

Functional trade-offs in the limb bones of dogs selected for running *versus* fighting

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Summary

The physical demands of rapid and economical running differ from the demands of fighting in ways that may prevent the simultaneous evolution of optimal performance in these two behaviors. Here, we test an hypothesis of functional trade-off in limb bones by measuring mechanical properties of limb bones in two breeds of domestic dog (*Canis lupus familiaris* L.) that have undergone intense artificial selection for running (greyhound) and fighting (pit bull) performance. The bones were loaded to fracture in three-point static bending. To correct for the effect of shear, we estimated the shear stress in the cross section and added energy due to shear stress to the tensile energy. The proximal limb bones of the pit bulls differed from those of the greyhounds in having relatively larger second moments of area of mid-diaphyseal cross sections and in having more circular cross-sectional shape. The pit bulls exhibited

lower stresses at yield, had lower elastic moduli and failed at much higher levels of work. The stiffness of the tissue of the humerus, radius, femur and tibia was 1.5–2.4-fold greater in the greyhounds than in the pit bulls. These bones from the pit bulls absorbed 1.9–2.6-fold more energy before failure than did those of the greyhounds. These differences between breeds were not observed in the long bones of the feet, metacarpals and metatarsals. Nevertheless, the results of this analysis suggest that selection for high-speed running is associated with the evolution of relatively stiff, brittle limb bones, whereas selection for fighting performance leads to the evolution of limb bones with relatively high resistance to failure.

Keywords: locomotion, aggression, bone mechanical properties, *Canis lupus familiaris*, greyhound, pit bull.

Introduction

Most characters are thought to serve multiple functions. If two functions impose conflicting demands on the same character, simultaneous optimization is impossible and a trade-off phenotype results (Maynard Smith et al., 1985; Gans, 1988; Lauder, 1991; Vanhooydonck et al., 2001; Van Damme et al., 2002). Two functions that may commonly result in such conflicts are terrestrial locomotion and fighting. Both locomotion and fighting are critical to survival and reproductive fitness in many species, but traits that make an individual good at fighting may, in many cases, limit locomotor performance and *vice versa*. Generally, this type of trade-off can be expected because rapid and economical terrestrial locomotion is dependent on long, gracile limbs and muscles that are specialized for the storage and recovery of elastic strain energy (Hildebrand and Goslow, 2001; Taylor, 1994), whereas specialization for fighting appears to be associated with short, stout limbs and muscles specialized for high force production. In a study comparing the architecture of limb muscles of a breed of domestic dog specialized for running with that of a breed specialized for fighting, we found that the running breed had relatively less muscle mass distally in their limbs, weaker

muscles in their forelimbs but stronger muscles in their hindlimbs, and a much greater capacity for elastic storage in their muscle–tendon systems (Pasi and Carrier, 2003). These observations are consistent with a trade-off in which specialization for running leads to a phenotype that is compromised for fighting whereas specialization for fighting negatively impacts locomotor ability.

Bones are adaptive structures that can vary in their mechanical properties (1) during an organism's lifetime, in response to changing developmental parameters and functional demands, (2) throughout an individual's body, due to varying functional requirements, and (3) among different members of a clade, associated with different life histories and environmental conditions (Currey, 1979; Currey and Pond, 1989; Biewener, 1990; Swartz et al., 1992; Carrier, 1996; Blob and Biewener, 1999; Heinrich et al., 1999; Blob and LaBarbera, 2001). Currey (1979) provided a dramatic illustration of the relationship between bone material properties and function with a comparison of red deer antler, cow femur and fin whale tympanic bulla. Of the three types of bone, antler was the least stiff but absorbed the most energy

before it failed, and cow femur resisted the greatest forces in bending. Currey suggested that these differences represent the need of antler to withstand large impact loads during male–male aggression and the need of limb bones to be stiff and strong to transmit muscular forces. This distinction between the mechanical properties of skeletal elements that function as weapons (i.e. antlers and tusks) *versus* those that function as limb elements has become well documented (Brear et al., 1993; Kitchener, 1991; Currey, 1987, 1989; Blob and LaBarbera, 2001; but see Zioupos et al., 1996). For example, axis deer have antlers that are composed of relatively stiff tissue (11.6 GPa; Kitchener, 1991), but the bone of their proximal limb elements is almost three times stiffer (31.6 GPa; Currey, 1999).

