiar Ursine bears, where the pattern does not parallel the humerus. Here, one finds that *Arctodus*' femur is practically indistinguishable from the larger Ursines. Mean W/L and α of *Arctodus* are not statistically distinct from polar bears, but more importantly, there is not much difference in femur proportions between large brown bears and small short-faced bears (see area of overlap in Fig. 15). *Arctodus* shows significant allometric transposition only from the much smaller black bears, as one would expect—but even here the deviation is less than it is between *Arctodus* and its closest small relative, *T. ornatus*. Thus, the femur of short-faced bears converges with the Ursine plan, and since there is a

substantial zone of size overlap between *Arctodus* and very large Ursines, it would be difficult to argue that the bending strength of their femurs was much different. The fact that mean W/L in *Arctodus* is greater than in Ursines argues that femur proportions in short-faced bears maintained similar strength despite their large size (i.e., they retained the same relative strength). Morphological convergence with Ursines does not necessarily imply functional convergence, even though it can be concluded that bending strengths were roughly similar between these distantly related bears. After summarizing data on the tibia, where a similar pattern arises, I will discuss possible reasons for this convergence and suggest a reason why the bones of *Arctodus*' hind limbs were heavily built whereas its front limbs were lightly built.

TIBIA (Fig. 16): Mean W/L is 10.1 in *Arctodus*, but only 9.0 in *T. floridanus* and 7.5 in *T. ornatus*, so in absolute terms *Arctodus*' tibia is quite robust compared to its Tremarctine relatives. Concordantly, its line of allometry is only slightly transposed (sample size is too small for *T. ornatus* to produce a reliable regression line, so this statement is made upon visual inspection and in comparison to *T. floridanus*). *Arctodus*' line of allometry for its tibia is only slightly transposed compared to other Tremarctines, and since all α values are essentially greater than 1 in this group (sample size is too small in *T. ornatus* to tell for certain), this suggests a lack of compensatory growth. As a result, the tibia of short-faced bears is relatively wide. The tibia is the only long bone in *Arctodus* which is truly more robust than in other Tremarctines, and therefore it must have been functionally stronger (relatively) and heavier.

Compared to Ursine bears, *Arctodus*' tibia is absolutely more robust and its line of allometry displays practically no compensation, similar to the pattern seen in its femur. The fact that its line of allometry seems to be an extension of the brown bear's line adds to the suggestion that the tibia in *Arctodus* was a strong bone, functionally on par with other bears, even considering its size. I would conclude that selection in *Arctodus* was for a strong tibia.

d. Overall Allometry and Functional Interpretations

In terms of the cursorial debate, the overall allometric trends and absolute limb dimensions in *Arctodus* demonstrate that this very large bear reduced the relative weight and strength of its limb bones, compared to both its closest relatives (Tremarctine bears) and Ursine bears. Some of these changes were implemented through compensatory growth, in which case the absolute proportions of *Arctodus*' limb bones are not much different than other bears. In the previous chapter, I emphasized that as geometrically similar

animals get larger, dynamic and static stresses in their bones increase faster than bone's ability to dissipate these forces. Therefore, geometrically similar animals of greatly different size cannot perform in geometrically similar ways; larger animals must curtail high force activities, or have bones that are relatively thicker. So while evidence such as limb weight reduction suggests that *Arctodus* was evolving cursorial tendencies, it does not seem plausible that this bear was built to withstand the high forces of fast running or radical high-speed maneuvers.

An important pattern to note in the limbs of *Arctodus* is that although this species did not evolve longer distal segments, it did reduce distal mass, especially in the front limbs. This is indicated by the highly transposed allometry of the radius and lack of compensatory growth in the ulna (earlier I noted that the metapodials of *Arctodus* also are relatively lighter). Previously, I commented that it is not logical to predict increased distal limb length in a cursorial bear because bear feet are so heavy, giving the limbs considerable distal weight. It is logical, however, to expect such a bear to reduce distal weight—and that is what *Arctodus* did.

Dimensional data showed that the hind limb bones of *Arctodus* are somewhat more robust (shorter and heavier) than its front limb bones. I believe this pattern is easily explained by the relative lengths of these bones. Table 6 presents data for the absolute and relative lengths of the major limb bones and axial segments of *Arctodus* and other bears discussed in this chapter. Table 7 shows two indices calculated from these data—Back Length Index (BLI) and Intermembral Index (IMI)(Fig. 17). BLI is calculated as the length of the thoracic and lumbar regions divided by the combined lengths of the four major limb bones; IMI is calculated as the combined length of the humerus and radius divided by the combined length of the femur and tibia¹. These data primarily will be used later in discussions on gait selection, but here I use them to point out how the IMI of *Arctodus* reveals that its front limbs were relatively much longer than its hind limbs. In terms of limb allometries and gracileness, changing limb bone lengths without changing patterns of relative growth will have obvious impacts on W/L values and allometric parameters. Simply shortening the hind limbs will make them relatively more robust and lengthening the front limbs makes them relatively more gracile. Kinematically, the relatively robust hind limbs of *Arctodus* would not have been disadvantageous since they

were short, meaning the mechanical encumbrance of their weight was minimal.

It is puzzling to note that both Kurtén (1967a) and Baryshnikov *et al.* (1994) conclude that *Arctodus* had relatively long hind limbs and relatively short front limbs compared to other bears. The data for IMI in Tables 6 and 7 and Fig. 17 clearly indicate that *Arctodus* was relatively tall in the shoulders and short in the hind quarters (also see Fig. 1a, Part I, which shows an accurate reconstruction of *Arctodus*' skeleton using skeletal data presented here). In Kurtén's case, I can only suggest that this conclusion was the result of using composite measurements for limb lengths in *Arctodus* (he used complete skeletons of modern species for comparison). At the time of his study, no complete skeletons of *Arctodus* were available (the data for the various bear species in Table 6 are all from single individuals). Kurtén reported lengths for the front and hind limbs as percentages of presacral length (lumbar, thoracic, and cervical vertebrae plus skull length), but as noted in footnote 8 of Table 6, he erred in his calculation of axial segment lengths for *T. floridanus* and *T. ornatus* (his values are too high). While this error does not affect comparisons of front and hind limb length, it does give the impression that the legs were shorter than they actually were in these two bears. The error also led Kurtén to the erroneous conclusion that the neck of *Arctodus* was substantially shorter than in these two relatives. Neck length, as a proportion of vertebral length, is about the same for all Tremarctines and does not differ much from Ursines (Table 6).

It is not clear how Baryshnikov *et al.* (1994) came to their conclusion about relative limb length in *Arctodus*, since the only surviving long bone in the specimen they studied was a single tibia. They do not cite data from other specimens or discuss comparative lengths of any limb bones in bears other than for the tibia. It is impossible to make a conclusion about intermembral ratios with data on only a single limb element, yet they state that, "the length of the hind leg bones indicate [sic] the animal was high in the hind quarters, not lowered as in *Ursus spelaeus*." (p. 350). Regarding their conclusion that *Arctodus* was a scavenger, but poorly adapted for this niche, these authors also make the statement that, "These limbs and locomotion are satisfactory for a scavenger." (p. 350), which would imply that selection for locomotor abilities necessarily will be lax in a scavenger. In the next chapter I present energetic and ecological arguments why there would be strong selective pressure on a large-bodied scavenger to evolve certain locomotor features, particularly the ability to cover large home ranges with maximum efficiency, contrary to the non-selectionist position of Baryshnikov *et al.* (1994).

Indeed, the relative changes in front and hind limb

¹ Length of each vertebral region was determined by measuring the anterior-posterior width of individual centra at their widest point and summing these widths for each region. Length of long bones was measured as the greatest length parallel to the long axis of the shaft.

TABLE 6. Absolute and relative lengths of limb and axial segments in *Arctodus* versus other bears¹. See Table 7 for comparison of BLI and IMI in these bears and other carnivores.

element(s) ²	short-faced bear ³ PM 24880	short-faced bear (Kurtén) ⁴	brown bear ⁵	brown bear (Kurtén)	polar bear ⁶	black bear ⁷	spectacled bear ⁸ (Kurtén) miss-calculated	spectacled bear (Kurtén) actual	Florida cave bear ⁴ (Kurtén) miss-calculated	Florida cave bear (Kurtén) actual
humerus (H)	594	—	304	357	369	321	235	235	—	—
radius (R)	480	—	273	307	321	278	195	195	—	—
femur (F)	651	—	352	395	446	355	259	259	—	—
tibia (T)	478	—	271	302	322	279	210	210	—	—
IMI ⁹	95	—	93	95	90	94	92	92	—	—
cervical vertebrae (c) ¹⁰	238	181.5	148	169.4	214.6	122.4	163.7	115.1	288	214.7
thoracic vertebrae (t)	584	538	360	425.5	522.6	398.4	308.4	308.4	472.0	472.0
lumbar vertebrae (l)	426	367.7	267	304.0	381.3	313.6	225.1	225.1	324.0	324.0
c + t + l	1248	1087	775	898.9	1118.5	834.4	697.2	648.6	1384.0	1010.7
c / c + t + l X 100	19.1	16.8	19.1	18.8	19.2	14.7	23.5	17.7	26.6	21.2
t / c + t + l X 100	46.8	49.5	46.5	47.3	46.7	47.7	44.2	47.5	43.6	46.7
l / c + t + l X 100	34.1	33.8	34.5	33.8	34.1	37.6	32.3	34.7	29.9	32.1
BLI ⁹	46	—	53	54	62	58	59	59	—	—

¹ The most accurate values will be derived from complete skeletons, not composite measurements from separate individuals. Values for short-faced bear, brown bear, polar bear, black bear, and spectacled bear are from complete skeletons. Kurtén's (1967a) values for Florida cave bear are composites, but fairly accurate because they are derived from several nearly complete skeletons. NOTE: Kurtén's (1967a; Table 9) values for axial composition include skull length, which is not included in this table; his values presented here have been adjusted to reflect this difference.

² vertebral lengths measured as greatest anterior-posterior length of centra; these lengths should not be taken to be actual lengths because they do not account for vertebral discs or spinal flexure

³ data calculated from PM 24880 in Richards and Turnbull (1996); several vertebrae missing; missing centra depths estimated from neighboring vertebrae; PM 24880 is a very large-bodied specimen

⁴ data from Kurtén (1967a)

⁵ UAM 14784, University of Alaska Museum

⁶ UAM 16545, University of Alaska Museum

⁷ UAM14783, University of Alaska Museum

⁸ Table 9 in Kurtén (1967a) reports relative lengths of axial segments for *T. ornatus* and *T. floridanus* based on raw data in Kurtén (1966); inspection of Kurtén's raw data reported for AMNH 2861 shows that he miscalculated the total for cervical vertebrae length. This total, when calculated directly from raw data in Kurtén's (1966) Table 8 is much lower than his total listed in Table 12. Apparently, his value in Table 12 includes the axis and atlas, which he excluded for other bears when calculating percentages in the 1967a paper's Table 9. The result is that his proportions for the neck are too high and those for the thoracic and lumbar are too low. As a result, Kurtén's conclusion that *T. floridanus* and *T. ornatus* were relatively longer necked than *Arctodus* is incorrect.

⁹ IMI (Intermembral Index) = H + R / F + T BLI (Back Length Index) = t + l / H + R + F + T

¹⁰ cervical portion does not include axis and atlas, for consistency with Kurtén (1966, 1967a)

TABLE 7. Intermembral Indices (IMI) and Back Length Indices (BLI) for *Arctodus* and other carnivores discussed in text.

species	\bar{x}	IMI ¹		BLI ²
		range	n	
spotted hyena ³	98	95 - 101	8	49
short-faced bear	96	95 - 96	2	46
black bear	93	88 - 97	6	58
brown bear	92	90 - 93	4	52
wolf	91	90 - 92	6	54
spectacled bear	90	84 - 95	4	59
polar bear	89	87 - 90	4	62
lion ³	86	83 - 88	10	63

¹ IMI = humerus length + radius length / femur length + tibia length x 100

² BLI = thoracic length + lumbar length / humerus length + radius length + femur length + tibia length x 100; values reported taken on single individuals for which complete vertebrae were available (bears are same specimens as in Table 8), but are corroborated by measurements from photos

³ data on lion and hyena from photos and scale drawings; values are less precise, but checks on data for bears and wolves confirm that accurate measurements can be made using this technique

proportions of *Arctodus* compared to other bears have important functional implications. The disproportionately long front limbs would have generated larger bending moments, yet their gracilenss meant they had less resistance to bending strains, relative to other bears. This means the front limbs could not withstand scaled up dynamic forces of locomotion on par with other bears. On the other hand, this change made the front limbs relatively lighter and kinematically less costly to oscillate. In later sections I will talk about how the long front limbs facilitated gait dynamics which also increased efficiency. There I will show that gait dynamics also explain the advantage of short hind limbs. The robustness of *Arctodus*' hind limbs is relative, and only stands out in comparison to the gracilenss of the front limbs. The femur, for instance, is still less robust than in *T. floridanus* and has proportions similar to those of Ursine bears. Because the hind limb bones were relatively shortened, and thus lighter overall, it would be difficult to argue that their robustness was kinematically disadvantageous. This is especially true if they oscillated at slow to moderate speeds because the kinematic effect of limb mass increases exponentially with speed. Also, because bones of the hind limbs were not lengthened as much as those of the front limbs, their distal mass would

not have been such a kinematic encumbrance. Therefore, their greater robustness adds little additional energetic costs at low speeds.

I think that last statement is the real key to understanding the type of cursorialism displayed by *Arctodus*. Since I showed evidence of cursorial modifications in *Arctodus*, but not a specific reduction in distal mass, this pattern suggests that *Arctodus* most likely was adapted for prolonged travel at moderate speeds, not for sustaining high speeds. In previous chapter's section on kinematics, I discussed how the energy required to oscillate a given mass and the force required to accelerate it are a product of its velocity and its length down the limb. In a courser built for sustained, but not fast locomotion, distal weight is not as critical in determining the limb's efficiency—because the velocity of distal masses is kept low, and the momentum which needs to be overcome four times per stride is much lower. For a courser of this type, the real key is limb length; increasing stride length is by far the most effective way to increase efficiency. However, the mass of the entire limb is still an important factor in the energetic (kinematic) equation and the overall weight reduction of the entire limb is most logically interpreted as a means to reduce the energy required to swing the limb as a whole. Therefore,

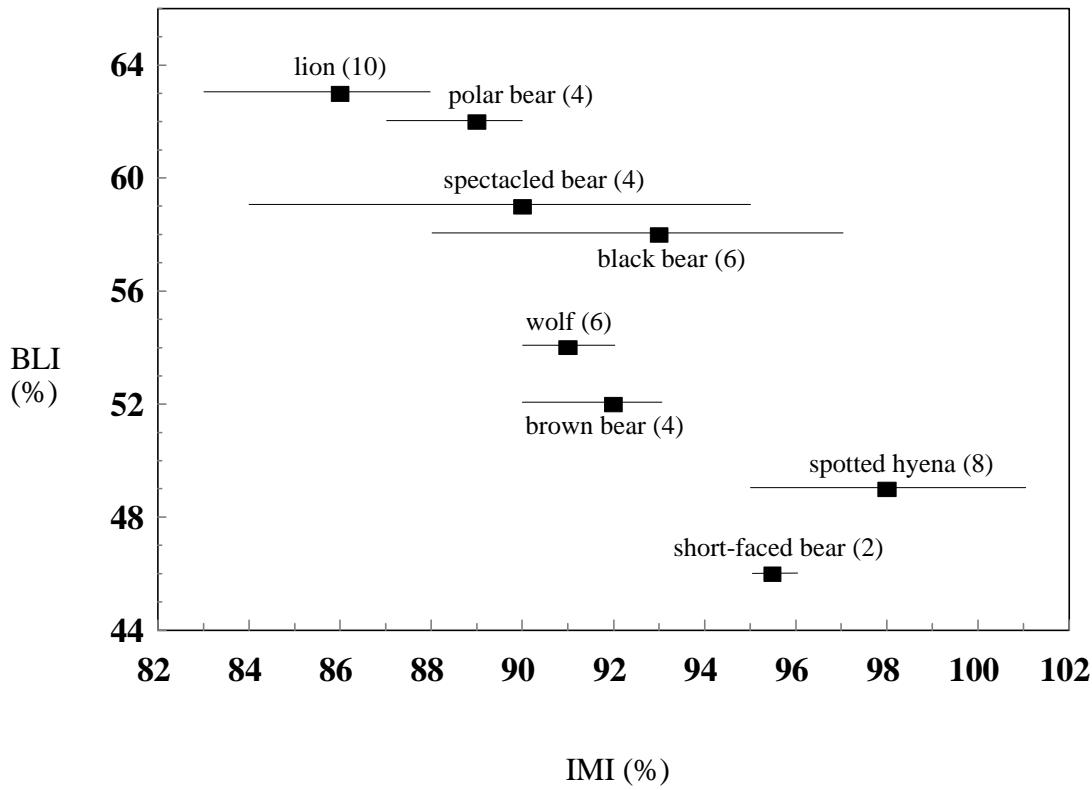


FIGURE 17. Back Length Index (BLI) and Intermembral Index (IMI) for short-faced bears compared to other bears and selected carnivores (plotted from data in Table 9). While short-faced bears were long-legged overall, the high IMI shows how their front legs were elongated the most, and that the hind legs were relatively short. The BLI reveals that the backs of short-faced bears also were short relative to leg length. In fact, their proportions are most similar to spotted hyenas. Large mammals with this type of conformation, especially those with high IMIs, use a pace as their mid-range gait because there is so much disparity between front and hind limb lengths. Of the species depicted, spotted hyenas are pronounced pacers, while the other species rarely pace. Pacing is an efficient gait for prolonged locomotion, and it is argued that short-faced bears were adapted for efficient long-range travel using such a gait. Species which accelerate well, such as felids, have relatively longer hind limbs (low IMI), which short-faced bears lacked. (sample sizes in parentheses; bars represent ranges of values for IMI; ranges not listed for BLI because actual vertebral lengths were only measured in bears-- in other species, back lengths were estimated from photos and lack the precision to warrant range bars.)

the key feature in the cursorialism debate in *Arctodus* lies with the fact that the entire limb, not just the distal ends, had evolved to be lighter and longer. This pattern suggests that *Arctodus* had evolved for sustained high-efficiency locomotion at moderate speeds, where the kinematic effects of distal weight are not so pronounced.

Critics of this interpretation may contend that all of these adaptations in *Arctodus'* limb morphology would also be adaptive for sustaining high speed and thus for predation. But this cannot be the case because of the bear's extreme mass. *Arctodus'* long, gracile front limbs would not have been strong enough to handle the forces of very high speed travel in such a large mammal, and, even if capable of sustaining high speeds, these legs would have been too weak to handle sudden force changes incurred during acceleration and maneuvering at high speeds— forces typically incurred by a predator. I would challenge proponents of the predatory model to demonstrate how such a “straight-line runner” could be a successful predator, or how *Arctodus'* specific morphology fits a particular predatory strategy. It would be contradictory for a courser the size of *Arctodus'* to have such gracile limbs (or more precisely, to not have robust limbs) if its cursorial style was characterized by high force locomotion involving rapid acceleration and maneuvering at high speeds.

Limb Posture and Conformational Features

In addition to limb mass and proximal-distal limb proportions there are other skeletal indicators in *Arctodus* which attest to its cursorialism. These features primarily involve modifications to limb posture, which either reduce the energy of oscillation or decrease lateral leg excursion during a stride. Both adaptations potentially increase locomotor efficiency, but could also increase the velocity of limb oscillation.

Compared to amblers, cursors swing their legs in a more parasagittal plane (parallel to the body), and their foot path tends to follow a nearly straight line that circumscribes a narrow horizontal ellipse or figure 8 on the ground (Jenkins and Camazine 1977) (Fig. 18). The limbs of less cursorially adapted mammals are swung with considerable lateral migration (abduction) during a stride, thereby traveling through a wider ellipse or figure-8 pattern (particularly in the hind limbs). Unlike cursors, the body's mass is lifted little during the stride of amblers, which is partially why amblers do not swing their hind limbs under the body so much as to the sides (Jenkins and Camazine 1977; Hildebrand 1985a, 1995). Consequently, their femurs are positioned in a more abducted (laterally splayed) position and there is considerable lateral pelvic rotation during a stride. This primitive pattern of motion would be inefficient at higher speeds or for prolonged travel, so more cursorial species

have made significant modifications to this plan (Hildebrand 1976, Jenkins and Camazine 1977). Joint angles (particularly the knees) in cursors also are more aligned with the sagittal plane, allowing the limbs to swing under the body simply by flexing them (i.e., without being swung laterally) (Jenkins and Camazine 1977, Hildebrand 1995).

The advantage of moving the limbs through a straight and parasagittal plane is twofold. First, the feet travel a shorter overall distance because there is less lateral migration. This reduces the energy needed to swing the limbs, increasing efficiency and endurance, but it also can increase the animal's speed since a limb which travels a shorter overall distance completes its stride more quickly. Second, fewer muscle groups, and thus less energy, are needed to swing a limb when it follows a parasagittal trajectory because skeletal mechanisms rather than muscles can be employed to constrain the direction of limb movement (Part I, Section 4). This process increases efficiency and endurance but probably does little to directly enhance speed. But, since muscle mass is reduced, it has the added effect of making the limb lighter, and, as shown in Part I, this can help increase top speed and acceleration in some animals (mainly small to medium ones less than about 100 kg). It also should be noted that nearly all of these modifications which restrict abduction and adduction of the limbs will limit their use for other dexterous functions.

With the preceding considerations in mind, I next will examine whether *Arctodus* displays cursorial modifications to its limb posture and line of travel. First, I will make a brief qualitative assessment of *Arctodus'* anterior limb conformation, followed by a more detailed evaluation of its hind limbs and pelvis using quantitative indicators of locomotor style. The hind limb assessment will include comparisons to other carnivores with diverse locomotor habits ranging from raccoons and modern bears (two non-cursorial carnivores) to felids and canids, two cursorial carnivore morphs which use their limbs quite differently.

a. Front Limbs:

Earlier, I showed that, compared to other bears, *Arctodus* had evolved long front limbs relative to its hind limbs. Now, I want to show that the conformation of its front limbs differed from other bears and that *Arctodus* must have swung its front limbs quite differently than contemporary bears. Evidence for these conclusions comes from the morphology of *Arctodus'* ribs and thoracic cavity. Richards and Turnbull (1995) and Kurtén (1966a) provide measurements on ribs in *Arctodus* and other bears. Their data show that the ribs of *Arctodus* had less bowing and were relatively longer than in other bears, indicating that its chest was taller and narrower. In

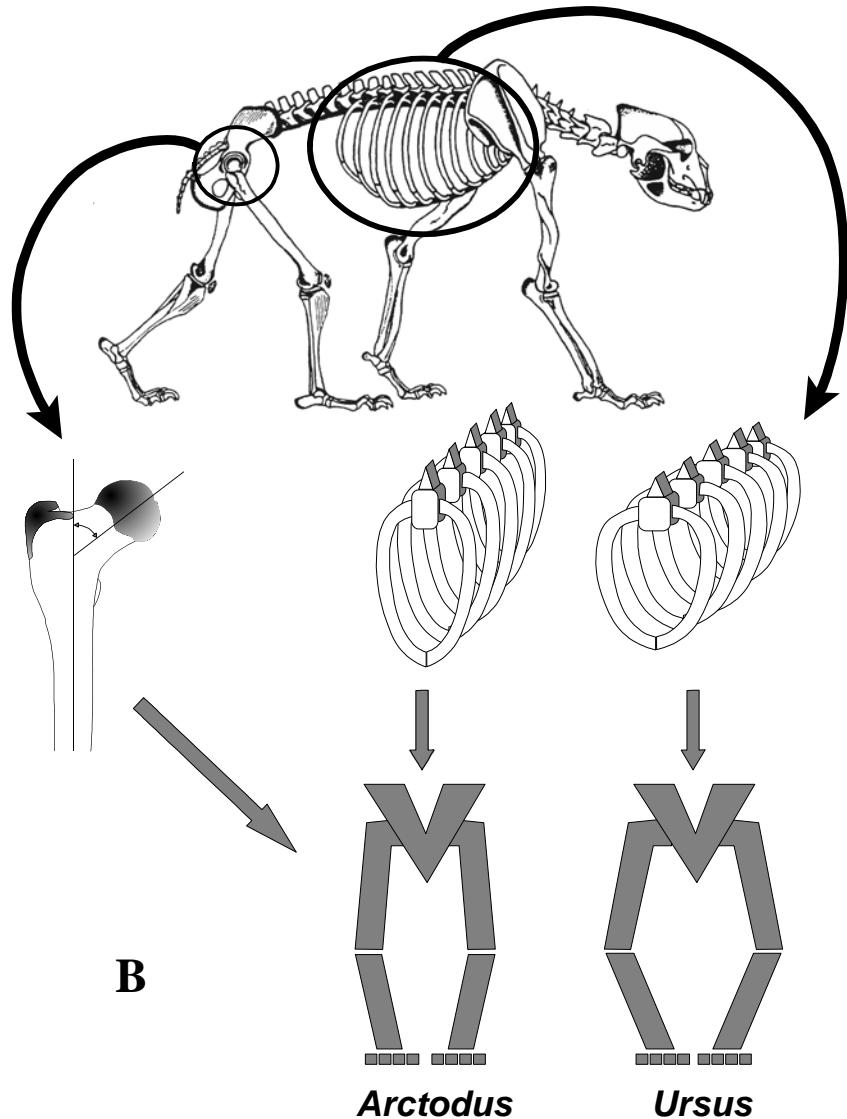
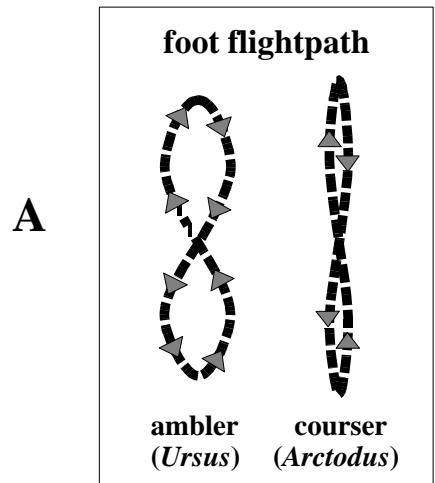


Figure 18. Schematic of some cursorial features in *Arctodus* compared to *Ursus*. **A** The foot flightpath of amblers, such as *Ursus*, circumscribes a wide figure 8, which is less efficient but a necessary accommodation for a wide body and a steady, wide-legged stance. Courisers, such as *Arctodus*, swing their legs in a tighter figure 8 or even an ellipse. This flightpath is energetically more efficient, but can be potentially unstable. **B** The conformation of the front and hind limbs and girdles in *Arctodus* allowed it to position its limbs more medially and to swing them in a more parasagittal plane compared to *Ursus*. The thoracic cavity was tall and narrow and widest at the 10th rib, as opposed to the 9th in Ursines. This latter feature means the widest part of the thoracic cavity was located more posteriorly in *Arctodus*, allowing the front limbs to take longer strides without significant lateral splaying. Reduced lateral splaying in the hind limb is brought about partially by a more acute angle in the neck of the femur and less medial-lateral bowing in the femur shaft.

addition, the 10th rib is the longest of the series in *Arctodus*; normally the 9th rib is longest in bears. Therefore, the chest's greatest depth was more posteriorly located. Functionally, these features of the thoracic cavity would have positioned *Arctodus'* front limbs more medially (closer together) and thus more directly beneath its body. The limbs also could have been swung farther posteriorly before flaring laterally, since the largest part of the chest was most posterior (Fig. 18). The locomotor advantages of these traits are that: 1) the front limbs could be swung in a near parasagittal plane more parallel to the body; by reducing lateral excursion in the front limbs, the feet circumscribed a tighter ellipse, 2) effective stride length could be increased, and 3) placing the limbs more directly beneath the body increases the stability of lateral gaits. The latter point is especially important in very large animals because they are inherently less stable (Hildebrand 1985a, 1995). In fact, one way of interpreting this repositioning of the front limbs could be that the condition had evolved specifically to facilitate a lateral gait with long strides, such as the pace— more on this later.

