

Functional trade-offs in the limb muscles of dogs selected for running vs. fighting

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Keywords:

aggression;
elastic storage;
limb mechanics;
locomotion;
mechanical constraint.

Abstract

The physical demands of rapid and economical running differ from those of physical fighting such that functional trade-offs may prevent simultaneous evolution of optimal performance in both behaviours. Here we test three hypotheses of functional trade-off by measuring determinants of limb musculoskeletal function in two breeds of domestic dogs that have undergone intense artificial selection for running (Greyhound) or fighting performance (Pit Bull). We found that Greyhounds differ from Pit Bulls in having relatively less muscle mass distally in their limbs, weaker muscles in their forelimbs than their hindlimbs, and a much greater capacity for elastic storage in the in-series tendons of the extensor muscles of their ankle joints. These observations are consistent with the hypothesis that specialization for rapid or economical running can limit fighting performance and vice versa. We suggest that functional trade-offs that prevent simultaneous evolution of optimal performance in both locomotor and fighting abilities are widespread taxonomically.

Introduction

The varied demands of survival and reproduction often require compromises in the design of organisms (Maynard Smith *et al.*, 1985; Gans, 1988; Lauder, 1991). One set of functional trade-offs that may be particularly important in the evolution of phenotypic diversity are the compromises entailed by the requirements of locomotion vs. the requirements of fighting. Both locomotion and fighting are critical to survival and reproductive fitness in many species, but characters that make an individual good at fighting may, in many cases, limit locomotor performance and vice versa. For example, among apes, sexual dimorphism in body size and male–male fighting are most dramatic in gorillas (Nowak & Paradiso, 1983). Large body size allows dominant male gorillas to defend multifemale groups against lone males interested in attracting the females and killing the infants (Fossey, 1983, 1984; Watts, 1989). Large size, however, severely limits the ability of male gorillas to climb trees (Schaller, 1963). In contrast, both male and female

gibbons brachiate with spectacular grace and agility. Gibbons exhibit little or no sexual dimorphism in body size and mate in monogamous pairs (Nowak & Paradiso, 1983; MacKinnon & MacKinnon, 1984). Both male and female gibbons participate in defence of territory and aggressive encounters rarely involve physical contact (Preuschoft *et al.*, 1984; Mitani, 1987). In this comparison, locomotion appears to be constrained in the fighting specialist whereas fighting ability appears to be limited in the locomotor specialist.

Possibly the most striking example of a trade-off between fighting and locomotor specialization is seen in species of fig wasps (Hamilton, 1979). Male winglessness and lethal fighting behaviour are common in species of fig wasps in which aggregations of females occur. The absence of wings is thought to improve mobility and therefore fighting ability in the tight quarters of figs in which the lethal battles are waged. In contrast, among fig wasp species in which population density is low, such that males must travel to find females, males are generally fully winged. These examples of apes and fig wasps illustrate anatomical and behavioural differences between closely related species that appear to be the result of differential specialization for locomotor vs. fighting ability.

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The mechanics of running in terrestrial tetrapods are likely to pose substantial trade-offs to fighting ability. In particular, the distribution and contractile performance of limb muscles are characters in which important differences between running specialists vs. fighting specialists can be expected. In this case, the hypothesized trade-off is between the design of limb muscles that facilitates economical and/or rapid transport vs. muscle design that provides the high force and power production needed for high agility, maintenance of balance and manipulating opponents.

This study attempts to test three hypotheses of difference between the limb muscles of runners vs. fighters. First, the rotational inertia of oscillating limbs (Cavagna & Kaneko, 1977; Fedak *et al.*, 1982; Willems *et al.*, 1995) leads to the expectation that animals specialized for high speed running will have relatively less muscle mass in their distal limbs (Hildebrand & Hurley, 1985; Steudel, 1991). In contrast, we expect the distal limbs of animals specialized for fighting to be well muscled to allow the production of large forces and high power for agility, balance and opponent manipulation.