We wondered if similar differences might exist within limb bones of animals specialized for running *versus* those specialized for fighting. Although the limb bones of most species are unlikely to experience the level of impact loads that deer antlers are subjected to during fighting, many mammalian species fight by striking and grappling with their forelimbs. Fighting can be expected to load limb bones with maximal muscle moments and in directions that are highly variable and unpredictable. Furthermore, during grappling, bending and torsional moments on limb bones induced by an opponent might exceed those that the animal's own muscles could produce. Limbs are also targets of bites during fighting. Biting could fracture limb bones outright or induce failure from bending or torsion as the two animals struggle. Indeed, fractures of bones do occur when dogs fight. In a survey of 284 bone fractures in dogs admitted to a metropolitan small animal hospital over a 2-year period, fights were the third most frequent cause of fracture and accounted for 14% of the bone fractures that were due to causes other than encounters with automobiles, human feet and slamming doors (Phillips, 1979; Cook et al., 1997). Dog attacks also produce bone fractures in humans, occurring at a frequency of 0.4% of the nonfatal dog attack-related injuries treated in USA hospital emergency departments in 2001 (Gilchrist et al., 2003). By contrast, other than in racing greyhounds (discussed below), we were unable to find reference to failure of limb bones during running in dogs. Thus, there is reason to suspect that selection for fighting ability might result in limb bones that are more resistant to failure than the bones of animals specialized for running. Obviously, specialization for fighting cannot be driven as far in limb bones as it has in deer antlers because of the conflicting demands of locomotion on the limbs. Nevertheless, we suspected that the limb bones of animals specialized for fighting would have lower stiffness and a greater capacity for absorbing energy before failure than the limb bones of animals specialized for running.

To test these expectations, we compared the mechanical properties of limb bones in two breeds of domestic dog: greyhounds and pit bulls. Greyhounds have undergone intense artificial selection for high-speed running and anaerobic (burst) stamina. By contrast, pit bulls have been selected for physical combat with other dogs. Specifically, we predicted that, to

avoid failure during fighting, the limb bones of pit bulls would exhibit lower elastic moduli, lower yield and maximum stresses but higher maximum resistive forces and higher levels of work to fracture than the limb bones of greyhounds. By contrast, we expected that the limb bones of greyhounds would have smaller second moments of area relative to bone length and body mass to minimize the inertia of the bones and thereby reduce the energetic cost of high-speed running. Additionally, because the primary loading direction is relatively predictable during running but unpredictable in a fight, we expected that the limb bones of greyhounds would have less circular diaphyseal cross sections than the bones of pit bulls.

Materials and methods

Subjects

We used two breeds of domestic dogs (*Canis lupus familiaris* L.). The American pit bull terrier's ancestors were imported to the USA from the UK in the mid-1800s and were bred to be fighting dogs (Clark and Brace, 1995). A number of fighting breeds have been credited with the early development of pit bulls, including bull terriers, mastiffs and bull dogs. Following the outlawing of bull-baiting in England in 1835, this lineage of dogs was bred for dog–dog fighting. The origin of greyhounds can be traced to the Egyptians, who used them to hunt wolves, deer and wild boar (Clark and Brace, 1995). More recently, greyhounds have been bred primarily for racing, and the breed is recognized as the fastest domestic dog, capable of running at 70 km h⁻¹.

The cadavers used in this study were the same as those used in a previous study of the limb muscle of these two breeds (Pasi and Carrier, 2003). All the subjects were osteologically mature, with fused epiphyseal plates. The four greyhound cadavers were donated by the School of Veterinary Medicine at Colorado State University. All appeared to be healthy at the time of death, and dissection revealed no visible adipose tissue. Their eviscerated body mass ranged from 27.34 to 30.80 kg, with a mean \pm s.d. of 28.52 \pm 1.98 kg. The four pit bull cadavers used were animals that had been euthanized at local (Utah) animal shelters and were donated to the study. These dogs also appeared to be healthy at the time of death and they did not have visible accumulations of subcutaneous adipose tissue. The eviscerated body mass of the four pit bulls ranged from 20.91 to 27.87 kg, with a mean \pm s.d. of 23.61 \pm 3.73 kg.