As a final note on the front limbs, it seems somewhat surprising that the scapula of *Arctodus* shows little variation from the typical ursid plan. Even the shape of its vertebral border (an evolutionarily and developmentally plastic trait (Wolffson 1950, Smith and Savage 1956) is essentially of the typical ursid form, and the postscapular fossa housing the powerful subscapularis minor muscle—a trademark of bears—is still prominent in *Arctodus*. This feature and others, such as its plantigrade foot posture (Kurtén 1967a) indicate that *Arctodus* was an incipient, not advanced, cursor.

b. Hip and Femur:

Next I discuss hind limb posture and morphology in various carnivores having diverse locomotor abilities and then place *Arctodus* into that spectrum. Many of my quantitative analyses closely follow those of Jenkins and Camazine (1977), and, unless stated otherwise, the data I cite for non-bear taxa comes from these authors. Conformational features I discuss will address the morphology of the pelvis and acetabular joint, along with the shape of the femur and its articulation with the hip. Comparisons will be made in terms of their effects on femoral posture, the limb's line of travel, and locomotor energetics. The carnivores being used for comparison are raccoons, brown bears, felids, and canids. Modern bears and raccoons both are amblers which have highly dextrous limbs capable of wide lateral excursions. When they walk their hind limbs circumscribe a broad figure-8 (Jenkins and Camazine 1977) (Fig. 18). Canids contrast most with amblers and other Carnivora in that their limbs are the most restricted in terms of lateral movement (Jenkins and

Camazine 1977). In this regard, canids can be considered “strict cursors” because their limbs are essentially useless for most other purposes (besides digging, which in canids has a motion parallel to running). Felids, on the other hand, use their limbs for many dextrous functions other than locomotion, such as climbing and handling large prey which require more limb mobility (Ewer 1973, Jenkins and Camazine 1977, Kitchener 1991).

The hip and femur morphology of raccoons—classic amblers—gives them a wide range of motion in the hind limb, including extensive abduction and adduction. The inferior surface of its pelvis forms a sharp angle when viewed posteriorly (Fig. 19). This angle between the lateral edge of the ischium and the horizontal plane is around 50° in raccoons (Table 8). The acuteness of this angle means that the femur is naturally splayed laterally (abducted). The neck and head of the femur project from the shaft at a relatively obtuse angle—only about 49°—adding further to the femur's naturally abducted position (Table 8, Fig. 19). The femur shaft, however, is bowed inward medio-laterally, which tends to bring the hind foot back to a more medial position under the body, giving raccoons a “bowleggedness” appearance. The acetabulum is shallow and the margins of the articular cartilage are broad. These two features allow for a greater range of rotation of the femur head when articulated. The articular surface of the femur head is quite broad and extends onto the neck, allowing for a broad extent of rotation in the acetabulum (Jenkins and Camazine 1977).

The utility of a mobile femur and hip articulation in raccoons is that it allows the animal to place its legs in almost unlimited postures, which greatly increases stability and maneuverability over broken terrain and during diverse activities. The raccoon commonly scrambles over objects and climbs, necessitating this flexibility. Evidently, there is little evolutionary incentive for raccoons to develop structures which limit femur rotation to a parasagittal plane, as these animals have little need to increase locomotor efficiency, nor are they required to maintain significant speeds for long periods or travel uninterrupted for long distances. Bear hips resemble those of raccoons in certain ways, but because I want to compare bears more with cursorial carnivores, it will be convenient to first describe hip morphology in the latter.

The canid pelvis and femur (a fox, *Vulpes vulpes*, in the case of Jenkins and Camazine's study) contrast strongly with those of the raccoon, as would be predicted based on the differences in locomotor habits. The inferior angle of the pelvis is only around 21° in the fox, but my own data show that this angle is considerably steeper in wolves—around 30° (Table 8). The fox's femur neck and head project from the shaft at an angle of approximately 65° (~53° in wolves) and the femur shaft is rather

Table 8. Inferior ischial angle (when viewed posteriorly) and angle that femur neck projects from shaft in carnivores that are discussed in text

species (n)	inferior ischial angle	angle that femur neck projects from shaft	source
raccoon	50°	49°	Jenkins and Camazine (1977)
domestic cat	34	63	Jenkins and Camazine (1977)
red fox	21	65	Jenkins and Camazine (1977)
wolf ¹ (10)	30	53	this study
brown bear ¹ (6)	62	52	this study
short-faced bear ² (2)	65	55	this study
spectacled bear (2)	60	n.a.	this study

¹ measured on specimens in the University of Alaska Museum Department of Mammalogy

² measured on F:AM 8027 (American Museum of Natural History, New York) and PM 24880 (Field Museum of Natural History, Chicago)

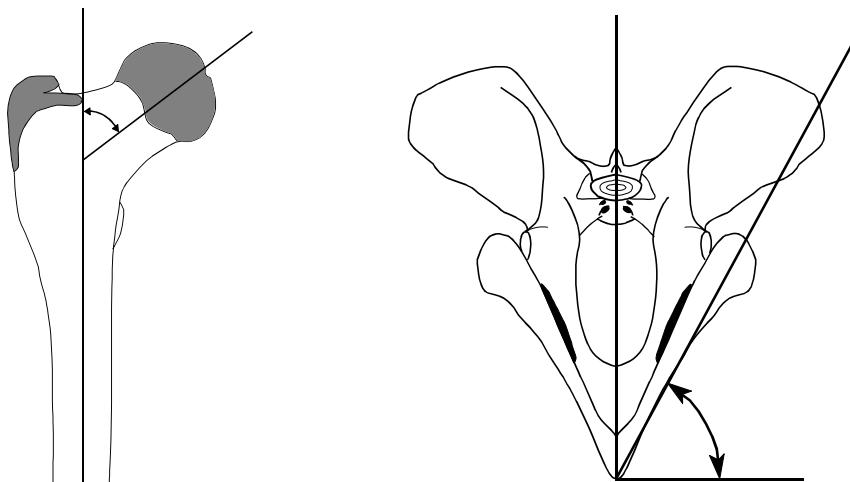


FIGURE 19. Angle of femur neck projection, viewed anteriorly, and inferior ischial angle viewed posteriorly (both examples represent *Arctodus*).

straight. The net effect of this pelvic angle, the projection of the femur neck, and a straight femur is that the hind limb has little lateral splaying (femoral abduction) compared to raccoons. Because foxes and raccoons are similar in size, it is not appropriate to invoke arguments about body size to explain the fox's straighter femur. That is, foxes (and other canids) most likely have evolved straighter femurs to position the leg so that they can swing more in-line with the body and to reduce splaying. The acetabulum in canids is deep and the margins form sharp inward angles, which effectively lock the femur head in place and limit most movement in all but the sagittal plane. The articular surface on the head in canids is the least extensive of the carnivores examined, and it does not extend onto the dorsal neck, being particularly reduced on the medio-ventral margins of the head, which further limits abduction (Jenkins and Camazine 1977). The neck of the femur also is very short in canids.

The femur and hip articulation in canids has the advantage of eliminating the need to control femur position using bulky and energetically costly adductor and abductor muscles. These muscles either have been eliminated, which decreases weight and locomotor effort, or they have been employed as flexors and extensors, which will help distribute the work of locomotion and thus increase endurance (Hildebrand 1995). The effect of these modifications is that canids swing their hind limbs in line with the body more than most carnivores (Jenkins and Camazine 1977). This singular dedication of the limbs increases efficiency, but limits dexterous activities. Thus, canids excel at long distance pursuit and prolonged running bouts, but they are for the most part poor climbers and their limbs are useless for grabbing large prey.

Felids have evolved quite different locomotor skills and activities than canids, and this is reflected in the morphology of their pelvis and femur. Domestic cats have an inferior ischial angle around 34° , considerably more than foxes, but less than raccoons (Table 8). However, because the neck of the femur projects at 63° (only slightly less than canids), their femur is positioned more vertically, with almost no lateral splaying. And like the fox, there is little lateral flexion of the femur shaft. (When the stance of canids and felids is compared, it can be seen that the canid femur splays outward (laterally) a few degrees, while the felid femur is held nearly perfectly vertical.) The acetabular depth is intermediate in cats, with broad coverage of the articular cartilage. In addition, the articular surface of the femur head extends more broadly onto the neck than in canids, but less than in raccoons (data on domestic cats from Jenkins and Camazine (1977)) (Table 8).

These features, characteristic of felids in general, agree well with their habits. Whereas canids have evolved

for more or less straight line travel and prolonged endurance, felids are agile, good climbers, and frequently use sharp maneuvers in their predatory tactics. They also use their limbs to handle and subdue prey. These demands require more medio-lateral mobility in the femur, and indeed, the structure of the felid hip articulation facilitates more adduction and abduction than in canids, though not as much as in raccoons. Speed also is vital to felids, and it is important to note that they are quite capable of rotating the femur through a narrow ellipse and in parasagittal plane. However, since felids lack skeletal features to direct this motion, it must require muscular control. In this regard, felids are a compromise morph, and might be said to have "sloppy" limbs because they are not kept in position by skeletal structures so much as by muscles. When felids run, they must be expending energy through adductor and abductor muscles to keep the legs swinging inclined with the body. This is a costly, but necessary, compromise, since when a lion (for example) catches its prey it must have flexible limbs in order to grab and manipulate the prey (even though the prey is killed by biting). Often, a lion may even stand on its hind limbs when pulling down large prey. This design probably has placed constraints on felid evolution, in particular preventing them from radiating into niches that necessitate long range, efficient locomotion.

The hips and femurs of bears also reflect a suite of functional compromises, but of a different sort than felids. Bears have pelvises with the steepest inferior angles measured in this study (Table 8). Theoretically, this should project the femur laterally at a strong angle. However, the head and neck of the femur typically project from the shaft at approximately 52° (in brown bears), which reduces the effective angle of femoral abduction. The acetabulum of bears is more similar to felids, being deeper than in raccoons and shallower than in canids. Furthermore, the articular surface of the femur head is broad in bears and extends onto the dorsal surface of the neck. However, bears are not nearly as extreme in this regard as raccoons.

These characteristics show how the hips of bears, when compared to all other carnivores, have a unique conformation. They resemble other amblers like the raccoon in that their hind limbs are free to move in many planes (but not nearly to the same extent), and their femurs tend to be splayed laterally and then bowed back medially. But bears also are a bit like felids in that the angle of the femur neck increases to compensate for a sharper ischial angle (a sharp ischial angle splays the femur laterally, but a commensurate rise in the neck angle brings the femur back to near-vertical). The ischial angle in bears, however, is extreme, and the angle of the femur neck is not nearly steep enough to bring the femur completely back to vertical. So it seems that bears are

doing something quite different in regard to hip conformation. Later, I will show how these features relate best to the ability of bears to use an upright, bipedal stance.

Before bringing short-faced bears into this comparison, I want to examine in detail the position of the fovea capitis femoris (FCF) in various carnivores, using techniques described in Jenkins and Camazine (1977). The FCF, located on the articular surface of the femur head, is the point of insertion for the ligamentum capitis femoris, the ligament directly connecting the femur head to the acetabulum (it originates in the acetabular fossa— see inset of Fig. 20). Since the FCF and the acetabular fossa should be aligned when the femur is positioned neutrally, its placement on the femur head is a good estimator of the femur's natural posture and degree of normal abduction at rest.

The position of the FCF can be quantified for comparison by projecting an equator and a prime meridian on the femur head and then measuring the latitude (E) and longitude (M) of the FCF in degrees (inset of Fig. 20)(Technique of Jenkins and Camazine 1977). In terms of femur posture, M measures the amount of deviation from the sagittal plane, or how much the femur is cocked with the toe inward or outward. E measures the proximal-distal position of the FCF and indicates the amount of normal femoral abduction. A bivariate plot of E and M can be used to visually separate animals by their locomotor specializations (Fig. 20). These values have been calculated for species of felids, canids, and amblers by Jenkins and Camazine (1977), and are plotted in Fig. 20, along with values calculated for *Arctodus* in this study.

The amblers in Fig. 20, including raccoons, skunks, and Ursine bears, cluster to the upper right, indicative of their highly abducted femurs (E) and toe-in stance (M). In these regards, Ursine bears appear to stand out as the most extreme, but I would argue that the position of the FCF in bears partially compensates for their strong ischial angles, working in conjunction with an acute angle of the femur neck. Nonetheless, Ursine bears cluster well with other amblers.

Felids have both low E and low M values, meaning their femurs normally have the least amount of abduction and toe-in positioning (i.e., their legs are most naturally inclined with the sagittal plane). This agrees with the observations made earlier and makes sense since felids need to keep their hind legs parallel to the body as much as possible during high speed locomotion. Felids, with their long backs, also have the least problem with front and hind leg interference (described in Part I) so they do not need to swing their hind legs laterally to clear the front legs nearly as much as other carnivores. Also, the pelvis is relatively wide in felids, so the hind legs are

naturally positioned farther apart. However, as the previous discussion indicated, felids still retain the ability to move the femur in other planes and its “normal” mode of swinging in the sagittal plane must be maintained by muscular effort.

Canids have E values that are much higher than felids, but their M values are nearly identical. This is consistent with the typical canid stance where the knees and toes face predominantly forward, in-line with the direction of travel (low M), but where the femur is somewhat abducted (high E). E in canids is on par with amblers, but this should not be taken to mean that actual femoral abduction is equal, since abduction is enhanced in amblers by a high ischial angle. Slight femoral abduction in canids probably reflects their need to swing the hind legs laterally as they move forward in order to avoid interference with the front legs. This compensatory motion must be necessary in canids, in contrast to felids, because canids have relatively short backs and narrow pelvises. Short backs in canids result in a longer period of front limb/hind limb overlap, and narrow pelvises mean that their hind legs are not far apart, which necessitates a slight bow to the legs.

Now I want to examine the hip and femur conformation of *Arctodus* by comparing it to the various modes described for amblers, felids, canids, and other bears. The inferior ischial angle of *Arctodus*' pelvis is high (~65°), but within the range observed for other bears, while higher than its closest relative, the spectacled bear (~60°)(Table 8) (statistical significance has not be determined since the measurement was made on only two *Arctodus* specimens and two spectacled bears). The neck of the femur projects at approximately 55° from the shaft, slightly higher than in *Ursus*, and commensurate with *Arctodus*' steeper ischial angle. However, the position of the FCF in *Arctodus* is quite divergent from other ursids (Fig. 20), and, in fact, its position is unlike amblers in general.

The low E and M of *Arctodus* indicate that its femur was less abducted and that short-faced bears required less of a toe-in stance than contemporary bears. In these regards, *Arctodus* had converged on the pattern in felids, having a hind limb that normally assumed a more vertical posture yet retained a high degree of flexibility in multiple planes. Evidence for this flexibility lies in the fact that the acetabulum is not particularly deep in *Arctodus* and that the articular surface of the femur head is fairly broad and extends well onto the dorsal surface of the neck— traits which are the norm for bears. The femur and tibia of short-faced bears do not display the bowing seen in other bears, which I think was necessary in part to reduce bending stresses in this huge bear. Recall from Part I that larger animals will reduce curvature in the long bones because it reduces bending moments by keeping

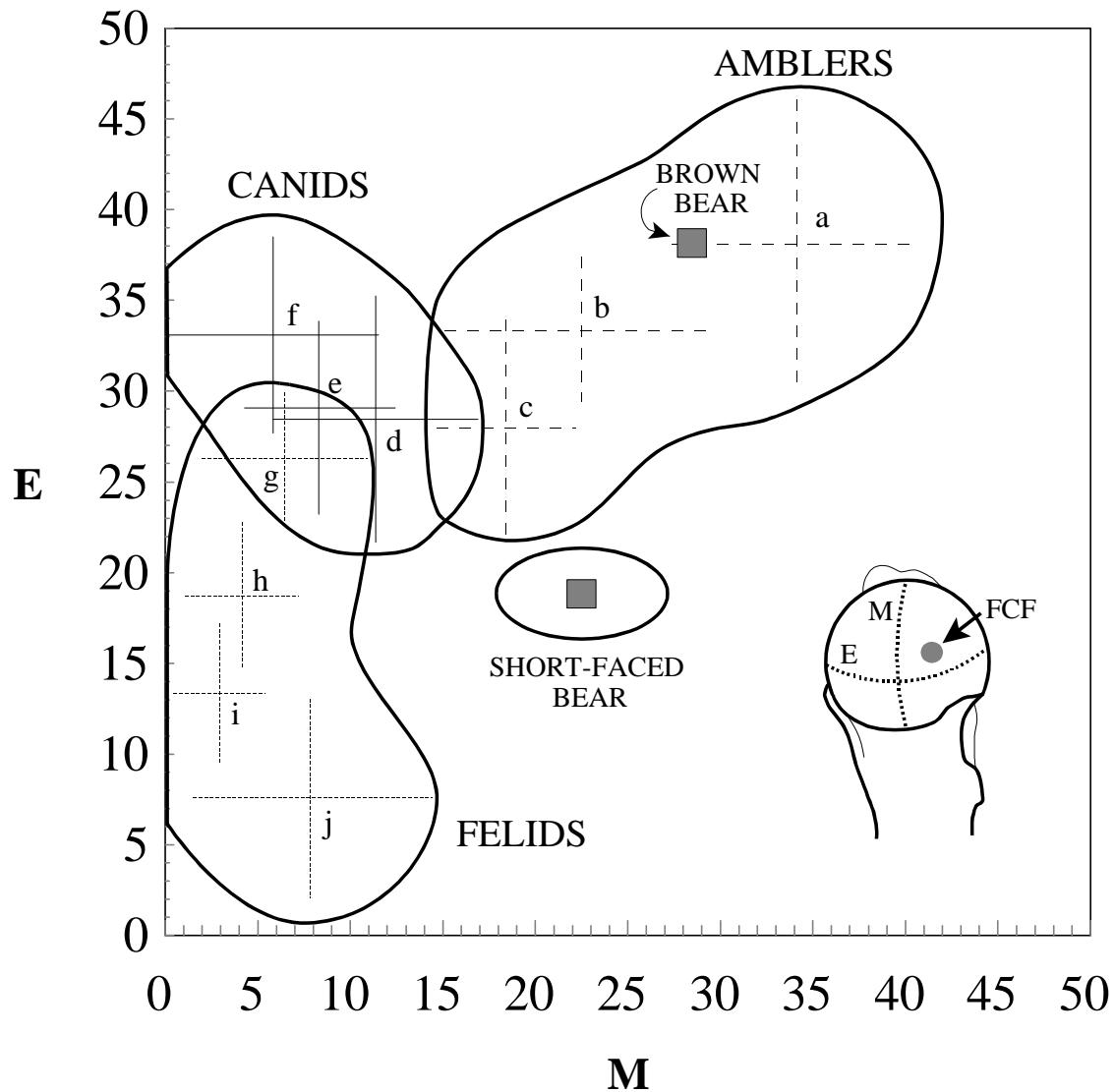


FIGURE 20. Position of the *fovea centralis femoris* (FCF) on the femur head in short-faced bears versus other carnivores. *E* (equator) measures the proximal-distal position of the FCF (in degrees “North”) and is an indicator of the extent of femoral abduction when the femur is in a neutral position. *M* (meridian) measures the amount of deviation from the sagittal plane (in degrees “East”) and is an indicator of how much the femur is normally chocked outward. Value for short-faced bears was obtained on F:AM 95654, American Museum of Natural History. Techniques for drawing a reference equator and prime meridian are imprecise, so resulting values of *E* and *M* are difficult to reproduce consistently. The ellipse drawn around the value for F:AM 95654 represents a qualitative estimate of its precision. Original graph and data from Jenkins and Camazine (1977, Fig. 9) with data for short-faced bears and brown bears added from this study. (a) bears (*Ursus* spp.), (b) skunks (*Mephitis* spp.), (c) raccoon (*Procyon lotor*), (d) red fox (*Vulpes vulpes*), (e) wolf (*Canis lupus*), (f) African hunting dog (*Lycaon pictus*), (g) puma (*Felis concolor*), (h) bobcat (*Lynx rufus*), (i) lynx (*Lynx canadensis*), (j) cat (*Felis domesticus*).

the bone more in-line with vertical ground forces.

Reduced femoral abduction and less of a toe-in stance mean that *Arctodus* swung its hind limbs in a near parasagittal plane, in-line with the body's long axis. If there was less lateral excursion to the hind limbs, then the feet most likely circumscribed a tight ellipse or figure 8 flight path during each stride. It has been a theme throughout this section that these traits increase locomotion efficiency (and thus endurance and economy of effort), since the legs travel less overall distance per stride, and because more of this distance contributes to forward motion. Furthermore, since these patterns are found universally among cursorial carnivores, their presence in *Arctodus* suggests that this bear was cursorially-adapted. However, it remains to be explained why *Arctodus* had evolved such an acute ischial angle, compared to its closest relatives, since that promotes abduction. Spectacled bears most closely resemble the primitive stock of Tremarctine bears. The fact that spectacled bears have a less acute ischial angle suggests that there was selective pressure on *Arctodus* to increase ischial steepness. I believe this is where the importance of bipedal standing comes into play.

When a bear stands upright, the femur is severely flexed relative to the pelvis and spine, but it also is highly abducted. Abducting the femur is important when a bear stands up because it provides a wide platform for stability. The extension of the femur head's articular surface onto the dorsal surface of the neck helps facilitate this action, as this is the region that would contact the acetabulum during extreme femoral abduction. Jenkins and Camazine (1977) have documented this trait in the femur heads of brown bears, and I have seen it expressed in brown bears, polar bears, American black bears, and spectacled bears. Since all of these species are able to stand upright, this is not surprising (however, this trait obviously is not unique to bears—see Jenkins and Camazine 1977).

The femur morphology of *Arctodus* is but one line of evidence suggesting that it used an upright stance. Additional evidence lies in the morphology of *Arctodus'* ilium and the length of its back and hind limbs. The ilium of *Arctodus* has a very wide neck compared to other bears. This has been noted by other authors (Merriam and Stock 1925, Kurtén 1967a, Richards and Turnbull 1995), but its function has remained elusive. I think the function becomes apparent if one considers the mechanics of a bear standing upright. Figure 21 models the mechanics of this action. There, it can be seen that the extensor muscles of the femur provide the force for the action, and the acetabular joint acts as the fulcrum. The in-lever of this system is formed by the portion of the pelvis posterior to the acetabulum, namely the ischium. The out-lever is formed by the ilium, spine, and head. The torque

opposing the lifting action is generated by the entire body mass anterior to the acetabulum. This mass must have been considerable, since it constitutes all of the torso and includes the heavy head. The great length of the out-lever relative to the in-lever magnifies this torque—all of which comes to bear most intensely at the out-lever's proximal end, which is the neck of the ilium.

Three prominent features unique to *Arctodus* (compared to other bears) would have had the effect of improving performance in this lever system (Fig. 21). First, the thick neck of the ilium strengthened the out-lever's weakest point in front of the fulcrum. Secondly, the short back of *Arctodus* reduced the length of the out-lever, and thus the torque it exerted in resistance against the extensor muscles. Third, the short hind legs of *Arctodus* would have made it more stable during a bipedal stance because its center of mass would have been kept low. Later, I will discuss back length and limb proportions in terms of locomotion, where it will be shown that they confer other advantages. However, none of these traits would have evolved exclusively for one function, and the fact that they increased the ease with which *Arctodus* could have stood upright probably is not insignificant. In the next chapter I will discuss why it seems logical that an upright posture in *Arctodus* would have been advantageous as an aggressive posture for use in intimidating other carnivores at carcasses.

Summary on Cursorialism

I showed that short-faced bears did not lengthen distal limb segments—a trait which might be predicted for a courser—but that this trait is only to be expected amongst advanced cursors because it is beneficial only if the distal segments are light, which they generally are not in bears. Furthermore, long distal segments are most important in cursors that use high speeds, so I suggested that if other cursorial traits could be found in *Arctodus* then this would indicate that it was a courser that emphasized endurance and locomotor efficiency at moderate speeds.

Additional evidence of cursorialism was found. First, patterns of allometry, as well as actual proportions in the long bones, show that *Arctodus* had reduced the overall weight of its limbs. These data also showed that short-faced bears had lightened their limbs distally, but not strongly so. But since gracile limbs are not only lighter, but also weaker, I emphasized that it is unlikely that *Arctodus* engaged in scaled-up, high-force locomotor activities equivalent to other bears.

