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Functional anatomy of the cheetah (*Acinonyx jubatus*) forelimb

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Abstract

Despite the cheetah being the fastest living land mammal, we know remarkably little about how it attains such high top speeds (29 m s^{-1}). Here we aim to describe and quantify the musculoskeletal anatomy of the cheetah forelimb and compare it to the racing greyhound, an animal of similar mass, but which can only attain a top speed of 17 m s^{-1}. Measurements were made of muscle mass, fascicle length and moment arms, enabling calculations of muscle volume, physiological cross-sectional area (PCSA), and estimates of joint torques and rotational velocities. Bone lengths, masses and mid-shaft cross-sectional areas were also measured. Several species differences were observed and have been discussed, such as the long fibred serratus ventralis muscle in the cheetah, which we theorise may translate the scapula along the rib cage (as has been observed in domestic cats), thereby increasing the cheetah's effective limb length. The cheetah's proximal limb contained many large PCSA muscles with long moment arms, suggesting that this limb is resisting large ground reaction force joint torques and therefore is not functioning as a simple strut. Its structure may also reflect a need for control and stabilisation during the high-speed manoeuvring in hunting. The large digital flexors and extensors observed in the cheetah forelimb may be used to dig the digits into the ground, aiding with traction when galloping and manoeuvring.

Key words: *Acinonyx*; anatomy; cheetah; forelimb; locomotion; muscle; speed.

Introduction

The cheetah is widely acknowledged to be the fastest living land mammal, capable of speeds up to 29 m s^{-1} (Sharp, 1997), and yet there is little scientific evidence to explain how it achieves such remarkable speeds. Here we investigate the musculoskeletal anatomy of the cheetah forelimb and compare it with the racing greyhound; an animal of similar gross morphology and mass, but which can only achieve top speeds of 17 m s^{-1} during a race (Usherwood & Wilson, 2005). Through quantifying and comparing the forelimb musculoskeletal anatomy of the cheetah and

racing greyhound, we will gain insight into anatomical adaptations that could explain how the cheetah achieves higher top speeds.

To maximise its speed, an animal must rapidly swing its limbs (to increase stride frequency) and support its body weight by resisting large ground reaction forces (GRF; Weyand et al. 2000). As a predator, the cheetah also uses its forelimbs for prey capture and therefore they must also be adapted for this function. Through examining the musculoskeletal anatomy of both species, insight into their ability to perform each of these functions will be obtained. Measurements of muscle mass and fascicle lengths enable calculations of muscle volume and physiological cross-sectional area (PCSA). These parameters can then be used to estimate muscle power output (proportional to its volume; Zajac, 1989) and its maximal isometric force (F_{max}; proportional to PCSA). Further to this, measurements of muscle moment arms (the perpendicular distance between the line of action of the muscle and the joint centre of rotation) enable linear muscle forces to be converted to rotational joint moments (Landsmeer, 1961; An et al. 1981; Spoor & van Leeuwen, 1992). This will provide us with a greater understanding of how each muscle can move the limb

during locomotion and indications of the forces that the limb may experience.

Increasing stride frequency is key to reaching faster speeds. This is mainly achieved through rapidly swinging the limb and thereby decreasing swing time. Muscles adapted for rapid joint rotations would have long fascicles (more sarcomeres in series enabling it to contract at a higher velocity) and short moment arms (enabling a greater change in joint rotation for a given change in muscle length). Muscle fibre type composition will also play a large role in determining a muscle's contraction velocity. Cheetah muscle has been shown to contain a high proportion of fast-twitch fibres (Williams et al. 1997), which would be highly beneficial for rapidly swinging the limb and reducing swing time; however, exact contraction velocities are unknown.

With increasing speed an animals' stance time (Cavagna et al. 1988; Heglund & Taylor, 1988) and duty factor (proportion of a stride in which the feet are in contact with the ground; Keller et al. 1996; Weyand et al. 2000) decrease. During the period of a stride in which the feet are in contact with the ground, an animal must support its body weight by resisting the GRF joint torques experienced by the limb (Alexander, 1985; Weyand et al. 2000; Usherwood & Wilson, 2006). Quadrupeds typically support a greater proportion of their body weight with their forelimbs during steady state locomotion (Alexander & Jayes, 1983, 1978; Witte et al. 2004), and with increasing speed, peak GRFs have been shown to increase (Witte et al. 2004). When travelling at top speed the cheetah's forelimbs are therefore likely to experience very high peak forces, and must be particularly adept at resisting large GRF joint torques. To resist large GRF joint torques, the extensor muscles of the limb are required to produce large isometric forces. Muscles adapted for such a function would have a large PCSA (more sarcomeres in parallel enabling a bigger F_{max}). A long moment arm would also increase the leverage the muscle has at the joint (enabling a bigger joint torque for a given change in muscle length), maximising the joint torques that can be achieved. Contrary to this, the forelimbs of quadrupeds are often thought of as springy struts (Blickhan, 1989; Blickhan & Full, 1993), where the GRF vector is aligned through the point of rotation of the forelimb on the body, resulting in small GRF joint torques, particularly at the shoulder (Carrier et al. 2008). This would be of great benefit to an animal, potentially allowing it to reduce the mass of muscle on its forelimb. This would reduce the limb's inertia (Lee et al. 2004) and enable the animal to swing its limb more rapidly and potentially increase its top speed.

Unlike the greyhound, the cheetah must also use its forelimbs for capturing prey. As the cheetah lacks the strength of other felids it is unable to fight its prey to the ground. Instead it must trip or pull its prey off balance when travelling at high speeds. To do this the cheetah will hook the rump of its prey with its dew claw (the cheetahs only retractile claw on digit 1; Gonyea & Ashworth, 1975; Turner &

Anton, 1997; Gorman & Londei, 2000; Russell & Bryant, 2001; Hunter & Hamman, 2003). Adaptations for such behaviours, such as increased supination ability, may therefore be observed.

Here we aim to describe and quantify the forelimb musculoskeletal anatomy of the cheetah and compare this with existing data on the racing greyhound to provide insight into how the cheetah achieves such high speeds.