Caveats and limitations

Although there are well-recognized limitations associated with two species (or breed) comparisons when studying adaptation (Garland and Adolph, 1994), the choice of greyhounds and pit bulls substantially reduces these problems. First, the types of selection on the two breeds are known and were very specific. In both cases, the financial incentives of the breeders have been high, driving the two breeds toward extreme specialization. Second, the environment in which the two breeds have evolved has been largely controlled. That is, both breeds have evolved as domesticated animals in which

humans provided their day-to-day care and survival. The ancestors of the subjects we studied grew up and lived in a temperature-controlled environment, their food and water was served to them and their mating opportunities were determined by their human owners. Thus, although differences between the two breeds may exist due to various founder effects or genetic drift, adaptive differences other than those due to selection for fighting or running are unlikely to exist. The study remains unreplicated, however, and that limits the confidence we can have in any conclusion.

A second limitation of the comparison used in this study is the lack of information about the ancestral configuration. We did not collect similar data from wolves, the species from which domestic dogs are derived. The lack of information about the ancestral state makes it impossible to say anything about the level of specialization in the two domestic breeds. It could be that any difference in bone properties observed between the two breeds is due entirely to selection on running performance in the greyhounds, with the pit bulls being very similar to the ancestral state. Alternatively, differences between the breeds could be entirely due to selection on fighting ability in pit bulls. In which case, the greyhounds would be similar to wolves. Without knowledge of the ancestral state, the level of specialization cannot be addressed. Nevertheless, knowledge of the ancestral state is not necessary to falsify the different hypotheses outlined above. If greyhounds and pit bulls do not differ in the predicted direction, a given hypothesis of conflict for specialization of running *versus* specialization for fighting would be falsified.

A final caveat that could compromise the interpretation of the results of this study is the possibility that the subjects of the two breeds experienced substantially different levels of 'functional adaptation' during their lives. Because the greyhound subjects came from the racing industry, we can be confident that their limb bones were exposed to the loading of high-speed running. The pit bull subjects, by contrast, were unlikely to have been exposed to frequent fighting that could result in functional adaptation. In most species, however, serious fighting is not a routine behavior and individuals prepare for true fighting through play (Pellis and Pellis, 1987; Pellis et al., 1993). Nevertheless, breed differences in functional adaptation could impact this analysis in unknown ways.

Mechanical testing

After they were euthanized, the subjects were sealed in plastic bags and frozen. For dissection, the subjects were thawed at room temperature. The humerus, radius, 4th metacarpal, femur, tibia, and 3rd metatarsal were dissected from one side of each dog and cleaned of all soft tissue. We chose to test the radius rather than the radius and ulna together, or just the ulna, because the dimensions of the radius, by itself, more closely approximate the shape of a beam. The bones were then stored in sealed plastic bags below 0°C until mechanical testing was performed. Before testing, the bones were thawed

at room temperature and placed in physiological saline at 25°C for 1–2 h.

The bones were removed from the saline and immediately tested to ensure negligible dehydration and temperature change. We used a servo-hydraulic material testing system (model 8500; Instron Corp., Canton, MA, USA) to load the bones in three-point static bending at a rate of 0.16 mm s⁻¹, producing fracture in 60–120 s. The loaded length of the bones included as much of the diaphysis as possible and so varied for each bone. Care was taken to orient the bones on the loading supports in a consistent manner, such that the load was applied perpendicular to the long axis of the bone and in the parasagittal (i.e. anterior–posterior) plane.

Bones were loaded until fracture occurred. This provided a measure of yield and fracture parameters. Yield represents the point at which the bone ceases to behave elastically and is difficult to determine precisely in bending tests. To calculate yield, we used the offset method (Turner, 1993), in which a line parallel to the linear portion of the stress–strain curve is calculated and then offset by a strain of 0.2%. Maximum load is the maximum resistance that the bone offers to loading. Fracture load is the force applied at the moment of failure (i.e. when fracture occurs) and is a measure of the strength of the bone as a whole. Yield and fracture stress were calculated from the relationship:

$$\text{Stress} = FLY(4I)^{-1}, \quad (1)$$

where F is yield or fracture force, L is the distance between supports (length of diaphysis), Y is the outer radius at load point, and I is the second moment of area at the site of loading (Turner, 1993).

