RESEARCH ARTICLE

High speed galloping in the cheetah (*Acinonyx jubatus*) and the racing greyhound (*Canis familiaris*): spatio-temporal and kinetic characteristics

Penny E. Hudson, Sandra A. Corr* and Alan M. Wilson[†]

Structure and Motion Laboratory, Royal Veterinary College, University of London, Hawkshead Lane, South Mymms AL9 7TA, UK

*Present address: Division of Surgery, School of Veterinary Medicine and Science, University of Nottingham, Sutton Bonnington Campus LE12 5RD, UK

[†]Author for correspondence (awilson@rvc.ac.uk)

SUMMARY

The cheetah and racing greyhound are of a similar size and gross morphology and yet the cheetah is able to achieve a far higher top speed. We compared the kinematics and kinetics of galloping in the cheetah and greyhound to investigate how the cheetah can attain such remarkable maximum speeds. This also presented an opportunity to investigate some of the potential limits to maximum running speed in quadrupeds, which remain poorly understood. By combining force plate and high speed video data of galloping cheetahs and greyhounds, we show how the cheetah uses a lower stride frequency/longer stride length than the greyhound at any given speed. In some trials, the cheetahs used swing times as low as those of the greyhounds (0.2 s) so the cheetah has scope to use higher stride frequencies (up to 4.0 Hz), which may contribute to it having a higher top speed that the greyhound. Weight distribution between the animal's limbs varied with increasing speed. At high speed, the hindlimbs support the majority of the animal's body weight, with the cheetah supporting 70% of its body weight on its hindlimbs at 18 m s⁻¹; however, the greyhound hindlimbs support just 62% of its body weight. Supporting a greater proportion of body weight on a particular limb is likely to reduce the risk of slipping during propulsive efforts. Our results demonstrate several features of galloping and highlight differences between the cheetah and greyhound that may account for the cheetah's faster maximum speeds.

Key words: galloping, cheetah, greyhound, speed, force.

Received 14 October 2011; Accepted 25 March 2012

INTRODUCTION

The galloping cheetah [*Acinonyx jubatus* (Schreber 1775)] is characterised by the extreme movements of its back, and its rapidly swinging limbs, but primarily for its remarkable top speed. The fastest recorded speed of a cheetah is 29 m s⁻¹ as an average over a 200 m course (Sharp, 1997), and thus its top speed is likely to be even greater. In contrast, the fastest canid, the racing greyhound (*Canis familiaris* L.), has a top speed of just 17 m s⁻¹ (Jayes and Alexander, 1982; Usherwood and Wilson, 2005), despite the two animals being of a similar mass and gross morphology. Anatomical studies (Hudson et al., 2011a; Hudson et al., 2011b) have presented no clear reason as to why there is such a large difference in their top speeds, and there is no clear consensus in the literature as to what fundamentally limits the maximum running speed of a quadruped. Here, we studied the kinematics and kinetics of galloping in the cheetah and racing greyhound to investigate how the cheetah attains faster speeds than the greyhound, and to explore some of the theorised limits to maximum running speed.

The determinants of maximum running speed have been examined in detail for humans, and three major limits have been proposed; peak limb force, minimum achievable swing time and muscular power; however, such limits in quadrupeds remain relatively unexplored. During a stride an animal must produce a vertical impulse that is equal to the product of its body weight and stride time in order to support its body weight. The impulses required to do this must be generated during stance, and therefore, because

of decreases in contact time and duty factor with increasing speed (observed in several animals) (Hoyt and Taylor, 1981; Kram and Taylor, 1990; Usherwood and Wilson, 2005; Weyand et al., 2000; Witte et al., 2006), greater peak ground reaction forces (GRFs) must be resisted by the limbs to support the body weight of the animal. An animal may therefore encounter a speed where its limbs cannot resist a higher peak GRF (a force limit) perhaps due to the contraction properties or architecture of its muscles, or the safety limits of the skeletal elements of the limb may be approached. The animal can therefore increase its speed no further, and should slow down to increase contact time and reduce peak force. This phenomenon appears to be true for humans, as they run slower with longer contact times when going round a bend; a situation that simulates an increase in body weight as a result of the centripetal forces experienced by the runner (Bowtell et al., 2007; Usherwood and Wilson, 2006). This allows them to maintain constant peak limb forces, suggesting that they have already reached a peak limb force limit when running on the straight. In a similar study on racing greyhounds, it became apparent that, unlike humans, greyhounds are not constrained by the peak GRFs experienced during maximal speed running (Usherwood and Wilson, 2005). Despite this, the maximum speed of a turning racehorse appears to be limited by peak limb force and thus whether this is a constraint that is universal for all quadrupeds remains unknown (Tan and Wilson, 2010). All of these studies, however, relied on estimates of peak GRF from duty factor, estimates of body weight distribution (Jayes and

Alexander, 1978), and an assumption that the GRF is sinusoidal; thus, the peak force estimates could be somewhat incorrect.