One of the most prominent signs of cursorialism in *Arctodus* is its advanced limb posture compared to other bears and amblers. *Arctodus'* deep but narrow chest allowed its front limbs to be held more medially beneath the body and facilitated longer strides with less lateral



FIGURE 21. *Arctodus* was configured well for a bipedal stance, which I propose was used as an intimidation posture. It also would have been important for surveying the environment and scenting-out carrion, important traits for a scavenger. The shortened back reduced the length of the outlever (out-L) formed by the anterior portion of the body. This reduced the torque of the body's weight (and heavy head) which opposes the action of the hind leg extensors when a bear stands upright. The neck of the ilium in *Arctodus* was unusually thick and strong compared to other bears. This is the point where the torque of the body's mass is the most intense when a bear stands up because it is immediately in front of the fulcrum in this lever system. Its short hind legs also mean the center of gravity would have been kept low while standing upright.

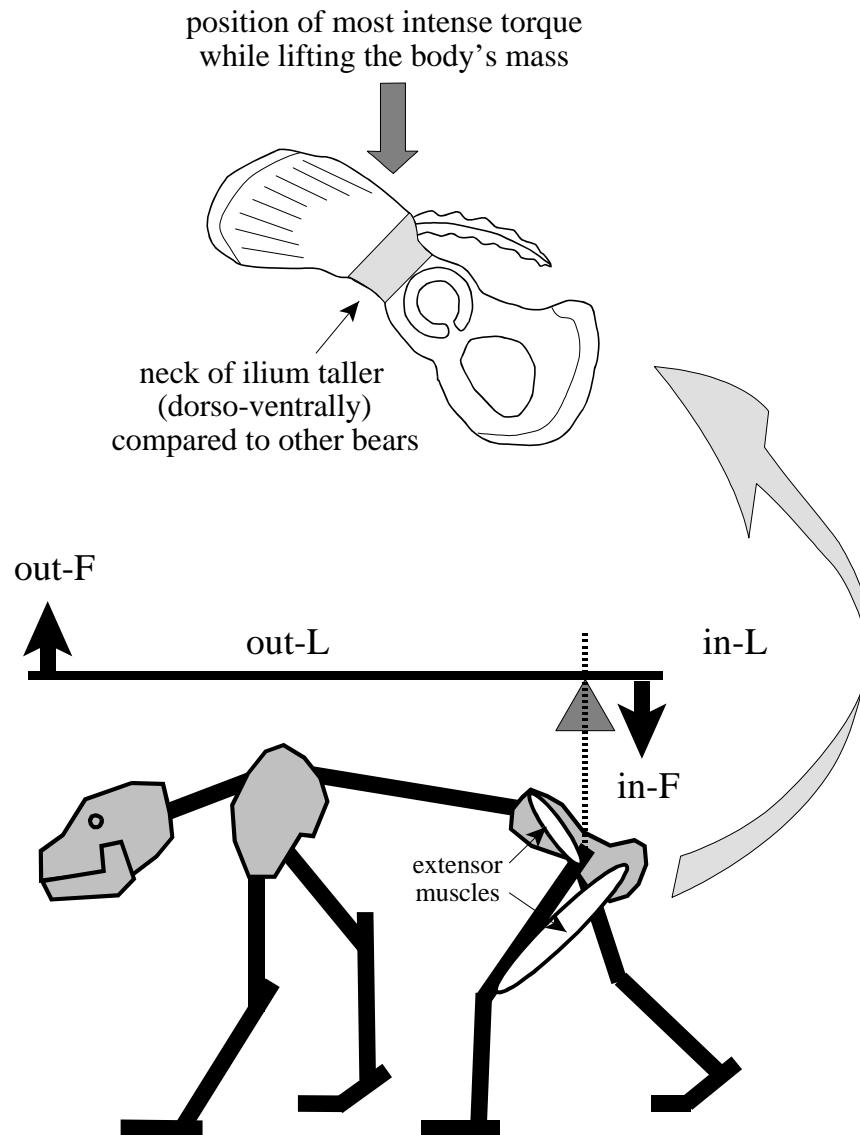


TABLE 9. General cursorial traits and their level of expression in a non-cursor (brown bear), a long distance cursor (short-faced bear), and a high speed sprinting cursor (cheetah).

cursorial trait	brown bear	short-faced bear	cheetah
proximal muscle attachments	no	yes?	yes
limbs placed medially under body	no	yes	yes
limbs swing in parasagittal plane	no	yes	yes
distal segments lightened (limb bones reduced, restructured)	no	slightly	yes
distal segments relatively elongated	no	no	yes
non-locomotor functions of limbs curtailed	no	no	yes
digitigrade / unguligrade	no	no	yes
distal segments lightened further through bone fusion and/or loss	no	no	no

degree of cursorial specialization



flaring than is typical for bears. The front limbs also were elongated, which further increased stride length and reduced the cost of transport. The configuration of the front limbs conforms with those of cursors that use laterally-supported gaits like the pace (see below). *Arctodus* swung its hind limbs in a near parasagittal plane by reducing femoral abduction and lateral excursions in ways that resemble more cursorial carnivores. However, *Arctodus* retained the ability to abduct the femur when necessary, probably to facilitate an upright stance.

Table 9 summarizes cursorial traits displayed in *Arctodus* and contrasts them with their level of expression in cheetahs (cursors specialized for extremely high speeds) and brown bears (non-cursors). As demonstrated by the patterns in this table, short-faced bears apparently were incipient cursors when they became extinct.

3. GAIT SELECTION AND SPEED: WHAT KIND OF COURSER WAS *ARCTODUS* ?

In the previous section, I concluded that *Arctodus* had evolved rudimentary cursorial abilities and that its cursorial adaptations are indicative of a cursor that had evolved to reduce the cost of locomotion at moderate speeds and for sustaining these speeds, rather than for running at high speeds or for other high force activities, such as acceleration or maneuverability—traits necessary for most kinds of predation. Next, I want to analyze other aspects of *Arctodus*' morphology in order to reconstruct its gait and estimate its speed of travel.

Gait Selection

In Part I, I correlated gait selection in carnivores to proportions in their limbs and back. I noted that a trotting mammal requires a moderate to long back, relative to leg length, so that front-hind limb interference is minimized. Large carnivores with short backs (relative to leg length), namely hyenas and long-legged dog breeds, do not trot but instead use a pace for moderate speed travel. I also contend that the front limbs of pacers (including non-Carnivora) tend to be elongated relative to the hind limbs, giving the back a sloped appearance. Trotting is difficult and inefficient for such an animal because front-hind diagonal pairs of feet cannot take equal-length strides. This is not a problem for pacers where lateral limbs swing as pairs, because flexure in the trunk increases the stride of the shortened hind limbs (this is not possible in the trot because the trunk must be kept stiff). But gait choice is more than just an accommodation for morphology, since gaits also influence energetics. Recall, for instance, that pacers are able to utilize trunk muscles to assist in oscillating the limbs, and pacers can take longer strides than non-pacers because there is no front-hind limb interference. Long strides correlate directly to a decrease in the cost of transport (Part I, Kram and Taylor 1990). Because of the association between limb morphology, gait selection, and energetics, it seems reasonable to assume that limbs and gaits co-evolve under strong forces of selection.

To quantify limb and back proportions and assess gaits in *Arctodus*, I will use the Intermembral Index (IMI)

and a Back Length Index (BLI) discussed earlier. These indices were calculated for the short-faced bear, brown bear, black bear, polar bear, spectacled bear, wolf, lion, and spotted hyena. These last three (non-ursid) species were analyzed because they represent a broad spectrum of locomotor styles in large carnivores. Modern bears were examined in order to investigate conformational similarities between them and *Arctodus*, which will help determine if they are appropriate analogs for reconstructing gaits in *Arctodus*.² The morphology and scaled proportions of these carnivores are compared in Figs. 1 and 2 (Part I).

Calculations of BLI and IMI show that 1) *Arctodus'* back was shorter (relative to limb length) than any of the modern carnivores tested, and 2) the disparity between front and hind limb length was considerable in *Arctodus*, being nearly as great as in spotted hyenas— known pacers (Table 7, Fig. 17).³ In fact, short-faced bears resemble spotted hyenas more than they do any other carnivore, including other bears, in terms of limb and back conformation. As noted, nearly all large mammals with short hind limbs and tall fore limbs relative to the length of their backs (i.e., tall shoulders) do not trot, but pace when traveling at moderate speeds. I conclude from the above data that *Arctodus* would have been a pacer, and perhaps locomoted in other ways similar to spotted hyenas. (After estimating speed of travel below, I will return to a detailed comparison with hyenas).

Acceleration

The IMI also can be used to assess some aspects of a carnivore's ability to accelerate. In Part I, I discussed how long limbs in general are not beneficial for acceleration. However, while the best accelerators tend to have short limbs, their hind limbs are long relative to their front limbs (Gonyea 1976). This is characteristic of felids, for example—the best accelerators among large carnivores (Ewer 1973, Gonyea 1976, Kitchener 1991). Relatively long hind legs in felids allow them to burst up to top speeds almost instantaneously because their first stride off the hind legs is essentially a leap from a crouched stance. The crouched stance greatly increases the length of the first stride, which gives the muscles of the hind limbs a longer contraction period to generate

² Complete skeletons were measured for all bears and wolves, including length of individual vertebrae. Data for lions and hyenas were taken from scale drawings and photographs. The validity of this technique was confirmed by performing it on photos/drawings of bears and wolves, for which the actual values were known.

³ Indices for bears were derived from data in Table 6.

their force (thus, they generate more power). This “leap” allows the limbs to reach a high velocity on the first stride (Biewener 1983b). In contrast to felids, short-faced bears had very short hind limbs relative to their front limbs (high IMI), a configuration that would have greatly reduced their ability to accelerate rapidly (Fig. 17). Likewise, it is reasonable to conclude that *Arctodus* had to take numerous strides to reach top speed.

A relatively long, flexible back, represented by a high BLI, also increases a quadruped's ability to accelerate because it allows the body to be flexed and extended during aerial phases, which increases stride length. Not surprisingly, felids have essentially the highest BLIs of the carnivores tested. The BLI of the polar bear appears to be higher, but this may likely be an artefact of small sample size; bears in general have low BLIs and are too large to flex and extend the back much while galloping. Flexing and extending the back during the aerial phase of a full gallop exposes the spine to sudden vertical forces upon landing, and since the forces of running increase with mass faster than skeletal strength, very large mammals (around 200 kg and above) do not run with flexed backs (Hildebrand 1960). This is not a liability for a large mammal that is able to sacrifice acceleration, and in fact, a stiff back seems to be preferred by mammals of all sizes which engage in prolonged travel. The long distance trotting wolf maintains a rigid back, as do the migrating bison and wildebeest, although for different reasons (Guthrie 1990).

The intermediate back length of wolves (Fig. 17) seems well-suited for an efficient trot because the back is long enough to prevent too much interference between front and hind feet, yet short enough to remain rigid without much muscular exertion. For a trotting wolf (or dog of comparable size), the whole body is noticeably non-compliant and a stiff back provides a rigid platform from which it can suspend its legs. In Part I, I showed that non-compliant gaits are more efficient than compliant gaits, and indeed, a wolf can keep up its trot for long periods without fatiguing (Mech 1970). In fact, efficient, long-range trotting could be considered one of the hallmarks of large canid evolution (Ewer 1973). The lion's long back, in contrast, forms a very long span (Fig. 17), which must be energetically more costly to support. Pennycuick (1979) suggested that large felids are generally less efficient at locomotion, compared to other carnivores, because of the dual function of their limbs and their specialization for ambush hunting. While the lion's long, flexible back may detract from locomotor efficiency, these traits enhance acceleration and top speed because they increase stride length during a gallop (Hildebrand 1960, 1985).

Guthrie (1990a) assessed the relationship between back/limb morphology and cantering gaits in wildebeest

and plains bison. Guthrie showed that these migratory ungulates need stiff backs to oppose the tension of stretch tendons in their necks in a complex arrangement whereby elastic strain energy is used to “kick-out” the hind legs as the head is lowered. Their back also needs to be stiff because these cantering ungulates take long strides with their front legs, during which the hind legs are suspended, thereby placing a heavy load on the spine for extended periods (Guthrie 1990a).

Given its size, a flexible and long back would have been fairly useless in short-faced bears. By all modern standards, *Arctodus* was too big to incorporate prolonged aerial phases in its gallop when the back was flexed and extended. The role of the back during locomotion in *Arctodus*, I believe, was comparable to large ungulates in that it transferred elastic strain energy. But an even better parallel is found amongst spotted hyenas, so I turn next to a discussion of locomotion in this carnivore, which may appear to have a strange build and unseemly gait, but which in fact is magnificently balanced for an unusual, but effective, form of locomotion.

The Hyena Analogy—Pros and Cons

In this discussion, I will not be arguing that *Arctodus* was a scaled-up hyena—it was not. Instead, I will show why an animal might evolve some proportions seen in both hyenas and *Arctodus* by discussing the advantages and disadvantages they confer. I begin with a relevant review of the way hyenas approach their prey using different gaits. These generalizations follow patterns established in Kruuk and Turner (1967), Kruuk (1972), and Mills (1989) and from my own observations of videotaped hyenas.

Hyenas are social carnivores, but even when part of a group, each hyena acts and hunts fairly independently or perhaps in pairs, except when specifically hunting for very large prey such as zebra (but even then, there is minimal co-ordination of hunting effort). Essentially, each hyena in a “group” is hunting on its own and a pursuit most often is initiated by a single hyena with others apparently joining in when the hunt looks promising. Hyenas seem to test their prey more than almost any other large predator, and it is typical to see an individual hyena move into a group of wildebeest (their primary prey in most regions) and force them to scatter, whereby the hyena can detect or create an opportunity which it can exploit. When such an opportunity arises—for instance the discovery of a wildebeest running awkwardly—other hyenas may join the pursuit or kill.

When hunting in this manner, a hyena uses three distinct gaits for different stages of the process. When approaching and scouting a group of wildebeest, the hyena will walk using a long-stridden pace. When it confronts and disrupts a group, the hyena will use a

faster, bouncy canter (slow gallop) as it assesses individual prey for vulnerabilities. If an animal is picked out for pursuit, the hyena accelerates from a canter to a full gallop and will pursue intently for usually less than 1 km. At this point, other hyenas may join in.

Kruuk (1972) specifically notes that hyenas often pursue and catch their prey at remarkably slow speeds—often around 15 km/hr. This is because their strategy of moving amongst the herds and constantly testing individuals frequently leads to serendipitous opportunities to kill prey. But it is important to note that hyenas still rely on high speed pursuit for a large amount of their hunting, and successful hunts at slow speeds are most common during group hunts after zebra. Therefore, it is not appropriate to extend this argument and suggest that short-faced bears could have been successful predators without high speed pursuit. All predators need high speeds, or at least rapid acceleration, at times and must be able to maneuver at those speeds. Plus there is no sound basis to argue that *Arctodus* was social (I believe that the only way a carnivore the size of *Arctodus* could be predatory would be if it used social hunting tactics, but calculations in the next chapter show that a “pack” of short-faced bears would require more prey biomass production than any terrestrial system could provide.)

In addition to the above course of events, five relevant patterns in hyena locomotion are: 1) hyenas continuously change speeds within their gallop (Kruuk 1972), 2) hyenas locomote over a wide range of speeds without changing gait (personal observation), 3) hyenas are on the move and work their prey for longer periods than most predators (Kruuk 1972, Mills 1989), 4) hyenas use a pace for moderate speed travel when scouting an area or moving from one point to another (Kruuk 1972, Mills 1989), and 5) in the Serengeti, hyenas regularly “commute” long distances (~50 km) during the dry season to hunt migratory prey (Kruuk 1966, Hofer and East 1993a).

I propose that the key to understanding locomotor strategies and gait selection in hyenas lies in understanding the role of their long necks and heavy heads. Both of these traits are related to the hyena’s ability to process large mammal carcasses quickly and thoroughly, and they probably have evolved for these purposes. Part of my contention will be that hyena locomotion and post-cranial morphology have evolved around these constraints.

The heads of hyenas are robust and heavily built to house strong masticatory muscles, massive teeth, and to be able to handle the stresses of forceful biting, including bone processing (Sutcliffe 1970, Kruuk 1972, Ewer 1973). The long, strong neck seems to relate most to competition at kills. Competition between individual hyenas at a kill is keen, and the strategy which seems to

have evolved is one where each hyena grabs what it can and eats as quickly as possible before the carcass is totally consumed by other hyenas (Kruuk 1972, Bertram 1979). For this reason, hyenas bolt large chunks of food, but they also remove large pieces—often entire limbs—and carry them a few meters away from the kill, especially when being chased by another hyena (Kruuk 1972). Doing so requires a strong neck since the piece being carried can weigh nearly as much as the hyena itself. For these muscles to evolve such strength, they would have had to become not only wider, but also longer—as per discussions in Part I, muscles need to contract over greater lengths to be strong.

To balance this long, heavy neck and head and to prevent their center of gravity from being too far forward, hyenas would have needed to evolve certain modifications to their post-cranial morphology. I suggest that the long front limbs and short hind limbs accomplish this by creating a radical pivot point at the shoulders. If one models the shoulder as a fulcrum with the axial skeleton on the anterior and posterior sides forming two levers, it can be seen how the low, heavy hind end has the effect of counterbalancing and passively lifting the heavy head and neck. If the hind end were tall and proportioned like other carnivores, then the hyena's center of balance would be too far forward, and it would be difficult (or at least costly) to keep the head up. Therefore, within this theory, hyenas have evolved short hind ends to mechanically counterbalance the head and keep it propped up.

Next, consider the situation when a hyena scouts a wildebeest herd using a pacing gait. Its head typically is held low (Kruuk 1972), which functions to tense the muscles and tendons of the neck and back, which in turn makes the back more horizontal and elevates the pelvis. This process increases clearance for the hind limbs and allows them to be swung more stiffly (without being flexed), which effectively increases their length and stride. Only when this is accomplished through lowering the head can one front and one hind limb be swung as a pair (pacing). This being achieved, the hyena can utilize a long-stridden, efficient pace which allows it to scout herds for long periods without fatigue. Hyenas spend most of their hunting time engaged in this scouting behavior (Kruuk 1972, Mills 1989), and they commonly commute distances of 30 - 60 km between dens and hunting areas (data reviewed by Hofer and East 1993b; also see Pennycuick 1979). Therefore, hyenas represent an example where pacing has evolved in a species where selection should be high for increased locomotor efficiency.

When breaking into a canter and entering a herd, a hyena has a totally different look, not only because of its slow galloping motion, but because its head is raised.

Referring back to the lever analogy, raising the head has the effect of releasing tension on the muscles and tendons of the back and lowering the hind end. Since the two hind and two front limbs each swing as couplets independent from each other during the canter, the stride lengths of each couplet do not need to match. Moreover, because the two hind limbs are moving together, they can be swung in a wide arc beneath the body. During this action, the back half of the body essentially moves as a unit, pivoting at the shoulder. When the back legs are then extended, they can make a long stride which propels the animal forward and slightly upward upon which it lands on semi-stiff front limbs. Because the front limbs are not very compliant, but act more as pivot points, the slow gallop has a bouncy, rocking motion. The gait also looks bouncy because the head bobs up and down to alternately tense and relax the back when the hind end flexes and extends. When used at high speeds, the rocking motion decreases because the front limbs flex (become compliant) and increase their propulsive contribution to the gait, rather than just acting as pivot points. During this style of fast galloping, the hind limbs still extend far forward and have an elongated step length because the back flexes considerably. In conventional gallops, the front limbs provide about 65 % of the propulsion (Manter 1938, Cavagna *et al.* 1977), but I would venture that the hind limbs are more important in the fast running hyena.

I also contend that the whole phenomenon of short, sloping backs has evolved in other mammals for the same reasons it did in hyenas—to accommodate a heavy front end. The same pattern can be found, for example, in giraffes and camels, whose long necks would act to amplify the mechanical leverage of the head's weight. Balancing this weight requires getting the back end low to the ground, which is accomplished through a rearward sloping back and elevated shoulders. It seems logical that this was driving body proportions and locomotion in *Arctodus* as well. While *Arctodus*' neck was relatively short (Table 6), its head was very massive (Kurtén 1967a), and either a long neck or a heavy head will place a mechanical encumbrance on the lever system I just described, requiring counter-balancing by the rear-end. Moreover, hyenas, giraffes, camels—and almost certainly short-faced bears—accommodate this morphology by using a pacing gait instead of a trot for moderate-speed travel. As a rough equivalent to trotting, pacing is a fairly fast gait, being quicker than the singlefoot walk (Hildebrand 1976, 1985). It can even be used as a running gait, and I showed that pacers are pre-adapted for efficient, long range locomotion (although non-pacers also may develop this trait). Furthermore, I will show below that because of its size, *Arctodus* would have been a fast pacer.

But is it realistic to extend the hyena analogy so far as to say that *Arctodus* and spotted hyenas galloped in similar ways? I think the answer is yes, to a limited degree. Mechanically, *Arctodus'* gallop must have looked like a hyena's gallop in that the hind end likely moved as a single unit, rocking at the shoulders, and being swung far forward beneath the tall front legs. But in application, its likely these two species differed substantially. The hyena's habit of changing speeds within its gallop allows the animal to break into faster speeds more quickly, which is useful for hyenas in their special form of predation. However, this is not energetically efficient. If my arguments are correct that *Arctodus* would not have engaged in high speed, high force locomotion, then there would be little reason for it to use a variable-speed gallop like that of hyenas. But by no means am I arguing that *Arctodus* could not gallop (run). In fact, it may have been capable of fairly high speeds— faster than a grizzly I would think. My argument simply has been that it would have been straight-line running, and a short-faced bear would have needed to take numerous strides to reach top speeds— very much unlike a grizzly. Next, I will attempt a more precise estimation of *Arctodus'* pacing and running speeds.

Speed of Travel

There are a number of techniques and formulae available for estimating speeds (but not necessarily top speeds) in extinct animals. Many of these were developed specifically for applications to fossilized trackways. These techniques provide general estimates of the speed of travel when the tracks were laid down, but say little about top speeds or normal speeds of travel. Other techniques involve linear correlations between body mass or limb length and running speed, but these techniques have been shown to be very imprecise, especially when applied to very large mammals. Moreover, these techniques have been applied mostly to dinosaurs and provide only very basic estimates of speeds for a group of animals which are essentially a mystery. However, *Arctodus* is essentially a modern mammal with close living relatives, so a more precise indicator of speed should be used. The two methods which seem most applicable are: 1) Alexander and Jayes' (1983) method for scaling locomotion using Froude numbers and linear dimensions, and 2) Garland's polynomial for maximum running speed (MRS) using body mass.

Alexander and Jayes' (1983) method scales locomotion in animals with similar builds but different size using Froude numbers— non-dimensional constants that scale size and motion in dynamic systems. Scaled animals move in dynamically similar ways at speeds that make their Froude numbers equal. Consequently, this method predicts the speed of animals during

physiologically-equivalent events, such as the speed of a gait change, using the following equation:

$$F = v^2 / g \cdot l \quad (20)$$

where F is the Froude number, v is ground speed, g is the force of gravity, and l is leg length (l could also be some other linear dimension of locomotion, such as stride length). Alexander and Jayes have shown further that quadrupeds generally change from a walk to a trot (or pace) at $F \sim 0.5$, and from a trot (or pace) to a gallop at $F \sim 2.5$ (these are approximate values and the generalization is somewhat oversimplified, but these are the most appropriate values to use for calculations performed below— see Alexander and Jayes (1983) for more detailed correlations between gait change and Froude number).

By scaling limb length (l) in *Arctodus* to that of hyenas, it would be possible to make a fairly accurate estimate of the speed at which *Arctodus* changed from a walking singlefoot to a pace and the speed at which it broke into a gallop. Unfortunately, these speeds have not been measured in hyenas. Nonetheless, it is possible to make rough calculations for *Arctodus* using its limb length and the above mentioned average Froude numbers. Then these estimates can be qualified from observations of how hyenas deviate from other large mammals. Using Formula 20 and values on *Arctodus'* hind limb length in Table 6, I derived the following estimates:

$$\begin{aligned} \text{speed}_{\text{walk-pace transition}} &= \sqrt{0.5 \times 1.129 \times 9.8 \text{ m/sec}} \\ &= 2.6 \text{ m/sec} (8.5 \text{ km/h}, 5.3 \text{ mph}) \end{aligned}$$

$$\begin{aligned} \text{speed}_{\text{pace-gallop transition}} &= \sqrt{2.5 \times 1.129 \times 9.8 \text{ m/sec}} \\ &= 5.3 \text{ m/sec} (18.9 \text{ km/h}, 11.8 \text{ mph}) \end{aligned}$$

These calculations suggest that *Arctodus* would not have broken into a gallop until reaching nearly 12 mph, a fairly high speed. Garland's (1983) polynomial formula⁴ relating MRS to body mass predicts a top speed of 51 km/hr (32 mph) in a short-faced bear weighing 700 kg (Table 10)(see Fig. 7 of Part I and its discussion of Garland's polynomial). But I showed that few mammals actually run with MRS similar to this theoretical prediction, and an animal's build must be assessed

⁴ $\log MRS = 1.47832 + 0.25892 (\log Mass\text{-kg}) - 0.06237 (\log Mass\text{-kg})^2$

TABLE 10. Maximum Running Speeds (MRS) in km/h for selected large mammals reported by Garland (1983) versus MRS calculated using his formula: $\log MRS = 1.47832 + 0.25892 (\log \text{Mass}) - 0.06237 (\log \text{Mass})^2$

species	mass ¹	MRS reported ²	MRS calculated
CARNIVORA			
<i>Lycaon pictus</i>	20	70	51
<i>Canis familiaris</i>	25	67	52
<i>Canis lupus</i>	40	64	54
<i>Acinonyx jubatus</i>	55	110	55
<i>Panthera pardus</i>	60	60	55
<i>Crocuta crocuta</i>	65	65	55
<i>Ursus americanus</i>	135	48	56
<i>Panthera leo</i>	150	59	56
<i>Panthera tigris</i>	230	56	55
<i>Ursus arctos</i>	300	48	55
<i>Ursus maritimus</i>	400	40	54
<i>Arctodus simus</i>	700	—	51
NON-CARNIVORA			
<i>Antilocapra americana</i>	50	100	55
<i>Rangifer tarandus</i>	120	80	56
<i>Ovis canadensis</i>	150	48	56
<i>Equus hemionus</i>	260	70	55
<i>Equus zebra</i>	300	64	55
<i>Equus caballus</i>	400	70	54
<i>Cervus elaphus</i>	300	72	55
<i>Alces alces</i>	450	56	53
<i>Camelus dromedarius</i>	500	32	53
<i>Bison bison</i>	900	56	50
<i>Loxodonta africana</i>	6000	35	37

¹ Masses represent species averages reported by Garland, which he collected from various general sources. Therefore, values for mass and MRS not from the same individual

² Speeds are those given by Garland. It is well known that many reported top speeds for mammals are unreliable (usually too high), and many of them in this table are undoubtably inaccurate. Despite this, they still represent the values used by biologists because they are the best or only ones available.

qualitatively in order to understand why its actual MRS falls above or below predicted values (Fig. 7, Part I). For instance, actual MRS in brown bears is about 40 km/h (25 mph), but Garland's polynomial predicts 55 km/h (34 mph) for a 300 kg brown bear. This and other values in Table 12 indicate that all modern bears have actual MRSs well below speeds predicted from their mass, while obligate predators have MRSs much higher than predicted.