Secondly, elastic storage and recovery of strain energy in the tendons of distal limb muscles is thought to greatly enhance the economy of transport during both low and high speed running (Cavagna *et al.*, 1964; Dawson & Taylor, 1973; Alexander, 1984; Roberts *et al.*, 1997; Biewener, 1998). For this reason we expect animals specialized for distance and/or high speed running to have a high capacity for elastic storage. In contrast, long stretchy tendons in series with extensor muscles would likely pose a handicap for any animal attempting to overpower an opponent during physical combat. Hence, we expect animals specialized for fighting to have relatively limited abilities to utilize elastic storage during running.

A third predicted difference between runners and fighters involves the distribution of extensor muscle strength in the fore vs. the hindlimbs. We expect animals specialized for running to have less muscle strength in their forelimbs than in their hindlimbs. This hypothesis emerges from two observations. First, there is a division of labour in the limbs in which the forelimbs of running animals play a greater role in deceleration and hindlimbs play a greater role in acceleration (Cruse, 1976; Cavagna *et al.*, 1977; Jayes & Alexander, 1978; Heglund *et al.*, 1982; Blickhan & Full, 1987; Full *et al.*, 1991). Secondly, active skeletal muscle generates much greater force when it is stretched (eccentric contraction) than when it shortens (Katz, 1939). Because the extensor muscles of the limbs must actively stretch to absorb energy during deceleration, but must actively shorten to produce acceleration, less muscle strength is expected in the forelimbs than in the hindlimbs of running specialists. In contrast, the strength of extensor muscles of the forelimbs of animals specialized for fighting can be expected to be as great or greater than that of the hindlimbs

because forelimb strength is needed to manipulate an opponent and is essential for rapid turning and agility.

To test these hypotheses of muscle specialization for running vs. fighting performance, we compare anatomical determinants of muscle function in two breeds of domestic dogs, Greyhounds and Pit Bulls. Although there are well recognized limitations associated with two species (or breed) comparisons when studying adaptation (Garland & Adolph, 1994; Garland, 2002), the choice of Greyhounds and Pit Bulls ameliorate the problems in substantial ways. First, the types of selection on the two breeds are known and were very specific. Greyhounds have undergone intense artificial selection for maximum running speed and anaerobic (burst) stamina. In contrast, Pit Bulls have been selected for physical combat with other dogs. In both cases, the financial incentives of the breeders have been high, driving the two breeds towards extreme specialization. Secondly, 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 all 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 genetic drift, adaptive differences other than those due to selection for fighting or running are unlikely to exist. In summary, the analysis used in this study represents an unreplicated selection experiment. But it is a selection experiment that has potential to falsify the three hypotheses mentioned above and one that may provide additional insight into the nature of functional trade-offs between running and fighting.

Materials and methods

Subjects

We used two breeds of domestic dogs, *Canis familiaris*, that have undergone intense artificial selection for very different functions. The ancestors of the American Pit Bull Terrier were imported to the United States from the British Isles in the mid-1800s and were bred to be fighting dogs (Clark & Brace, 1995). A number of fighting breeds have been credited with the early development of Pit Bulls, including Bull Terriers, Mastiffs and Bull Dogs. Since the outlawing of bull-baiting in England in 1835, this lineage of dogs has been 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 & 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 four Greyhound cadavers used in this study 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 and SD of 28.52 ± 1.98 kg. The five Pit Bull cadavers used were animals that had been killed at local (Utah) animal shelters and were donated to the study. These dogs also appeared to be healthy at the time of death. One of the five had a slight accumulation of subcutaneous adipose tissue. The eviscerated body mass of the five Pit Bulls ranged from 20.91 to 27.87 kg, with a mean and SD of 23.61 ± 3.73 kg. Dissection and analysis were performed on fresh, nonpreserved tissue.

Proximal to distal distribution of muscle mass in the limbs

We restricted this analysis to the muscles that have the greatest influence on the rotational inertia of the limb during running, namely those that are associated with the stylopodia (humerus and femur) and the zeugopodia (radius and ulna, and tibia and fibula). The proximal to distal distribution of muscle mass in the forelimbs and hindlimbs of the two breeds was addressed in two comparisons. We measured the percentage of the total mass of the stylopodia and zeugopodia muscles constituted by the muscles of the zeugopodium [i.e. all muscles located below the elbow (forelimb) and below the knee (hindlimb)]. We also measured the percentage of the total mass of the stylopodia and zeugopodia *extensor* muscles constituted by the *extensor* muscles of the zeugopodium (i.e. extensor muscles distal to the elbow and knee). The muscles included in these two analyses are listed in Table 1. The belly of each muscle was dissected free of its in-series tendons and weighed.