Another proposed limit to speed is the minimum time in which an animal can reposition its limb during swing. There are several adaptations that can minimise the muscular work required to swing the limb, some of which have been observed in both the cheetah and greyhound. Reduced distal limb mass is observed in both species and will reduce the inertia of the limb (Hudson et al., 2011a; Hudson et al., 2011b; Williams et al., 2008a; Williams et al., 2008b). Muscle insertions that are close to the joint will allow faster joint rotational velocities for a given change in muscle length and are observed in the greyhound, but the cheetah hip and shoulder muscles tend to have long moment arms by comparison (Hudson et al., 2011a; Hudson et al., 2011b). Finally, the recruitment of fast glycolytic or long muscle fibres that will contract at higher velocities than slow oxidative or short fibres will rotate the limb more rapidly. Fast fibres have been shown to be prevalent in cheetahs (Hyatt et al., 2010; Williams et al., 1997), and in the greyhound when compared with other dog breeds (Rodriguez-Barbudo et al., 1984). Weyand highlighted the importance of this limit in humans, illustrating there to be no variation in the minimum limb swing times (0.37 s) achieved by elite athletes and non-runners (Weyand, 2000). In horses, protraction of the limb is believed to be a rapid catapult process (Lichtwark et al., 2009; Wilson et al., 2003), as there is no significant variation in swing time (0.35 s) with increasing speed in the horse (Witte et al., 2006). To achieve high speeds, an ability to minimise swing times is crucial.

The final limit is the muscular power that an animal has to replace losses in centre of mass (CoM) energy during a stride. An animal may reach a speed at which the power requirements to maintain a constant horizontal speed are so great that it is unable to accelerate further. This limit has been studied by increasing the power requirements on an individual through incline running. In humans, the cost of locomotion has been shown to increase with increased gradient. This results in a decrease in running speed (Minetti et al., 1994); however, such studies were performed at sub-maximal speeds and thus as a limit to maximal speed, muscular power remains relatively unexplored.

There is minimal information on the stride parameters used by the cheetah. One study reported that at $25\,\mathrm{m\,s^{-1}}$ a cheetah completes a stride in 0.28 s with a stride length of 7 m, but no other temporal information or any GRF information is known (Hildebrand, 1961).

Two studies have investigated limb forces during galloping in dogs (Bryant et al., 1987; Walter and Carrier, 2007), but none have examined steady-state galloping in the greyhound, which has a highly specialised morphology compared with other canids (Williams et al., 2008a; Williams et al., 2008b).

Both the cheetah and greyhound use a galloping gait at top speeds. Early studies identified that two defined types of gallop exist: a transverse gallop and a rotary gallop (Muybridge, 1957). The cheetah and greyhound both use a rotary gallop. This is an asymmetrical gait where the feet fall in a circular sequence around the body (Hildebrand, 1959), and it contains two aerial phases: a gathered aerial phase where the back is flexed and the hindfeet pass in front of the forefeet, and an extended aerial phase where the feet are stretched away from the body and the back is extended.

There are several theories as to why the rotary gallop may be beneficial, including reducing momentum losses during stance (Bertram and Gutmann, 2009), and allowing internal work to be stored in the elastic structures of the back, increasing efficiency (Alexander, 1988). Here, we examined the temporal parameters and limb forces used by the cheetah and greyhound when galloping at various speeds. We aimed to explore some of the potential limits to maximum running speed (limb force and swing time) by comparing two of the fastest quadrupedal animals: the cheetah and the racing greyhound.

MATERIALS AND METHODS
Subjects

Data were collected from three cheetahs at ZSL Whipsnade Zoo, Dunstable, UK, and six cheetahs at the Ann van Dyk Cheetah Centre, Pretoria, South Africa. These were compared with data from six ex-racing greyhounds from the Retired Greyhound Trust, Hertfordshire, UK. All subjects were mature (over 2 years of age), considered fit (as they were regularly exercised) and free from any musculoskeletal pathologies. See Table 1 for subject information. The protocols for this study were approved by the Royal Verterinary College's Ethics and Welfare committee, as well as the committees associated with each of our collaborators.

Limb lengths were measured in a standing posture for each subject using a flexible measuring tape. The forelimb length was measured from the top of the scapular to the ground, hindlimb length from the greater trochanter of the femur to the ground, and back length as the distance between the base of neck (c1) and the base of tail (sacrocaudal junction).

Table 1. Subject information and the number of strides and single limb contacts (SLCs) analysed for each individual