Materials and methods

The experimental protocol was identical to that described in Hudson et al. (2011). In brief, forelimbs from eight captive cheetahs (from the Anne van Dyk Cheetah Centre and the research department of the National Zoological Gardens of South Africa) and three ex-racing greyhounds (obtained from greyhound racing track vets) were dissected, and their musculoskeletal anatomy described and quantified (known subject information is given in Table 1). Measurements of muscle mass, fascicle length (average of 10 from each muscle) and pennation angle (average of three from each muscle) were taken, from which muscle volume and PCSA were calculated (see Table 2 for muscles analysed). To enable species and subject comparison, all muscle architecture measurements were scaled. Unfortunately total body mass was often unavailable, and thus all architecture measurements were scaled geometrically to total forelimb muscle mass. The mass, length and mid-shaft diameter of the humerus and radius were also measured and scaled to body mass for species comparison. Published data from six greyhounds (Williams et al. 2008a) were then combined with our greyhound data for comparison.

Muscle moment arms were measured for cheetah subjects 4–8 using the tendon travel method (Landsmeer, 1961; Spoor & van Leeuwen, 1992), and compared with published values for four greyhounds (Williams et al. 2008a). Moment arms were measured for the major limb muscles acting at the shoulder, elbow and carpus (see Table 3 for muscles analysed). To enable species and subject comparison, moment arms were scaled to humerus length (for muscles acting at the shoulder) and radius length (for muscles acting at the elbow and carpus).

Species comparisons were made using a Mann–Whitney U-test, due to the small numbers of subjects. Comparisons with P-values of < 0.05 were taken to be significant, and instances where $P < 0.01$ are also indicated throughout the results.

Results

Muscle name abbreviations are provided in Table 2.

Forelimb muscle anatomy and architecture

Thirty individual muscles were identified and measured from the forelimbs of eight cheetah cadavers, but only 29 muscles were identified in the greyhounds. In the three greyhound cadavers examined, no brachioradialis muscle was found, nor was it mentioned in the published results (Williams et al. 2008a). In the cheetah this muscle originated from the lateral supracondylar crest of the lateral epicondyle of the humerus and inserted onto the medial

Table 1 Known subject information – greyhounds 1–3 were dissected in this study, and greyhounds 4–9 were from data published by Williams et al. (2008a). For species comparison data were normalised geometrically to body mass and a Mann–Whitney *U*-test was performed to test for significant species differences. The cheetah has a significantly heavier humerus (*P* < 0.05) and radius (*P* < 0.05) than in the greyhound. Its humerus (*P* < 0.01) and radius (*P* < 0.05) are also significantly longer, but no species differences in bone radius were observed.

Subject	Age (years)	Gender	Mass (kg)	Humerus Length (mm)	Humerus Mass (g)	Humerus Diameter (mm)	Radius Length (mm)	Radius Mass (g)	Radius Diameter (mm)
Cheetah 1	8.5	Female							
Cheetah 2	15.5	Female							
Cheetah 3	11.5	Male							
Cheetah 4	13.5	Male	31	267	214	18.2	253	83	20.4
Cheetah 5	12	Female	29.5	242	162	23.7	232	67	16.5
Cheetah 6	6	Male	27.5	254	171	24.8	247	68	11.5
Cheetah 7	12.5	Male	32	257	214	17.6	248	82	11.4
Cheetah 8	6.5	Female	45.5	243	164	25	232	63	17.1
Greyhound 1		Female	25	215	118	21.4	196	46	14.3
Greyhound 2		Male	28	230	124	21.5	208	47	15.3
Greyhound 3		Male	29	221	141	22.3	218	51	16.2
Greyhound 4		Female	27	200			220		
Greyhound 5		Male	33						
Greyhound 6		Male	34	200			240		
Greyhound 7		Male	33	200			220		
Greyhound 8		Male	28	190			230		
Greyhound 9		Male	33						

aspect of the distal radius. The origins and insertions of all other muscles showed no species variation (Fig. 1).

Overall, the combined cheetah forelimb musculature (assuming symmetry between limbs) represented 15.1 ± 1.2% of total body mass, which was not significantly different to that observed in the greyhound at 16.7 ± 2.3% of total body mass. When arranged by their point of insertion onto the limb, a proximal-to-distal reduction in muscle mass was not apparent (Fig. 2), largely because of several heavy muscles (latissimus dorsi and long head of triceps brachii) inserting onto the distal humerus and proximal radius and ulna.

The majority of the cheetah's extrinsic muscles were either lighter or of a similar mass when compared with the greyhound. This was most evident in the pectoralis profundus (*P* < 0.01) and the cervical portion of the rhomboid muscle (*P* < 0.05), both of which were significantly lighter in the cheetah. For some muscles, species differences in their internal architecture were apparent even when their masses were the same (Table 2). For example, the masses of the cervical (SVc) and thoracic portions of the serratus ventralis muscle (SVt) were the same in both species, but those of the cheetah had significantly longer fascicles (*P* < 0.05), and a significantly lower PCSA (*P* < 0.01 for SVt and *P* < 0.05 for SVc).

The proximal intrinsic muscles of the forelimb; infraspinatus, supraspinatus, subscapularis and teres major were all significantly (*P* < 0.01) heavier in the cheetah than in the greyhound (Fig. 2). All had larger PCSAs in the cheetah, but only teres major and subscapularis were significantly so (*P* < 0.01). The cheetah's supraspinatus muscle also had sig-

nificantly (*P* < 0.05) longer fascicles when compared with that of the greyhound (Table 2).

Several significant differences were apparent when comparing the distal limbs of the two species. The cheetah's extensor digitorum communis (*P* < 0.05), pronator teres (PT; *P* < 0.01) and flexor digitorum superficialis (SDF; *P* < 0.01) and profundus (DDF; *P* < 0.05) were all significantly heavier than those of greyhound. In the cheetah, the extensor digitorum communis had significantly (*P* < 0.01) longer fascicles and a significantly (*P* < 0.01) smaller PCSA. PT and the DDF and SDF muscles exhibited no species differences in fascicle length; however, all had significantly (*P* < 0.01 for PT, *P* < 0.05 for SDF and DDF) larger PCSAs in the cheetah compared with the greyhound.