Strength of fore- and hind-limb extensor muscles

To access the relative strength of the fore- and hind-limb extensor muscles in the two breeds we compared the cross-sectional area of the extensor muscles of the wrist vs. ankle joints and the elbow vs. knee joints. The physiological cross-sectional area of a muscle provides a reliable estimate of its capacity to generate force (Ker *et al.*, 1988). The muscles included in this analysis are listed in Table 2. To calculate the cross-sectional area of a muscle we followed the methods of Ker *et al.* (1988). Briefly, we measured the mass and average fascicle length of the muscle, assumed a tissue density of 1.06 g cm^{-3} (Mendez & Keys, 1960) and then calculated cross-sectional area from the equation:

$$\text{CSA}_m = m_m \cdot (d_m \cdot l_f)^{-1},$$

where CSA_m is the cross-sectional area, m_m is the mass, d_m is the density and l_f is the fascicle length of the muscle. Fascicle length was determined by measuring the distance parallel to the fibres between sites of fascicle attachment

Table 1 Muscles included in the analyses of proximal to distal distribution of muscle mass.

	Forelimb	Hindlimb
Proximal	Triceps (all heads)*	Biceps femoris
	Biceps	Semitendinosus
	Brachialis	Semimembranosus
		Tibial head
		Lateral head
		Sartorius
		Cranial head
		Caudal head
		Gracilis
		Adductor
		Rectus femoris*
		All Vasti*
Distal	Extensor carpi radialis	Cranial tibialis
	Common digital extensor	Long digital extensor
	Ulnaris lateralis	Peroneus longus
	Flexor carpi ulnaris*	Gastrocnemius*
	Ulnar head	Medial head
	Humeral head	Lateral head
	Flexor carpi radialis*	Superficial digital flexor*
	Superficial digital flexor*	Deep digital flexor*
	Deep digital flexor*	Lateral head
		Medial head

*Muscles used in the analysis of the proximal to distal distribution of extensor muscles.

Table 2 Muscles included in the analysis of the strength of the extensor muscles of the fore- and hind-limbs.

Wrist	Elbow	Ankle	Knee
Flexor carpi radialis	Triceps	Gastrocnemius	Rectus femoris
Superficial digital flexor	Long head	Superficial digital flexor	Vastus lateralis
Flexor carpi ulnaris	Accessory head		Vastus medialis
Deep digital flexor	Lateral head		Vastus intermedialis
	Medial head		

on aponeuroses or tendons. The cross-sectional areas of the synergists acting on a joint were then summed and divided by the eviscerated mass of the dog to yield the mass specific cross-sectional area of the extensor muscles at each of the four joints.

Potential for storage and recovery of elastic strain energy at the ankle joint

To gain an estimate of the capacity of the two breeds to store and recover elastic strain energy we analysed the extensor muscle-tendon systems of the ankle. We used the measures of muscle cross-sectional area to estimate the forces that the muscles could produce, and the length and cross-sectional area of the in-series tendons to estimate the strain energy that these muscle forces could store in the tendons. Muscle cross-sectional area of the gastrocnemius and superficial digital flexor muscles were

measured as described above. Muscle force was estimated from the equation:

$$F_m = F_i \cdot \text{CSA}_m \cdot \cos(A_p),$$

where F_i is the maximum isometric force of the muscle (assumed to be 0.3 MPa, Ker *et al.*, 1988) and A_p is the pennation angle of the muscle.

Length of the in-series tendons was measured from the point of insertion to the start of the muscle belly (i.e. we measured the tendon distal to the muscle belly). Although aponeuroses within muscle bellies also store elastic energy (Roberts *et al.*, 1997), it is not possible to estimate the amount of energy storage in the aponeuroses of a fully activated muscle. Thus, we used a measure of the distal tendon length and our estimate of potential for elastic storage applies to the in-series (distal) tendons only. For the sake of comparison, we assumed that any difference in the potential for elastic storage in the in-series tendons would be proportional to the difference in the potential for elastic storage in the aponeuroses of the muscle bellies.