| Subject	Institution	Mass (kg)	Back length (m)	Hindlimb length (m)	Forelimb length (m)	No. of strides analysed	No. of SLCs analysed
Cheetah 1	ZSL Whipsnade Zoo	–	0.83	0.59	0.63	4	–
Cheetah 2	ZSL Whipsnade Zoo	30	0.63	0.48	0.54	14	19
Cheetah 3	ZSL Whipsnade Zoo	35	0.76	0.51	0.59	17	21
Cheetah 4	Ann van Dyk Cheetah Centre	35	0.65	0.54	0.61	2	–
Cheetah 5	Ann van Dyk Cheetah Centre	33	0.68	0.53	0.58	4	–
Cheetah 6	Ann van Dyk Cheetah Centre	35	0.8	0.60	0.66	5	–
Cheetah 7	Ann van Dyk Cheetah Centre	41	0.72	0.55	0.61	2	–
Cheetah 8	Ann van Dyk Cheetah Centre	40	0.68	0.52	0.59	3	–
Cheetah 9	Ann van Dyk Cheetah Centre	45	0.73	0.56	0.63	2	–
Greyhound 1	Retired Greyhound Trust	32	0.71	0.50	0.59	6	22
Greyhound 2	Retired Greyhound Trust	30	0.71	0.54	0.61	6	22
Greyhound 3	Retired Greyhound Trust	31	0.66	0.52	0.60	4	14
Greyhound 4	Retired Greyhound Trust	35	0.69	0.50	0.59	4	14
Greyhound 5	Retired Greyhound Trust	28	0.69	0.49	0.57	6	23
Greyhound 6	Retired Greyhound Trust	30	0.68	0.50	0.56	5	15
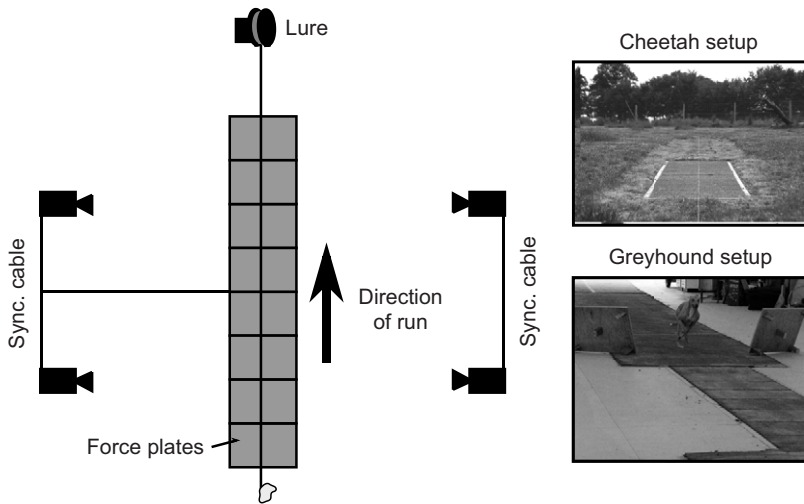
Fig. 1. Diagram of the experimental setup. The cheetahs and greyhounds both chased a mechanical lure across eight Kistler force plates. A set of two AOS cameras filmed the subject from each side of the run and each set was synchronised to global positioning system (GPS) time.

Stride parameters

All subjects were trained to chase a mechanical lure along a track of approximately 90 m. Four AOS high speed cameras (AOS Technologies AG, Dättwil, Switzerland; 1280×560 pixels; ~0.24 pixels mm^{-2} for cheetahs and 0.5 pixels mm^{-2} for greyhounds) were positioned 50 m from the start of the runway, with two on each side of the track to capture both sides of the animal; the two sets of cameras were synchronised to global positioning system (GPS) time (Fig. 1). A frame rate of 1000 Hz was used to film the cheetahs, and a lower frame rate of 350 Hz was used to film the greyhounds because of the different lighting conditions. The greyhound data were also combined with measurements made during a race, recorded at 250 Hz (Usherwood and Wilson, 2005).

Limb forces

Force plate data were collected from two of the cheetahs at ZSL Whipsnade Zoo. For this, a hole was dug into the track and the edges stabilised with a wooden frame. The hole was filled with compacted and levelled sand to provide a solid base, on top of which a custom-built steel frame was placed. Eight Kistler force plates (model 9287A and 9287B, Kistler group, Winterthur, Switzerland) were positioned onto the frame. Each individual plate was topped with a plywood top-plate onto which an artificial grass surface (commercial artificial football surface, 20 mm thick, which was filled with sand) was attached.

Force plate data were collected from all six greyhounds at the Structure and Motion Lab, Royal Veterinary College, on an artificial grass runway (as above), across the same array of eight Kistler force plates.

For both species, the force plate array was positioned ~50 m along the 90 m runway, and the force plate data were synchronised to the high speed video. Data were collected at 1000 Hz for both species.

Data analysis

Body mass calibration

For interspecies and individual comparisons, all force plate data were normalised to body mass. For each subject, body mass was calculated for five strides, where all four feet in the stride were in contact with the plates. The subject's body mass (m) was then calculated as:

$$m = \frac{\int_{t_{end}}^{t_{start}} \mathbf{F}_z \, dt}{\mathbf{g}} \times \text{Stride frequency}, \qquad (1)$$

where $\mathbf{F}_z$ is vertical force, g is acceleration due to gravity, t_{start} is the stride start time and t_{end} is the stride end time. The body masses were then averaged and used for normalising the data. See Table 1 for subject's body masses.

Stride parameters

Temporal stride parameters: stride time, limb stance time and limb swing time were measured from the high speed video using VirtualDub (v.1.9.9, www.virtualdub.org). Microsoft excel (Microsoft office 2007) was then used to calculate duty factor (stance time/stride time). Videos were calibrated for distance by placing an object of known size in the field of view. Lens distortion and parallax effects were accounted for, to enable stride lengths to be calculated. This analysis was performed using custom-built software in Matlab (Mathworks Inc., Natwick, MA, USA). Only strides in which the subjects performed a smooth rotary gallop were included in the analysis.

GRFs

Force data were filtered using a 3rd order low pass Butterworth filter (400 Hz cut off) using custom-written software in Matlab. Individual stances (where the limb was fully on a plate) were identified and cut. Peak forces were calculated in each direction (cranio-caudal, vertical and medio-lateral), and impulses were calculated as the integral of force with respect to time during each stance phase.

Statistics

Correlations between stride parameters and limb forces with speed were examined using linear mixed models (LMMs) in MLwiN (v2.21, www.bristol.ac.uk/cmm/software/mlwin/), because of the nested, multi-level structure of the data. A variable intercept and variable slope model was created in which subject and trial were included as nested random effects. Species and speed were included as fixed effects to examine their effect on the dependent variable, i.e. the particular stride parameter of interest. To determine whether the correlation was quadratic, a speed × speed term was included in the model. Similarly, to determine whether the slope of the lines for each species were significantly different from one another, a species × speed term was included in the model. Significance of each parameter in the model was determined using a chi-squared test. The results, including the effect size of each parameter and the result of the chi-squared test, are provided in Table 2.