Based purely on the kinematic implications of *Arctodus*' build (i.e., its reduced limb mass), one could conceivably argue that its morphology had evolved to increase top speeds relative to other bears. This essentially was Kurtén's contention, but I have been trying to show throughout these chapters that such an argument is unrealistic: because of its extreme mass, such high speeds most likely would have exceeded *Arctodus*' skeletal strength—at least if it tried to maneuver at these speeds. Without the ability to maneuver, high speeds are of limited value to a predator that hunts solitarily. Given these considerations, a reasonable estimate of MRS in *Arctodus* might be closer to 40 - 45 km/h, rather than the value of 51 km/h predicted by Garland's formula.

Interestingly, the above calculations using Froude numbers indicate that *Arctodus*' moderate speed gait—its pace—would have been fairly fast. In Fig. 5, Part I, it was shown that mammals normally (and optimally) trot or pace at a speed roughly halfway between their walk-pace transition and their pace-gallop transition. In *Arctodus* this would be about 13.7 km/h (8.5 mph). That is a fairly high value for moderate speed travel, but it does not seem out of line. Mills (1989), for instance, reports that spotted hyenas typically travel cross country at approximately 10 km/h (6.2 mph).

I have argued that short-faced bears were not built specifically to be runners, but I am not contending that they were incapable of running, or never encountered occasions where it was necessary to run. Moreover, my estimates of top running speeds up to 40 - 45 km/hr mean that short-faced bears were not slow. In Part III, I explain why competition between Pleistocene carnivores for control over carcasses probably was intense, and why it seems likely that *Arctodus* had evolved to dominate this rivalry. Given this assumption, it is likely that any carcass on the Pleistocene landscape would have attracted quite a bit of attention and would have led to direct conflict among carnivores. In such a situation, short-faced bears would have needed to express their dominance through aggressive behavior and intimidation. As I alluded to earlier, standing upright would have been one likely means to accomplish this, but it also is likely that *Arctodus* would have needed to drive carnivores off of carcasses, in which case it could have used its modest gallop. *Arctodus* also may not have successfully

dominated every situation because some of its rivals were social, and would have aggregated into formidable groups (see Part III). In those cases, *Arctodus* actually would have needed to run away from a carcass and recalcitrant pursuers. Neither of those types of running (aggressive and defensive) require rapid acceleration or even very high speeds, nor do they demand much maneuverability in the form of sharp turns. These activities seem to be quite within the range of *Arctodus'* structural capacities.

Furthermore, I stated from the onset that it is unrealistic to think that *Arctodus* never would have killed its food directly. I simply am arguing that predatory skills did not form the basis for selection in *Arctodus'* evolution. Even though it seems to have evolved specifically as an exploiter of scavenging opportunities, *Arctodus* undoubtably killed prey that presented itself as an easy target. At times, this would have required a galloping form of running. Finally, although it is speculative, I can imagine a short-faced bear harassing its competitors at a carcass by patrolling around them, demonstrating its presence with a type of bouncing slow gallop similar to hyenas. In fact, this very behavior can be observed today in hyenas which are vigilant in trying to drive lions off of carcasses.

4. POSTLOGUE AND PREVIEW OF THE PART III

At the beginning of this chapter, I stated that there were three credible foraging hypotheses which could explain *Arctodus'* carnivory: 1) it was a powerful predator that overwhelmed very large but slow megafauna, 2) it was a fast cursorial pursuit predator, or 3) it was a scavenging specialist. Each of these hypotheses makes specific predictions about the locomotor adaptations one would expect to find in such a carnivore, since each implies selective pressure for very disparate locomotor and dextrous abilities. I have tried to show that the morphology of *Arctodus* does not support the predictions of the two predatory hypotheses, but is consistent with those of the scavenging hypothesis. Foremost, *Arctodus'* skeleton was too weak to handle the locomotor forces normally incurred by predators, and indeed, no predator today comes close to *Arctodus'* size. The reason for this is because the relative strength of bone decreases with body size, as does running ability.

In *a priori* evolutionary terms, it is difficult to understand how selection under a predatory lifestyle would lead to the suite of morphological traits found in *Arctodus*. For instance, if *Arctodus* preyed on large, slow-moving pachyderms (hypothesis 1), then why did it evolve such a gracile build? It would seem that such a predator would need to be as strong as possible and built more like a typical bear. If *Arctodus* preyed on fast prey (hypothesis 2), then why was it so large? To capture fast

prey, *Arctodus* would have evolved in a direction that increased speed, maneuverability, and acceleration. Since smaller carnivores are more adept at these skills than larger ones, selection is predicted to have favored smaller body size in short-faced bears. Even if evolution did lead to a predator the size of *Arctodus* which engaged in high force running (something that I showed was highly improbable), then it most certainly should have evolved a more robust, not more gracile, skeleton.

Although not a fast or agile runner, *Arctodus* was an incipient courser with features indicating it was built for locomotor efficiency and for sustaining moderate speeds over extended periods using a pacing gait. Stable isotope data indicate that *Arctodus* was carnivorous (Matheus 1994, 1995; Bocherens *et al.* 1995), so I suggested that

these morphological traits would be most advantageous in a scavenger which needed to cover a very large home range. This seemed logical since one might predict that carrion resources were widely scattered and unpredictably distributed during the Pleistocene. A scavenger searching for large mammal carcasses on the landscape would need to cover a large area and stay on the move in order to increase its chances of finding enough carcass biomass to sustain itself.

Part III examines the energetic ecology of these predictions and tests them in a model of Pleistocene carcass production. There, I also discuss the necessary conditions leading to the evolution of a pure scavenging niche in a large carnivore, and I finish by suggesting probable mechanisms underlying *Arctodus'* extinction.

LOCOMOTOR ADAPTATIONS AND ECOMORPHOLOGY OF SHORT-FACED BEARS (*Arctodus simus*) IN EASTERN BERINGIA

PART III: FORAGING ENERGETICS, CARCASS PRODUCTIVITY, AND THE EVOLUTION OF *ARCTODUS*' SCAVENGING NICHE

1. INTRODUCTION

In Parts I and II, I established arguments contending that *Arctodus*' post-cranial morphology had evolved for increased locomotor efficiency within a scavenging niche. Part III explores probable ecological and energetic reasons for the association between locomotor efficiency and scavenging.

Energetic axioms predict that a very large, carnivorous endotherm will require an extremely large home range and will not have a high population density (Clutton-Brock and Harvey 1978, 1983; McNab 1963, 1980; Eisenberg 1981). Trophic principles and rules of ecological efficiencies also dictate that terrestrial carnivores have much lower population densities than herbivores and that larger carnivores will have even lower densities (Elton 1927, Slobodkin 1961, McNab 1980, Gittleman and Harvey 1982). These generalities suggest reasons to hypothesize that a pure carnivore the size of *Arctodus* would have existed at low population densities and needed to forage over an extremely large home range in order to obtain enough food to meet its energetic requirements.

Consider the case where such an animal also foraged on highly dispersed food items and invested considerable search effort into each unit of food—food units such as large mammal carcasses that are widely distributed in space and time. Optimal foraging theory predicts that this “big investment, big reward” system should provide selective pressure for both larger size and increased locomotor efficiency. Increased size is predicted because a larger animal 1) can eat more at one feeding when it finds a large food item, 2) can go longer between meals, and 3) has a reduced cost of transport. Increased locomotor efficiency is predicted because such an animal should not expend more energy searching for highly dispersed food items than it gains from them (Emlen 1966; Schoener 1969, 1971, Rapport 1971; Pyke *et al.* 1977; Houston 1979; Krebs *et al.* 1981; Eisenberg 1981).

These sorts of predictions provide the ecological reasoning to argue that *Arctodus*' morphology would have been most adaptive within a scavenging niche. Without this rationale, it would remain unclear why a

carnivore would evolve the morphological traits found in *Arctodus*, including its extremely large size. This reasoning also provides an additional means to test the scavenging hypothesis. Namely, it should be possible to model the energetic needs of a population of scavenging short-faced bears and then examine whether Pleistocene ecosystems were capable of supporting these needs. If these ecosystems did not produce enough carrion biomass to support the population, then the scavenging hypothesis can be rejected. In Part III, I perform this test by modeling energetic and life history parameters of the *Arctodus* population in eastern Beringia, and the likely amount of carrion that Beringia would have been producing.

Throughout this modeling exercise I will rely heavily on established correlations between body size and energetic life history parameters in modern carnivores, but frequently I will draw back from these strictly mathematical correlations and modify them by using direct observations and analogies in modern carnivores. Even though *Arctodus* inhabited a variety of landscapes and ecosystems in North America, I will be constructing input variables based purely on ecosystem parameters in eastern Beringian, to keep the model manageable. This approach also should provide the most rigorous test of the scavenging hypothesis because Beringia was relatively less productive than many other northern, Pleistocene ecosystems (Hopkins *et al.* 1982, Guthrie 1990a). To construct the model, I will estimate the annual food requirements (kg of meat/km²/year) of a carnivore the size of *Arctodus* (700 kg), followed by an estimation of individual home range size and population densities so that I can determine the annual carrion requirements (kg/km²/year) of a minimum viable population of short-faced bears. Then it will be necessary to compare this requirement to the amount of carcass production which could be reasonably expected from Beringian ecosystems. To do this, I will estimate carcass biomass production via both predation by large carnivores and natural mortality in Beringia's large herbivores (kg/km²/year). Both of these latter tasks will require secondary modeling of population dynamics and productivity in both herbivores and carnivores.

2. FORAGE REQUIREMENTS AND POPULATION PARAMETERS

In order to model the energetic ecology of the entire population of short-faced bears in eastern Beringia, I first will need to estimate the foraging area and annual energy budget of a single bear. Then, after making certain demographic considerations, this budget can be extrapolated to the whole population, whose size also will need to be estimated. Fortunately, numerous studies have documented correlations between body size and a wide range of energetic life history traits in mammals; many of these relationships have been specifically developed for carnivores (summaries in Kleiber 1932, 1961; McNab 1963, 1980, 1983, 1989, 1990; Gittleman 1985, 1986; Damuth 1987; Peters 1983; Calder 1984; Eisenberg 1981; Schmidt-Nielsen 1984).

As with other scaling relationships, these correlations are described in terms of the allometric equation:

$$P = b M^a \quad (21)$$

where P is the parameter in question and M is body mass. The regular log-linear relationship between various biological parameters and body size is premised on the scaling of metabolic rate to body size in endotherms. Using these empirical relationships, one can cautiously predict general features about a species, such as its home range, foraging (energetic) requirements, and minimum viable population density, based solely on its body mass and trophic level. Many authors warn that such scaling relationships are purely descriptive of the species they are measured on, and are not intended to be used as predictors in unstudied species. However, these relationships provide a good starting point to estimate such variables in an extinct population since they certainly suggest general trends within a group of animals. Naturally, it may be necessary to qualify a prediction based on ancillary information, and I will be doing this throughout the following sections.

Forage Requirements

Harestad and Bunnell (1979) showed that the amount of flesh consumed per day by a carnivore (FC in grams) is equal to:

$$FC = 1.7 M^{0.68 \pm 0.02} \quad (22)$$

(in this equation, M also is in grams). For a large 800 kg male short-faced bear this would be equivalent to 17.6 kg (17561 g) of food eaten every day, or 6424 kg per year. A 600 kg female would require 5271 kg/year, and the population average (assuming 700 kg) would be 5853

kg/year. Farlow (1993) derived an estimate of annual mass-specific food intake for predators as:

$$FC = 48.87 M^{-0.30} \quad (23)$$

where FC is kg food consumed per kg body mass per year. Using this equation, the annual kg of flesh eaten annually by the average 700 kg short-faced bear would have been 4793 kg, somewhat less than the first estimate.

Harestad and Bunnell's equation is derived from actual values on grams of food consumed per day by mammalian carnivores as reported in field studies, but includes all types of food eaten (i.e., flesh and vegetable matter) and their data were derived mostly from small carnivores. Farlow's equation is more theoretical. First, he uses food consumption rates (in watts) reported for a wide range of birds and mammals, including herbivores. Then he converts watts to kg of flesh required by a carnivore using the energy content of animal tissue (~ 7,000,000 joules/kg). Farlow's method yields a lower value probably because it unrealistically assumes that all food eaten by a carnivore is pure flesh, which is relatively high in energy content. I am inclined to use Harestad and Bunnell's equation because it is derived from data on actual mammalian carnivores, and its higher prediction of flesh requirements will be a more rigorous test of the scavenging hypothesis.

The predictive power of Equation 22 can be examined using known rates of food consumption in large predators. Spotted hyenas in the Serengeti consume 3 kg of prey per day, equal to 1095 kg per year (Kruuk 1972). Using a value of approximately 60 kg for the weight of an average Serengeti hyena (Kruuk 1972, Nowak 1991), the equation predicts this consumption rate perfectly. However, as I will discuss later, hyenas in the Ngorongoro ecosystem consume only 2 kg/day. The disparity arises probably for two reasons: 1) the method by which "consumed" prey is calculated (see below), and 2) because hyenas in Serengeti make long "commutes" between denning areas and foraging areas to hunt migratory prey, whereas hyenas in Ngorongoro do not commute (Kruuk 1972, Hofer and East 1993a). Therefore, Serengeti hyenas truly may eat more because they incur greater costs of locomotion.

In comparison, Kolenosky (1972) estimated that wolves hunting white-tailed (*Odocoileus virginianus*) deer in Ontario consume 0.1 kg of prey per kg of 1 kg of body mass, which is twice the rate of hyenas. Mech *et al.* (1971) estimated 2.5 kg of deer per day for wolves in Minnesota, which is only slightly greater than the amount predicted for a 40 kg wolf (2.3 kg/day) by Equation 22. Numerous other studies on wolf foraging also have shown that individuals consume about 1.5 - 3.0 kg/day (e.g., Pimlott *et al.* 1969; Mech 1970, 1977; Peterson 1977;

Peterson *et al.* 1984; Fritts and Mech 1981; Ballard 1981, 1993; Ballard *et al.* 1987). Field data on consumption rates can only be taken as rough approximations of food requirements because these calculations are made by dividing the estimated prey mass killed by total predator mass. Prey mass almost always is estimated, and the assumption that this entire mass is consumed, or consumed by the predator in question, is seldom valid. Wolves also have been known to consume over 12 kg of food at one feeding (Mech 1970), and Kruuk (1972) recorded one hyena eating 14.5 kg and another eating 9.3 kg in single feeding bouts. Incidents like these can potentially lead to an overestimation of daily food intake and energy requirements.

Carcass Requirements

In order to estimate carrion requirements of a scavenging short-faced bear, consumption data must be converted to carcass biomass. For modeling purposes, I will assume that carrion in the Beringian system was being produced by the hunting activities of large predators and natural mortality in the three dominant large herbivores—mammoth, bison, and horse (Guthrie 1968, 1982, 1984a, 1990a). The following values for herbivore body mass will be used:

mammoth	3800 kg
bison	650 kg
caballine horse	175 kg

These represent an approximation of mean adult body mass averaged for males and females, but they differ from estimates used in other studies, so I will explain their derivation.

Mammoth: The wooly mammoth (*Mammuthus primigenius*) was the smallest species of mammoth. Shoulder height was about 2.8 m according to Kurtén and Anderson (1980), which means it stood a little shorter than the African bush elephant (*Loxodonta africana cyclotis*) and a little taller than the African forest elephant (*Loxodonta africana africana*). Its shoulder height is more on line with the Asiatic elephant, to which it is more closely related (Kurtén and Anderson 1980). Haynes (1991) notes that mammoth limb bones are 20 % wider than *Loxodonta* bones of similar length, meaning mammoths were either engaging in higher stress activities or were carrying more body weight for their height—most likely the latter, since mummies of mammoth show that they carried large amount of fat through the winter (Guthrie 1990a). Using this information and the weights listed in Table 11 (from Nowak 1991), I will assign mammoths a weight of 2700 kg for females and 4900 kg for males, with an average of 3800 kg. Guthrie (1968) used an estimate of 3000 kg, while Bliss and Richards

(1982) (in a model discussed later) used 2230 kg, for unspecified reasons. My estimate is higher because I am interpreting the mammoth's stouter bones as an indication that these proboscideans were more heavily built for their height compared to modern elephants.

Horse: It is now apparent that two size classes of horses probably inhabited Beringia during latter stages of the Pleistocene, a moderate-sized hemione (*Equus (hemionus)* cf. *kiang*) and a smaller caballine (*E. (caballus) lambei*) (Guthrie 1968, 1982, 1990a; Guthrie and Stoker 1990; Sher 1974, 1986, 1987; Harrington and Clulow 1973; Harrington 1977, 1978, 1980; Burke and Cinq-Mars 1996). The temporal range and taxonomy of these two equids are unclear but it seems likely at present that they were contemporaneous. However, the fossil record indicates that the smaller caballine was much more common, especially in the late Pleistocene (one theory holds that nearly all large horses in eastern Beringia date to the early and mid Pleistocene), so I will use it as the representative equid (biomass representation is balanced by the fact that the smaller species would have had higher population densities). Modern domestic and feral horses have a considerable size range, often averaging 350 - 500 kg, but some may approach 1000 kg. Their large size in general is a product of domestication. Primitive wild caballines such as the tarpan and Przewalski's horse are smaller and stockier and weigh 200 - 300 kg; Ponies, such as the Shetland are about 150 - 175 kg (Nowak 1991). Since the small caballine of Beringia was, on average, a little larger than a Shetland (Guthrie 1984a), I will assign it a weight of 175 kg. In Guthrie's (1968) biomass estimates, he assigned horses a mass of 250 kg, but this was before it was recognized that two size classes inhabited eastern Beringia. Bliss and Richards (1982) used an estimate of 150 kg in their model.

Bison: To my knowledge, no one has systematically estimated the mass of Pleistocene steppe bison (*Bison priscus*) using skeletal indicators. However, it is widely accepted that they were larger than either present day plains or wood bison (Skinner and Kaisen 1947; Guthrie 1968, 1970, 1990a; Harrington 1977, 1978, Kurtén and Anderson 1980, Anderson 1984, McDonald 1981). Data in these studies indicate that steppe bison may have been 15 - 20 % larger than either modern plains (*Bison bison bison*) or wood bison (*Bison bison athabascae*). Nowak (1991) listed a size range of 350 - 1000 kg for modern plains bison, with an average weight around 450 kg for females and 750 kg for males. Carbyn *et al.* (1993) estimated the average weight of modern male and female wood bison to be 625 kg and 450 kg, respectively. Adding 15 - 20 % to the average weight of modern bison (~550 kg, combined for males and females), yields 633 - 660 kg. Considering these data, I will use a weight of 650 kg for *Bison priscus* in this model. Guthrie's (1968)

TABLE 11. Weights of modern elephants (from Nowak 1991) and estimates of male and female mammoth weights.

	female		male	
	weight- kg	shoulder ht.- cm	weight- kg	shoulder ht.- cm
<i>L. africana cyclotis</i>	range 2400 - 3500 mean 2800	240 - 340 250	range 4000 - 6300 mean 5000	300 - 400 320
<i>L africana africana</i>	range — mean 2700	160 - 240 210	range — - 6000 mean —	160 - 286 250
<i>Elaphus maximus</i> (Nowak makes no distinction for male-female shoulder ht.)	range — mean 2720	250 - 300 —	range — mean 5400	250 - 300 —
<i>Mammoth primigenius</i>	mean 2700	—	mean 4900	—
average mammoth estimates for model = 3800 kg; shoulder ht. = 2.8 m				

approximation for the average weight of steppe bison was 500 kg, and Bliss and Richards (1982) used 450 kg in their model, based on the weight of modern bison (Bliss and Richards did not adjust for Pleistocene body size).

Total Carcasses: In terms of whole carcass mass, 5853 kg (the annual dietary requirement of an average short-faced bear) is equivalent to:

- 1.5 wooly mammoth, or
- 9.0 bison, or
- 33.4 caballine horses

Obviously, certain qualifications to these estimates are in order. First, roughly 10% of a large mammal's body mass is composed of skeleton, which I will consider to be inedible for now. In terms of edible, caloric portions, about 45% of body mass is muscle, and the balance is comprised of skin, digestive organs, fat, blood, and liver in descending order (Calder 1984). Considering that the energy content and digestibility of these tissues differs, and accounting for skeletal weight, I will use a value of 75% for the edible and accessible body mass of a whole mammal. This also is the value used by Peterson (1977), while Schaller (1972) suggests it is lower and Pimlott (1967) estimates 80% (also see Fuller and Keith 1980). With a 75% adjustment, the number of carcasses required annually for one short-faced bear becomes:

- 2.0 wooly mammoth, or
- 12.0 bison, or
- 44.6 caballine horses

It is just as important to consider that a scavenger will seldom encounter a complete carcass and that

carcasses putrefy over time, at a rate that is dependent on temperature. For instance, in subtropical grassland and savannah ecosystems with high densities of competing carnivores, carcasses usually do not last more than a few hours to a few days, depending on their size. Carcasses < 113 kg are completely consumed within 4 hours in the Serengeti and Ngorongoro ecosystems, usually by the predators that killed them (Blumenschine 1987). Adult African buffalo (*Synacerus caffer*; 300 - 900 kg), however, persist for nearly four days on average, and elephants can last 11 days before putrefying if they are not found by carnivores (Blumenschine 1987). These estimates are also in line with those of Houston (1979).

Carcasses of ungulates in northern North America tend to last longer than similar-sized African species. Ungulate carcasses in Alaska, Minnesota, and northwestern Canada remain on the landscape for about 4 to 5 days in late winter and spring and 2 - 10 days in summer, but they are repeatedly visited and fed upon by carnivores during that time (Magoun 1976, Magoun and Valkenburg 1996, Haynes 1982, Oosenbrug and Carbyn 1982). The main large-bodied, carcass-consumers are brown bears, wolves, and wolverines. In Wood Buffalo National Park, Alberta, wolves spend an average of 2.5 days on a bison kill in winter before moving on, but they may return to the carcass again later in the season; soft tissue can be found on bison carcasses in the park for up to 1 month, after which only bone remains (Oosenbrug and Carbyn 1982). On Isle Royale, wolves preying on moose utilize nearly the entire carcass over the course of a few days (Mech 1966, 1970).

In Africa, carcasses are processed very rapidly mostly because of intense competition amongst large carnivores, but in North America the competition is less

intense and dominance hierarchies are simpler: brown bears dominate over both wolves and wolverines at carcasses unless highly outnumbered. However, brown bears are only competitors in the summer, leaving just wolves and wolverines along with raven and fox in the winter. In Alaska, brown bears and wolverines process and protect carcasses more thoroughly than do wolves, although carcass utilization increases in all three carnivores when carcasses are not abundant, or when these carnivores are denning and feeding young (Murie 1944, 1981; Magoun 1976; Magoun and Valkenburg 1996; Haynes 1982; Gardner 1985).

This information suggests that competition for carcasses would have been a key issue for any scavenger in Pleistocene North America, when carnivore diversity was higher than at present. But *Arctodus* almost certainly would have been dominant over other Pleistocene carnivores, except perhaps for large groups of social carnivores (Matheus 1995, 2001), so it would be inaccurate to envision *Arctodus* as being dependent on random carcass availability in the form of “leftovers” from other carnivores. At the end of Part III I evaluate the level of sociality in Pleistocene carnivores and their competitive interactions with *Arctodus*. There I will make the argument that competition for carcasses was indeed keen, and that body size in *Arctodus* most likely was driven by its need to exert dominance. Likewise, body size and the size of social units in other Pleistocene carnivores most likely were shaped by this highly competitive environment.

Population Density and Home Range Size

As a starting point for modeling carcass availability, I first will estimate the population density and home range size (HR) for short-faced bears. In the next section I will calculate the required carcass density for such an area. Both population density and HR size have been scaled to body size in mammals and are tied to the scale effects of metabolism, the density of food energy (productivity) on the landscape, and trophic level (McNab 1963, 1980, 1983; Harestad and Bunnell 1979; Eisenberg 1981; Damuth 1981, 1987). It is important to note that an individual's HR may not translate directly to population density, unless it is an exclusive HR, which is rare (Sandell 1989). In addition, HR can include areas that an animal occupies for reasons other than foraging. Still, it will be instructive to explore predictions for both density and HR in a carnivore the size of *Arctodus*, and then discuss them in terms of other large carnivores.

Harestad and Bunnell (1979) provide the most recent estimate of home range size specifically for carnivores:

$$HR = 0.11 M^{1.36} \quad (r^2 = 0.81) \quad (24)$$

where mass is in grams and HR is in hectares. Note that the scaling exponent is >1 , meaning home range requirements increase faster than body size in carnivores. The exponents for herbivores and omnivores range between < 1 to not significantly different from 1. According to Equation 24, each 700 kg short-faced bear is predicted to have a home range of 9,788,722 ha ($97,887 \text{ km}^2$; equivalent to 24,471,805 acres, or 38,237 miles 2) — an area nearly as large as the state of Ohio, which is obviously unrealistic. This is a good example of how it does not work well to scale some life history parameters over a large range of body sizes, and why these types of relationships often fail as predictive tools. However, this calculation emphasizes the fact that *Arctodus* would need to forage over an enormous area simply because of its size and trophic level. Indeed, the positive scaling of foraging area to body size in secondary consumers is the primary reasons why it is believed that carnivores do not attain such large sizes (Elton 1927, Colinvaux 1978, McNab 1980, Eisenberg 1981) and indirectly why Emslie and Czaplewski (1985) argued that *Arctodus* could not have been carnivorous.