Cross-sectional area of each tendon was determined from the equation

$$\text{CSA}_t = m_t \cdot (d_t \cdot l_t)^{-1},$$

where m_t is the mass of the tendon, d_t is the density of tendon and l_t is the length of the tendon. We assumed that the density of the tendons was 1.120 g cm^{-3} (Ker, 1981).

To calculate the amount of strain (S_t) a muscle could induce in its tendon we assumed that the tendon followed Hooke's law over the range of force its muscle could exert and that the tendon had an elastic modulus (E_t) of 1500 MPa (Ker *et al.*, 1988). We then calculated the strain of the tendon from the equation:

$$S_t = l_t \cdot ((F_m \cdot \text{CSA}_t^{-1}) \cdot E_t^{-1})$$

The potential for each muscle–tendon system to store and release elastic strain energy (W_{mt}) was calculated as:

$$W_{mt} = 0.5 \cdot F_m \cdot S_t.$$

Statistical analysis

Testing of differences between Greyhounds and Pit Bulls was assessed using one-tailed Student's *t*-tests. One-tailed tests were used because we had specific predictions for the direction of difference between the breeds before we began the investigation (see Introduction). All results are presented as mean \pm 1 SEM.

Results

The proximal to distal distribution of muscle mass differed in the two breeds. The Greyhounds had a smaller percentage of appendicular muscle mass in their distal limbs than did the Pit Bulls. Of the total muscle mass of

the forelimb, $22.6 \pm 0.7\%$ was below the elbow in Greyhounds compared with $27.5 \pm 0.6\%$ below the elbow in Pit Bulls ($t_7 = 5.311$, $P < 0.001$). In the hindlimb, $12.4 \pm 0.3\%$ of the muscle mass was distal to the knee in Greyhounds compared with $15.7 \pm 0.6\%$ distal to the knee in Pit Bulls ($t_7 = 4.323$, $P < 0.005$). The same pattern emerged when the comparison was restricted to the extensor muscles of the limb joints. The mass of the wrist and digit extensors was $18.5 \pm 0.9\%$ of the total forelimb extensor muscle mass in Greyhounds vs. $23.0 \pm 0.5\%$ in Pit Bulls ($t_7 = 4.810$, $P < 0.001$). Similarly, the mass of the ankle and digit extensors was $31.1 \pm 0.6\%$ of the total hindlimb extensor muscle mass in Greyhounds compared with $34.6 \pm 1.3\%$ in Pit Bulls ($t_7 = 2.252$, $P < 0.05$). Hence, distal muscle mass constituted a significantly smaller portion of total limb muscle mass in the Greyhounds than in the Pit Bulls.

The relative strength of the fore- and hind-limb extensor muscles differed between the two breeds. In the Greyhounds, the average mass specific cross-sectional area of the elbow extensor muscles ($2.11 \pm 0.05 \text{ cm}^2 \text{ kg}^{-1}$) was 21% less (Paired *t*-test, $t_3 = 4.054$, $P < 0.05$) than the average cross-sectional area of the knee extensors ($2.56 \pm 0.12 \text{ cm}^2 \text{ kg}^{-1}$). In contrast, in the Pit Bulls the average mass specific cross-sectional area of elbow extensors ($2.32 \pm 0.05 \text{ cm}^2 \text{ kg}^{-1}$) was 11% greater ($t_4 = 1.758$, $P = 0.077$) than the average cross-sectional area of the knee extensors ($2.08 \pm 0.09 \text{ cm}^2 \text{ kg}^{-1}$). The extensors of the wrist and ankle joints exhibited a similar pattern. In the Greyhounds, the average mass specific cross-sectional area of the wrist extensor muscles ($1.98 \pm 0.13 \text{ cm}^2 \text{ kg}^{-1}$) was 29% less ($t_3 = 3.878$, $P < 0.05$) than the average cross-sectional area of the ankle extensors ($2.55 \pm 0.03 \text{ cm}^2 \text{ kg}^{-1}$). In contrast, in the Pit Bulls the average cross-sectional area of wrist extensors ($2.20 \pm 0.13 \text{ cm}^2 \text{ kg}^{-1}$) was not significantly different ($t_4 = 0.211$, n.s.) from the average cross-sectional area of the ankle extensors ($2.17 \pm 0.08 \text{ cm}^2 \text{ kg}^{-1}$). Hence, in our sample of Greyhounds the extensor muscles of the hindlimb had a greater cross-sectional area than the serially homologous extensor muscles of the forelimb. The Pit Bulls exhibited the opposite pattern, greater or equal extensor muscle cross-sectional area in the forelimbs than in the hindlimbs.