Forelimb muscle moment arms

Muscle moment arms were measured for five cheetahs (subjects 4–8) and compared with those of four greyhounds from previously published work (Williams et al. 2008a). Moment arms were measured for seven muscles functioning at the shoulder, six at the elbow and four at the carpus. Maximum and minimum moment arm values are given in Table 1, along with the moment arm at mid-stance. Figure 3 shows a comparison between the cheetah and greyhound maximum moment arms when scaled geometrically.

At the shoulder, all of the moment arms were longer in the cheetah than in the greyhound, with the exception of biceps brachii. At the elbow, the long head of triceps and

Table 2 Muscle data; number of subjects (*N*), muscle mass, mean fascicle length and PCSA of the cheetah and greyhounds. Values indicated are mean (bold) and SD (italics). For species comparison data were normalised geometrically to body mass and a Mann–Whitney *U*-test was performed to test for significant species differences, with *indicating $P < 0.05$ and **$P < 0.01$.

Muscle name	Abbreviation	Cheetah N	Muscle mass (g)		Mean fascicle length (cm)		PCSA (cm²)		Greyhound N	Muscle mass (g)		Mean fascicle length (cm)		PCSA (cm²)	
Latissimus dorsi	LAT	8	**272.8**	*68.9*	**32.5**	*9.6*	**10.8**	*7.5*	9	**310.9**	*47.6*	**36.8**	*5.5*	**9.1**	*1.6*
Trapezius cervicis	TC	8	**25.9**	*11.4*	**14.4**	*4.2*	**2.0**	*0.8*	9	**35.6**	*16.3*	**14.0**	*2.6*	**2.9**	*1.9*
Trapezius thoracis	TT	8	**32.3**	*10.8*	***12.9**	*4.9*	***3.7**	*3.6*	9	**50.3**	*22.8*	**9.1**	*1.4*	**5.9**	*2.5*
Rhomboideus capitis	Rcap	8	**9.9**	*2.6*	**26.1**	*4.8*	**0.4**	*0.1*	3	**8.5**	*5.5*	**28.2**	*5.3*	**0.3**	*0.2*
Rhomboideus cervicis	Rcer	8	***26.3**	*14.3*	**11.2**	*7.6*	**3.9**	*3.1*	3	**52.7**	*12.9*	**15.3**	*5.8*	**4.5**	*3.2*
Rhomboideus thoracis	Rthor	8	**38.0**	*8.0*	**9.7**	*3.4*	**4.7**	*1.9*	3	**51.4**	*5.2*	**8.1**	*0.5*	**6.8**	*0.2*
Omotransversarius	OMO	8	****26.3**	*5.4*	**22.6**	*8.9*	***1.7**	*1.3*	9	**53.5**	*10.0*	**25.3**	*2.1*	**2.3**	*0.5*
Cleidocephalicus	Cc	8	**34.5**	*15.3*	**26.4**	*3.4*	**1.4**	*0.7*	3	**39.9**	*10.3*	**23.0**	*4.1*	**1.9**	*0.5*
Cleidobrachilalis	Cb	8	**36.6**	*8.6*	**17.4**	*7.0*	**2.7**	*1.3*	3	**39.4**	*21.7*	**18.1**	*4.1*	**2.2**	*0.7*
Serratus ventralis cervicis	SVc	8	**94.8**	*21.4*	***12.2**	*3.1*	***8.5**	*2.0*	8	**143.7**	*36.7*	**7.7**	*5.4*	**27.7**	*13.4*
Serratus ventralis thoracis	SVt	8	**98.4**	*31.5*	***8.8**	*2.2*	****12.5**	*5.2*	8	**117.9**	*14.5*	**5.0**	*0.9*	**25.6**	*5.9*
Pectoralis superficialis descending	PSd	8	**42.0**	*27.6*	**15.5**	*4.7*	**3.6**	*3.5*	9	**54.0**	*29.1*	**13.8**	*1.2*	**4.3**	*2.6*
Pectoralis superficialis transverse	PSt	8	****96.0**	*29.2*	**13.6**	*7.7*	**9.1**	*4.4*	9	**80.8**	*22.1*	**17.2**	*8.9*	**6.6**	*3.5*
Pectoralis profundus	PP	8	****221.3**	*62.7*	**25.2**	*12.0*	**12.0**	*7.4*	9	**378.3**	*56.1*	**30.7**	*1.9*	**13.0**	*1.8*
Supraspinatus	SS	8	****206.4**	*28.4*	***7.9**	*1.7*	**28.4**	*5.3*	9	**144.8**	*13.3*	**6.1**	*0.8*	**25.5**	*4.5*
Infraspinatus	IS	8	****148.3**	*18.5*	**5.1**	*1.4*	**33.5**	*10.5*	9	**108.8**	*13.6*	**4.2**	*0.9*	**28.9**	*7.8*
Deltoid acromial	DA	8	**22.6**	*8.3*	****2.9**	*0.4*	***8.2**	*3.0*	9	**26.2**	*5.4*	**6.6**	*2.7*	**4.8**	*1.8*