The modulus of elasticity (E) is a measure of the stiffness of the bone. It was calculated from the relationship:

$$E = C_S F_y L^3 (48ID)^{-1}, \quad (2)$$

where F_y is the force at some deflection, D , at a low strain (prior to yield; i.e. F_y/D is the slope of the initial linear portion of the curve), L is the length of the loaded beam, and I is the second moment of area at the site of loading. Because the loaded length of the bones was less in the pit bulls than the greyhounds, and was in all cases less than is typically needed for application of simple beam theory (i.e. aspect ratio >15), the analysis was corrected for effects of shear stresses using the C_S term (see Eqn 4). To correct for shear, we first approximated shear stresses in the cross section of the beam by modifying methods used to evaluate shear in solid beams (Gere, 2001) to the geometry of a hollow beam. By using force balance within a hollow beam, the total shear stress (τ) on any radial cross section of the hollow beam was found to be:

$$\tau = F_y (r_1^2 + r_1 r_2 + r_2^2) \cos \theta / (6I), \quad (3)$$

where r_1 and r_2 are the inner and outer radii of the bone cylinder, respectively, and θ is the angle from the horizontal plane to the position of the radial cross section. These shear stresses are maximal, as expected, in the horizontal cross

section of the beam ($\theta=0^\circ$) and zero on the vertical cross section ($\theta=90^\circ$). We next equated the energy in the beam due to both normal stresses and the above shear stresses to the energy of deformation ($F_y D/2$) and found the correction term to be:

$$C_S = 1 + [8 E_{\text{mod}} (r_1^2 + r_1 r_2 + r_2^2)^2] / [3 G_{\text{mod}} L^2 (r_1^2 + r_2^2)]^{-1}, \quad (4)$$

where E_{mod} is the elastic modulus and G_{mod} is the shear modulus. We used values for E_{mod} and G_{mod} from human cortical bone (Martin and Burr, 1998) to evaluate C_S . Note that the correction only depends on the ratio $E_{\text{mod}}/G_{\text{mod}}$ for bone, and this ratio is fairly uniform among species of mammals: 2.74 for humans *versus* 2.85 for cows (Martin and Burr, 1998).

Thus, to correct for shear stress, the bones were modeled as hollow or thick-walled cylinders with an inner radius r_1 and an outer radius r_2 . Although this is an approximation of the bone shape, we believe it is reasonable for extracting shear correction. Taking into account actual cross sections and variations in cross sections along the bone would require numerical analysis and would be unlikely to change the results from any of the comparisons.

After mechanical testing, the broken ends of the bones were cut as near to the fracture as possible for dimensional analysis. To measure the second moment of area of the cross sections, we analyzed digital images of the cut cross sections with Optimas, version 6 software (Media Cybernetics, San Diego, CA, USA). Because the bones of the two breeds differ significantly in length, we calculated an index of shape that relates the second moment of area (I) of the bone cross section to a reference force moment:

$$\text{Shape index} = I (M_b L Y_{\text{md}})^{-1} \quad (5)$$

where I is the second moment of area of the mid-diaphysis, M_b is body mass, L is the length of the diaphysis, and Y_{md} is the outer radius at mid-diaphysis. Length of the diaphysis was measured between epiphyseal lines (estimated when not visible) on the cranial surface of the bone for the radius, metacarpal, femur and metatarsal and measured on the caudal surface of the bone for the humerus and tibia. High values of this index indicate a relatively large second moment of area for the bone's length and the animal's mass.

Lastly, we determined whether or not there were differences in the cross-sectional shape of the mid-diaphysis by calculating an index of circularity (Cornhill et al., 1980; Hueck, 2000) of the cross sections for the two bones that most closely approximated a circular cross section, the humerus and femur. The circularity index (CI) is defined as a dimensionless ratio of the total area contained within the periosteal perimeter at the mid-diaphysis (A) divided by the square of the periosteal perimeter (P):

$$CI = [A/(P^2)] 4\pi, \quad (6)$$

The ratio of area to perimeter-squared was normalized by 4π so that the ratio has a value of unity for a circle. This CI gives a value less than one for noncircular cross sections.