Table 2. LMM model analysis of correlations between stride parameters and limb forces with speed, controlling for individual and trial

Model term	Species			Speed			Speed^2			Species × speed		
	Estimate	d.f.	χ^2	Estimate	d.f.	χ^2	Estimate	d.f.	χ^2	Estimate	d.f.	χ^2
Stride frequency (Hz)	1.962	1	19.414**	0.090	1	25.815**	–	–	–	–0.100	1	10.734**
Stride length (m)	–2.133	1	13.067**	0.211	1	84.174**	–	–	–	0.940	1	5.633*
Normalised stride length:												
by back length	–0.873	1	7.754**	0.332	1	132.459**	–	–	–	–	–	–
by hindlimb length	–0.858	1	6.352*	0.453	1	136.403**	–	–	–	–	–	–
NLFL												
Stance time (s)	–0.002	1	0.334	–0.020	1	74.861**	0.001	1	48.555**	–	–	–
Swing time (s)	–0.175	1	19.788**	–0.005	1	9.875**	–	–	–	0.009	1	10.218**
Duty factor	0.133	1	13.960**	–0.051	1	35.273**	0.002	1	25.470**	–0.008	1	9.507**
Peak vertical force (BW)	0.190	1	1.390	–0.017	1	0.045	–	–	–	–	–	–
Vertical impulse (BW ms)	4.664	1	0.546	–6.731	1	31.548**	–	–	–	–	–	–
Accelerative impulse (BW ms)	–15.974	1	4.755*	0.879	1	3.625	–	–	–	1.178	1	4.19*
Decelerative impulse (BW ms)	–27.947	1	11.172**	–0.275	1	0.272	–	–	–	2.178	1	10.944**
LFL												
Stance time (s)	–0.002	1	0.934	–0.018	1	43.949**	0.001	1	26.561**	–	–	–
Swing time (s)	–0.174	1	18.404**	–0.005	1	8.966**	–	–	–	0.009	1	9.538**
Duty factor	0.166	1	19.763**	–0.050	1	30.992**	0.002	1	22.899**	–0.010	1	14.802**
Peak vertical force (BW)	0.419	1	6.112*	–0.023	1	0.746	–	–	–	–	–	–
Vertical impulse (BW ms)	13.095	1	4.11*	–6.103	1	37.268**	–	–	–	–	–	–
Accelerative impulse (BW ms)	–1.167	1	0.929	1.638	1	32.022**	–	–	–	–	–	–
Decelerative impulse (BW ms)	–23.255	1	4.783*	–0.642	1	0.970	–	–	–	1.875	1	5.495*
NLHL												
Stance time (s)	–0.003	1	0.506	–0.015	1	34.799**	0.000	1	20.151**	–	–	–
Swing time (s)	–0.162	1	16.320**	–0.005	1	9.263**	–	–	–	0.008	1	7.825**
Duty factor	0.025	1	11.423**	–0.008	1	48.508**	–	–	–	–	–	–
Peak vertical force (BW)	–0.245	1	2.387	0.152	1	12.543**	–	–	–	–	–	–
Vertical impulse (BW ms)	–9.188	1	1.587	2.306	1	1.362	–	–	–	–	–	–
Accelerative impulse (BW ms)	–2.247	1	1.082	2.400	1	19.038**	–	–	–	–	–	–
Decelerative impulse (BW ms)	3.334	1	9.411**	–0.133	1	0.204	–	–	–	–	–	–
LHL												
Stance time (s)	–0.006	1	10.343**	–0.011	1	18.748**	0.000	1	9.906**	–	–	–
Swing time (s)	–0.159	1	16.025**	–0.006	1	12.487**	–	–	–	0.008	1	8.177**
Duty factor	0.011	1	2.818	–0.006	1	37.500**	–	–	–	–	–	–
Peak vertical force (BW)	–1.083	1	5.302*	0.094	1	4.681*	–	–	–	–	–	–
Vertical Impulse (BW ms)	8.055	1	13.039**	1.701	1	1.132	–	–	–	–	–	–
Accelerative impulse (BW ms)	–7.785	1	4.786*	2.397	1	12.426**	–	–	–	–	–	–
Decelerative impulse (BW ms)	4.958	1	10.383**	–0.693	1	2.668	–	–	–	–	–	–

A correlation with speed^2 was examined to establish whether the relationship was curvilinear, and species × speed to allow the slope of the species to vary.
   Species variations were also examined in the linear mixed models (LMM).
The table shows parameter estimates, d.f. and associated test statistic (χ^2) for fixed effects.
*$P<0.05$; **$P<0.01$.

RESULTS
Stride parameters

Stride parameters were collected for nine cheetahs (53 strides) and six greyhounds (47 strides). The cheetahs galloped at speeds ranging from 8.7 to 17.8 m s^{-1}, and the greyhounds at speeds from 9.9 to 19.0 m s^{-1}. Both species used a rotary gallop at these speeds (Fig. 2). The cheetah often changed its lead limb during a trial, in response to the position/bounce of the lure. The cheetah used a longer gathered aerial phase time than the greyhound (LMM: χ^2=17.598, d.f.=1, $P<0.01$), and for both species the duration of the gathered aerial phase did not change with increasing speed. In contrast, the extended aerial phase duration increased with increasing speed in both species (LMM: χ^2=32.897, d.f.=1, $P<0.01$).