Deltoid spinous	DS	8	****29.9**	*4.3*	**10.3**	*2.0*	****3.2**	*1.1*	9	**51.0**	*15.2*	**8.7**	*1.3*	**6.5**	*2.4*
Teres major	TMJ	8	****77.6**	*10.8*	**11.3**	*2.6*	****7.8**	*2.7*	9	**52.5**	*9.0*	**14.2**	*1.4*	**3.9**	*0.7*
Subscapularis	SUB	8	****121.0**	*15.7*	**3.2**	*0.6*	****40.6**	*8.4*	9	**82.1**	*9.3*	**3.3**	*0.3*	**26.7**	*3.3*
Teres minor	TMN	8	**8.5**	*1.2*	**2.2**	*0.3*	**4.1**	*0.6*	9	**29.4**	*20.9*	**2.0**	*0.3*	**16.8**	*12.4*
Coracobrachilalis	COR	5	****2.1**	*2.5*	**2.0**	*1.8*	***1.2**	*0.8*	9	**30.4**	*21.0*	**2.5**	*0.5*	**12.6**	*9.3*
Triceps brachii – Long	Tlong	8	**255.4**	*23.6*	**6.0**	*1.2*	**46.8**	*9.2*	9	**323.8**	*53.5*	**7.1**	*0.9*	**49.3**	*12.4*
Triceps brachii – Lateral	Tlat	8	**98.9**	*9.9*	**10.4**	*1.9*	**10.5**	*2.8*	9	**119.3**	*24.3*	**10.8**	*1.0*	**11.9**	*3.0*
Triceps brachii – Medial	Tmed	8	****16.9**	*4.0*	****13.1**	*1.8*	****1.4**	*0.4*	9	**70.2**	*35.8*	**4.4**	*4.0*	**34.7**	*26.1*
Triceps brachii – Accessory	Tacc	8	****11.8**	*6.3*	**9.1**	*3.8*	****1.5**	*0.9*	9	**40.3**	*14.7*	**11.3**	*1.3*	**3.8**	*1.2*
Biceps brachii	BB	8	****88.8**	*19.1*	****3.6**	*0.7*	**26.9**	*5.7*	9	**51.1**	*15.4*	**2.2**	*0.6*	**28.4**	*17.3*
Brachialis	BCH	8	**20.8**	*5.8*	**8.0**	*2.1*	**2.8**	*1.0*	9	**23.2**	*3.4*	**7.0**	*4.8*	**4.8**	*2.3*
Anconeus	ANC	8	**4.0**	*1.8*	**4.3**	*2.4*	***1.4**	*1.1*	9	**6.1**	*2.4*	**2.2**	*1.7*	**3.8**	*2.1*
Extensor carpi radialis	ECR	8	****12.0**	*5.4*	**4.7**	*2.6*	****3.2**	*1.6*	9	**30.7**	*6.5*	**3.5**	*0.8*	**9.7**	*2.9*
Extensor digitorum communis	EDC	7	***14.0**	*2.7*	****3.8**	*0.7*	**3.9**	*0.8*	9	**10.4**	*2.5*	**2.8**	*0.4*	**4.0**	*1.0*
Extensor digitorum lateralis	EDL	7	**5.4**	*0.8*	**1.7**	*0.5*	**3.6**	*1.0*	9	**9.8**	*6.9*	**1.5**	*0.2*	**7.6**	*5.0*
Ulnaris lateralis	UL	7	**11.3**	*2.6*	**1.5**	*1.5*	**12.0**	*6.7*	9	**10.4**	*1.9*	**0.9**	*0.2*	**12.9**	*3.8*
Flexor carpi ulnaris – Ulnar head	FCUu	7	**4.6**	*4.3*	**1.6**	*1.8*	**8.9**	*12.0*	3	**3.7**	*1.2*	**1.1**	*0.5*	**7.8**	*5.0*
Flexor carpi ulnaris – Humeral head	FCUh	7	**13.1**	*5.2*	**1.8**	*0.5*	***7.9**	*3.3*	3	**18.2**	*3.0*	**1.5**	*0.4*	**13.4**	*3.6*
Brachioradialis	BCR	7	**12.3**	*3.8*	**5.1**	*2.8*	**3.2**	*1.7*							
Supinator	SUP	7	**1.8**	*0.4*	**0.8**	*0.4*	***3.3**	*3.3*	9	**4.9**	*3.3*	**0.5**	*0.3*	**14.7**	*12.7*
Pronator teres	PT	7	****10.6**	*1.7*	**1.2**	*0.4*	****10.0**	*2.5*	9	**4.8**	*1.0*	**1.2**	*0.2*	**4.4**	*1.7*
Pronator quadratus	PQ	7	**3.3**	*2.1*	**2.0**	*2.2*	***2.4**	*0.8*	9	**2.7**	*0.6*	**0.6**	*0.2*	**5.2**	*3.0*
Flexor carpi radialis	FCR	7	**6.9**	*2.5*	***1.9**	*0.6*	**4.4**	*3.1*	9	**9.0**	*1.7*	**2.9**	*0.8*	**3.5**	*1.0*
Flexor digitorum superficialis	SDF	7	****23.4**	*2.8*	**1.0**	*0.3*	****27.6**	*11.4*	9	**18.0**	*3.2*	**1.2**	*0.2*	**16.5**	*2.5*
Flexor digitorum profundus – Humeral head	DDFh	7	**38.7**	*10.9*	**4.0**	*1.4*	**11.2**	*5.4*	3	**31.5**	*13.6*	**3.0**	*0.2*	**11.1**	*4.3*
Flexor digitorum profundus – Radial head	DDFr	7	***9.3**	*6.7*	**3.8**	*1.9*	***4.3**	*4.7*	3	**2.2**	*1.3*	**3.4**	*1.1*	**0.8**	*0.5*
Flexor digitorum profundus – Ulnar head	DDFu	7	**9.6**	*1.3*	**3.8**	*2.3*	**4.4**	*4.0*	3	**9.8**	*11.5*	**2.4**	*0.3*	**4.2**	*4.8*
Abductor pollicis longis	APL	7	**3.4**	*0.8*	**1.3**	*1.1*	**5.6**	*6.1*	3	**2.8**	*0.4*	**1.8**	*0.7*	**3.1**	*1.7*