The two breeds differed by more than two-fold in our estimate of potential to store and recover elastic strain energy in the in-series tendons of the extensor muscle–tendon systems of the ankle joint. The average potential for elastic work was $0.223 \pm 0.018 \text{ J kg}^{-1}$ in the Greyhounds and $0.095 \pm 0.013 \text{ J kg}^{-1}$ in the Pit Bulls. These estimates of elastic work were based on estimated muscle force from measurements of muscle cross-sectional area, estimated in-series tendon stress from the muscle force and measurements of tendon cross-sectional area, and estimated tendon stretch from tendon stress and measurements of tendon length. Of these variables, only the

	Muscle area (cm ² kg ⁻¹)		Pennation angle (°)	
	GH	PB	GH	PB
M. Gastrocnemius	0.67 ± 0.08	0.56 ± 0.04	27.2 ± 1.0	24.8 ± 2.1
L. Gastrocnemius	0.72 ± 0.01	0.64 ± 0.07	23.7 ± 1.4	24.4 ± 0.9
Superficial digital flexor	1.16 ± 0.05	0.97 ± 0.08	27.2 ± 0.7	29.4 ± 2.4
	Tendon length (cm kg ⁻¹)		Tendon cross-sec. area (cm ² kg ⁻¹)	
	GH	PB	GH	PB
Gastrocnemius	0.48 ± 0.03	0.37 ± 0.01*	0.0055 ± 0.0006	0.0065 ± 0.0004
Superficial digital flexor	1.06 ± 0.04	0.91 ± 0.03*	0.0094 ± 0.0007	0.0107 ± 0.0007

*Mean of breeds significantly different. $P < 0.05$, Student's *t*-test.

length of the tendons was found to be significantly different between the two breeds (Table 3). The in-series portion of the gastrocnemius and superficial digital flexor tendons were on average 30 and 16% longer, respectively, in the Greyhounds than in the Pit Bulls. In contrast, although there was a trend towards greater muscle cross-sectional area in the Greyhounds and greater tendon cross-sectional area in the Pit Bulls, these variables were not significantly different between the two breeds. Nevertheless, when the potential for elastic work was calculated for each dog from these variables the difference between the two breeds was highly significant ($t_7 = 6.012$, $P < 0.001$).

Discussion

Limitations of the study

This study required a number of assumptions. First, we assumed that differences in the anatomical determinants of muscle function we measured have a significant impact on the fighting and running performance of the two breeds. Although this may not be true, our understanding of muscle physiology gives us confidence that the anatomical differences observed in this study do produce performance differences in the two breeds. The effect of distal limb mass on the mechanical work of running (Cavagna & Kaneko, 1977; Hildebrand & Hurley, 1985), the division of labour between fore- and hind-limbs during running (Cruse, 1976; Cavagna *et al.*, 1977; Jayes & Alexander, 1978), the force consequences of eccentric vs. concentric muscle contractions (Katz, 1939), and the energetic consequences of elastic storage (Cavagna *et al.*, 1964; Dawson & Taylor, 1973; Alexander, 1984) and its physiological basis (Roberts *et al.*, 1997; Biewener, 1998) are well established. Hence, the anatomical variables we measured are expected to confer performance differences. Nevertheless, whether or not these performance differences influence the relative running and fighting abilities of the two breeds remains untested.

The second major assumption of this study is that the two breeds have both diverged from a common ancestor

with generalized, wolf-like, fighting and running abilities. Because we do not have similar measurements from the common ancestor of Greyhounds and Pit Bulls, this assumption cannot be tested. Observed differences could be the result solely of selection for running ability in Greyhounds or solely of selection for fighting ability in Pit Bulls, in which case any difference between the breeds would reflect divergence of only one breed. Alternatively, observed differences between the two breeds may be the result of divergence of both breeds from their common ancestor. Because both breeds appear to be morphologically divergent from wolves, and because we believe it is reasonable to suggest that Greyhounds are compromised in their fighting ability relative to wolves, whereas Pit Bulls are compromised in their running ability relative to wolves, we suspect that both breeds have diverged from a wolf-like ancestor along different pathways. Nevertheless, knowledge of the actual extent of divergence from the ancestral state and the polarity of the divergence are not needed to address the questions posed in this study.