Statistics

Data were collected for 48 bones (six bones per dog, four dogs per breed, two breeds). To address whether or not there were differences between the breeds for a given bone (e.g. radius), we grouped the data by bone and checked for breed differences using unpaired t -tests with a sequential Bonferroni correction (Sokal and Rohlf, 1981). To address whether the breeds differed for each parameter (e.g. whether the modulus of elasticity was higher on average in the greyhound bones than in the pit bull bones), we used Fisher's combined probability test (Sokal and Rohlf, 1981), comparing the P -values of all six bones. A fiducial limit for significance of $P<0.05$ was chosen.

Results

Bone shape

Mass-specific second moment of area of the mid-diaphysis did not differ between the two breeds for the four proximal bones: humerus, radius, femur and tibia (Table 1). This metric, however, was substantially larger for the two distal bones, metacarpal and metatarsal, in the greyhounds than in the pit bulls.

Diaphyseal length was 1.48 (± 0.02) times greater on average in the greyhounds than in the pit bulls. This difference made a functional comparison of mid-shaft diameter or second moment of area inappropriate for the two breeds because of the effect that bone length has on bending moment. Hence, we compared the two breeds with a shape index (Eqn 5) that relates the second moment of area of the bone's cross section to a reference moment. High values of this index indicate relatively large mid-diaphyseal second moments of area for the bone's length and the animal's mass. For three of the proximal limb bones (humerus, radius and femur), the pit bulls had significantly higher mid-diaphyseal second moments of area for their length than did the greyhounds (Table 1). The shape index did not differ between the two breeds for the distal bones (metacarpal and metatarsal). Nevertheless, using the P -values from all six bones, the shape indexes were higher in the pit bulls than in the greyhounds ($P<0.005$; Fisher's combined probability).

The two breeds also differed in the cross-sectional shape of the proximal limb bones (Fig. 1). The circularity indexes for the humeri and femurs of the pit bulls were closer to unity, indicating a more circular cross section than was the case in the greyhounds ($P<0.05$; unpaired t -test).

Material properties

Elastic modulus was higher in the greyhounds than in the pit bulls in the four proximal limb bones: humerus, radius, femur and tibia (Table 2). The bones of the foot, metacarpal and metatarsal, also exhibited a trend of greater stiffness in the greyhounds but the difference between the two breeds was not significant. In the greyhounds, the mean and S.D. of the elastic modulus of the six limb bones was 10.4 ± 3.6 GPa. The mean elastic modulus of the six bones of the pit bulls was 35% lower (6.7 ± 2.2 GPa). Comparing all six bones, the difference

Table 1. Cross-sectional shape

	Greyhound		Pit bull		<i>P</i>
	Mean	± S.E.M.	Mean	± S.E.M.	
Second moment of area (m ⁴ kg ⁻¹)*					
Humerus	1.845×10 ⁻¹⁰	5.77×10 ⁻¹¹	2.48×10 ⁻¹⁰	3.36×10 ⁻¹¹	0.67
Radius	2.99×10 ⁻¹¹	3.11×10 ⁻¹²	3.83×10 ⁻¹¹	8.27×10 ⁻¹²	0.38
Metacarpal	9.23×10 ⁻¹²	1.73×10 ⁻¹²	4.27×10 ⁻¹²	4.93×10 ⁻¹³	0.03
Femur	1.38×10 ⁻¹⁰	9.5×10 ⁻¹²	1.49×10 ⁻¹⁰	3.35×10 ⁻¹¹	0.77
Tibia	1.17×10 ⁻¹⁰	8.83×10 ⁻¹²	9.21×10 ⁻¹¹	1.34×10 ⁻¹¹	0.17
Metatarsal	1.47×10 ⁻¹¹	2.66×10 ⁻¹²	5.51×10 ⁻¹²	6.82×10 ⁻¹³	0.02
Shape index (m ² N ⁻¹)					
Humerus	1.27×10 ⁻⁸	4.11×10 ⁻⁹	2.61×10 ⁻⁸	4.73×10 ⁻⁹	0.038
Radius	3.69×10 ⁻⁹	3.72×10 ⁻¹⁰	6.37×10 ⁻⁹	1.20×10 ⁻⁹	0.039
Metacarpal	4.36×10 ⁻⁹	6.80×10 ⁻¹⁰	4.41×10 ⁻⁹	3.03×10 ⁻¹⁰	0.476
Femur	9.92×10 ⁻⁹	8.02×10 ⁻¹⁰	1.74×10 ⁻⁸	3.32×10 ⁻⁹	0.036
Tibia	8.79×10 ⁻⁹	4.51×10 ⁻¹⁰	1.20×10 ⁻⁸	1.70×10 ⁻⁹	0.06
Metatarsal	4.58×10 ⁻⁹	7.62×10 ⁻¹⁰	4.10×10 ⁻⁹	5.95×10 ⁻¹⁰	0.5
Fisher's combined probability <0.005					

P-values are from unpaired *t*-tests.
*Second moment of area per kilogram body mass.

between the breeds was significant ($P<0.001$; Fisher's combined probability).