Table 3 Muscle moment arms (cm); maximum, minimum and mid-stance moment arms for the cheetah and greyhound (Williams et al. 2008a). Values are means (bold) and SD (italics).

Joint	Muscle	Muscle abbreviation	Cheetah						Greyhound
			Max MA (cm)		Min MA (cm)		Mid-stance MA (cm)		Max MA (cm)
Shoulder	Biceps brachii	BB	**2.6**	*0.23*	**1.0**	*0.23*	**1.0**	*0.23*	**2.4**
Shoulder	Deltoid acromial	DA	**4.4**	*0.72*	**0.4**	*0.49*	**1.1**	*0.51*	**0.8**
Shoulder	Deltoid scapula	DS	**9.1**	*2.4*	**0.3**	*2.66*	**2.0**	*2.5*	**5.3**
Shoulder	Infraspinatus	IS	**2.8**	*0.30*	**0.2**	*0.22*	**0.5**	*0.17*	**0.7**
Shoulder	Supraspinatus	SS	**7.1**	*0.53*	**0.9**	*0.82*	**1.8**	*0.46*	**3.4**
Shoulder	Teres major	TMJ	**11.2**	*0.67*	**1.1**	*0.19*	**2.8**	*0.41*	**3.5**
Shoulder	Triceps brachii – Long	Tlong	**16.6**	*1.1*	**3.9**	*0.95*	**5.3**	*1.0*	**4.9**
Elbow	Biceps brachii	BB	**4.3**	*0.58*	**1.7**	*0.58*	**1.7**	*0.58*	**1.9**
Elbow	Brachialis	BCH	**3.4**	*0.41*	**1.3**	*0.41*	**1.3**	*0.41*	**2.3**
Elbow	Extensor carpi radialis	ECR	**4.0**	*1.0*	**0.5**	*0.34*	**1.1**	*0.55*	**2.5**
Elbow	Extensor digitorum communis	EDC	**3.6**	*0.53*	**1.4**	*0.53*	**1.4**	*0.53*	**0.23**
Elbow	Triceps brachii – Lateral	Tlat	**4.6**	*0.70*	**1.3**	*1.0*	**1.6**	*0.73*	**4.3**
Elbow	Triceps brachii – Long	TLong	**6.8**	*0.46*	**2.1**	*0.50*	**2.4**	*0.25*	**3.6**
Carpus	Extensor carpi radialis	ECR	**1.79**	*0.21*	**0.06**	*0.47*	**0.10**	*0.50*	**1.5**
Carpus	Flexor carpi radialis	FCR	**1.33**	*0.31*	**0.27**	*0.33*	**0.51**	*0.29*	**0.57**
Carpus	Flexor carpi ulnaris	FCU	**9.7**	*1.1*	**0.47**	*0.48*	**3.6**	*1.0*	**2.6**
Carpus	Ulnaris lateralis	UL	**3.6**	*0.80*	**0.05**	*0.12*	**1.3**	*0.76*	

the extensor digitorum communis exhibited longer moment arms in the cheetah. At the carpus, moment arms showed little species difference with the exception of flexor carpi ulnaris, which was almost twice as long in the cheetah than in the greyhound. Unfortunately a value for the moment arm of ulnaris lateralis was unavailable for the greyhound.

Forelimb skeleton

When scaled to body mass, the cheetah's radius ($P < 0.01$) and humerus ($P < 0.05$) were found to be significantly longer than that of the greyhound (Table 1). Both bones were also significantly heavier ($P < 0.05$) when compared with those of the greyhound, but no significant species differences in mid-shaft diameter were found.

Discussion

The cheetah and greyhound are of a similar mass and morphology, yet the cheetah can attain significantly faster speeds. In this study, the forelimb muscle architecture, moment arms and skeleton of both species were compared to investigate differences that may account for the cheetah's higher top speed. Unfortunately no data regarding fibre contraction properties are available for the cheetah, therefore muscle function has been determined solely from muscle architecture, position and electromyographical information. Until such data regarding the contraction properties of cheetah muscle are available, our knowledge will remain somewhat incomplete. Despite this we feel that

our results provide great insight into the functional capabilities of the muscles investigated.

In the cheetah, the forelimb musculature comprised 15.1 ± 1.2% of its total body mass, substantially less than for its hindlimb at 19.8 ± 2.2% of total body mass (Hudson et al. 2011); however, in the greyhound this difference was reduced, with the forelimb comprising 16.7 ± 2.3% of its total body mass and the hindlimb 18.8 ± 2.4% of total body mass (Hudson et al. 2011). Pasi & Carrier (2003) suggested that the forelimbs of highly specialised runners would contain less muscle mass than the hindlimbs, as the forelimbs play a greater role in deceleration compared with the hindlimbs, which accelerate the centre of mass. This is because during deceleration muscles contract eccentrically (high force output), actively stretching to absorb energy, compared with the concentric (low force output) contractions used during accelerations, and therefore the forelimbs can contain muscles with smaller PCSAs to obtain the same force output. Despite this, in the greyhound we see just a 2% of total body mass difference in the mass of muscle comprising the forelimbs and hindlimbs. Williams et al. (2008a,b) suggested that the large mass of muscle they observed in greyhound forelimbs may be used in propulsion or for body weight support.

There were no species differences in the origins and insertions of the forelimb musculature; however, the cheetah did possess an additional muscle – the brachioradialis. This muscle is always present in domestic cats and but often absent in canids (Nickel et al. 1977). It functions to supinate the paw, which is of crucial importance to the cheetah for prey capture (Gorman & Londei, 2000; Russell & Bryant, 2001). Its
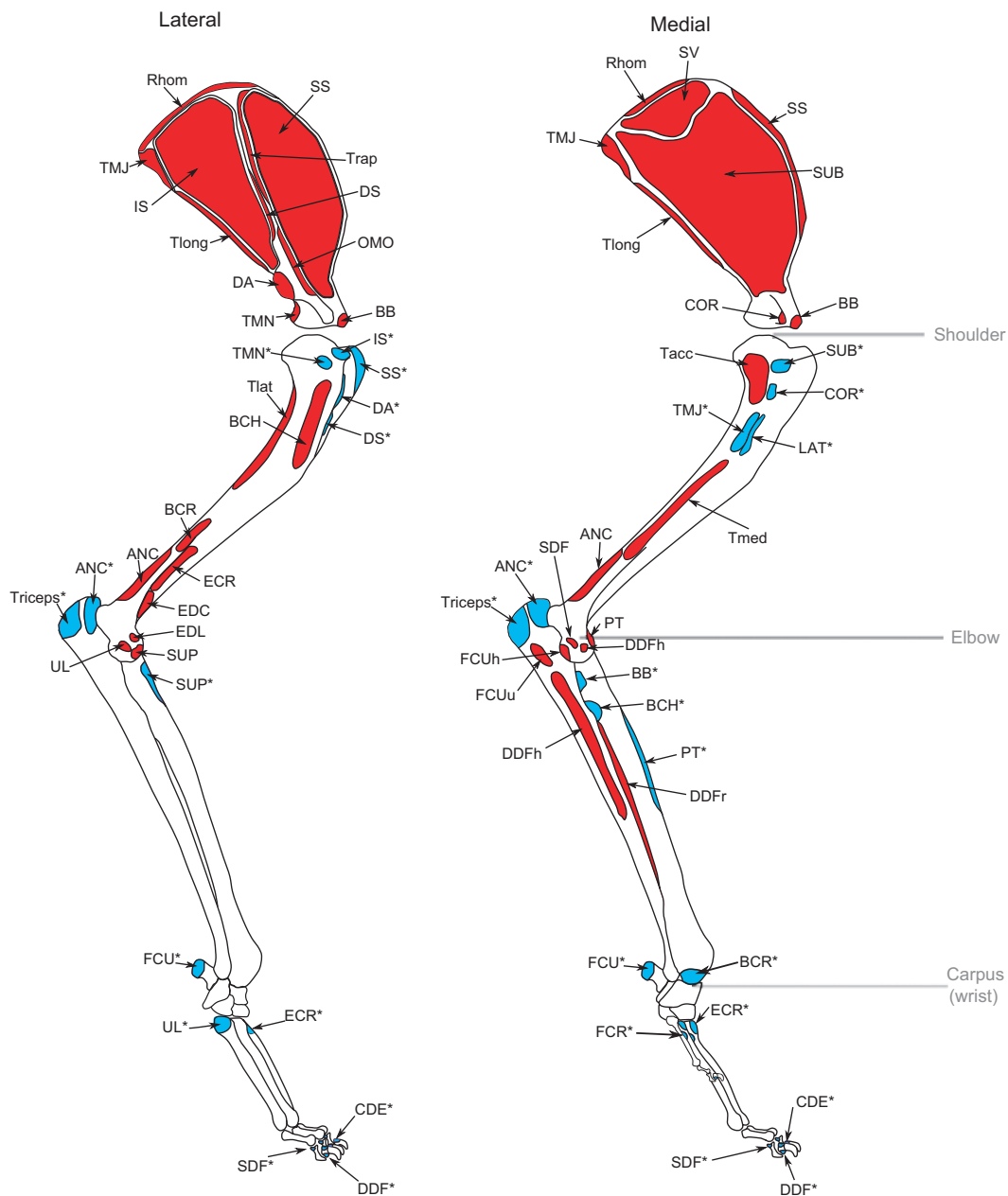
Fig. 1 Schematic illustration of all muscle origins and insertions in the cheetah. Origins are in red and insertions are in blue (insertions are also given a * after the muscle name). Muscle name abbreviations are given in Table 2.