A lack of information on the history of the nine dogs used in this study necessitated a final assumption. We assumed that the difference in limb musculature of these two breeds is a function of the different genetic composition and developmental trajectories of the two breeds rather than a function of differences in the environment in which the dogs were raised or a function of differences in training. Although we cannot discount the possibility that training effects influenced our results, we know of no reason to believe that differences in proximal to distal muscle mass, fore- vs. hind-limb muscle strength, or potential for elastic storage would be due to differences in developmental environment or training.

Proximal to distal muscle distribution

Elongate limbs with reduced distal muscle mass have evolved many times in animals specialized for rapid and/or efficient running (Hildebrand & Goslow, 2001). This convergence has been attributed to selection to increase locomotor stamina at high speeds by reducing the mechanical work required to oscillate the limbs

Table 3 Greyhound (GH) and Pit Bull (PB) mean and standard errors for parameters used to calculate potential elastic storage.

during each locomotor cycle (Hildebrand & Hurley, 1985; Steudel, 1991). Measurements of the mechanical work of limb oscillation (i.e. the internal work of locomotion) have confirmed that at moderate and high speed running the internal work can be as large or larger than the work to accelerate and decelerate the mass of the entire animal (Cavagna & Kaneko, 1977; Fedak *et al.*, 1982; Willems *et al.*, 1995). Nevertheless, several studies have been unable to demonstrate a relationship between limb inertia and the cost of locomotion (e.g. Taylor *et al.*, 1974; Taylor, 1994). These energetic studies, however, have all been restricted to relatively low running speeds; speeds at which the energetic consequences of limb inertia are expected to be least important.

The difference in proximal to distal distribution of muscle mass in Pit Bulls and Greyhounds is consistent with the hypothesis that reduced distal mass in cursors is associated with selection to reduce limb rotational inertia. Compared with Pit Bulls, Greyhounds have relatively less muscle mass in their distal limbs than their proximal limbs. This pattern was observed in both the fore- and hind-limbs. Such an arrangement could both enhance maximum running speed, by increasing the rate at which the limbs could be accelerated, and increase anaerobic stamina at the high speeds at which Greyhounds race. Alternatively, the difference in distal to proximal muscle mass between the two breeds could be the result of selection for fighting ability in the Pit Bulls. Rapid acceleration, rapid turning, balance control and opponent manipulation are behaviours that are expected to be important during fighting and are behaviours that would be enhanced by relatively strong distal limb muscles.

Relative muscle strength in fore- vs. hind-limbs

Two observations lead to the hypothesis that animals specialized for running will have less muscle strength in their forelimbs than in their hindlimbs. First, when animals run there is a division of labour such that the forelimbs produce most of the fore-aft deceleration of the body, whereas the hindlimbs produce most of the acceleration (Cruse, 1976; Cavagna *et al.*, 1977; Jayes & Alexander, 1978; Heglund *et al.*, 1982; Blickhan & Full, 1987; Full *et al.*, 1991). Secondly, muscle that is stretched while it is active produces more force than muscle that actively shortens (Katz, 1939). Because muscles must actively lengthen to absorb energy during deceleration and shorten to produce acceleration we would expect specialized cursors to have extensor muscles of smaller cross-sectional area, and therefore, strength, in the forelimbs. This is the pattern we observed in our comparison of Pit Bulls and Greyhounds. The Greyhounds had extensor muscles of smaller cross-sectional area in their forelimbs than in their hindlimbs, whereas the Pit Bulls had extensor muscles of equal or greater cross-sectional area in their forelimbs than in their hindlimbs. This observation is consistent with

specialization for high speed running in the Greyhounds and for fighting in Pit Bulls.