Turning to density estimates, Damuth (1987) compiled data on population densities in hundreds of terrestrial mammals, including 46 carnivores ranging in size from small mustelids to bears. His regression for population density (D) in “vertebrate-consumers” is:

$$D = 3.47 M^{-0.96} \quad (r^2 = 0.67) \quad (25)$$

Assuming an average weight of 700 kg for *Arctodus* (half males, half females), Damuth's equation predicts a density of 0.0064 bears/km 2 , equivalent to 156 km 2 for each bear (134 km^2 for a 600 kg female, and 176 km^2 for an 800 kg male). It is important to note, however, that Damuth's equation is derived almost entirely from carnivores that are predatory. In other words, estimates based on his equation are indirect estimates of prey densities, not carcass densities. Naturally, carcass densities will be much lower than prey densities. Therefore, the calculation of 156 km 2 for each short-faced bear will be regarded as the maximum theoretical density of individuals in prime habitat, but it cannot be construed as an estimate of individual HR size.

Lacking an accurate mathematical predictor of HR or density in such a large scavenger, I will make a some approximations using comparisons to other large, solitary Carnivora. The HR of barren ground grizzlies in arctic Canada, where bear densities are very low, is around 414 km 2 for males and 73 km 2 for females (Pearson 1975, 1976), but values as high as 3029 km 2 have been reported for individual bears (Servheen 1983). Ballard *et al.* (1981) estimated an average HR between 313 - 382 km 2 for grizzlies in southcentral Alaska. Again, these are HR

sizes, not population densities. For perspective, the HR predicted for a 200 kg grizzly using Harestad and Bunnell's equation for carnivores is 1,781,531 HA, or 17,815 km² — again, extremely divergent from any realistic value. But grizzly bears may not be good analogs for HR in short-faced bears, since grizzlies are not strict carnivores. Harestad and Bunnell's equation for HR in omnivores is:

$$HR = 0.059 M^{0.92} \quad (r^2 = 0.90) \quad (26)$$

For a 200 kg grizzly, Equation 26 predicts 44 km² — close to the minimum HR in a female grizzly in some habitats, but it still is a poor estimate for the species' average.

Nowak (1991) lists a wide range of HR values for brown bears, from an average of 80 km² in Yellowstone, to upwards of 600 km². Over the course of a lifetime individual brown bears can inhabit an area covering thousands of km², and males tend to have much larger HRs. There can be considerable overlap in brown bear HRs, and population densities are on the order of one bear per 100 km². In Denali National Park, Alaska, the density is one bear per 30 km², while in tundra areas of northern Alaska and Canada it is one bear per 150 km² (Nowak 1991).

Data from puma may be instructive since it is a wide-ranging solitary carnivore that lives in low densities. Puma have HRs as large as 277 km² according to sources cited in Sandell (1989), and as large as 293 km² according to Nowak (1991). But a cougar in Texas was reported to have roamed over 1826 km² (Lindzey 1987). Based on data in cumulative sources cited by Nowak (1991), a good approximation for average puma HR seems to be around 150 km². Population densities for puma range from 0.048 - 0.005 puma/km², or 1 puma every 21 - 200 km² (Nowak 1991), so even this solitary, reclusive carnivore may experience considerable overlap in HR (mostly between males and females).

Next, I will discuss data on wolf demographics in a fair amount of detail because the information will be used later when I model population parameters in Pleistocene carnivores.

Harestad and Bunnell (1979) calculated a mean HR size for wolves of 2027 km², based on published data. I believe their value is erroneous and represents the HR of entire packs, not individual wolves (this mistake probably is partially responsible for their inaccurate line of allometry correlating HR to body size in very large carnivores). A closer look at specific data shows that individual HRs are much smaller.

Wolf packs in northern Alaska and northwestern Canada typically range over an area around 500 - 1000 km² through the course of a year, and generally are

comprised of 5 - 9 permanent members, equivalent to 56 - 143 km² per wolf (Murie 1944; Mech 1970; Ballard 1982; Ballard *et al.* 1981, 1990; Stephenson and James 1982; ADFG Wolf Report 1994). Wolves hunting bison in Wood Bison National Park, however, form packs averaging around 10 individuals (Oosenbrug and Carbyn 1982). Stephenson and James (1982) reported that wolf densities in northwestern Alaska are around 0.0026 wolves/km² in the foothills of the Brooks Range, but down around 0.0019 wolves/km² on the Arctic Slope. The later value is the same reported by Nowak (1991) for the lowest known density of wolves. Home ranges are large in northwestern Alaska, around 1300 km² for packs of about 5- 8 individuals. Ballard (1993) found local areas in this region with wolf densities ten times as great in prime habitat, but area-wide densities are on the order of 0.004 wolves/km² according to estimates by the Alaska Department of Fish and Game (ADFG Wolf Report 1994). Statewide estimates from this report show that overall wolf densities in northern Alaska are generally between 0.002 - 0.005 wolves/km², pack size is around 5 - 9 wolves, and HR size for an average pack commonly reaches 1000 - 2000 km².

In south-central Alaska, Ballard (1982) reported that the 61,595 km² Nelchina basin supported approximately 450 individuals in 1965. This is equivalent to 0.007 wolves/km², or 137 km² per individual wolf. However, a fair amount of this area— about 18,798 km²— is high altitude, and Ballard implies that this area is not part of normal wolf habitat. Adjusted density in the Nelchina basin using the 1965 population then would be 0.011 wolves/km², or 95 km² per wolf. This agrees with Ballard's estimate of 73 - 119 km² per wolf during the mid-1970s. Since this population was recovering from a previous predator control project, it was nowhere near carrying capacity in 1965. Home range size in these packs was on the order of 500 - 800 km², and an average pack had around 8 individuals. The ADFG 1994 Wolf Report indicates that densities of wolves in interior and southcentral Alaska generally are around 0.005 - 0.01 wolves/km², pack size is around 6 - 9, and pack HRs are on the order of 600 - 1000 km². Pack size tends to be larger for wolves that hunt large prey like moose (Earle 1987).

Home ranges for wolves south of Alaska are smaller and their densities are considerably higher than in the north. In Algonquin National Park (Ontario), where wolves feed mainly on white-tailed deer, packs of 4 - 7 wolves typically have a HR around 100 - 300 km², or approximately 35 - 40 km² per wolf. Overall densities in Algonquin are 0.038 wolves/km² (Pimlott *et al.* 1969). In northern Minnesota, wolves also primarily hunt white-tailed deer, but their HR size tends to be larger— around 200 - 350 km² for a pack of 5 - 8 wolves, or around 50

km^2 per wolf. Average densities there are approximately 0.015 - 0.040 (Mech 1970, Van Ballenberghe *et al.* 1975, Fritts and Mech 1981, Nelson and Mech 1981, Keith 1983, Fuller 1989). On Isle Royale, about 20-25 resident wolves use the 544 km^2 island to hunt moose, yielding a density of 0.037 - 0.046 wolves/ km^2 , or $\sim 24 \text{ km}^2$ per wolf (Mech 1966, 1970; Pimlott 1975; Peterson 1977; Peterson and Page 1983). Pimlott (1975) believes this is about the highest sustainable density for wolves.

Nowak (1991) also reviewed wolf HR size and population densities, and arrived at similar generalities to the ones made here. From these compilations, I conservatively estimate that it takes at least 100 km^2 to support one wolf for energetic purposes, equivalent to a population density of 0.01 wolves/ km^2 . But it is not rare for populations to exist at densities as low as 0.002 wolves/ km^2 or as high as 0.02 wolves/ km^2 .

I showed that Harestad and Bunnell's (1979) equation grossly overestimates HR in large carnivores, and that Damuth's equation has similar inadequacies estimating population densities. Using actual carnivore population data discussed above as a guide, I will make a rough estimate of exclusive HR size and population density for short-faced bears for use in subsequent discussions. A conservative (low) estimate will make the model more rigorous. Following that guideline, and assuming that *Arctodus* foraged on a highly dispersed food resource, a first estimate might be that each short-faced bear required 500 - 1000 km^2 of exclusive HR; probably closer to the latter. Since I am assuming that HRs are exclusive, this yields a population density of 0.001 - 0.002 bears/ km^2 . For purposes of this model, I will use 0.001 bears/ km^2 because it will err on the side of rarity.

As an additional consideration, Sandell (1989) observed three key patterns relating HR size to food distribution in solitary carnivores, which I will use to further narrow my estimates for *Arctodus*: 1) HR size, at least for females, seems to be determined by the abundance and distribution of food biomass during the most critical times of the year, such as during gestation and lactation. When food is abundant during critical times and not dispersed, this leads to smaller HRs. 2) HRs will be exclusive when food resources are stable and evenly distributed; they overlap when there is much temporal variation in food supply, and 3) Exclusive HRs will be smaller than overlapping HRs. In discussions at the end of this paper, I will be showing why it is likely that short-faced bears had large HRs with a fair amount of overlap because carcasses would have been widely dispersed and seasonally scarce. Sandell also recognized two ways that solitary carnivores are spatially arranged which are relevant to this discussion: 1) because males are larger and require more energy, their HR is usually larger than

females. 2) males will keep to territories when females are evenly distributed; when females roam, so do males. 3) male HRs do not overlap when females are evenly and densely distributed. 4) when males roam, their HRs are largest and overlap more during mating seasons, but their foraging HRs are smaller than their overall HR. I will be working under the assumption that female short-faced bears roamed widely because of the random and dispersed nature of their food resource (carcasses), and thus so were males. Males would have had larger HRs because of their size, but HRs would have overlapped considerably. Territoriality in males would have been nearly non-existent because females and carcasses would have been randomly and distantly distributed; there would have been little reward for a male which guarded a territory, since there would have been little predictability in where carcasses (or females) would occur, and it would have been energetically inefficient to guard such a huge area. The only thing worth guarding was a carcass, and, for the most part, they are small, ephemeral, and their location is not permanent. All of these factors lead me to predict that the short-faced bear had a very large HR somewhere on the order of 1000 km^2 .

Earlier, I estimated that the average short-faced bear (700 kg) needed to consume 5853 kg of flesh per year, equal to about 16 kg per day or $\sim 100 \text{ kg}$ of edible carrion every 6.25 days.. If its HR was 1000 km^2 , this necessitates that its habitat had to produce an available carcass biomass of at least 5.85 kg flesh/ km^2 /year. I want to test whether east Beringian ecosystems were capable of this level of carcass productivity, but first I will briefly examine whether a HR of 1000 km^2 represents a reproductively-viable population of short-faced bears.

Minimum Viable Population

Even if it can be shown that the Beringian system was able to produce 5.85 kg flesh/ km^2 /year, the question arises whether a population density of 0.001 short-faced bears/ km^2 represents a minimum viable population—that is, one that is able to resist chance extinction. Goodman (1987) developed a method for predicting the probability of chance extinction in a species over time based on its body size and variability in its growth rate (r). Goodman's method actually estimates the minimum breeding population size (N_m) required for a species to have a 95 % chance of surviving chance extinction every 1000 years. Belovsky (1987) expanded the method by taking into account the influence of environmental variability on r in a species. In this modified model, Belovsky derived two allometric equations relating body mass to N_m , one for species with high variance in r :

$$N_m = 409,540 M^{-0.36} \quad (27)$$

and one for species with more constant r :

$$N_m = 19,018 M^{-0.40} \quad (28)$$

The two equations yield vastly different results, so it is important to have information about r . For instance, with an average mass of 700 kg, these two equations predict *Arctodus* would have required a minimum breeding population size of either 38,731 (Equation 27) or 1384 (Equation 28). When addressing variation in r , Belovsky was mainly concerned with how much r is influenced by variation in environmental and climatic factors. Within a given bear species, reproductive output varies and variation is correlated to environmental factors (Bunnell and Tait 1981), but in general bears are conservative breeders and their population growth rates do not seem tightly linked to levels of climatic variation. Therefore, I would expect a value for N_m in *Arctodus* to be closer to the lower value.

For the sake of these calculations, I will consider all the short-faced bears in eastern Beringia to constitute a single population (In comparison, Farlow (1993) made similar calculations for carnivorous dinosaurs and considered all individuals inhabiting the entire continental United States to be one population). Using maps in Hopkins *et al.* (1982) I estimate that unglaciated eastern Beringia was about 2,000,000 km². A minimum breeding population of 1384 bears would yield a density of one bear per 0.0007 km². My density estimate of 1 bear per 1000 km² (0.001 bears/km²) requires a population of 2000 bears in eastern Beringia—a number not far from 1384. In comparison, a population of 38,000 bears yields a density of 1 bear per 53 km² (0.02 bears/km²)—an unrealistically high density for such a large carnivore.

It is important to place some perspective on the numbers just calculated. First, 2000 individuals in all of eastern Beringia is a very small number. For comparison, the population of brown bears in Alaska today is estimated to be around 29,000 - 40,300, not including Kodiak Island; another 6000 - 7000 bears inhabit the Yukon Territory (Brown 1993). This is just about equal to the average value predicted by Belovsky's two equations (assuming 200 kg mass). Therefore, because brown bear populations in these areas are well above minimum breeding numbers, this is a good reason to suspect that the second equation (low variation in r) is the better predictor of minimum viable population size in bears. Still, 2000 short-faced bears seems like a very small number.

Table 12 shows the density of carrion, and its equivalent in large mammal carcasses, required to support a population of 2000, 4000, and 20,000 short-faced bears in eastern Beringia (densities of 0.001, 0.002, and 0.010 bears/km² respectively).

3. MODELING CARCASS ABUNDANCE

Next, I address the rate at which carcasses were produced on the Beringian landscape, in order to see if any of the population densities depicted in Table 12 can be supported. Keep in mind that I am testing the hypothesis that *Arctodus* made a living just by foraging on available carcasses, without killing any prey itself. Carcasses therefore should be available from two sources: predation by other carnivores and natural mortality among large herbivores.

Carcass Production from Predation

A good modern analog for mammalian communities or predator-prey relationships of Pleistocene east Beringia does not exist. In addition to short-faced bears, fossils of large carnivores from the region include wolf (*Canis lupus*), lion (*Panthera leo atrox*), brown bear (*Ursus arctos*), wolverine (*Gulo gulo*), scimitar (sabertoothed) cat (*Homotherium serum*), and dhole (*Cuon alpinus*) (listed in order of descending abundance).

Recently (Matheus 2001), I examined the carnivore guild of eastern Beringia and compared it to other guilds in the Pleistocene Holarctic. There, I made the assertion that it is unlikely that more than three or four of these large carnivores inhabited the region at any given time during the mid to late Pleistocene (also see Harrington 1977, 1978; Guthrie 1990a). Patterns of fossil abundances also led me to conclude that wolves and lions were the only significant, long-term, predators that occupied eastern Beringia during the late Pleistocene. The other carnivores either are not significant predators (brown bear, wolverine), or appear to have a limited (or at least unknown) chronological range in Beringia (scimitar cat, dhole). I discuss predation in lions and wolves in detail below, but first I will make brief comments on the other species.

Brown Bear: Brown bears migrated to eastern Beringia from Asia probably in the early Wisconsinan Glaciation (Kurtén 1960, 1963, 1966b, 1968, 1973a, 1976a; Kurtén and Anderson 1974, 1980; Guilday 1968; Harris 1985) but they should not be considered significant predators in the system. Stable isotope ratios (C, N) in fossil brown bears from eastern Beringia indicate that they ate mostly vegetation, but also varying amounts of terrestrial meat (Matheus 1994, 1995). Today, no population of brown bears relies primarily on carnivory, even though predation and scavenging can be locally or seasonally important. Predation by brown bears on ungulates in Alaska, for instance, occurs mostly during the brief period of calving seasons when caribou, moose, and occasionally sheep are taken. At these times, brown bear predation can be intense, but brief, and the biomass harvested is relatively small (Magoun 1976, Murie 1981,

Ballard 1982, Boertje *et al.* 1988, Gasaway *et al.* 1992). But being adept scavengers, brown bears will compete with other carnivores for existing carcasses throughout the year, and brown bears will cache and defend carcasses (Mysterud 1973, Magoun 1976, Ballard 1982, Magoun and Valkenburg 1996).

Wolverine: Wolverines were minor members of the Pleistocene large carnivore guild. They can be highly carnivorous and are adept at processing large mammal carcasses. They mainly operate as scavengers and exist in low population densities. While wolverines are somewhat predatory, and even can kill caribou, they are not significant predators of large herbivores. However, because of their abilities to find carrion and defend it voraciously, they would have been a competitor to any scavenger on the landscape (Rausch and Pearson 1972; Magoun 1985; Hornocker and Hash 1981).

Homotherium: *Homotherium*'s importance to the carcass economy of eastern Beringia is unclear, as their temporal and geographic range in the region is sketchy. *Homotherium* fossils are rare, and it is possible that these scimitar cats were extinct in Beringia before the Wisconsinan period (Harington 1977, Guthrie personal communication, Matheus 2001). However, in terms of sabertooths, both *Homotherium* and *Smilodon* would

have coexisted with *Arctodus* in other areas of North America south of Beringia.

Dhole: The abundance and temporal range this small canid in eastern Beringia is even more uncertain. Currently, there is no good evidence to suggest that they even coexisted in a guild with all or any of the previously mentioned species. Dholes are advanced cursorial social predators and adept processors of carcasses. Packs of dholes can be formidable defenders of carcasses.

Next I want to examine typical predation rates for eastern Beringia's two main predators, wolves and lions. I will examine not only normal rates of carcass production by these predators, but also rates of surplus killing in order to assess their potential to kill additional prey when other predators confiscate carcasses. But first, it is worth considering an example of extreme carcass production—that of spotted hyenas in Africa's Ngorongoro Crater, a system where predator and prey densities are high and where predators take a very large percentage of the prey population each year (Kruuk 1972, Schaller 1972, Hilborn and Sinclair 1979).

Spotted Hyena: Kruuk (1972) calculated that 430 spotted hyenas in the 250 km² Ngorongoro ecosystem each consumed 2 kg of prey per day, including adults and calves of wildebeest, gazelle, zebra, and miscellaneous

TABLE 12. Carcass requirements of an average short-faced bear (700 kg) in eastern Beringia (an area of 2,000,000 km²) and necessary carcass densities as a factor of population size.

energetic parameter, per individual bear	population size (bears/km ²)		
	2000 (0.001) ¹	4000 (0.002)	20,000 (0.010)
size of mutually exclusive home range (km ²)	1000	500	100
required annual carcass production (kg/km ² /year) ²	5.85	11.70	58.53
equivalent in carcass numbers / densities ^{3, 4} (average distance between carcasses) ⁵			
<i>small caballine horse</i> (175 kg x 75 %)	45 / 0.045 (22.2)	45 / 0.090 (11.1)	45 / 0.450 (2.2)
<i>bison</i> (650 kg x 75 %)	12 / 0.012 (83.3)	12 / 0.024 (41.7)	12 / 0.120 (8.3)
<i>mammoth</i> (3800 kg x 75 %)	2 / 0.002 (500)	2 / 0.004 (250)	2 / 0.020 (50)

¹ minimum viable breeding population, estimated in text

² assumes an average bear weighs 700 kg, and requires 5853 kg of carcass flesh per year (\approx 16 kg per day) according to equation in text

³ number of carcasses required by a single bear per year; density of carcasses expressed as number of animals per km²

⁴ carcass masses are reduced by 25 % to reflect non-caloric body parts — see text

⁵ calculated as the inverse of carcass density

species for a total of 313,787 kg annually. (Kruuk made his calculation by totaling average weights for carcasses on which hyenas were observed feeding and dividing this by the number of resident hyenas; total animals consumed = 2331, average weight = 135 kg.) This equates to 9.3 carcasses of 135 kg each, or 1255 kg/km²/year. But only about 62 % of this biomass was confirmed as being killed directly by hyenas; a good deal of the remainder probably was scavenged. Hyenas scavenge far less in the Ngorongoro Crater, however, than they do in the Serengeti. Assuming hyenas kill 70 % of their food, direct carcass production by hyena predation becomes 879 kg/km²/year, which means that at least 376 kg/km²/year still is being "produced" by other means (other predators and natural mortality) in this system.

Kruuk also noted that during certain seasons hyenas will kill a large surplus, and that hyenas in general are not limited by their ability to kill prey, but rather on seasonal prey abundance. In fact, in the Serengeti each hyena "consumed" 3 kg of prey per day (as opposed to 2 kg in Ngorongoro)¹ according to Kruuk (consumed is in quotes because Kruuk derived this value by dividing prey biomass by the number of hyenas— not all of this biomass is necessarily consumed). During wildebeest calving season, Kruuk recorded a daily carcass production of 5.4 kg/hyena in the Serengeti— more than double their daily needs.

The theoretical confiscation of 5.8 kg/km²/year (the minimum requirement to support short-faced bears) of the hyena's prey in the Ngorongoro would represent only 0.7% of the edible carcass mass produced directly by hyena predation. However, the density of prey and predators in the Ngorongoro, and tropical savannahs/grasslands in general, is exceptionally high (Petrusewicz 1967, Kruuk 1972, Schaller 1972, Sinclair and Norton-Griffiths 1979). Furthermore, there are other carnivores competing with hyenas for their carcasses. But these predators also add more carcasses to the system. More will be said on hyena carcass losses in the following discussion on lions.

Lion: Guthrie (1990a) stated that lions probably were Beringia's most prevalent carnivore (based on fossil abundance). However, based on the number of fossils in the Alaska collection of the American Museum of Natural History it seems that wolves may have been just as common, or more so. Lions are highly predatory but they readily turn to scavenging when it is beneficial and

available (Kruuk 1972, Schaller 1972). They also are good processors of carcasses, but not on par with hyenas (Kruuk 1972; Ewer 1973; Van Valkenburgh 1989, 1996).

Schaller (1972) found that lions in the Seronera area of the Serengeti consume approximately 2500 kg of prey per lion annually, yielding a daily individual consumption rate of 6.8 kg. The mean body mass of five female and 14 male lions weighed by Schaller was 166 kg. For this weight, the expected daily food consumption predicted by Harestad and Bunnell's equation (Equation 22) is 6.0 kg per day. Schaller was able to confirm that 75 % of this 2500 kg was killed directly by lions, while 16 % definitely was scavenged and 9 % was of uncertain origin. At 75%, it is reasonable to assume that each lion killed 5.1 kg of its own food per day, or 1875 kg annually (variations in edibility rates do not need to be accounted for because Schaller reported actual consumption).

Schaller estimated that about 2,000 - 2400 lions (including nomads) live within the 25,500 km² Serengeti ecological unit, for a density of one lion every 10.6 - 12.75 km², or 0.078 to 0.094 lions/km². This means that lions in the system were producing up to 176 kg/km²/year (1875 kg/lion/year x 0.094 lions/km²), which can be considered an extreme rate because of the high density of lions. Kruuk (1972) reported densities for lions in Ngorongoro in the range of 0.12 - 0.23 lions/km², the highest anywhere, but Nowak (1991) compiled data from numerous more recent studies in the Serengeti and estimated an average density of 1 lion every 10.0 - 12.7 km², or 0.01 - 0.08 lions/km², including nomadic individuals. Using Nowak's average value, annual carcass production from lion predation is roughly 166 kg/km²/year. Removing 5.8 kg/km²/year from such a system by scavenging short-faced bears would represent only 3.5 % of the lions' kills.

Schaller provided little data on the biomass of surplus killing by lions, but stated that 1.4 - 4 % of wildebeest and zebra killed by lions (by far the two most common prey species for lion) were left uneaten or mostly whole (for unknown reasons). Extrapolating from his data on total prey killed (and subtracting 25% for inedible material), this represents nearly 20-56 kg/lion/year, or 3.2 - 11.2 kg/km²/year of surplus uneaten prey (20 kg/lion/year x 0.16 lions/km = 3.2; 56 kg/lion x 0.20 lions/km² = 11.2). These "scraps" represent only 0.9 - 3.0 % of the lion's normal kill rate, but represent practically the entire annual requirement of a population of short-faced bears in eastern Beringia (assuming each bear has an exclusive HR of 1000 km²). Schaller also stated that whole, untouched carcasses can be found on the Serengeti landscape (mostly in wooded areas) but he gave no estimate of their biomass or density. (Blumenschine (1987) studied carcass availability in Serengeti, but he also did not record data on biomass. His

¹ It is unclear how much of this discrepancy is due to methodological errors or the likelihood that hyenas in the Serengeti have higher energetic costs because they commute long distances to hunt on migratory prey, whereas hyenas in the Ngorongoro Crater do not (Kruuk 1972, Hofer and East 1993a).

study examined carcass longevity.)

Some additional surplus killing from lions could be expected because of losses to other large carnivores, especially spotted hyenas. In general, however, lions tend to be dominant over other carnivores. The fact that hyenas engage in substantial surplus killing also suggests that predators in general are capable of killing at higher rates when forced to do so by competition. Consider further that hyenas in Ngorongoro nearly double their predation rate during wildebeest calving season when prey are easy to obtain (Kruuk 1972). Hyenas normally lose 21% of their kills to lions in Ngorongoro, according to Kruuk, and in 63% of these cases lions confiscate a substantial part of the carcass. This means hyenas in Ngorongoro need to kill about an additional 15% because of losses to lions. Recall that the normal predation rate in these hyenas is about $879 \text{ kg/km}^2/\text{year}$. Therefore, hyena losses to lions in the Ngorongoro Crater are about $132 \text{ kg/km}^2/\text{year}$. This is about one third of the lions' diet, which is right in line with Kruuk's estimates for scavenging rates by lions in Ngorongoro. In the Serengeti, lions kill a much larger proportion of their own food, and hyenas lose fewer kills to lions. I will show below that a roughly analogous competitive relationship exists between brown bears and wolves today in Alaska.

Now I want to cautiously extrapolate some of this information about modern lions to Pleistocene lions in Beringia. Guthrie (1990a) provides compelling evidence that Beringian lions formed small prides or even hunted alone or in pairs as do some modern nomadic lions. He cites data in Van Orsdal *et al.* (1985) which shows that pride size correlates positively with prey density and territory size correlates negatively with prey density. Since Guthrie (1990a) argues that herbivore population densities would have been low in Beringia, it follows that lions would have formed small social groups that occupied large territories. Guthrie also uses paleolithic paintings in Europe as an indication that lions formed small groups. He shows that where lions live in high densities today, males have elaborately developed social organs because competition to control prides is intense (social display organs advertise condition and status). But paleolithic paintings depict males with small manes, and they frequently show scenes of males and females hunting together. Today males primarily hunt cooperatively with females only when pride associations are loose and when individuals are somewhat nomadic (Bertram 1975). The notion that Pleistocene lions hunted in pairs or alone also is supported by observations of fossil frequencies at Rancho La Brea. There, equal numbers of male and female lions representing all age classes are found (Jefferson 1992). If these lions had formed prides, one would not expect such a good cross-section of the population, but rather some sort of biased sampling—

perhaps more young dispersing males or old infirm males looking for an easy meal, since both are excluded from access to female-killed carcasses in modern populations that form prides.