long fibred internal architecture is well suited to this function, enabling it to contract at a high velocity, and rotate the joint through large angles. Despite this, previous work on the cheetah's elbow has highlighted a reduced ability for supination when compared with other felids, with a conformation much like canids and other cursorial carnivores (Andersson, 2004) contradicting the muscular anatomy.

Limb length

The cheetah's radius and humerus are longer than the greyhound's, and are also proportionally longer than that of other felids (Day & Jayne, 2007). We therefore propose that the cheetah has a proportionally longer forelimb than the greyhound. Assuming that stride frequency is unaffected, a longer forelimb should enable the cheetah to increase its stride length and therefore its speed. It would also enable the cheetah to use a longer contact length [distance the centre of mass (CoM) moves whilst the foot is in contact with the ground], and therefore have a longer stance time when travelling at a given speed. Maintaining a longer stance time will help to limit the peak vertical forces that the cheetah's limb experiences whilst maintaining the impulse required to support its own body weight when
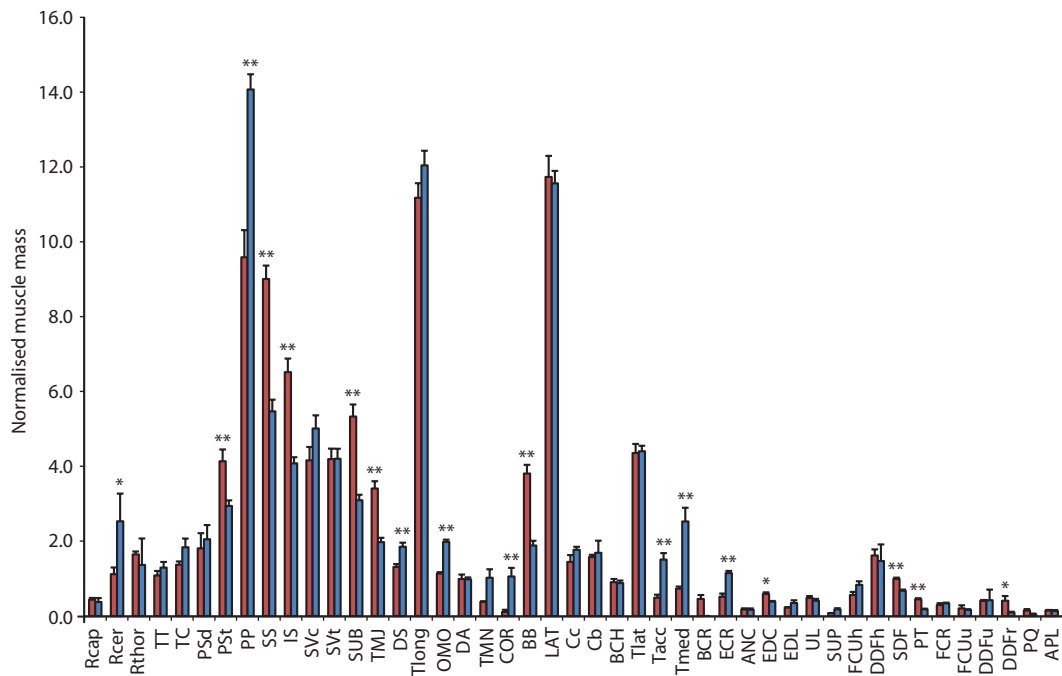
Fig. 2 Proximal to distal distribution of muscle mass within the cheetah (red) and greyhound (blue) forelimb. Bars are means ± standard error. Species comparison performed using a Mann–Whitney U-test (*P < 0.05 and **P < 0.01).
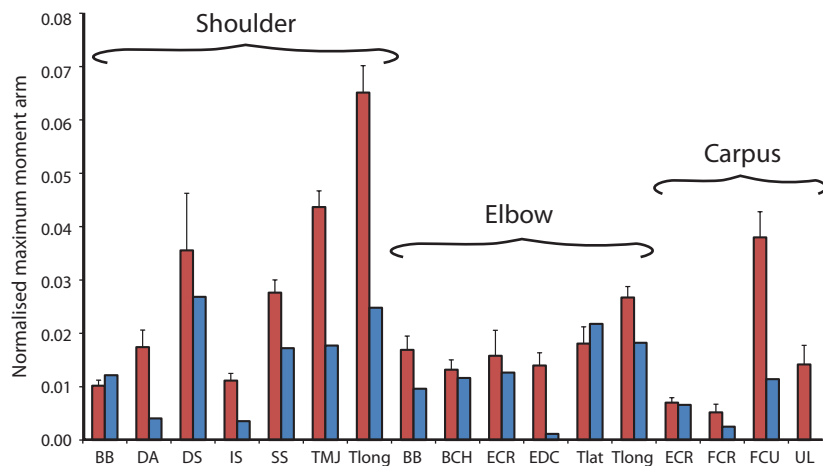