The pattern of greater muscle strength in the hindlimbs of Greyhounds vs. equal or greater strength in the forelimbs of Pit Bulls was observed in the extensor muscles of both the mid joint (i.e. elbow and knee) as well as the distal joint (i.e. wrist and ankle). We anticipated the result at the elbow and knee joints, but were surprised to find a similar pattern at the wrist and ankle. The extensor muscle-tendon systems of the wrist and ankle joints are generally recognized as being instrumental in the storage and recovery of elastic strain energy (Alexander, 1984) and this mechanism provides a significant energetic saving during running (Cavagna *et al.*, 1964; Dawson & Taylor, 1973; Biewener, 1998). For elastic storage to be effective in providing an energetic saving the active muscle fibres must undergo very little shortening (Roberts *et al.*, 1997). Hence, if the extensor muscle-tendon systems of the distal joints functioned primarily as springs during running we would expect the force produced per unit cross-sectional area of the wrist and ankle extensor muscle to be the same because the active fibres remained isometric. We would not therefore expect greater muscle cross-sectional area in the extensor muscles of the ankle than in the wrist. This is particularly the case given that the forelimbs support a greater percentage of body weight than do the hindlimbs. Thus, the observation in Greyhounds that the extensor muscles of the ankle joint have greater cross-sectional area than do the extensor muscles of the wrist suggests that shortening and lengthening contractions are important enough in the distal muscles of at least some cursorial mammals to have an influence on relative muscle strength.

Elastic storage

Our estimates of the potential to store and recover elastic strain energy in the in-series tendons of the extensor muscles of the ankle joint suggest that Greyhounds have more than a 2.3-fold greater capacity to use elastic storage than do Pit Bulls. Such a large difference in two breeds of the same species is surprising until one considers the factors that have governed the artificial selection of the two breeds. Although Greyhounds are bred for speed, the lengths of their races are such that anaerobic stamina also plays a very large role in determining which dogs win. In one set of 15, 518-m races, there were 33 instances in which one dog passed another dog in the last 300 m of the race. Of these 33 passes, 51% occurred in the last 50 m and 30% in the last 10 m of the race (D.R. Carrier, Unpublished observations). The relatively high frequency of passes in the last few metres of the race not only adds to the excitement and unpredictability of the race, but is also consistent with the suggestion that anaerobic stamina plays an important role. If anaerobic stamina is an important component of Greyhound racing, an ability to

store and recover elastic strain energy would enhance performance by reducing the metabolic energy needed to accomplish the mechanical work. Additionally, having ankle and toe extensor muscles that function as springs during running would reduce the distal mass and therefore the rotational inertia of the hindlimb, allowing the limb to oscillate faster and the dogs to run at higher maximum speeds. In contrast, a high potential for elastic storage in the extensor muscles of the ankle joint could pose a serious problem for a fighting dog. In dogs, fighting often involves pushing contests, in which each dog attempts to push its opponent over onto its back. In this behaviour, compliant tendons in series with the ankle extensor muscles would be a handicap because energy would be dissipated in stretching the tendons rather than doing work on the opponent. Stretchy, in-series tendons would also likely inhibit control of balance when an opponent applied perturbing forces to one's body. Hence, the observed difference in potential to store elastic strain energy appears to be consistent with the expected demands of economical, high speed, running vs. those of physical combat.

Implications

The results of this study are consistent with the hypothesis that there are often functional trade-offs that prevent simultaneous evolution of optimal performance in (1) economical and/or rapid transport and (2) fighting ability. Greyhounds differ from Pit Bulls in having relatively less muscle mass distally in their limbs, weaker muscles in their forelimbs than their hindlimbs and a much greater capacity for elastic storage in the extensor muscle-tendon systems of their ankle joints. We believe each of these differences help to make Greyhounds faster and more efficient runners than Pit Bulls and help to make Pit Bulls more effective fighters than Greyhounds. We suggest that the three differences observed in this study are examples of a broad set of characters that require functional trade-offs between locomotor and fighting abilities, and that locomotor/fighting functional trade-offs are widespread taxonomically.