The limb bones of greyhounds sustained higher stresses at yield than the limb bones of pit bulls ($P<0.025$; Fisher's combined probability; Table 2). The maximum stress sustained by the bones, however, was not different between the two breeds.

Differences were observed in the material properties of the

bones of the forelimb *versus* the hindlimb, as well as among the bones within each limb (Table 2). Comparing serially homologous elements between the fore- and hindlimb in both breeds, the bones of the hindlimb had higher elastic moduli than those of the forelimb ($P=0.046$; paired *t*-test). Of the three skeletal elements within each limb, the central elements (i.e. radius and tibia) had higher elastic moduli ($P=0.006$; unpaired *t*-test) and higher yield stresses ($P=0.004$, unpaired *t*-test) than

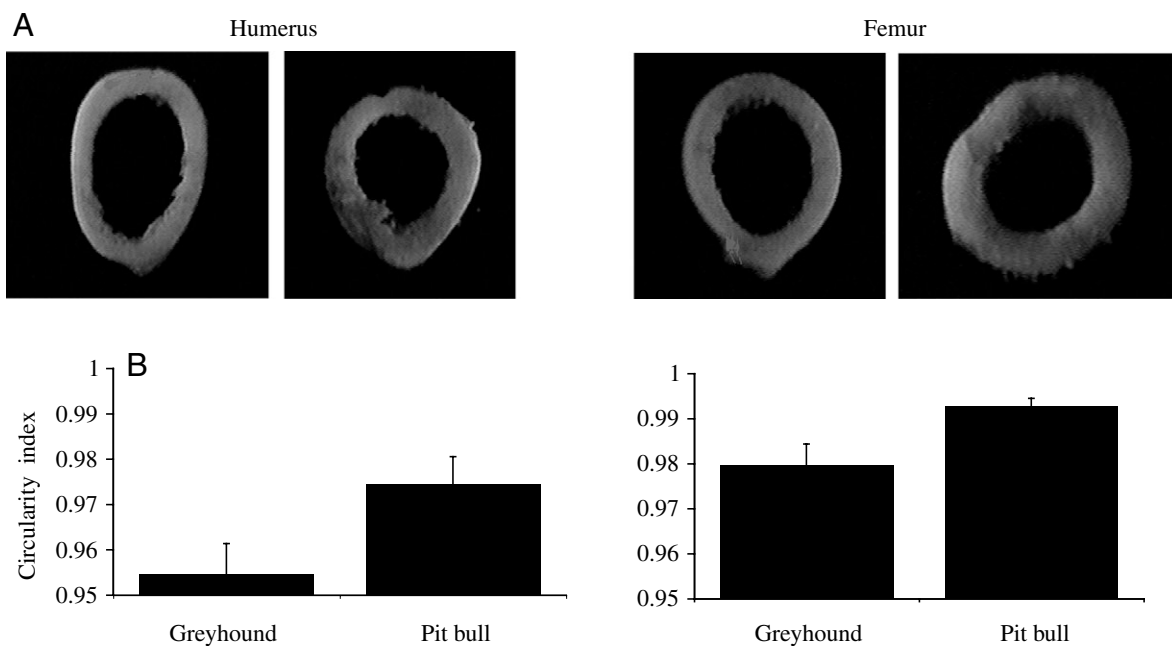


Fig. 1. Mid-shaft cross-sectional shape of the humeri and femurs of greyhounds and pit bulls. (A) Comparison of representative mid-shaft cross sections of the humeri and femurs from a greyhound and a pit bull. In both cases, the greyhound bone is on the left. The anterior-posterior axis is oriented vertically, with anterior at the top. (B) Mean \pm S.E.M. of circularity index (*CI*) for the mid-shaft cross sections of the humeri and femurs of four greyhounds and four pit bulls. The *CI* is 1 for a circular cross section and is <1 for noncircular cross sections.