The effect of speed on stride length and stride frequency was examined (Fig. 3). In both species, stride length shows a strong linear increase with increasing speed and the cheetah used significantly longer strides than the greyhound at any given speed (Table 2). Two statistical tests were performed to test for the influence of species/individual size on the stride lengths observed; initially, stride lengths were normalised by either back length or hindlimb length and the same LMM was performed (Table 2). For the second test, segment lengths were included as random variables in the LMM (Table 2). Both forms of normalisation removed the interspecies variation in stride length. The stride frequency data were highly variable but showed a trend to increase with increasing speed in the cheetah, but not in the greyhound (Table 2).

For each limb, similar patterns in stance time, swing time and duty factor with increasing speed (Fig. 4) were observed. A decrease in stance time with increasing speed was apparent for all limbs (Table 2). The cheetah's lead hindlimb (LHL) had significantly longer stance times than those in the greyhound, but no other limbs exhibited species variation in stance time. Swing times proved to be highly variable in both species with only weak correlations apparent. The cheetah showed a weak trend to decrease swing time with increasing speed; however, the greyhound showed a weak trend to increase swing time with increasing speed. For all limbs, the
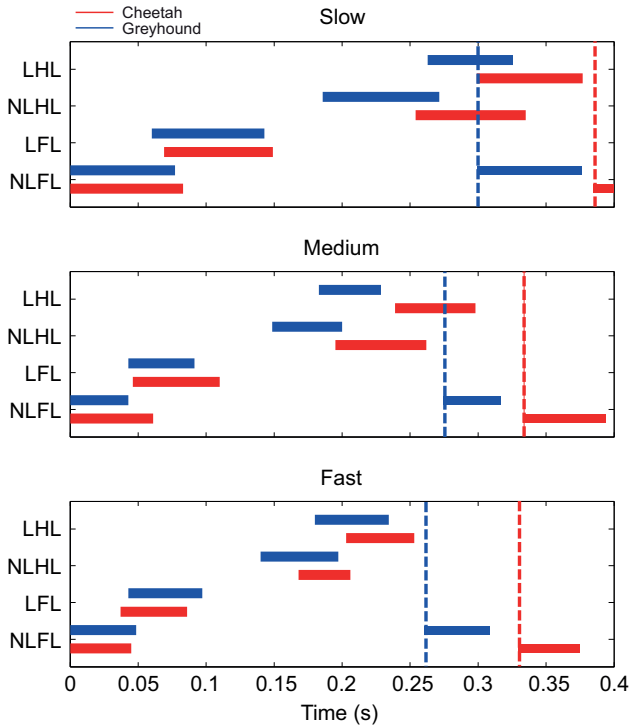
Fig. 2. A representative example of stance timing during strides at various speeds. Red bars represent the stance periods of each limb of the cheetah and blue bars those of the greyhound during a complete stride at different speeds. The dashed vertical lines represent the end of the stride. Both animals use a rotary gallop whereby the non-lead forelimb (NLFL) contacts first followed by the lead forelimb (LFL). This is followed by the gathered aerial phase when the feet are pulled together prior to the non-lead hindlimb (NLHL) contact. Last to contact is the lead hindlimb (LHL); this is followed by the extended aerial phase where the feet are extended away from the body before the stride cycle starts again. Slow: 8 to <12 m s^{-1}; medium: 12 to <14 m s^{-1}; fast: >14 m s^{-1}.

significantly lower duty factors than the greyhound with the exception of the LHL, where no species variation was observed.

Limb forces

For two cheetahs and all six greyhounds, we were able to simultaneously collect GRFs and high speed video. In total, 40 single limb contacts (SLCs) were analysed for the cheetahs and 110 for the greyhounds. A SLC was defined as a stance period when only one limb contacts a single plate. Trials ranged from 8.7 to 15.0 m s^{-1} for the cheetah and from 9.9 to 16.3 m s^{-1} for the greyhound. Data were divided into three speed categories (slow: 8 to <12 m s^{-1}; medium: 12 to <14 m s^{-1}; fast: >14 m s^{-1}) and averaged (Fig. 5).

Both hindlimbs showed an increase in peak limb force with increasing speed and vertical limb impulse remained constant (Table 2). The forelimbs exhibited a significant decrease in vertical impulse with increasing speed (Table 2) and no variation in peak force with speed was observed. The LHL exhibited species differences in vertical impulse but not in peak force (Table 2).

In three cheetah trials ($N=2$, 9–15 m s^{-1}) and 12 greyhound trials ($N=6$, 10–15 m s^{-1}), SLCs were obtained for every footfall in a complete stride. From these, the percentage of body weight supported on each limb was calculated from the impulses each limb applied. The cheetah supported ~25% of its body weight on each limb. This was significantly different in the greyhound, which supported a greater proportion (56±5.5%) of its body weight on its forelimbs (non-lead forelimb, NLFL LMM: $\chi^2=4.157$, d.f.=1, $P<0.05$). There was a large difference in the amount of body weight supported by the two hindlimbs, with the non-lead hindlimb (NLHL) supporting 26±5.7% and the LHL just 18±5.5%, significantly less than in the cheetah (LHL LMM: $\chi^2=6.478$, d.f.=1, $P<0.05$). Despite this, the decreases in forelimb vertical impulse with increasing speed indicate that the front–back weight distribution varies with speed.