According to data summarized in Nowak (1991), modern nomadic lions typically form groups of 2 to 4 individuals, and such a pride may occupy an area as large as 4000 km^2 (at the extreme). For the sake of calculations, I will work off of Guthrie's arguments and make the conservative assumption that lions in Beringia were nomadic and that 2 lions hunted together over an exclusive territory of 500 km^2 , for a density of 0.004 lions/km^2 . For perspective, this equates to only 8000 lions in all of eastern Beringia and is $1/100$ the density of Serengeti lions; Equation 28 predicts a minimum viable population size of 2438 lions in Beringia, assuming an average mass of 170 kg. From the previous calculations, each lion is predicted to consume 2500 kg of prey each year. Assuming that scavenging opportunities for lions were limited (by the presence of *Arctodus*), nearly all of this 2500 kg would have had to come from predation, yielding a carcass production rate of $10 \text{ kg/km}^2/\text{year}$. It was shown that hyenas can double their kill rate during calving seasons, and can be induced to kill at least an extra 15 % when they loose carcasses to a dominant carnivore. Below, it will be shown that wolves can be forced to increase predation by nearly 50% in areas where brown bears steal carcasses. Therefore, under the assumption that Beringian lions could be forced to increase predation rates by a minimum of 20%, we might expect them to minimally provide an additional $2.0 \text{ kg/km}^2/\text{year}$ under pressure from a dominant carnivore such as *Arctodus*. That is about one third of *Arctodus'* annual requirement.

Wolf: In northern North America today, wolves are the most significant predators of large herbivores. (Puma rely heavily on deer and elk in western North America, but puma typically do not exist in high densities.) In the arctic and subarctic of North America, wolves typically exist in low densities compared to wolves farther south (see earlier discussion). In these northern regions caribou are the wolf's main prey in tundra habitat, whereas moose are the its primary prey in the taiga. In the southern part of their range, wolves mainly hunt white-tailed deer but also moose in some areas. In terms of understanding secondary productivity in Pleistocene Beringia, data from these systems will be highly instructive.

I discussed earlier how pack sizes in arctic wolves preying on caribou are highly variable, and population densities are low—as low as $0.002 \text{ wolves/km}^2$ on the arctic coastal plain. Area-wide densities seem to be on the order of $0.003 \text{ wolves/km}^2$ (around 1 wolf per $300 - 400 \text{ km}^2$), but better habitats in the arctic support densities near 0.01 wolves/km^2 . As a generality, arctic wolves kill

a caribou about once every 4 days, and a moose every 7 days if moose are available. Wolf densities for the arctic coastal plain and northern foothills of the Brook Range are around 1 wolf per 350 - 450 km² (Stephenson and James 1982, ADFG Wolf Report 1994, Stephenson 1978, Ballard *et al.* 1990, Haber 1977, Murie 1944, Peterson 1977, Dale 1993).

In a study of two wolf packs in northwest Alaska, Stephenson and James (1982) found that caribou constituted 96 - 97 % of their prey biomass. Collectively, these packs hunted over an area of 2600 km², and killed a caribou every 3 - 4 days on average (mostly adults; \bar{x} mass = 104 kg), for a total of about 10,846 kg/year, or 4.2 kg/km²/year. Accounting for a 75 % edibility factor, the realized values become 8135 kg/year and 3.1 kg/km²/year. This is a fairly typical kill rate for wolves feeding on large cervids (Mech 1966, 1970; Peterson 1977; Peterson *et al.* 1984; Fritts and Mech 1981; Ballard 1982; Ballard *et al.* 1987). Wolf densities in the region were 1 wolf per 390 km², so this amount of predation represents the activities of about 6 wolves, for a realized average of 1356 kg/wolf/year, or 3.7 kg/wolf/day.

In the same study, Stephenson and James measured actual consumption rates (as opposed to kill rates) for a 4 month period, during which the wolves were observed eating 1861 kg of adult caribou. Extrapolating this value for the remainder of the year (1861 kg x 3), the consumption rate becomes 2.5 kg per wolf per day, or 2.1 kg/km²/year. This seems like a very accurate estimate of daily meat consumption since it agrees with results from other studies (Pimlott *et al.* 1969; Mech 1970, 1977; Kolenosky 1972; Peterson 1977; Peterson *et al.* 1984; Fritts and Mech 1981; Ballard 1982; Ballard *et al.* 1987) and it is 91 % of the value predicted by Equation 22 (2.3 kg/day for a 40 kg carnivore). This is very close to the actual percentage of caribou in the diet of these wolves noted above (96 - 97 %).

If annual predation is 3.2 kg/km²/year and consumption is 2.1 kg/km²/year, then approximately 1.1 kg/km²/year of surplus carcass biomass is produced by these low density predators. For comparison, this is a little less than the amount of surplus predation I predicted for a population of Beringian lions.

Today, grizzlies, wolverines, foxes, and ravens consume surplus carcass biomass in northern Alaska and Canada (Magoun 1976, Murie 1981, Carbyn *et al.* 1993), but competition generally is less intense compared to other carnivore systems I discussed, mainly because carnivore densities are low in northern North America. Ballard (Ballard 1982, Ballard *et al.* 1981) conducted a study on wolf-grizzly interaction and predation rates on moose in the Nelchina Basin of southcentral Alaska where competition for carcasses between these two carnivores can be intense. He noted two important

patterns. First, areas with high moose densities had higher wolf densities but lower levels of wolf-grizzly competition for carcasses, compared to areas with low moose densities (grizzly density did not vary). Second, wolves increased their predation rates in areas where they lost carcasses to grizzlies.

Ballard (1982) reports that the carcass biomass produced by Nelchina wolves in all areas was around 4.6 kg/wolf/day, but in areas with competition, wolves had to produce 6.2 kg/wolf/day — an increase of nearly 50 %. These are numbers calculated by Ballard, and already reflect the 75 % edibility of carcasses. Two packs of wolves (7 and 8 individuals) foraged over a combined area of 1399 km² yielding an effective average density of 1 wolf for every 93 km²; wolf density for the entire Nelchina basin below 1200 m is around 100 wolves/km². Using the later value and the two predatory rates above, annual carcass production would be at least 16.8 kg/km²/year in low competition areas and 22.6 kg/km²/year in high competition areas. This yields a surplus predation rate of 5.8 kg/km²/year induced by the loss of carcasses to grizzlies. Even 16.8 kg/km²/year in areas of low competition is equivalent to nearly 8 kg/km²/year of surplus production, assuming that wolves require around 2.3 kg of meat per day. Therefore, carcass production, in general, is higher in the Nelchina Basin than in northwest Alaska because both predator and prey densities are greater in the Nelchina Basin (see arguments in Fuller 1989).

In areas of southern Canada and the northern contiguous U.S. states, wolves feed mainly on white-tailed deer, but also varying amounts of moose. In these areas, wolf packs average about 4 - 8 individuals and area-wide wolf densities are around 0.02 wolves/km², or 1 wolf per 50 km². Exclusive pack territories are approximately 200 km², or around 33 km² per wolf, and they kill a deer about once every 3 - 4 days (\bar{x} mass = 50 kg) (Mech 1970, Pimlott 1969, Fritts and Mech 1981, Nelson and Mech 1981, Fuller 1989, Keith 1983). Studies in these southern areas of the wolf's range also confirm that an average wolf eats a little over 2 kg of meat per day.

It is informative to note that, in the southern part of their range, the size of wolf packs does not differ much among packs that hunt moose and packs that hunt white-tailed deer (Mech 1970). However, the population density of wolves that hunt moose (in the south) can be greater than those that hunt white-tailed deer. As an extreme example, wolf densities on Isle Royale average around 0.04 wolves per km², or 1 wolf per 25 km². Wolves in this system typically kill 13-19% of the moose population per year and kill a moose every 3 days. This feeds 18 - 20 individuals (pack sizes are unusually high on Isle Royale), so assuming a modest average moose mass of

300 kg, wolves on Isle Royale produce at least 46.8 kg/km²/year of carcass mass annually, equivalent to approximately 1.9 kg/km²/year of carcass production from each wolf (Mech 1966, 1970; Jordan 1970; Peterson 1977). In the north (Alaska and northern Canada), wolves that feed on moose have densities 2 - 3 times lower than wolves that feed on moose in the south. Moreover, northern wolves feeding on caribou have densities that are about 1/10 of those in the south (Mech 1970; Ballard 1982; Ballard *et al.* 1981, 1990; Stephenson and James 1982; Oosenbrug and Carbyn 1982; ADFG Wolf Report 1994).

Using these generalities, it is possible to infer certain aspects of wolf densities and predation on the mammoth steppe of Pleistocene east Beringia. With the presence of lions, it is quite possible that wolves were competitively excluded from utilizing some larger prey which they otherwise would have hunted. This may explain why late Pleistocene wolves in Beringian were smaller than present (Matheus 2001). If wolves were smaller-bodied and were hunting smaller prey, they probably existed in higher densities during the Pleistocene, but in order to remain conservative (i.e., emphasize minimum values) in my calculations, I will assume an approximate wolf density of 1 wolf per 300 km² in eastern Beringia (0.0033 wolves/km²) — similar to area-wide densities in the modern arctic.

I showed that wolves require about 2.5 kg of meat per day (912.5 kg/year) but they kill about 3.0 - 3.5 kg of meat per day (1095 - 1277.5 kg/year) in areas with little or no competition, yielding a surplus of about 100 - 365 kg/wolf/year (11-40 %). Assuming a density of 0.01 wolves/km², the typical northern wolf population today provides (in principle) approximately 1.0 - 3.7 kg/km²/year of carcass flesh to scavengers. In my theoretical, modest Beringian population with 0.0033 wolves/km², the normal surplus (i.e., without competition) is predicted to be 0.33 - 1.2 kg/km²/year. But I also showed that in areas where competition is high and wolves lose carcasses to bears, they can be induced to produce an additional 5.8 kg/km²/year (in an area with a density of 0.01 wolves/km²). Extrapolated to a hypothetical population with 0.0033 wolves/km² this equates to an additional surplus of 1.9 kg/km²/year, for a combined total surplus of 2.3 - 4.9 kg/km²/year from wolves. That is, 1.0 - 3.7 kg/km²/year from normal surplus, plus 1.9 kg/km²/year from induced predation. These estimates are very conservative.

Earlier, I showed how Beringian lions might be expected to provide a surplus of at least 2.0 kg/km²/year when pressured by competition from a dominant carnivore. According to these conservative estimates, *the two primary predators of the Mammoth Steppe could collectively produce at least 4.3 - 6.9 kg/km²/year of*

edible surplus carcass biomass via both natural over-kill and when induced to do so by aggressive competition (reductions for inedible carcass mass were made in the initial calculations). This would have been just about the right amount of biomass to support a minimum viable population of short-faced bears (needing 5.85 kg/km²/year).

Carcass Production from Natural Mortality

1. Modeling Herbivore Populations in Eastern Beringia

The preceding calculations show that the predatory actions of wolves and lions alone could arguably support the dietary needs of a minimum viable population of scavenging short-faced bears in Pleistocene east Beringia. I was conservative throughout these estimates, but they still cannot be considered to be very precise. Furthermore, reflecting on the densities of other large mammals today, it is not completely convincing that a density of 1 short-faced bear per 1000 km² constitutes a viable breeding population. Therefore, evidence of additional carcass production is necessary for the scavenging hypothesis to be accepted as wholly credible from an energetic standpoint.

So far I have made no consideration of natural mortality in herbivore populations, a factor which certainly would have been adding carrion to the system. A thorough modeling of ungulate population dynamics is beyond the scope of this paper, and I think it is necessary only to estimate the general magnitude of carrion being produced by the system through natural mortality. Furthermore, whereas Pleistocene carnivore population dynamics have not been modeled, attempts have been made to qualitatively and quantitatively model Pleistocene herbivore populations and secondary productivity. I will discuss and modify two such models— Redmann (1982) and Bliss and Richards (1982). Both were designed to address the issue of secondary productivity in Beringia, but I believe there are shortcomings in each: Redmann stopped short of making specific estimates for Beringia; his model was more a reflection of productivity in northern grasslands. Bliss and Richards were primarily interested in determining how many humans could be supported by the Beringian landscape, so they modeled harvestable levels of big game. While Bliss and Richard's model sounds very applicable to the issues in this paper, I think there are serious flaws with its assumptions about ecosystem structure and function on the Mammoth Steppe of eastern Beringia, as well as the data they use to establish input parameters.

Redmann's (1982) Model: Redmann's model estimates the biomass density of large herbivores in a northern grassland using the following conditions and

assumptions: 1) primary productivity of edible above ground biomass is set at 150 kg/km²/year; this is the amount of forage (“herbage” in Redmann) available to herbivores and is a conservative approximation based on productivity rates measured in modern cold-temperate grasslands, 2) a positive linear relationship exists between the rate of forage production and herbivore biomass density, 3) annual consumption (C) by herbivores scales to body mass (M) in a manner consistent with metabolic scaling:

$$C = 32.85 M^{0.75} \quad (29)$$

4) energy is the only dietary factor limiting secondary production; protein and other nutrients are not limiting, 5) energy (herbage) is available throughout the year. Redmann’s model is a general predictor for north temperate grasslands, and some of its assumptions will have to be adjusted to fit Beringia.

The key element of this model is that it accounts for the observation that herbivore biomass and diversity are strongly influenced by levels of species dominance in the community. When a large-bodied herbivore dominates, higher overall biomass is achieved, but most of it is allocated to the dominant species. The lowest biomass occurs in herbivore communities dominated by a small-bodied species.

Redmann uses his model to predict the biomass density for five theoretical northern grasslands, each with the same five herbivore species but at different levels of dominance (relative density): 1) strong dominance by a large species, 2) strong dominance by a small species, 3) weak dominance by a large species, 4) weak dominance by a small species, and 5) no dominance. When one large herbivore dominates the system, 150 kg/km²/year of herbage production yields a standing herbivore biomass density of 13,500 kg/km², of which 84 % is in the form of the dominant species. The other four scenarios in Redmann’s model yield 6720, 12,000, 8300, and 10,200 kg/km²/year respectively.

The first estimate, based on a dominant large herbivore, yields an unrealistically high density for Beringia, since equivalent levels in modern ecosystems only can be found in tropical grasslands and savannahs and in one ecosystem in Alberta (see Table 13). The system modeled in this scenario might resemble the community dominated by bison on the far northern great plains of Canada 200 years ago. Past great bison herds of the plains have been estimated to have densities on the order of 10 - 14 bison/km² (Seton 1909, Roe 1970, McHugh 1972, Dary 1974), but Redmann’s equation predicts approximately 25 bison/km², assuming that the average bison weighed 450 kg (modern weight) and that bison constituted 84 % of the system’s biomass.

Redmann’s scenario which assumes no dominance may be more appropriate than one which assumes the presence of one large dominant species because there were three co-dominant herbivores in Beringia — mammoth, bison, and horse. The “no dominance” scenario predicts a somewhat reduced herbivore biomass of 10,200 kg/km². One possible way to distribute this biomass would be among 1 mammoth (3800 kg), 4 bison (2600 kg), and 15 caballines (2650 kg), along with 1175 kg of other less common herbivores on each km² of Beringia. If only bison were present, their density would be nearly 16 bison/km² — as dense as the former herds on the great plains. These values still seem unreasonably high and exceed the biomass densities given by Redmann himself for many modern temperate grasslands.

Redmann sets annual herbage production at 135 kg/km²/year in all scenarios of his model. However, it may be unrealistic, and unnecessary, to invoke such high rates to account for high levels of secondary productivity in Pleistocene Beringia, and even though Redmann’s estimate is conservative for grasslands, it probably is too high for Beringia. Secondary productivity and herbivore diversity in Beringia are best explained by models relying on increased digestibility and extractable nutrition in Pleistocene vegetation (i.e., increased consumption efficiency and assimilation efficiency in herbivores), along with staggered spikes in the timing of green-up, a longer growing season, and increased habitat heterogeneity (Guthrie 1976, 1982, 1984a, 1984b, 1990a, 1990b). This assessment of Guthrie’s casts doubt on two assumptions in Redmann’s model: 1) that energy (herbage) is available all year, and 2) that energy, not protein, is the limiting factor determining biomass density. While the first assumption is necessary to keep the model manageable, and it is a standard assumption when comparing ecosystems, Guthrie’s arguments show that the timing and duration of available high quality forage probably are the key factors regulating populations in Beringian mammals, past and present. High quality forage means high protein forage, and it is protein, not energy, that limits herbivore populations (Janis 1976, Hanley 1980, Robbins 1993).

Moreover, biomass density is not equivalent to population density (i.e., number of individual animals), and Guthrie’s model mainly addresses patterns not of biomass quantity, but biomass distribution and its impact on mammalian body sizes. At an ecosystem level, however, a population composed of fewer, but larger, individuals is energetically “more efficient,” and it would take less energy to maintain such a population. Therefore, a greater diversity of species can be maintained for a given amount of trophic energy if their average body size is larger and population numbers are fewer.

The above arguments suggest that it is best to use a

TABLE 13. Large mammal standing biomass densities of modern ecosystems and the predicted density for late Pleistocene east Beringia

ecosystem (type of biomass reported)	large mammal biomass (kg/km ²)	source
entire Serengeti Plain (large herbivore prey)	annual $\bar{X} = 4222$ seasonal range = 998 - 7234	Schaller 1972
woodlands of western Serengeti (large herbivore prey)	3110	Bell 1967 (in Schaller 1972)
savannah of Kruger Park (large herbivore minus elephant)	7785	Schaller 1972
savannah of Kruger Park (large herbivore minus elephant)	9000	Watson and Turner 1965 in (Schaller 1972)
grassland/savannah of Ngorongoro Crater (large herbivore prey)	16,200	Kruuk 1972
Ruwenzori Park, Uganda plains-tropical forest ecotone (large herbivores, but includes many elephants/hippos)	20,000	Eltringham 1974 (in Redmann 1982)
boreal forest of Alberta (large herbivores)	5700	Telfer and Scotter 1975 (in Redmann 1982)
semidesert of southcentral Russia (saiga biomass in a protected park)	5200	Bannikov 1967 (in Redmann 1982)
grassland of South Dakota (large herbivores)	3640	Petrides 1956 (in Redmann 1982)
grasslands of Nebraska (large herbivores)	919	Petrides 1956 (in Redmann 1982)
parkland of Alberta (large herbivores)	2530	Flook 1970 (in Redmann 1982)
dry tundra of St. Elias - Kluane region, Yukon (large mammals)	89 (actual estimated) 175 (potential estimated)	Geist 1978 (in Redmann 1982)
tundra of Southampton Island, Northwest Territories (caribou)	36	Parker 1975 (in Redmann 1982)
alpine tundra of southern Norway (caribou)	233	Østbye 1975 (in Redmann 1982)
southern boreal forest on Isle Royale (moose)	401	calculated from data in Mech 1970
northern boreal forest of interior Alaska and Yukon (moose)	9 - 289 (assumes \bar{X} moose = 200 kg)	calculated from data in Gasaway <i>et al.</i> 1992
tundra of Alaskan arctic slope (caribou- Western Arctic Herd)	91 (assumes \bar{X} caribou = 100 kg)	calculated from data in Ballard <i>et al.</i> 1990
tundra of south-central Alaska (Nelchina Basin) (large mammal)	< 300	Guthrie 1968
Mammoth Steppe of Eastern Beringia (total large herbivore biomass)	1000	models revised in this study

cautious, conservative, estimate of secondary productivity in Beringia when calculating the carcass biomass produced by natural mortality. Since Redmann's estimates appear too high for Beringia, I will use half his value— 5100 kg/km²/year— and examine the herbivore populations this could support. To do so, I need values for the division of biomass in the system. Guthrie (1968) estimated the relative biomass of Pleistocene large mammals from four sites in Interior Alaska based on their fossil abundance, and derived the following biomass percentages for the top three herbivores: 46% Bison, 33% mammoth, and 17% horse (averaged over the four sites). I will modify Guthrie's numbers slightly to reflect subsequent finds from around Beringia which suggest a higher frequency of minor taxa; the values I will use for relative biomass are 40% bison, 30% mammoth, 18% horse, and 12 % other herbivores. Table 14 shows the resulting population densities calculated for this theoretical system assuming a total standing large herbivore biomass of 5100 kg/km²/year. Results show that this system would simultaneously support population densities of 0.402 mammoth/km², 3.138 bison/km², 5.246 caballines/km², and still leave another 612 kg/km² divided between other minor species (e.g., caribou, muskox, saiga, elk, camel, etc.). This latter amount would support 2.5 individuals/km² of a species weighing 250 kg, for instance. Before estimating carcass production from natural mortality in these populations, I will check their validity using Bliss and Richard's model.

Bliss and Richard's (1982) Model: Bliss and Richards constructed a model of finer detail specifically for Beringia. Their model essentially takes the view that

the Mammoth Steppe was a tundra biome, but with a higher percentage of dry sedge-grass tundra compared to today's northern tundra. Under this view, the Mammoth Steppe supported a more diverse and productive large herbivore community than today's ecosystem because dry sedge-grass tundra is the most productive type of tundra habitat. As I mentioned, the goal of these authors was to determine how much meat such a system could provide for humans, and in turn, whether this was enough to sustain a viable human population— a question very similar to the one I am addressing.

These authors began their reconstruction by collecting data on primary and secondary productivity in a variety of modern habitats in the arctic and subarctic, including well-drained upland sedge fields, tussocky tundra, shrubby tundra, alpine tundra, and sedge-moss meadows. Then, using published data on Pleistocene vegetation patterns, they reconstructed the percentages of these habitat types in a hypothetical Beringian river valley spanning 1000 km². Next, they used consumption data in analogous modern mammals to estimate the forage requirements of the system's predominant herbivores, which they concluded were mammoth, horse, bison, muskox, caribou, and moose. Finally, they used modern values of net primary production (NPP) and consumability for each habitat, and extrapolated them to the presumed distribution of each habitat on the mammoth steppe, in order to estimate how much herbivore biomass would be supported for each species in each habitat. I will briefly review the results of their simulation.

Bliss and Richard's hypothetical system contained

TABLE 14. Estimated population densities and total numbers of dominant large herbivores in eastern Beringia according to a modified biomass estimate using Redmann's (1982) model. Total biomass predicted by the modified model is 5100 kg/km², which was divided amongst each species according to relative biomass estimates modified from Guthrie (1968)¹. Values generated from this modified model are considered too high, as discussed in text. Compare values to those in Table 15 (Bliss and Richard's 1982 model) and Table 16 (values ultimately derived from this study).

species (mass in kg)	% of biomass ¹	resultant biomass density (kg/km ²)	resultant population density (animals/km ²)	total population in eastern Beringia (= pop. density x 2,000,000 km ²)
mammoth (3800)	30	1527	0.402	804,000
bison (650)	40	2040	3.138	6,276,000
horse (175)	18	918	5.246	10,491,429
others ($\bar{x} = 250$)	12	612	2.448	4,896,000

¹ Biomass percentages modified from Guthrie's (1968) estimates, which were based on fossil abundances at four sites near Fairbanks, Alaska. Guthrie's values were modified by the present author based on subsequent discoveries and data from a larger region.

65% upland sedge-grass tundra, 20% upland cushion plants (alpine tundra), 10% wet sedge tundra (tussocky tundra), and 5% tall willow tundra (shrub tundra). They estimated the amount of forage each herbivore would extract from each habitat based on their presumed diet and the ability of each habitat to provide for it. For example, mammoth were presumed to get 40% of their forage from tall willow habitat, 40% from wet sedge, and 20% from upland sedge-grass. The amount of standing herbivore biomass and the predicted population density for each species using Bliss and Richards' model is presented in Table 15. Comparing Tables 14 and 15 shows that Bliss and Richards' model predicts about 80 % less standing biomass than my modified Redmann model (~1000 kg/km² vs. 5000 kg/km²).

Bliss and Richards are highly regarded experts on the subject of productivity in modern tundra ecosystems, and while the productivity estimated by their model could have supported the Pleistocene herbivore community, I have strong reservations about their assumptions regarding ecosystem structure and function on the Mammoth Steppe. First, while some authors, relying mainly on floral evidence, subscribe to the idea that the mammoth steppe was a modified tundra ecosystem (e.g., Schweger and Habgood 1976; Cwynar and Ritchie 1980; Ritchie and Cwynar 1982; Colinvaux 1980, 1986; Colinvaux and West 1984; Ager 1982; Giterman *et al.* 1982; Schweger 1982), the idea has been strongly refuted by others (e.g., Guthrie 1968, 1982, 1984a, 1984b, 1990a, 1990b; Sher 1974, 1986; Matthews 1982; Yurtsev 1982). This latter group argues that the full glacial fauna of Beringia was dominated by herbivores which had evolved as grazing specialists, indicating the indisputable presence of a cold grassland (steppe) biome. Even though grassy elements grow in tundra environments, true grasslands are distinct from tundra and each is maintained by vastly different processes (Walter 1973, Tieszen and Detling 1983, Guthrie 1990a).

Therefore, Bliss and Richards' decision to use tundra analogs, especially to model energy flow, seems a poor choice. For instance, they use data on secondary productivity, consumption rates, and population turnover rates from modern tundra systems across arctic Alaska, Canada, and Russia, and they often rely on microtines as mammalian models for the conversion of primary productivity into herbivore biomass. Furthermore, as I emphasized earlier, the key to higher levels of secondary productivity in Pleistocene Beringia was not higher NPP; instead, more of the primary production was available to consumers—a trait of grasslands, not tundra. In these regards, Redmann's model is preferred because it is based on grassland systems.