Because many animals must, at some point in their lives, be effective at both transport and physical combat against competitors, predators or prey, functional trade-offs between running and fighting performance may have had an important influence on the evolutionary trajectories of many species. The comparisons of gorillas and gibbons, and species of fig wasps, mentioned above, are obvious examples of the extent to which selection for fighting specialization on the one hand and selection for locomotor specialization on the other may lead to anatomical, functional and behavioural diversity among closely related taxa. We can point to many other possible examples of this type of divergence along a running-fighting specialization continuum. Among

felids, for example, cheetahs are the fastest runners on the planet, exhibit little sexual dimorphism in body size (Nowak & Paradiso, 1983), and although coalitions of territorial males are known to kill individual male intruders (Caro, 1994), cheetahs are recognized as exhibiting relatively little physical aggression towards conspecifics (Eaton, 1974). In contrast, lions are characterized by fierce male-male fighting and sexual dimorphism in which males are about 35% larger in body mass than females (Nowak & Paradiso, 1983). Consistent with the trade-off hypothesis, lions are not fast runners (particularly males) and can sprint at only half the maximum speed of cheetahs (Schaller, 1972). Among grouse, Willow and Rock Ptarmigan migrate seasonally (Kaufman, 1996) and are usually monogamous (Johnsgard, 1975). In contrast, Ruffed and Sage Grouse are mainly permanent residents, with little or no seasonal migration (Kaufman, 1996), and are highly polygynous, with intense male competition (Johnsgard, 1975).

Another noteworthy example of conflict between specialization for fighting and locomotion comes from a consideration of the evolution of prey immobilization systems in colubrid snakes (Savitzky, 1980). Basal snakes are thought to have killed their prey by constriction (Greene & Burghardt, 1978). In these snakes the axial musculoskeletal system must have been used for both subduing prey and locomotion. Powerful constriction appears to preclude rapid locomotion (Ruben, 1977). The evolution of a serous gland (Duvernoy's gland) in colubrid snakes may have provided a mechanism for uncoupling locomotor and prey capture activities by providing a venomous secretion for the immobilization of prey (Savitzky, 1980). Among colubrids, the five genera in which serous cells are few or absent are those that use constriction for prey capture. In contrast, the most strongly terrestrial and rapid genera (*Chironius*, *Coluber*, *Drymarchon*, *Drymobius*, *Masticophis* and *Salvadora*) do not constrict, but have well-developed Duvernoy's glands. Hence, Savitzky (1980) suggests that the dramatic colubroid radiation during the Miocene may be a response to the spread of open habitats, with taxa that were characterized by slow locomotion and immobilization of prey through constriction being supplanted by taxa characterized by rapid locomotion and immobilization of prey by envenomation.

These examples support the suggestion that functional trade-offs that prevent simultaneous evolution of optimal performance in locomotion and fighting ability may be (1) widespread taxonomically and (2) influence behavioural and social characters in addition to aspects of the musculoskeletal system. For example, selection for greater locomotor speed or stamina is expected to reduce the ability of males to compete in physical combat. Reduced ability of males to fight might effect a species' mating system by reducing a male's ability to defend and attract

multiple females (Darwin, 1874; Andersson, 1994). In contrast, selection that improves a species' ability to defend territory, protect young from predators or compete in intraspecific combat would lead to reduced locomotor speed and stamina and, thus, possibly influence a species' predator-prey relationships, its migratory behaviour or its foraging behaviour. Hence, the importance of both locomotion and fighting combined with the often-conflicting nature of characters that enhance these two skills lead us to suggest that dichotomies in locomotor and fighting specialization may have strongly influenced the evolution of many species.

Acknowledgments

We thank S. Johnson of Recycled Racers for her help in related studies and the Veterinary School of Colorado State University for donating the greyhound cadavers. We thank N. Kley for drawing our attention to Savitzky's work on the conflict between prey constriction and locomotion in snakes. S. Deban, C. Farmer, T. Garland, J. Seger, E. Stakebake, R. Walter and two anonymous reviewers read and provided comments on the manuscript. This investigation was supported by The National Science Foundation (IBN-9807534).

Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEB/JEB512/JEB512sm.htm>

Figure S1 Frontal view of representatives of the two breeds used in this study: Pit Bulls and Greyhounds. Both individuals in this photograph are adult males with a body mass of 33 kg. These individuals were not subjects in this study. Modified from Chase et al., 2002.

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Received 24 May 2002; revised 13 August 2002; accepted 16 September 2002