Fig. 3 Maximum moment arms of muscles functioning at the shoulder, elbow and carpus in the cheetah (red) and greyhound (blue; Williams et al. 2008a). Bars represent means ± standard error. Only means were available for the greyhound. For species comparison data were normalised to humerus length (for muscles acting at the shoulder), and radius length (for muscles acting at the elbow and carpus).

travelling at a given speed. Therefore, if peak force is a limit to an animal's maximum speed, this may be a way for the cheetah to maintain higher duty factors when travelling at low speeds, enabling it to attain higher maximal speeds. This will be of great importance in the forelimb, as the forelimbs tend to support a larger proportion of an animal's body weight during steady state locomotion (Alexander & Jayes, 1983; Witte et al. 2004). Despite this, there are several disadvantages to having a longer limb. Our results showed

the cheetah's humerus and radius to be heavier than the greyhound's, which will be essential for maintaining bone strength and safety factors (Alexander, 1993; Sorkin, 2008), but this will increase the inertia of the limb. Increased inertia would result in a longer swing time or more muscular work to accelerate and decelerate the limb through swing.

In the cheetah, we found the SV muscles to have longer fascicles than in the greyhound. A recent study in dogs suggested that the SVt muscle functioned for weight
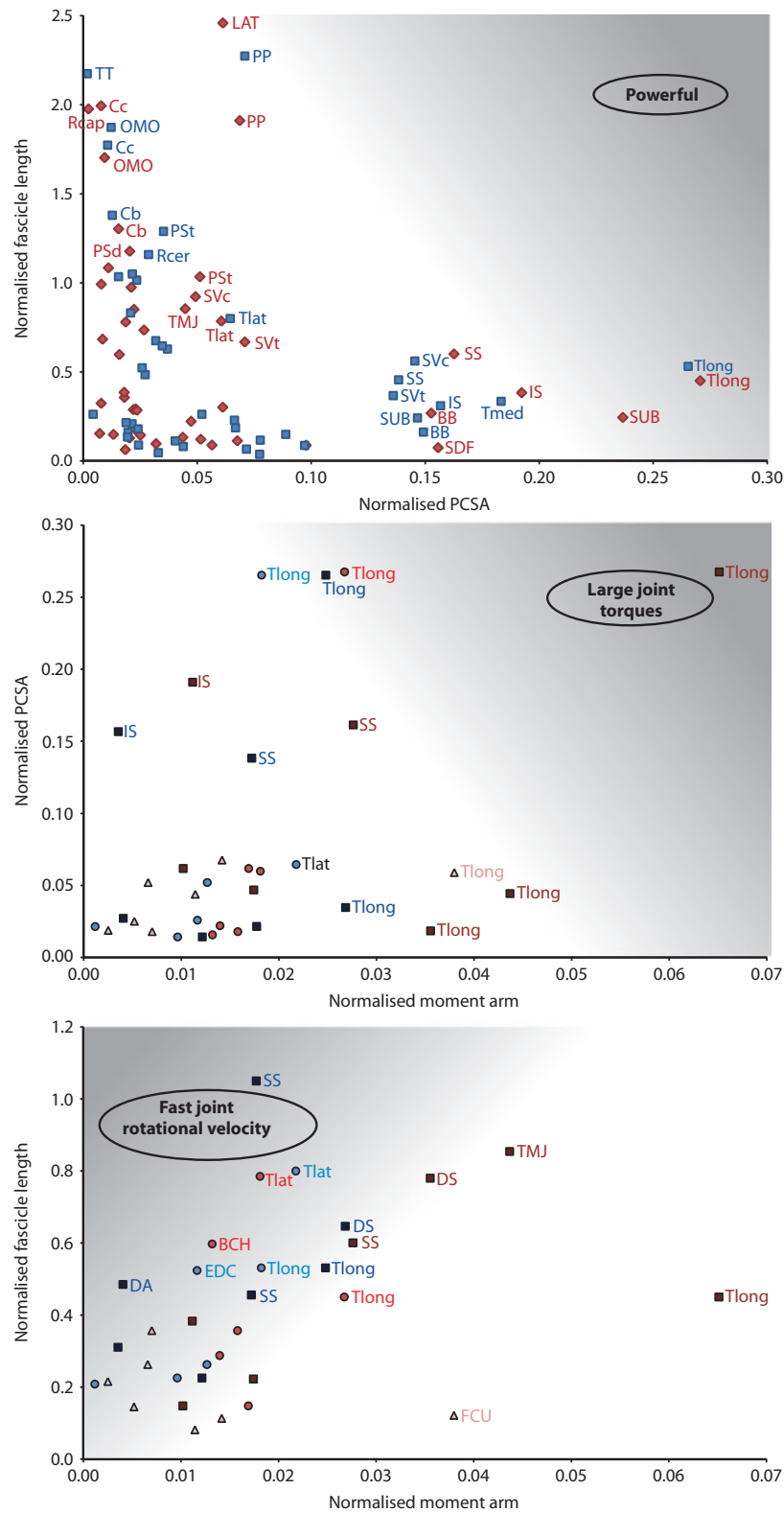
Fig. 4 (a) PCSA against FL to illustrate the power output of the muscle. (b) Moment arm against PCSA to illustrate the muscles ability to produce large joint moments. (c) Moment arm against fascicle length to illustrate the muscles ability to rotate the joint rapidly. Darker shaded areas of the graphs represent increased power output (a), large joint torques (b) and faster joint rotational velocity (c). Cheetahs are in red and greyhounds in blue. (b,c) Dark red and blue are muscles acting at the shoulder; mid-shades are muscles acting at the elbow; light colours are muscles acting at the carpus. Refer to Table 2 for muscle name abbreviations.