Combined Model: Despite their shortcomings, I will use the results of these two models to conservatively

estimate that large-herbivore biomass (standing crop) in late-Pleistocene Beringia was in the range 1000 kg/km². Considering the level of productivity achieved in northern grasslands today, 1000 kg/km² is not unreasonable (Table 13), although it is 3 to 10 times higher than what one finds in modern taiga and tundra systems (Table 13). I will propose the following conservative, round-number estimates of herbivore standing biomass in late Pleistocene (full glacial) eastern Beringia using Guthrie's (1968) modified estimates of relative biomass and 1000 kg/km² total standing biomass (values also presented in Table 16):

mammoth (3800 kg) @ 30 % of biomass:
 $= 300 \text{ kg/km}^2 = .079 \text{ mammoths/km}^2 = 158,000 \text{ mammoths}$

bison (650 kg) @ 40 % of biomass:
 $= 400 \text{ kg/km}^2 = .615 \text{ bison/km}^2 = 1,230,000 \text{ bison}$

horse (175 kg) @ 18 % of biomass:
 $= 180 \text{ kg/km}^2 = 1.029 \text{ horse/km}^2 = 2,058,000 \text{ horses}$

others = 12 % of biomass

2. Non-Predatory Mortality in Eastern Beringia

Non-predatory mortality rates are known for enough modern large mammals that it should be possible to estimate such rates for Beringian herbivores using the preceding population estimates.

Hilborn and Sinclair (1979) calculated that non-predatory mortality for adult wildebeest in Serengeti was 5% annually in years without catastrophic die-offs, although Talbot and Talbot (1963) and Houston (1979) suggested it may be nearer 8% and 12%, respectively. Kruuk (1972) stated that non-predatory mortality for wildebeest living in Ngorongoro was somewhat higher than in the Serengeti, as was the population turnover rate as a whole. Zebra lost 3% of the adult population annually to non-predatory mortality, according to references cited in Kruuk (1972), and 16.5 % of the adult hyenas in his study died each year. Sinclair (1977) reported that adult African buffalo experienced 4-12% non-predatory mortality annually, and average around 8%. In Manyara, Tanzania, a system where half the deaths are from hunting by humans, adult elephants suffer 3-4% annual losses (Owen-Smith 1988). Owen-Smith presented similar mortality rates for other populations of elephants, and he suggested that they are somewhat higher than natural rates because of hunting. Over-all, Owen-Smith indicated that adult natural mortality in megaherbivores is around 2-5% per year.

In the boreal forest of interior Alaska and the Yukon Territory, moose mortality varies depending on each population's stability. Annual adult mortality is 6 - 6.8 % in steady or increasing moose populations, but as high as 19 % when populations are declining (Gasaway

TABLE 15. Estimated biomass, population densities, and total numbers of dominant herbivores in Pleistocene east Beringia according to the model of Bliss and Richards (1982). Biomass estimates come directly from the model; densities and population numbers calculated first using body weights given by Bliss and Richards, then using weight estimates from this study. Compare values to those in Table 14 (Redmann's model) and Table 16 (values derived from this study).

species	standing biomass density from model (kg/km ²)	body weight used by Bliss and Richards (kg) ¹	adjusted body weight used in this study (kg) ¹	population density per Bliss and Richards (animals/km ²)	population density using adjusted body weights (animals/km ²)	total population in Eastern Beringia per Bliss and Richards (= 2,000,000 km ²)	total population in Eastern Beringia using adjusted body weights (= 2,000,000 km ²)
<i>mammoth</i>	96 - 136	2230	3800	.043 - .061	.025 - .036	86,000 - 122,000	50,000 - 72,000
<i>horse</i>	84 - 236	150	175	.560 - 1.573	.480 - 1.349	1,120,000 - 3,146,000	960,000 - 2,698,000
<i>bison</i>	127 - 305	450	650	.282 - .678	.195 - .469	564,000 - 1,356,000	390,000 - 938,000
<i>caribou</i>	132 - 270	100	200	1.320 - 2.700	.660 - 1.350	2,640,000 - 5,400,000	1,320,000 - 2,700,000
<i>musk ox</i>	151 - 289	180	400	.840 - 1.605	.320 - .578	1,680,000 - 3,210,000	640,000 - 1,156,000
<i>moose</i>	209	300	400	.697	.523	1,394,000	1,046,000
total	799 - 1445						

¹ Body weights used by Bliss and Richards are weights from modern species or estimated from modern relatives. Adjusted body weights are those proposed in this study. Adjusted body weights only change estimates of population size and density, not biomass density.

TABLE 16. Conservative estimates of herbivore populations and carcass densities in late Pleistocene east Beringia, based on an overall herbivore biomass density of 1000 kg/km².

species (kg)	biomass density ¹ (kg/km ²)	population density (no./km ²)	total population in eastern Beringia (2,000,000 km ²)	annual adult mortality rate (%)	edible carcasses from natural mortality = <i>carcass production minus 50%</i> ²	edible carcass biomass from surplus predation ³	total carcass biomass from predation and natural mortality
<i>mammoth</i> (3800)	300	0.079	158,000	3	4.50	.0012	833
<i>bison</i> (650)	400	0.615	1,230,000	5	10.00	.0154	65
<i>horse</i> (175)	180	1.029	2,058,000	7	6.30	.0360	28
<i>other herbivores</i>	120	— ⁴	— ⁴	— ⁴	— ⁴	— ⁴	— ⁵
TOTAL	1000	1.723⁵	3,446,000⁵	—	20.80⁵	.0526⁵	19⁵
							6.3 kg/km²/year
							27.10 kg/km²/year

¹ based on the following biomass percentages: bison 40 %, mammoth 30 %, horse 18 %, others 12 %

² 25 % loss assumed for inedible portions of carcass, 25 % loss due to losses to other carnivores and undiscovered carcasses

³ see text for derivation of edible carcass biomass from surplus predation

⁴ not an appropriate calculation unless species and weight are specified

⁵ calculating predation levels for individual species requires too many assumptions and is beyond the resolution of this model

⁶ only includes mammoth, bison, and horse

et al. 1983, 1992). In a five-year study on bison in the badlands of South Dakota, Berger and Cunningham (1994) found that adult bison experienced a maximum of only 3.2 % annual mortality. However, this is a protected system without significant predation, and bison numbers are increasing and well below carrying capacity. Bison mortality in natural systems must therefore be higher.

Earlier, I discussed ecological arguments which predict that Beringia's Pleistocene herbivores most likely existed in small populations of larger bodied individuals (following Guthrie 1984a). Species such as this, where more biomass is housed in fewer, but larger, individuals, tend to have relatively lower population turnover rates—that is, longer lifespans and lower mortality rates (Eisenberg 1981, Hennemann 1983, Calder 1984, Owen-Smith 1988). Large-bodies species like mammoth and bison would have had even longer lifespans and even lower mortality rates. A general allometric model scaling mortality rates to body size does not exist, but many other life history parameters scale in accordance with metabolic scaling—that is, $\propto M^{0.75}$. This is believed to be the reason why longevity, for instance, scales reciprocally $\propto M^{0.25}$ (Calder 1984), and why the rate of population increase scales $\propto M^{-0.26}$ (Hennemann 1983). Calder also reviews data showing that age-specific death rate increases $\propto M^{-0.25} - 0.36$. Since mortality is inversely proportional to longevity and should scale similar to the rate of population increase, it seems reasonable to generally assume that mortality scales nearly $\propto M^{-0.25}$.

Using this logic and the data listed above for mortality in modern mammals, I will calculate a rough approximation for annual adult mortality in mammoth, bison, and horse. Starting with a conservative assumed adult mortality rate of 5 % for the 800 kg steppe bison, and applying a -0.25 scaling constant (scaled to body mass), the rates in horse (175 kg) and mammoth (3800 kg) are predicted to be 7.2 % and 3.3 % respectively. But considering that both equids and proboscidian have conservative life history strategies relative to bison, it seems best to lower these latter two estimates somewhat. I will use values of 6 % for horses and 3 % for mammoth.

Inputting these mortality rates onto my population model, it is possible to estimate the rate of carcass production from non-predatory mortality in each species. The results using conservative population estimates are shown in Table 16. Assuming a standing live biomass of 1000 kg/km², arrived at in the earlier discussion, the total carcass biomass resulting from natural mortality in all major large herbivores is estimated to be around 41.38 kg/km²/year. As before, 25% should be subtracted for the non-caloric portion of a carcass. It also seems prudent to subtract an additional 25% to account for carcasses that are partially consumed by other predators and carcasses which go undiscovered, leaving a total of 20.80

kg/km²/year.

Adding my earlier estimates on surplus predation (average of 6.3 kg/km²/year), *total carcass production on the Pleistocene landscape is predicted to be roughly 27.10 kg/km²/year. That is over four times the amount needed to maintain a minimum viable population of short-faced bears, thereby supporting the hypothesis that Beringian ecosystems could have sustained a 700 kg carnivore that obtained all of its meat through scavenging.* Terrestrial ecosystems of Pleistocene Beringia were far more productive than today, but they probably were less productive than most other ice-free regions of North America (Guthrie 1968, 1982, 1984a, 1984b, 1990; Hopkins *et al.* 1982). Therefore, from this “worst case scenario,” it is plausible to argue that *Arctodus* could have functioned as scavenger across its entire range in North America.

3. Corollaries to the Model

Short-Faced Bear Population Levels: Throughout this modeling exercise, I started with a minimal viable population of scavenging short-faced bears and looked for ways that Beringia's Pleistocene ecosystem could support it energetically. Now that these conditions seem to be met, I want to turn the equation around and ponder the maximum number of short-faced bears the ecosystem could support. If the annual requirements of a 700 kg short-faced bear was 5853 kg of carrion, then 27.10 kg/km²/year of carrion should support an *Arctodus* density of ≈ 0.005 bears/km², equivalent to one short-faced bear every 200 km² or 10,000 bears in all of eastern Beringia. Considering *Arctodus*' size, these estimates are very much in line with densities of other large carnivores I discussed, and it supports my earlier prediction that *Arctodus* may have had an exclusive home range as small as 500 km². Relying on conventional wisdom, 10,000 bears in a 2,000,000 km² area seems like a much more reasonable population than 2,000—yet it still is not a lot, and I will be arguing later that a primary reason for *Arctodus*' demise may have been the inherent untenability of a carnivorous niche for such a large mammal due to the fact that it would be difficult for to maintain a minimal viable population density that still allowed each individual to extract enough energy *year-round* from the ecosystem.

Predator-Prey Ratios: My model's estimates of secondary productivity also can be turned around and used to predict predator densities in Pleistocene Beringia. This also will provide a secondary test of my model, since one can ask whether the predicted densities seem realistic. Trophic principles dictate that carnivore biomass will be far less than herbivore biomass (Slobodkin 1961; Clutton-Brock and Harvey 1978, 1983; Gittleman and Harvey 1982). Conventional wisdom is

that ecological efficiencies in secondary consumers will be around 10 % (Slobodkin 1968, Pimm 1982), but Turner (1970) showed that they really are much lower—generally < 2% in endotherms, with maximum values reaching about 3%. Since the system in question is one of endotherm consuming endotherm, predator-prey biomass ratios should then be around 1:100. Ratios in terrestrial vertebrate food webs often are lower than this (discussed below), but many certainly no longer represent natural systems. Because there is no regular, predictive pattern of predator size to prey size in nature, the numbers ratio of predator:prey (as opposed to biomass ratio) will have to be examined from empirical evidence.

Data in the Alaskan wolf studies cited earlier suggest a general wolf:prey numbers ratio of a little over 1:100 and a general biomass ratio of around 1:250, in areas where wolves experience some population control by hunting or management. Both ratios are higher (relatively more wolves) in areas without significant human control (data also reviewed in Keith 1983). On Isle Royale, the biomass ratio is similar, although the number ratio is higher (~ 1:30) because large-bodied moose constitute the vast majority of prey (on Isle Royale, wolves and moose are not hunted or controlled). In southern boreal forests of Ontario and Minnesota, where deer are the main prey, predator prey ratios are about 1:100 - 1:150, but biomass ratios still are around 1:200.

Puma, North America's only other significant predator of large mammals, have extremely low numbers compared to their prey (Hornocker 1970). Numbers ratios are as low as 1:600, but approach 1:200 in more pristine areas (Nowak 1991). Respective biomass ratios are around 1:524 and 1:46 (puma frequently kill prey larger than themselves, leading to a higher biomass than numbers ratio)(Longhurst *et al.* 1952, Hornocker 1970, Seidensticker *et al.* 1973, Lindzey 1987).

Ratios for African lions can be difficult to calculate because much of their prey is migratory. If only resident prey are considered, Serengeti lions experience an overall predator-prey ratio of approximately 1:129 and a biomass ratio of 1:118 (calculated from data in Schaller 1972 and Van Orsdol *et al.* 1985). Ratios for individual prides are usually much higher. For example, Schaller's data for the Masai pride in the Serengeti show a predator-prey numbers ratio as high as 1:20. For my purposes, area-wide numbers are more useful.

Serengeti hyenas have a predator-prey numbers ratio of 1:86 and a biomass ratio of 1:266 (Kruuk 1972) (for consistency sake, Schaller's numbers for Serengeti prey were used for this calculation, but hyena numbers came from Kruuk). Considering lion and hyena together, total ratios are around 1:51 for numbers and 1:82 for biomass. But both of these ratios underestimate herbivore

numbers and mass because they do not include migratory animals, which constitute over twice as much biomass as the resident herbivores (Schaller 1972). Since they are part of the system for only part of the year, their contribution is hard to estimate, but they are an important part of the diet for both predators and probably reduce the actual ratios by nearly one-half.

There is a higher density of both predators and prey in Ngorongoro than in Serengeti. Hyena densities, for instance, are about 14 times greater. Yet, using data in Kruuk, I estimate that the ratio of hyena (385) to prey (23,660) actually is 1:62 with a biomass ratio of 1:140. The relatively fewer lions (50) in Ngorongoro leads to a total (lion plus hyena) predator prey ratio of 1:54 and a biomass ratio of 1:97, nearly identical to those calculated for Serengeti. But considering the number and biomass of ungulates moving into Serengeti seasonally, predator:prey ratios in Ngorongoro truly are higher.

The above data suggest that the pristine ecosystems of late Pleistocene Beringia might reasonably be expected to have a predator-prey numbers ratio of at least 1:100, while the biomass ratio could be set conservatively at around 1:200, yielding an ecological efficiency of 0.5%. The two ratios imply that carnivores were consuming prey which was generally twice their own mass. Guthrie (1968) estimated Beringian predator:prey ratios from fossil frequencies and derived a numbers ratio of 1:130 for wolves and 1:250+ for lions, for a combined ratio of around 1:86. Even though there are reasons to suspect preservational and collector biases against the smaller-bodied carnivores, Guthrie's ratios are very close to my theoretical predictions. Using a ratio of 1:200, the herbivore biomass of eastern Beringia (1000 kg/km^2) would have supported approximately 5.0 kg of predators per km^2 . Based on modern population dynamics and the fossil record, one might expect this biomass to be divided evenly between wolves and lions at 2.0 kg/km^2 each, leaving 1.0 kg/km^2 for other minor predators. This translates into 1 wolf every 25 km^2 (0.04 wolves/km^2 ; assuming a Pleistocene body size of 50 kg) and 1 lion every 100 km^2 (0.01 lions/km^2 ; assuming a Pleistocene body size of 200 kg).

These numbers are well in-line with modern demographics, and even suggest somewhat higher densities than present in the case of wolves. Of course the estimate is not very precise, and the 50-50 split between lion and wolf is only a best guess based on fossil frequency. The predicted lion density compares very well to densities of modern lions (average values around 0.01 - 0.08 according to Nowak 1991). The wolf estimate is exactly on order with the density of wolves in areas of Minnesota and Ontario, where they feed mostly on white-tailed deer in forest ecosystems (no parallel in ecosystem structure is implied)(Mech 1973, Van Ballenberghe *et al.*

1975, Fritts and Mech 1981, Fuller 1989). To expect such wolf densities in Pleistocene Beringia may be too optimistic, but the fact that Pleistocene wolves were smaller and may have been relegated to smaller prey items suggests that this estimate may not be too far off. It certainly is within the range of my conservative suggestion of 0.0033 wolves/km² and compares reasonably well with the density of wolves in modern Alaska.

Prediction for both wolf and lion densities based on predator:prey ratios suggest that my initial general predictions (0.01 for wolves, 0.004 for lions) may have been too conservative. Alternatively, these levels of tertiary productivity suggest that the Pleistocene large carnivore guild may have been fairly rich, and able to support scimitar cats, and dholes along with lions and wolves. Either way, the implication to a population of scavenging short-faced bears is that there would have been many opportunities to confiscate carcasses from other carnivores, in addition to scavenging on herbivore carcasses resulting from non-predatory mortality.

4. RELYING ON CARCASSES AS A CONTINUOUS FOOD SOURCE AND THE EVOLUTION OF *ARCTODUS'* SCAVENGING NICHE

Some authors have made the point that no large mammalian carnivore today is able to make a living by pure scavenging (see Houston 1979), and this is true — in modern ecosystems (vultures are the only large-bodied endotherm that does so today). In this section, I will show how a pure scavenging niche may be tenable for a large mammal under certain ecological and environmental conditions. I already demonstrated how it seems likely that North American ecosystems produced enough carcass biomass annually during the Pleistocene to support scavenging short-faced bears. It is another question all together, however, whether that carrion would be available year-round and on a regular basis. If mortality among Pleistocene herbivores was highly seasonal, for instance, then short-faced bears would have faced seasons of huge dietary surpluses followed by long, lean periods and certain energetic bottlenecks. The following discussion will explore such issues. In the process I will try to show that the key to *Arctodus'* extinction probably lies in changing patterns of carcass availability caused by changes in herbivore demographics at the end of the Pleistocene. I will conclude by proposing a theory for the events which may have driven the evolution of a pure scavenging niche in *Arctodus*.

Feasibility of A Pure Scavenging Niche

I contend that there are two reasons why no large terrestrial carnivore today subsists solely by scavenging.

First, few ecosystems provide enough carrion biomass distributed evenly throughout the year. Second, no large carnivore living in such an ecosystem today has the large body size necessary to monopolize and defend carcass resources from its competitors and to survive long bouts without food. I address these reasons in order and explain how bears, and particularly short-faced bears, were pre-adapted to overcome them.

Seasonal Carcass Abundance: The most critical tenet of the scavenging hypothesis may be the question of seasonal carcass abundance and whether carrion would have been a reliable year-round food source for *Arctodus*. While this is probably the most difficult aspect of the hypothesis to test, I believe light can be shed on the issue by re-examining aspects of the large herbivore populations in Pleistocene Beringia versus those of today. In my model of Beringian herbivore populations I followed Guthrie's (1982, 1984a, 1984b, 1990a, 1990b) rationale that Pleistocene herbivores were large-bodied and existed in low population densities. In the simplest terms, the reason for this pattern, according to Guthrie, is that Beringia's Pleistocene winter range supported fewer individuals of any given species and heavy winter mortality kept most populations of large herbivores understocked. Selection was for larger-bodied individuals which were able to take advantage of a longer and more productive growing season and invest conservatively in reproduction, often delaying reproduction for a season or two. Such individuals and their offspring would experience increased fitness because they were more likely to survive subsequent winter bottlenecks in Pleistocene environments.

Guthrie emphasized that this large-body strategy only applies to ruminants, not monogastric herbivores, because the latter have slow growth potentials and thus are not adapted to take advantages of seasonal spikes of high quality forage. As a result, Pleistocene monogastrics like horses and mammoths were not giants, but actually diminutive compared to their ruminant counterparts. However, since monogastrics are better adapted to using poor quality winter range, more of them may have been able to overwinter and thus summer productivity could be turned into more, but smaller, individuals.

This sets up the following likely situation in Pleistocene Beringia: ruminants, dominated by bison, would have been in their worst condition and mortality rates would have been highest in late winter to early spring just before green-up. Carcasses of bison would have been plentiful for *Arctodus* at that time, but perhaps rare during other seasons. Today, mortality is highest in winter and spring among northern ungulates, including bison (Soper 1941, Kline and Olson 1960, Clutton-Brock *et al.* 1982, Ballard *et al.* 1981, Leader-Williams and Ricketts 1982, Berger and Cunningham 1994). In

contrast, mortality amongst Beringia's horses and mammoths (the dominant monogastrics) should have been more evenly distributed throughout the year. Both proboscidian and equids have conservative growth strategies and live long lives (Klingel 1969, Janis 1976, Owen-Smith 1988, Haynes 1991), and rates of natural mortality in both are predicted to be low. Mortality in most populations of modern African elephants — a monogastric roughly analogous to mammoths — is not particularly seasonal, according to causes of death listed by Haynes (1991) and Owen-Smith (1988). Mass die-offs do occur in elephants, but are related mostly to droughts (Hanks 1979, Owen-Smith 1988). They also occur most frequently in extremely arid areas such as western Hwange Park, Zimbabwe, where it can be difficult for elephants to fulfil their requirement for daily water (Haynes 1991). Still, the earlier model showed how even low natural mortality rates in horse and mammoth alone could provide ample carcass biomass for short-faced bears — as long as it was evenly distributed throughout the year. Given Guthrie's demographic predictions, this seems plausible.

In stark contrast, the large herbivore guild of Holocene Beringia is composed exclusively of ruminants. In the most recent millennia, caribou and moose have dominated, but muskox, sheep, bison, and wapiti were common in the early to mid Holocene. All of these species experience highly seasonal mortality, and this factor, combined with low overall ungulate biomass leads to a situation whereby there are not enough carcasses available year-round to support an exclusive scavenger, much less such a large one.

Even wolverines, the carnivore most dependent on scavenging in the region today, do not subsist completely on carrion (Rausch and Pearson 1972, Hornocker and Hash 1981, Magoun 1985, Gardner 1985). It is my impression that carcasses are a rare commodity overall in present day Beringia but that they can be a nutritional windfall at times when happened upon by wolves, wolverines, and brown bears. If a carcass has been mutually located by any two of these carnivores, competition can be high, but there is a clear dominance hierarchy — bears dominate. Wolves will harass bears for access to a carcass, but they seldom prevail (Murie 1944, 1981, Ballard 1982, Magoun and Valkenburg 1996). Wolverines, while known for their ferocity, also are no match for brown bears (Murie 1981). Brown bears, wolves, and wolverines all will cache carrion presumably to prevent detection by other scavengers (Mysterud 1973; Murie 1981; Magoun 1976, 1985; Gardner 1985). This is understandable in wolves and wolverines, but there seems to be little reason for brown bears to cache carcasses, since they normally remain near a carcass until it is consumed, as Murie's many anecdotes describe, and no

other present-day carnivore can realistically steal a carcass from an attendant brown bear, except maybe a pack of wolves. Perhaps this behavior in brown bears is a reflection of past habits, when another, larger bear monopolized all carcasses unless they could be hidden from detection (especially by smell). A test of this hypothesis would be to examine whether brown bears in Eurasia habitually cache carcasses, since those populations have evolved in the absence of *Arctodus*.

I hypothesized earlier that no modern carnivore subsists totally by scavenging because few modern ecosystems provide enough carrion biomass distributed more or less evenly throughout the year, and in those ecosystems that might, there is no large carnivore big enough to monopolize and defend carcass resources and survive lean seasons. Now I have presented reasons to suspect that Beringia's Pleistocene ecosystem may have been structured in a way such that carcasses were more evenly distributed throughout the year — mainly because of the former prominence of more monogastric herbivores.

The argument extends equally well to most of North America, which had even more monogastrics and other large herbivores with conservative growth strategies, including camellids, edentates, additional horse species, and another proboscidian (mastodons). In addition, western North America was occupied by a diverse group of antilocaprid species (Kurtén and Anderson 1980), which may fit well into the present *Arctodus* model, but for a different reason. Antilocaprids are ruminants, but they are small-bodied, which means they have rapid population turnover rates (higher rates of both mortality and fecundity) than larger ungulates (Eisenberg 1981, Hennemann 1983, Calder 1984, Owen-Smith 1988). The American pronghorn, the only extant antilocaprid, experiences fairly high mortality rates, even though it is moderately protected (Baker 1954, Folkner 1956, Fichter and Nelson 1962, Kitchen 1974). Baker (1954), for example, recorded a 10% (non-hunting) winter mortality in 1952 for Wyoming pronghorn, while Hailey *et al.* (1966) reported a Texas population that experienced a 30 % decrease in numbers in a single year. Twinning also is the norm in pronghorns, which adds to their rate of production (Chattin and Lassen 1950, Folkner 1956, Kitchen 1974).

A diversity of such antilocaprid species would collectively contribute more, but smaller, carcasses to the system on a more regular basis. These species still may have experienced a peak of seasonal mortality in the winter, as do modern pronghorn, but overall this pattern of high herbivore turnover would work well for an obligate scavenger, even a very large one, because such a scavenger does not need large carcasses so much as it needs a "large-enough" carcass at frequent intervals. A 50

kg pronghorn, for instance, represents about one week of food for *Arctodus*. Therefore, I predict that a system supporting an obligate scavenger will have one or both of the following two characteristics. First, it will provide carcasses on a regular basis, which occurs when the system contains herbivores with conservative growth patterns and herbivores that do not have marked seasonal mortality. Second, the system should have a fair number of smaller-bodied herbivores with rapid populational turnover rates.

Carcass Dominance and Carnivore Body Size: Having addressed the question of ecosystem structure, there still remains my second point about the scavenger's body size. In this regard, it seems that only bears, with their inherent large size, are preadapted to a niche of exclusive scavenging because only they are able to reach body sizes which allow them to monopolize carcasses. One could argue that big bears exist today in the Holarctic, yet none are exclusively scavengers. I would counter that Holarctic ecosystems today do not provide large amounts of carcass biomass throughout the year. Some modern temperate and tropical ecosystems may provide the necessary carcass biomass year-round, but they do not have bears or any other carnivore large enough to monopolize carcasses and survive occasional starvation bouts, and I would argue that no other group of terrestrial carnivores is big enough to cross that critical size threshold because they and their ancestors have come from the ranks of obligate predators. In Part I, I showed how being a predator encumbers a species with certain morphological and size constraints, and that there is an upper size limit for mammalian predators because of locomotor demands involved with successful predatory tactics. From that standpoint, it is difficult to envision a group of predators evolving a large enough body size to then cross over to a mode of searching out, and, more importantly, defending carcasses. There also are energetic barriers to overcome, as I have been discussing in the present chapter. Namely larger predators need to capture larger prey or many smaller prey more frequently. Their bigger size makes the latter more difficult, and being dependent on larger prey means dependence on a food source that is inherently less abundant. All of these factors keep predators relatively small, making it difficult for them to evolve body sizes large enough to be dominant at carcasses.