Table 2. *Material properties of the bone*

	Greyhound	Pit bull	<i>P</i>
Elastic modulus (GPa)			
Humerus	7.70±0.65	3.22±0.34	0.0014*
Radius	15.07±0.47	8.64±0.68	0.0001*
Metacarpal	6.62±0.85	5.52±0.40	0.1461
Femur	11.22±1.18	6.77±0.62	0.0077*
Tibia	14.05±0.85	9.29±0.44	0.0012*
Metatarsal	7.51±0.31	6.97±0.91	0.2959
Fisher's combined probability <0.001			
Yield stress (MPa)			
Humerus	121.03±21.10	103.63±28.75	0.591
Radius	202.36±8.12	168.39±10.86	0.046
Metacarpal	149.34±11.44	139.73±7.74	0.513
Femur	166.50±11.26	119.56±10.14	0.021
Tibia	177.94±3.22	163.31±2.90	0.015
Metatarsal	157.89±7.40	147.14±12.82	0.495
Fisher's combined probability <0.025			
Max stress (MPa)			
Humerus	147.94±5.52	161.02±35.39	0.728
Radius	235.26±9.43	190.78±9.93	0.018
Metacarpal	184.93±10.69	195.77±12.55	0.536
Femur	172.70±11.68	146.22±10.34	0.14
Tibia	193.02±6.10	177.84±3.89	0.081
Metatarsal	189.77±6.67	191.91±18.13	0.915
Fisher's combined probability <0.10			

Values are means ± S.E.M. *P*-values are from unpaired *t*-tests.

*Significant after sequential Bonferroni correction.

the proximal and distal elements. These intra-limb patterns were observed in both breeds.

Whole bone properties

The mass-specific maximum resistive force that the bones sustained during three-point bending was not different between the breeds ($P>0.4$; Fisher's combined probability; Table 3). There was a clear trend of higher maximum resistive force among the four proximal bones in the pit bulls but none of these bones exhibited a significant difference under the constraint of a sequential Bonferroni test.

The mass-specific energy absorbed (i.e. work) at fracture was greater in the pit bulls ($P<0.001$; Fisher's combined probability; Table 3). This was the most dramatic difference observed between the two breeds. The work to fracture was on average 2.2-fold greater in the pit bulls than in the greyhounds. All four of the proximal bones exhibited a significant difference (Table 3). The work to fracture the long bones of the feet, however, did not differ between the two breeds.

Discussion

The trade-off we are proposing is based on our understanding of limb characteristics that enhance rapid and economical running *versus* those that can be expected to facilitate fighting performance. Among tetrapods, rapid and economical running

is associated with long, gracile limb bones. Long limbs reduce the number of steps that an animal must take to cover a given distance (Hildebrand and Goslow, 2001), and reduction of the mass of limb bones, particularly the distal elements, decreases the energy required to swing the limbs back and forth in each step (Hildebrand and Hurley, 1985; Steudel, 1991). Because the energy required to oscillate the limbs increases dramatically with running speed (Cavagna and Kaneko, 1977; Fedak et al., 1982; Willems et al., 1995), selection for reduction of limb mass is expected to be most pronounced in those species that are the fastest runners. Indeed, relatively long and slender limbs have evolved repeatedly in those lineages that have become specialized for high speed and economical running (Pough et al., 1999). The observations that greyhounds have relatively less muscle mass distally in their limbs and relatively less muscle strength in their forelimbs than pit bulls (Pasi and Carrier, 2003) suggests that selection for high-speed running can produce cursorial specialization in domestic dogs. Much less is known about the characters that enhance fighting ability, but strength and agility are generally thought to be important in most types of fighting. During fighting, an individual must generate large limb forces to accelerate its body and to manipulate an opponent. Additionally, the direction of force application by limbs is likely to be much more variable during fighting than during running. Thus, stout bones with a circular cross section that can transfer large muscle forces over a large range of