The cranio-caudal impulses were small in comparison to the vertical impulses, with a mean total (across all four limbs) decelerative impulse of −16.0±0.5 BW ms and an accelerative impulse of 13.4±0.9 BW ms for the cheetah and values of −14.1±0.5 and 12.0±0.5 BW ms, respectively, for the greyhound. The decelerative and accelerative impulses applied by the cheetah's NLFL and LHL were significantly larger than those in the greyhound

cheetah used significantly longer swing times than the greyhound at all speeds. These differences in swing times and stance times are reflected in the duty factor results where the cheetah used
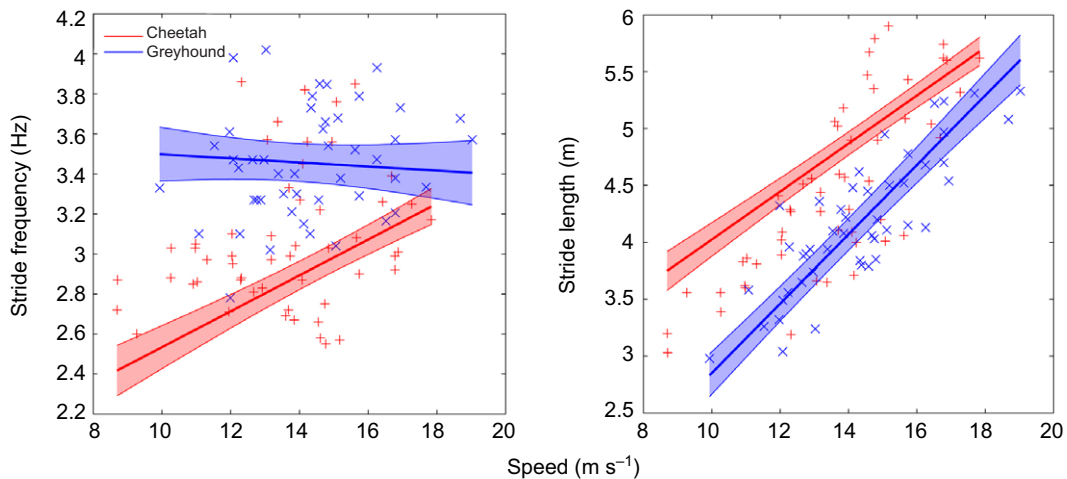
Fig. 3. Variation in stride frequency (left) and stride length (right) with increasing speed in the cheetah (red +) and greyhound (blue x). Stride length significantly increased with speed ($P<0.01$) and cheetahs used significantly longer strides than greyhounds ($P<0.01$). Stride frequency showed a gradual increase with speed in the cheetah ($P<0.01$) but no significant change in the greyhound. Across the whole speed range the greyhound used significantly higher stride frequencies than the cheetahs ($P<0.01$). Lines represent predicted means from the linear mixed models (LMM) ± s.e.m.
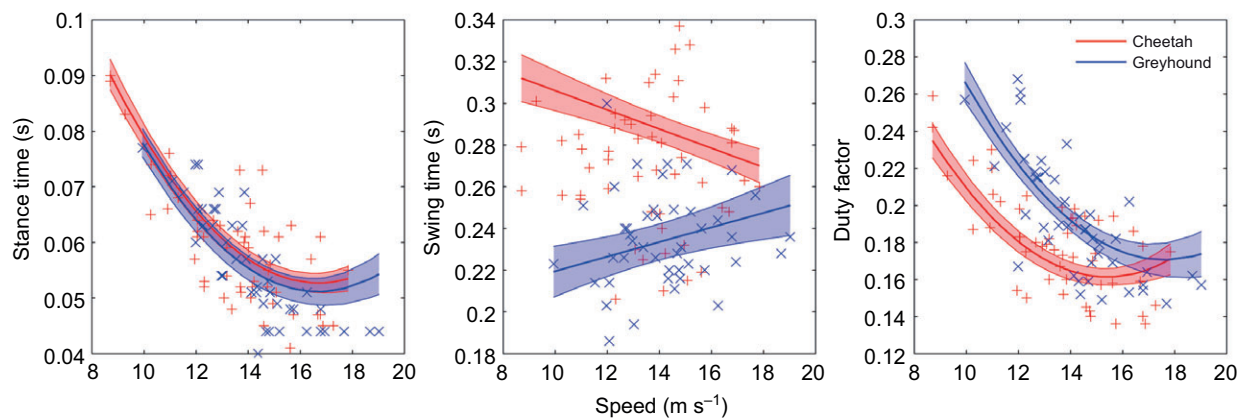
Fig. 4. Variations in stance time (left), swing time (middle) and duty factor (right) with increasing speed in the cheetah (red +) and greyhound (blue x) for the NLFL. Both stance time and duty factor showed a curvilinear decrease with speed ($P<0.01$). In the cheetah, swing time decreased with increasing speed, but a weak increase with increasing speed was observed in the greyhound. Cheetahs used significantly longer swing times ($P<0.01$) and significantly lower duty factors ($P<0.01$) than the greyhounds. This pattern was observed on all limbs except the LHL, for which cheetahs used significantly longer stance times and swing times, and there were no significant species differences in duty factor. Lines represent predicted means from the LMM ± s.e.m.

(Table 2). Medio-lateral forces were highly variable and very small in magnitude for both species.