support (Carrier et al. 2006); however, its long fibred low PCSA structure in the cheetah suggests it would not be particularly adept at this function. An electromyography study on domestic cats found both the SVt and SVc muscles to be active during the end of swing and the majority of stance (English, 1978a,b), and it was suggested that co-activity of these muscles causes the scapula translation and rotation that is observed in domestic cats. The fan-shaped SV muscles suspend the trunk from the scapula, and will allow both vertical and cranio-caudal displacement of the scapula relative to the trunk. In the horse it is pennate with short fibres (Payne et al. 2005), and has been proposed to potentially act to modulate limb stiffness (McGuigan & Wilson, 2003). The fibres are considerably longer in the cheetah, which indicates a greater capacity for modulation of the muscle force–length relationship, and hence limb stiffness and mechanical work during stance. In the cheetah the scapula moves both vertically and horizontally relative to the trunk during locomotion (Hildebrand, 1961), demonstrating that SV muscles have an important role in both the vertical and horizontal direction. In contrast, the greyhound's SV muscle has shorter fascicles and thus appears less well adapted for such movements of the scapular, but may still play an important role in regulating the stiffness of the limb.

The cheetah's ability to translate its scapula and therefore the point of rotation of its entire forelimb will have the functional benefit of increasing its effective limb length, without any of the previously mentioned disadvantages of increasing limb inertia. It will therefore enable longer strides, contact lengths and a more vertical limb at the extremes of stance, potentially aiding faster top speeds.

Comparative forelimb anatomy and function

Many of the cheetah's proximal intrinsic limb muscles (infraspinatus, supraspinatus, subscapularis and teres major) were larger in mass, had a larger PCSA and were more powerful than in the greyhound (Fig. 4A). They also had longer maximum moment arms (Fig. 3) in the cheetah when compared with the greyhound, enabling them to produce larger joint torques (Fig. 4C) but reducing their capacity to produce high joint rotational velocities (Fig. 4B). These muscles are all active during stance and are thought to support body weight by resisting GRF torques at the shoulder joint (English, 1978a,b). The ability of these muscles to create larger joint torques in the cheetah will aid in this function, which will be of great importance at high speeds, when peak limb forces are likely to be higher (Witte et al. 2006, 2004). The high speed manoeuvring that is characteristic of the cheetah's hunting style also results in high limb forces. These force vectors will be somewhat unpredictable in magnitude, orientation and position. It is therefore critical that the cheetah's musculoskeletal system can modulate and control these to prevent excessive joint torques, damage or instability. The large proximal muscle mass may fulfil this function through the highly appropriate force velocity characteristics of activated muscle; large muscles contain more crossbridges and are inherently better for high positive and negative work and active stabilisation (Woledge et al. 1985; Wilson et al. 2001). This is also true at the elbow where the long head of triceps, which functions to extend the joint during stance (English, 1978a,b), has a very similar architecture and mass but a substantially larger moment arm (Fig. 3). This suggests that the cheetah's forelimb is not functioning as a typical strut (Blickhan, 1989; Blickhan & Full, 1993), and that substantial joint moments are occurring. This has also been shown to be important in the highly elastic equine forelimb (Wilson et al. 2001; Lichtwark et al. 2009).

The pectoralis muscles (superficialis transverse and profundus portions) exhibited species variation in mass but little variation in fascicle length or PCSA. The pectoralis superficialis muscles have been shown to function during rapid deceleration (Carrier et al. 2008). The larger mass of the pectoralis superficialis transverse muscle in the cheetah may increase the muscular power available for deceleration. This would be crucial for the cheetah as during prey capture it will initially trip its prey, after which it must decelerate rapidly and get back to its prey to perform the killing bite. The pectoralis profundus muscle functions to retract the forelimb (Carrier et al. 2008). The cheetah's pectoralis profundus is significantly lighter in the cheetah than in the greyhound. It has been suggested that the greyhound uses its forelimbs for propulsion, and therefore may have developed a powerful pectoralis profundus for this function (Williams et al. 2008a).

To capture prey the cheetah often uses its dew claw to hook their rump and pull them off balance. The cheetah's dew claw is retractile, unlike its other claws, with an ungual claw sheath to help it remain sharp (Gonyea & Ashworth, 1975; Russell & Bryant, 2001). To protract its dew claw, co-contraction of the extensor digitorum communis and DDF is required (Gonyea & Ashworth, 1975). Both these muscles were larger in the cheetah than the greyhound, and we suggest this is to protract the dew claw during prey capture. The digital flexors (SDF and DDFr) were also heavier in the cheetah, and we hypothesise that this helps to flex the phalanges whilst galloping such that the claws are dug into the ground. This will aid with traction, which is especially important during the rapid accelerations and manoeuvres that the cheetah performs. The larger mass and PCSA of these muscles may also play a role in resisting hyperextension of the metacarpophalangeal joint during stance.

Study limitations

Study limitations are described in Hudson et al. (2011).

Conclusions

In conclusion, we have quantified the forelimb anatomy of the cheetah and compared it with existing data on the racing greyhound, identifying features that may contribute to the cheetah's superior speed.

(1) The cheetah has long fibred SV muscles that may aid scapula translation along the rib cage, resulting in an increase in the cheetah's effective limb length. This will enable the cheetah to take longer strides and have a longer contact length for a given speed, potentially increasing their top speed.

(2) When compared with the greyhound, we saw little specialisation for generating propulsion or strut-like behaviour in the cheetah's forelimbs, but it is instead a limb that is capable of resisting large GRF joint torques through having large PCSA muscles with long moment arms. This may reflect a need for control and stabilisation during high-speed manoeuvring in hunting.

(3) The digital flexor muscles and the extensor digitorum communis were significantly heavier in the cheetah than in the greyhound, which we hypothesise is an adaptation for protraction of the dew claw during prey capture. These muscles will also flex the digits, potentially enabling the claws to be dug into the ground and aid with traction during accelerations and manoeuvres.

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