Table 3. Whole bone properties

	Greyhound	Pit bull	<i>P</i>
Work to fracture (N m ⁻¹ kg ⁻¹)			
Humerus	0.374±0.068	0.908±0.110	0.006*
Radius	0.315±0.043	0.588±0.022	0.001*
Metacarpal	0.071±0.019	0.106±0.016	0.222
Femur	0.326±0.078	0.837±0.103	0.008*
Tibia	0.305±0.044	0.643±0.044	0.002*
Metatarsal	0.118±0.016	0.125±0.021	0.813
Fisher's combined probability <0.001			
Max force (kN kg ⁻¹)			
Humerus	0.088±0.007	0.147±0.018	0.022
Radius	0.035±0.005	0.049±0.012	0.317
Metacarpal	0.032±0.006	0.032±0.004	0.914
Femur	0.067±0.004	0.098±0.016	0.106
Tibia	0.067±0.005	0.084±0.013	0.279
Metatarsal	0.034±0.006	0.031±0.007	0.761
Fisher's combined probability >0.4			

Values are means ± S.E.M. *P*-values are from unpaired *t*-tests.

*Significant after sequential Bonferroni correction.

motion can be expected to enhance fighting performance. As argued above, high resistance to bone fracture is also expected to improve fighting ability.

Based on these expected differences in specialization for running *versus* fighting, we predicted that, under three-point static bending, the limb bones of greyhounds would exhibit higher elastic moduli, higher yield and maximum stresses, lower levels of work to fracture and lower maximum resistive force than the bones of pit bulls. We also expected that the limb bones of greyhounds would have smaller second moments of area relative to bone length and body mass and less circular diaphyseal cross sections than the bones of pit bulls. We found that elastic moduli and yield stresses were higher in the greyhounds whereas the work to fracture was much higher in the pit bulls. On average, the elastic modulus was 60% greater, yield stress was 17% greater and the work to fracture was 57% less in the greyhound bones than in the pit bull bones. The second moments of area relative to bone length and body mass were higher in the pit bulls, and the diaphyseal cross-sectional shape of the humerus and femur was more circular in the pit bulls. These observations are consistent with expectations based on specialization for running *versus* fighting.

Two of the measured variables, however, did not fit our expectations. No significant differences between the breeds were found in maximum stress and maximum resistive force. Peak loads and stresses in most materials are highly dependent on material flaws that facilitate crack growth. Thus, the lack of significant difference in these variables is not surprising. In contrast to failure stress, which represents flaw-dominated crack growth, the onset of yielding is typically a bulk process associated with shear deformation rather than crack growth. Yield stresses are therefore less variable than flaw-dominated strength properties, making them a more reliable metric.

The long bones of the feet, metacarpal and metatarsal,

presented a consistent contrast to the more proximal limb bones. Although the long bones of the feet differed between breeds in mid-diaphyseal second moment of area (Table 1), they did not differ in the other parameters we measured. In greyhounds, the metacarpal and metatarsal tended to have low elastic moduli and yield stresses relative to the other greyhound bones. It is possible that loading of the skeletal elements of the feet during high-speed running in greyhounds roughly equals that which typically occurs in dogs during fighting, such that these bones in greyhounds need to have a high capacity to absorb energy. Indeed, the highest rates of skeletal injury in greyhound during races occur in the bones of the feet rather than the more proximal limb bones (Prole, 1976; Sicard et al., 1999; Johnson et al., 2000). Alternatively, the demands of high-speed running may constrain the mechanical and shape properties of the distal elements to be lightly built for efficient locomotion regardless of the specialization of the more proximal elements. The similarity might also be due to a simple lack of genetic variation in the two breeds for mechanical traits in these two bones. Whatever the explanation, the mechanical properties of the long bones of the feet appear not to differ in these two breeds.

The most dramatic differences we observed between the two breeds, in terms of both amplitude and statistical significance, were the higher elastic moduli of the greyhound bones and the higher work to fracture of the pit bull bones. Our analysis did not address which aspects of the bone material account for these differences between the breeds, and this issue warrants future investigation. Nevertheless, differences observed in this study mirror those that Currey (1979) found between the femur of a cow and the antler of a deer. He suggested that because male deer crash their antlers together with considerable force and speed, they are loaded in impact and should therefore have a high work to fracture. By contrast, he suggested that limb

bones need to be stiff to function effectively as levers and struts. Currey acknowledged that limb bones must also bear large stresses and be resistant to impact but that, in general, the danger of impacts is less in limb bones than in antlers because limb bones are protected by muscle and skin. Although this is true, the results of this analysis suggest that the physical demands of high-speed running influence the evolution of limb bones differently than do the physical demands of fighting.

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