DISCUSSION

To date, we have limited knowledge of the galloping gaits used by quadrupeds. This is the fastest gait quadrupeds use, and thus a good understanding of it may prove crucial when investigating the limits of speed. The aim of the present study was to investigate some of the proposed limits to maximum running speed in the cheetah and greyhound, and to determine how the cheetah attains a top speed of $29\,\mathrm{m\,s^{-1}}$ (Sharp, 1997) whilst the greyhound, which is of a similar mass and morphology, can only attain a top speed of $17\,\mathrm{m\,s^{-1}}$ (Jayes and Alexander, 1982; Usherwood and Wilson, 2005). Studies of galloping mechanics have often been limited by the technology available, with earlier studies based solely on kinematic measurements (Minetti et al., 1999). More recent work using inertial sensors (Pfau et al., 2006; Witte et al., 2004) has provided some insight into the transverse gallop in horses, but the rotary gallop remains poorly understood. Here, we implemented a traditional 'in lab' protocol combining force plates and high speed video in a field environment, allowing for accurate collection of GRFs and kinematics simultaneously.

From the kinematics, we can confirm that both species adopted a rotary gallop gait (Fig. 2) at high speed, as has been highlighted by many authors (Bertram and Gutmann, 2009; Hildebrand, 1959; Maes et al., 2008; Walter and Carrier, 2007). The cheetahs often changed their lead limb in response to the bounce/movements of the lure, and thus they frequently completed the footfall sequence associated with a transverse galloping stride, a phenomenon noted previously (Hildebrand, 1959). This would help the cheetah respond to turns made by the prey (or the lure in this case). In our study, the cheetahs galloped between 8.7 and $17.8\,\mathrm{m\,s^{-1}}$, and the greyhounds between 9.9 and $19.0\,\mathrm{m\,s^{-1}}$. For the greyhounds, this is close to what is often considered their maximum running speed (Usherwood and Wilson, 2005); however, this is far below the maximum speed reported for a cheetah (Sharp, 1997). The cheetahs used in this study were all captive bred but were regularly (2–3 times per week) run with the lure, and thus could be considered fit, but being captive bred, may never have had the motivation to run at full speed or chase live prey. It is believed that a lack of motivation rather than

a lack of ability is the main reason why the cheetahs studied here did not run faster.

It has been suggested that a plateau in stride frequency is reached at just $4.0\,\mathrm{m\,s^{-1}}$ in most animals, and that stride length increases with speed thereafter (Maes et al., 2008). For the data collected in this study there was substantial variation in the stride frequencies used by greyhounds at any one speed, but no consistent trend with increasing speed was observed. In contrast, an increase in mean stride frequency from 2.4 to $3.2\,\mathrm{Hz}$ was observed in the cheetah. Across the whole dataset, maximum stride frequencies of $3.9\,\mathrm{Hz}$ were used by both species; a maximum that far exceeds that used by other fast quadrupeds (Heglund and Taylor, 1988; Witte et al., 2006) and that previously observed for the cheetah (Hildebrand, 1961). For both species, a linear increase in stride length with speed was observed, and the cheetah used longer stride lengths than the greyhound, which can be explained by the cheetah's slightly longer limbs and back (Hudson et al., 2011a; Hudson et al., 2011b). During a gallop, the greyhound therefore appears to only increase its stride length; however, the cheetah uses a combination of increased stride frequency and stride length to achieve higher speeds.

There are three major theories as to what limits the maximum speed an animal can achieve. The first is the minimum achievable swing time limit (Weyand et al., 2000). With the exception of the LHL, the cheetah exhibits a significant decrease in swing time with increasing speed, whereas the greyhound exhibits a weak increase. This is in contrast to work on both humans (Weyand et al., 2000), where no variation in swing times was observed between people of varying running abilities, and horses (Witte et al., 2006), where no significant correlation between swing time and speed was found. In horses, protraction of the limb is thought to be a largely passive movement (Lichtwark et al., 2009; Wilson et al., 2003). There may be a passive component to limb protraction in the cheetah and greyhound; however, the decrease in the swing times used by the cheetah, at ~0.05 s across the speed range examined here, suggests that limb protraction in the cheetah may be an active motion. This is supported by the presence of large psoas muscles in the cheetah, which have the main function of protracting the hindlimbs (Hudson et al., 2011b).