In contrast, bears have evolved their large size as an integral part of their evolution away from pure carnivory and predation (Kurtén 1964, 1966a, 1967; Martin 1989; Stirling and Derocher 1990). Still, all bears retain a predisposition for carnivory. But their size and build makes them poor predators in all but the most opportune situations. At least one bear lineage — the brown bear-polar bear line — has secondarily increased its level of

carnivory (Kurtén 1964), and this propensity seems to persist in the Ursidae. What is important to this discussion, however, is the ability of a bear to exploit its size for the purpose of dominating other carnivores. Bears today clearly are aggressive towards other carnivores (e.g., Rogers and Mech 1981, Ramsay and Stirling 1984, Miller 1985), and the original impetus for size evolution in bears during the Miocene seems best explained, at least in part, as a defense against predators, since bears could no longer outrun them.

A Theory for the Evolution of Scavenging in Short-Faced Bears

Given these dispositions in bears, I propose that short-faced bears diverged from a more generalized stock of forest-dwelling Tremarctine bears (around 1.5 - 2.0 Mya) as they increased their use of open habitats. Carrion is more easily located in non-forested environments (Schaller and Lowther 1969, Schaller 1972, Blumenschine 1989), so a critical factor in this evolution may have been the increased percentage of open savannahs and parklands in the western half of North America at the end of the Pliocene. Carcasses are difficult to find in forested environments and frequently they go undiscovered there presumably because they are hard to detect, as odors do not travel far and carcasses are difficult to spot in closed habitat (Craighead and Craighead 1972, Mysterud 1973). Therefore, it would seem unprofitable for a carnivore to focus its foraging efforts searching for carcasses in forests, and indeed, *Arctodus* fossils are associated with non-forested environments (Harington 1973, Kurtén and Anderson 1980, Harris 1985, Richards *et al.* 1996). In an open environment the scent of a carcass will carry farther and, once its direction is determined, visual detection is far easier than in a closed environment. Carcasses could be detected and found with little addition to a bear's normal foraging efforts. But this statement holds true for any carnivore in open terrain. What other carnivores lack, however, is size — enough size to dominate a carcass they find and monopolize carcass resources in general. Without this ability, it is hard to imagine how a carnivore could evolve a niche dependent on large mammal carcasses as its primary or exclusive food source.

Because of their size, bears are uniquely preadapted to evolve into a scavenging niche if the appropriate environmental conditions arise. Once a bear moves into such a niche and increases its dependence on carrion, and competition from other carnivores is keen, I would predict there to be selective pressures for even larger body size in order to ensure its dominance. But larger size has other key advantages for a scavenger. A larger animal can go longer between feeding bouts, and if it finds a large meal, it can eat more at one time (Houston 1979,

Eisenberg 1981). These are ideal traits for a scavenger that depends on large carcasses for food— larger carcasses come from larger animals, which in turn have lower population densities and therefore will be less abundant.

Likewise, a larger animal has a lower cost of transport (previous paper) and thus can more efficiently traverse a foraging area. Reciprocally, it can cover a larger area at a reduced cost. But such a strategy means the scavenger must find an absolutely greater amount of carrion to meet the energetic needs of a large body, even if it is metabolically more efficient. If such a large-bodied scavenger begins to focus primarily or exclusively on large carcasses for food, then selection should favor morphological changes that increase locomotor efficiency even further. These would include a reduced musculoskeletal mass, increased leg (stride) length, cursorial limb posture, and an economical gait for moderate speed travel— traits which all are found in *Arctodus*.

But why did *Arctodus* evolve such a huge size? Those who subscribe to predatory models have used *Arctodus*' size as an indication of its prey size— in other words, as a reflection of herbivores in the mammal community. Under the scavenging model, *Arctodus*' size becomes a reflection of other carnivores in the community — that is, it is an indicator of the level of aggression, and perhaps the degree of sociality in Pleistocene carnivores. If *Arctodus* only needed to defend carcasses against a few wolves or a lion or two, then it is hard to see why it had evolved to be so large. Even the energetic reasons I have discussed may not be reason enough to explain its size. Given corroborating evidence, I think it is reasonable to conclude that *Arctodus*'s size is an indicator of high levels of competition amongst carnivores and that *Arctodus* was defending itself and its resources against groups of social carnivores which had a large cumulative biomass (i.e., group size need not have been large if individuals were large-bodied).

Today clear examples can be found of competition driving the size of carnivore social units as well as body size. Lions and spotted hyenas are classic examples. Two female lions (weighing about 150 kg each) can keep 5 - 6 spotted hyenas (weighing about 50 - 60 kg each) from stealing their kills, but the mere presence of a male lion (weighing 200 - 250 kg) can keep up to 12 hyenas at bay (Eaton 1979). Indeed, the large size of male lions is believed to have evolved in part because of their role in defending kills and prides against the smaller, but highly social hyena (Kruuk 1972, Schaller 1972, Eaton 1979). (Male lion size also appears to be driven by male-male competition as coalitions of males vie for control of prides (Packer *et al.* 1988)). Even a small pride of female lions is nearly invincible to hyenas with a male present.

Competitive dynamics of body size and group size also play out in interactions between these two dominant carnivores and hunting dogs, leopards, and cheetahs. The solitary nature of leopards and cheetahs ranks them very low in their competitive abilities, but the large packs of the highly social African hunting dog make them nearly equal competitors to the larger-bodied hyena (Estes and Goddard 1967; Kruuk and Turner 1967; Kruuk 1972; Lamprecht 1978, 1981; Eaton 1979).

Earlier I summarized arguments showing why Pleistocene lions probably existed in very small groups and most likely did not form typical prides, at least in Beringia. But still, two or three large lions constitute quite a threat to any mammal, even to a 700 kg short-faced bear. This is especially true considering the revised carnivore body mass estimates of Anyonge (1993); according to Anyonge, Pleistocene lions weighed 344 - 523 kg. Previous estimates have placed them about 1 ½ times the size of modern lions, in the range of 200 - 375 kg (Anderson 1984, Stock and Harris 1992). In Part I, I tried to show that body size severely limits predatory abilities in carnivores over about 250 kg. If this analysis is correct, then Anyonge's estimates are hard to believe, since a 523 kg lion would have been an inept predator. Using either of the above estimates of lion body size, the presence of lions in North America seems like a compelling force driving increased body size evolution in *Arctodus*.

Other Pleistocene felids in North America almost certainly were not social, with the possible exception of sabertooths. Pumas are not social cats; neither are Jaguars, which inhabited western North America during warmer intervals of the Pleistocene (Kurtén 1973b, Kurtén and Anderson 1980, Shultz *et al.* 1985). The American Cheetah (*Miracinonyx*) was most closely related to pumas (Van Valkenburgh *et al.* 1990), and is unlikely to have been social. Traditionally, it has been argued that Smilodine and Homotherine sabertooths probably did not form prides, mainly because a solitary lifestyle is the rule for felids, with lions being the only exception. Radinsky (1975) and Hemmer (1978) argued further that sabertooths were non-social based on brain size and morphology. Turner (1997) questions the validity of comparing brain size, even when scaled to body size, because accurate estimates of body size do not exist for the morphologically-unique sabertooths. Turner (citing Graham 1976) further argues that the high occurrence of *Homotherium* deciduous teeth and juvenile mammoth remains at Friesenhahn Cave provides circumstantial evidence that these cats may have hunted young proboscidians, and Turner believes this would have been inconceivable for a predator the size of *Homotherium* unless it hunted in groups. The high incidence of bone lesions found on *Smilodon* fossils at

Rancho La Brea, and the case of a sabertooth canine being lodged in the skull of another sabertooth, have been cited as evidence that sabertoofths were aggressive towards each other and generally asocial (summarized in Turner 1997). But Shaw *et al.* (1991) and Heald (1989) have interpreted healed wounds in *Smilodon* as a sign that this sabertooth was social because it is difficult to see how an injured sabertooth with bone pathologies could survive unless it had access to kills made by pride-mates.

In groups, or alone, sabertoofths probably were formidable competitors in Pleistocene North America, and Anyonge's (1993) latest estimates for body mass are 146 - 231 kg in *Homotherium* and an amazing 347 - 442 kg in *Smilodon*. Marean and Ehrhardt (1995) argue that *Homotherium* was capable of disarticulating large mammal carcasses, but this is questionable due to the extreme specialization of sabertooth dentition for killing and cutting at the cost of bone processing abilities (Ewer 1967, 1973; Blumenschine 1987, 1989; Marean 1989). Either way, sabertoofths were the least adapted of all large carnivores for processing carcasses to their fullest, and it is likely they left considerable edible material on the bodies of animals they killed (Schaller and Lowther 1969; Ewer 1967, 1973). Sabertooth kills thus would have been a real boon for a scavenger with abilities to process carcasses more thoroughly—an idea which has been proposed for hominid scavengers as well (Schaller and Lowther 1969; Marean 1989; Blumenschine 1986, 1987, 1988).

Potential large canid competitors of *Arctodus* in North America included wolves, dire wolves, and perhaps coyotes (*Canis latrans*). Modern coyotes depend on carcasses from other predators' kills perhaps more than any other large canid (Young 1951) and coyotes will form temporary associations at carcasses to defend them (Bueler 1973, Bekoff and Wells 1986). Coyotes also have an occasional tendency to form cohesive social groups when hunting cooperatively for large prey in areas where coyotes and wolves are not sympatric (Bowen 1981). Coyotes were larger in the Pleistocene (Nowak 1979), but given the tendency of coyotes to be subordinate to larger canids (namely wolves), the presence of two other (social?) canids in Pleistocene North America suggests that Pleistocene coyotes were solitary.

There is probably little descent for the assertion that Pleistocene wolves were social, but it is difficult to estimate their pack size. Wolves today can form large packs, sometimes upwards of 15 to 20 individuals, but this is rare (Rausch 1967, Mech 1970, Haynes 1982). Also, the mechanisms driving pack size remain elusive (Rausch 1967, Pimlott *et al.* 1969, Mech 1970, Rodman 1981, Pulliam and Caraco 1984, Earle 1987). There is some evidence that wolves form larger packs in situations where they frequently lose carcasses to grizzlies (Ballard

1982), but the prevailing theories implicate prey size and prey density as the determinants of pack size: packs that hunt larger prey and/or prey with low-densities have more individuals (Murie 1944, Burkholder 1959, Rodman 1981, Oosenbrug and Carbyn 1982, Pulliam and Caraco 1984, Earle 1987). Body size in wolves is only loosely associated with prey size, and it seems that the strategy of wolves is to match pack size rather than body size to prey size. Pleistocene wolves were slightly smaller than today (Matheus 2001), but for the reason just stated, this may not have reflected prey size. Instead, it may suggest that packs were larger, since a pack of given total mass can be composed of many small individuals or few large individuals.

In this regard, Pleistocene wolves may have hunted more like the smaller African hunting dog of today, which specializes on small to moderate-size bovids by hunting in large packs—averaging around 7 - 11 individuals (Kruuk 1972, Bertram 1979). Hunting dogs can kill animals as large as adult wildebeest (at least 5 - 7 times their own size), but their small size excludes them from hunting the very largest African bovids. The hunting dog's forte is using its speed and large numbers to chase down swift bovids, mainly gazelles, which they capture when the gazelle makes a sharp evasive turn and runs into a well-positioned pack member (Kruuk and Turner 1967). Hunting success rates are high in hunting dogs, but they must hunt often because each kill must feed many individuals, and because their prey is relatively small-bodied. If Pleistocene wolves were hunting this way, it would explain how prey resources were partitioned between them and lions, which because of their size must have been focusing on much larger-bodied prey. The large pack size of hunting dogs also makes them rank on par with the larger spotted hyena for access to carcasses (Eaton 1979). The same could be said for a pack of small Pleistocene wolves trying to defend carcasses from lions or short-faced bears. Also, the prediction that these small wolves killed smaller prey, but more frequently, compliments *Arctodus'* niche, as presented in this paper, because it would increase the average number of carcasses on the landscape at any given time.

There is no direct evidence of pack size in dire wolves, but their exceptionally high numbers at Rancho La Brea—where they are more abundant than any other species—has been interpreted as an indication that they formed large packs (Stock and Harris 1992). Compared to grey wolves, the dire wolf was slightly larger and more heavily built in both its limbs and cranium. Its canines and carnassials were larger, too, and the latter were highly sectorial. Because of its robust build and dentition, it has often been suggested that the dire wolf may have done substantial amounts of scavenging (Kurtén and Anderson 1980, Stock and Harris 1992, Van Valkenburgh 1989),

but I find little logic in this. First, the canines of the dire wolf were long and compressed, an adaptation for piercing and killing (Van Valkenburgh and Ruff 1987). While its larger premolars would function better as bone crackers, bone-cracking does not necessarily signify a scavenging lifestyle, so much as it indicates the degree to which a carcass is utilized. As I have tried to show in this chapter, an argument for specialized scavenging requires one to demonstrate that the whole animal has evolved to maximize its access and ability to utilize carrion resources, often at the expense of predatory skills. Yet, the number of traits in dire wolves that point to a predatory lifestyle are equally great, such as canine size and shape. Moreover, all predators will engage in scavenging behavior when the opportunity arises, so to speculate on whether an extinct predator scavenged, or to what degree, can be pointless. Of course, this is different than building the argument that a species evolved specifically within a scavenging niche.

If any of these predators faced a constant threat of losing their prey to an exceptionally large, carcass-stealing specialist, then there would have been clear impetus to increase body size and/or pack size for defense. Lions displayed large body size, as did dire wolves. Both may have had only small social units, but their size and strength may have made them competitive with short-faced bears, even in small numbers. Wolves apparently took a different route in this competitive scheme. They were smaller-bodied, but they likely formed larger packs than today. In response to this competition, selection in *Arctodus* would have been for even larger size, as long its scavenging niche remained energetically tenable (later, I will discuss how this tenability may have been lost).

In Part II, I noted that *Arctodus'* inflected pelvis, short hind limbs, and short back were well suited for a bear that used an upright stance. In context of the current discussion, I would argue that this behavior would be valuable in an animal that intimidated other aggressive and social carnivores either while defending a carcass or stealing one. If a scavenger wants to ensure its control over a carcass, it must make an unmistakable presentation to other carnivores that clearly states its dominance, and size is the clearest indicator. Larger social groups of competitors require the impression of even larger size, and an upright stance has the effect of greatly increasing an animal's apparent size, especially during a frontal display. I estimate that when the average *Arctodus* stood upright it would have been about 2.5 m tall at head height. Harrington (1996) and Voorhies and Corner (1982) estimate that the largest short-faced bears would

have stood 3.4 m tall, with a vertical reach of 4.3 m!² As with the propensity for large size, being able to stand upright in an intimidating posture is a trait uniquely available to bears, as no other large carnivore can realistically stand bipedally. It should be noted that an upright stance is not the standard aggressive posture or threat display of Ursine bears. Hererra *et al.* (1991: 67) noted, however, that spectacled bears, the only surviving Tremarctine bear and *Arctodus'* closest living relative, have a reputation amongst local people for chasing humans while standing upright. They stated: "... bears will chase people away and are very dangerous when they get up on their hind legs."

Elsewhere (Matheus 1995), I argued that *Arctodus'* cranial and dental morphology also supports the scavenging hypothesis (also see comments in Voorhies and Corner 1985, Guthrie 1988, Baryshnikov *et al.* 1994). Its massive jaw musculature and shortened outlevers of its teeth would have yielded a very strong bite force, and its carnassials, which were ill-adapted for sectorial action, would have been positioned well to function as bone-cracking hammers (Matheus 1995). Such a suggestion can almost be taken for blasphemy amongst mammalogists, but Van Valkenburgh (1996) recently showed that African large carnivores display considerable "slop" in the use of their teeth for prescribed functions, and indeed she records the regular use of carnassials as bone cracking devices in spotted hyenas and hunting dogs (also see Sutcliffe 1970).

Such features of the skull in *Arctodus* are indicative of a carnivore that had the ability to open and process large mammal carcasses, and I disagree with Kurtén (1967a) that the skull is adaptive in any significant way for predation. Kurtén argues, for instance, that *Arctodus'* wide palate was adaptive for "worrying prey," but this trait may just be coincident with a wide snout that was used to smell-out carcasses over a large area. Standing alone, neither proposal is more or less reasonable than the other, but the latter fits more congruously with other data on *Arctodus*.

Likewise, *Arctodus'* canines do not suggest any adaptation for predation, such as lateral compression (using criteria of Van Valkenburgh and Ruff 1987). Instead, they are round and generic like those of other

² My estimate of bipedal height is based on the length of the hind legs (femur and tibia) plus the length of the spine and the height of the skull. Using data from Table 6 in Part II, these lengths total ~ 2.5 m. It is unclear how other authors have derived such large estimates.

bears, only larger. Speculating on the role of *Arctodus* as a flaker of Pleistocene bone, Voorhies and Corner (1986) seem to imply that short-faced bears could have used their canines to break bones, and Guthrie (1988) comments on the ability of brown bears to puncture steal with their canines. Larger canines may have evolved in *Arctodus* from this selective pressure, but it seems unlikely to me. One of the primary functions of canines is to pull and rip flesh. This ability is important for any carnivore in the initial stages of consuming a carcass, whether it was hunted or scavenged. Amongst other alternatives is the possibility that *Arctodus'* canines were used agonistically against other short-faced bears. Indeed, the degree of sexual dimorphism in canine length is correlated to breeding systems (e.g., monogamy, polygyny) in Carnivora, not diet (Gittleman and Van Valkenburgh 1997). I did not examine the degree of canine sexual dimorphism in short-faced bears, but this question should be pursued as a possible clue into *Arctodus'* breeding biology.

Furthermore, if *Arctodus* had evolved as a predator, there should be a greater dissimilarity between its teeth and those of other bears. For instance, during its rapid and relatively recent radiation from brown bears, the highly predatory polar bear has developed teeth that are clearly distinct from those of brown bears. Polar bear teeth are smaller, higher crowned, narrower, and more trenchant, than brown bear teeth giving polar bear teeth more sectorial qualities. Over its 1.5 to 2.0 million year history, *Arctodus* never developed comparable traits. Kurtén (1967a) argued that the protocone of *Arctodus'* P⁴ was positioned more posteriorly, giving this cusp a blade-like quality (Stock and Harris 1992 concur). I have examined most of the *Arctodus* dentitions in existence and do not see this trait in the P⁴. Therefore, I can not agree with the conclusion of these authors. Instead, I find that there is high variability in the position of the protocone both in *Arctodus* and other bears (except polar bears), and, if anything, the P⁴ has a broader and more pyramidal shape in *Arctodus*. As I mentioned, this tooth would function best as a bone cracker, and it typically has a fairly flat anterior-posterior wear-facet inclined lingually about 20°, a pattern similar to that found on premolars of spotted hyenas. Given the fact that the remainder of *Arctodus'* cheek teeth remained so "bear-like," it seems most congruous to argue that they retained their function as crushing apparatuses. This configuration would suit a carcass-processing animal well because such an animal could use its broad posterior molars to crush smaller bone and it could fracture large cortical bone using the apex of its P⁴ and the triconid of the M₁ as cracking hammers. It is even possible, but as yet untested, that *Arctodus* had evolved the ability to digest bone as modern hyenas have. Energetically, osteophagy extends

the feasibility of the scavenging niche, and perhaps is a key component of it (Martin and Martin 1993).

Repeatedly, I have made the point that simple one-to-one comparisons between *Arctodus* and other carnivores could lead to spurious conclusions, and that a first-principles approach is more appropriate. The former approach led Baryshnikov *et al.* (1994: 350) to conclude that, "*Arctodus simus* was not as highly specialized a scavenger as *Crocuta* or *Canis dirus*. Their carnassials lay [too far] forward, to be effective. *Crocuta* can 'cut' and 'crush' bones... . *Arctodus simus* could less effectively crush small bones; big bones of mammoths were probably not accessible for *Arctodus*." (secondary quotes are mine). I find these conclusions puzzling because they do not agree with the morphology of *Arctodus*, and to expect such a strict morphological recipe for bone processors is unreasonable. Moreover, *Crocuta* appears to have evolved as an osteophagous predator, and the carnassials are not the fundamental tooth used by *Crocuta*, or any other modern carnivore to process bone (Sutcliffe 1970; Ewer 1967, 1970; Kruuk 1972; van Valkenburgh 1989, 1996). Also, hyenas do not "cut" bone, they crack and crush it. Bone "cracking," as opposed to "crushing," is a process by which strong biting forces are transmitted usually to a single, well-backed apex on a tooth so that these forces are focused on a narrow point of the bone. This initiates a fracture in the crystalline bone matrix. When the wider basal portion of the tooth is driven into the bone, this expands the fracture and causes it to propagate as a long crack. Any tooth of the proper configuration and position in the tooth row can be employed for such a function (as long as the action does not generate so much torque as to dislocate the jaw, which is more likely with more posterior teeth because they have shorter outlevers). In contrast, "crushing" occurs when one solid object obliterates the structural integrity of another softer and less dense object. There is less need when crushing bone to focus the biting force in a single apex, in which case broad, flat teeth which are close to the jaw articulation suffice.

Baryshnikov *et al.*'s (1994) contention that *Arctodus'* carnassials were too far forward to process bone, also is difficult to accept. If these authors were looking for analogous structures in *Crocuta*, they should have compared *Arctodus'* carnassial to *Crocuta*'s P³ and P₄, which are conical-shaped and the primary teeth used by *Crocuta* to crack bone. Also, the forward position of *Arctodus'* carnassials in the tooth row is less significant than the fact that the face was shortened overall, which brought the carnassials closer to the jaw articulation and gave them increased mechanical advantage. Finally, Baryshnikov *et al.*'s statement that "*Arctodus simus* could less effectively crush small bones" seems to go against reason. A bear that large and with such a powerful

masticatory anatomy would have no problem crushing small bones, as discussed above. Even the much smaller wolverine can crush and crack large mammal long bones (Krot 1959, Haglund 1966, Magoun and Valkenburg 1996).

Extinction

Throughout these chapters I alluded to two possible contributing factors in *Arctodus* extinction, both relating to its huge size. Here I will briefly summarize them in the form of two hypotheses.

1) When discussing home range size and population densities, I suggested that *Arctodus* faced a fundamental conflict due to its size: how does such a large-bodied carnivore exist in population densities low enough so that each individual has a large enough exclusive foraging area, yet still retain a minimal viable population size? The first tenet of this question is an energetic one relating to the prediction that a carnivore the size of *Arctodus* must forage over a tremendous home range just to find enough food to meet its energetic requirements. Indeed, that is why I argued that *Arctodus* was built for increased locomotor efficiency. But it is conceivable that large mammal carcasses became so widely scattered that each bear would have to forage over an increasingly larger area, to the point where the environment supported a population density so low that the species fell victim to inevitable chance extinction. This process would have been amplified by the likelihood that home range overlap decreased as densities dropped, leading to populations that were further fragmented, whereby the chance of random extinction increased further.

Stated in another way, decreasing carcass densities would have increased the size of individual foraging areas to a point where each bear would have had to travel so far to find carcasses that it became impossible to balance its energetic budget between foraging costs and foraging gains. This may have even become a limiting factor before population sizes fell below minimum levels required for reproduction.

2) Rather than a reduction in absolute carcass production, the most important factor in *Arctodus'* extinction may have been a change in the regime of carcass abundance—namely, from a Pleistocene regime, characterized by weakly seasonal carcass availability, to a Holocene regime, characterized by strongly seasonal carcass availability. In my modeling, I suggested that increased herbivore diversity during the Pleistocene and the presence of monogastric herbivores with more conservative growth strategies (i.e., equids, proboscideans, and other non-ruminants) would have made carcasses readily available year-round in Beringia and the rest of North America. The abundance of small

ungulates with rapid turnover rates also would have produced more carcasses more consistently. In contrast, Holocene ecosystems are marked by seasonal spikes of carcass availability because of reduced herbivore diversity and the predominance of ruminants. Today, carcass spikes are a nutritional windfall for northern carnivores, but none can make a living completely from carrion.

Regardless of the proximal cause for its extinction, it must have been *Arctodus'* huge size that ultimately brought on its demise. An obligate carnivore the size of *Arctodus* would have required such a large mass of flesh at regular intervals that, despite its energy-conserving design, this bear's annual energetic budget could not be balanced in Holocene ecosystems of North America. Those large carnivores that did survive Pleistocene extinctions are antitheses to *Arctodus*. Wolves switch types and size of prey (small prey will have higher turnover rates), and their foraging unit—the pack—has a flexible “body size” that changes seasonally. Brown bears are the hallmark of dietary and ecological plasticity; they have the behavioral flexibility *Arctodus* probably lacked, and, perhaps most important, brown bears do not need to eat for more than half the year because they hibernate. It is not known whether short-faced bears could hibernate. I have suggested that it was unlikely (Matheus 1995), one reason being that winter and spring would be the most productive seasons for a carcass-dependent scavenger. In some ways, wolverines are like miniature short-faced bears in that they are the most focused of all extant carnivores on carrion resources. Yet, like the wolf, they do not require such large amounts of meat year-round. Most important, however, is their size—because they are so small, wolverines can get significant energy from both small and large carcasses. *Arctodus'* size made it dependent on carcasses of large mammals. The wolverine also is a capable predator, able to find it profitable to hunt prey in a variety of sizes, from ground squirrels to small caribou. While I will not claim that *Arctodus* never killed any of its food, this monograph has been devoted to making the point that it was not an adept predator and does not show signs of a carnivore that had evolved in a predatory niche. And unlike the wolverine, if *Arctodus* was a predator, its size dictates that it could not have gained any significant energetic benefit from hunting prey the size of a ground squirrel. Puma are the only solitary obligate large predators extant in northern North America, but their persistence also may relate mostly to their size. Like the wolf, they are able to use large and small prey items and can switch prey seasonally. The puma's ability to use a variety of broken terrain, from dense forest to badlands, gives it a flexibility *Arctodus* may have lacked, since it needed to be in environments where it could detect carrion. Indeed,

Arctodus' distribution indicates that it had a strong preference for open terrain (Harington 1973, Kurtén and Anderson 1980, Harris 1985).

In closing, I submit that if short-faced bears were predatory, and had a penchant for larger prey, then they should have persisted into the Holocene as hunters of the great bison herds inhabiting central North America. Of all late Quaternary carnivores, *Arctodus* would have been

best able to follow the bison herds because of its size and ability to travel long distances efficiently. Alas, *Arctodus'* inability to catch and kill bison meant it could not follow such a strategy. Today, wolves follow caribou herds in northern Alaska and Canada (Kuyt 1972, Stephenson and James 1982) but they do not wait for caribou to die, or for another predator to kill them. Instead, the wolf is built to both follow the caribou and to kill it. *Arctodus* was not.

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