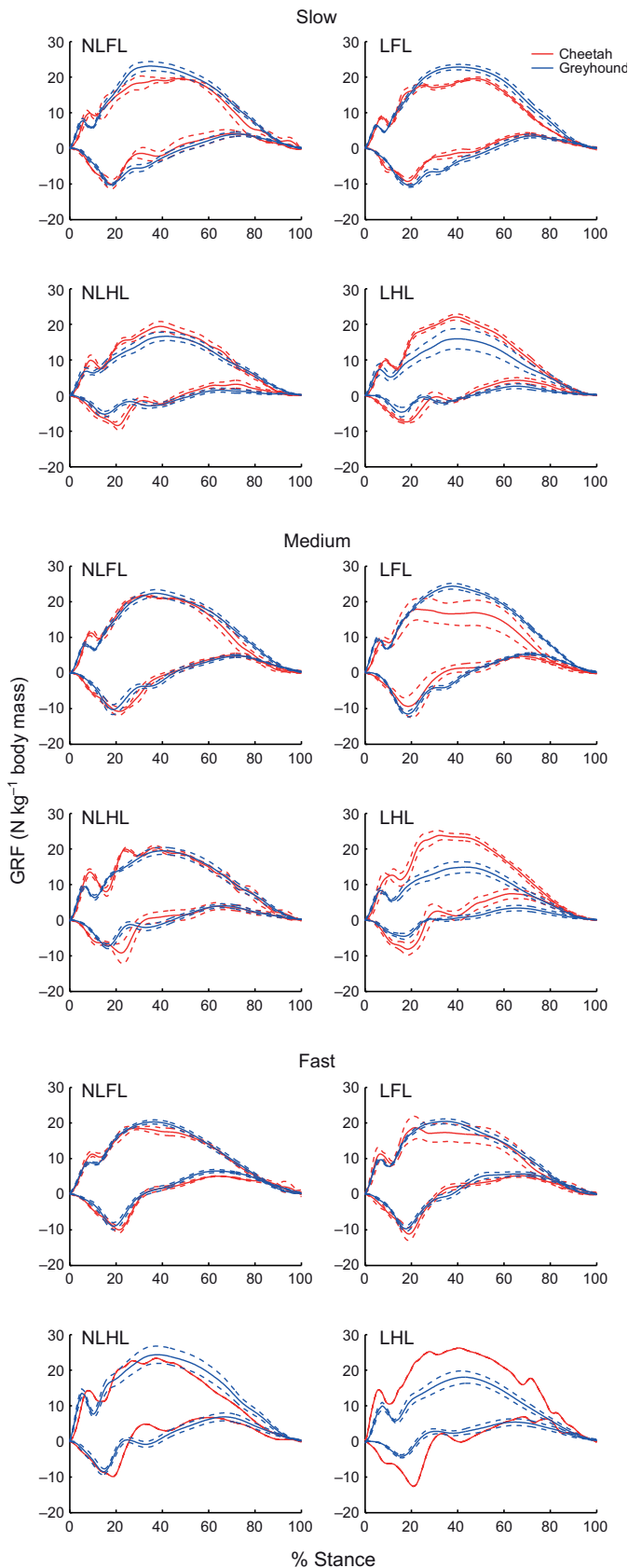The cheetah's swing time, at a mean of 0.27±0.01 s, is significantly longer than the greyhound's (0.24±0.02 s) for the

Fig. 5. Mean vertical and cranio-caudal ground reaction force (GRF) curves (±s.e.m.) for stances of each limb for cheetahs (red) and greyhounds (blue) within various speed ranges: slow: 8 to <12 m s⁻¹; medium: 12 to <14 m s⁻¹; fast: >14 m s⁻¹.

NLFL. Despite this, the minimum swing times observed for the two species are similar at 0.20 s for the cheetah and 0.19 s for the greyhound, suggesting that the animals are capable of using similar minimum swing times and are not usually limited by their muscular capabilities or limb inertia. It therefore appears that the greyhound galloping at 19 m s⁻¹ has attained its maximum stride frequency whilst the cheetah is usually capable of a further increase in frequency. It is interesting to speculate whether a cheetah with a stride frequency of 3.9 Hz could use its higher observed stride length to run even faster or whether some other mechanical factor would limit speed.

The second theory concerns the peak force that the limbs can withstand (Usherwood and Wilson, 2005; Usherwood and Wilson, 2006; Weyand et al., 2000). Within the speed ranges studied, the cheetahs used significantly lower duty factors than the greyhounds (with exception of the LHL). The lower duty factors used by the cheetah would normally indicate that the cheetahs are experiencing higher peak limb forces than the greyhound; however, the small differences in duty factor did not result in significant differences in peak limb force, probably because of the variability within the dataset. Despite this, an interesting trend in peak vertical limb force and impulses was observed with increasing speed. The cheetah's hindlimbs maintained constant impulses at higher speed by increasing peak vertical force to counteract the decreasing stance time. Peak force increased from 200 to 900 N as speed increased, and the cheetah's LHL used significantly larger peak vertical forces and impulses than the greyhound's. The forelimbs, however, exhibited no correlation between peak vertical force and speed, with peak vertical force remaining between 500 and 900 N across all speeds. As stance times decreased, the vertical impulses applied by the forelimbs therefore decreased. This could be interpreted as the forelimbs attaining a peak force limit at ~900 N (3.0 body weights) and impulse decreasing with stance time. Whilst running during a hunt, a cheetah will often lift up one of its forelimbs to swipe at the prey and pull it off balance and the cheetah also performs sharp and rapid turns, and rapid deceleration (Hunter and Hamman, 2003). Each of these situations is likely to require a higher forelimb impulse than steady-state maximal running, so it appears unlikely that a simple forelimb force limit to speed exists.

The third theory relates to the muscular power available for external work. Unfortunately, we are unable to infer anything about this limit in cheetahs and greyhounds. Further work on fluctuations in mechanical work during galloping, maximal accelerations and maximal uphill galloping would be required to investigate this further.

There are many other factors that could be limiting the maximum speed that a quadruped can achieve which were not explored in this paper. Such limits include ground speed matching (retraction speed of the limb), maintaining stability and simply motivation. It is unlikely that there is one confounding factor that limits maximum speed in quadrupeds, but rather several limits exist, both mental and physical.

For three cheetah trials (speeds of 9.3–14.8 m s⁻¹) and 12 greyhound trials (speeds of 11.1–14.8 m s⁻¹) we were able to calculate how body weight was supported by each individual limb during a stride. Traditionally, quadrupeds are believed to support 60% of their body weight on their forelimbs and 40% on their hindlimbs; however, most of these studies have been performed on standing or walking animals (Jayes and Alexander, 1978), with walking dogs supporting 61% and sheep 57% of their body weight on their forelimbs. A more recent study on horses found no
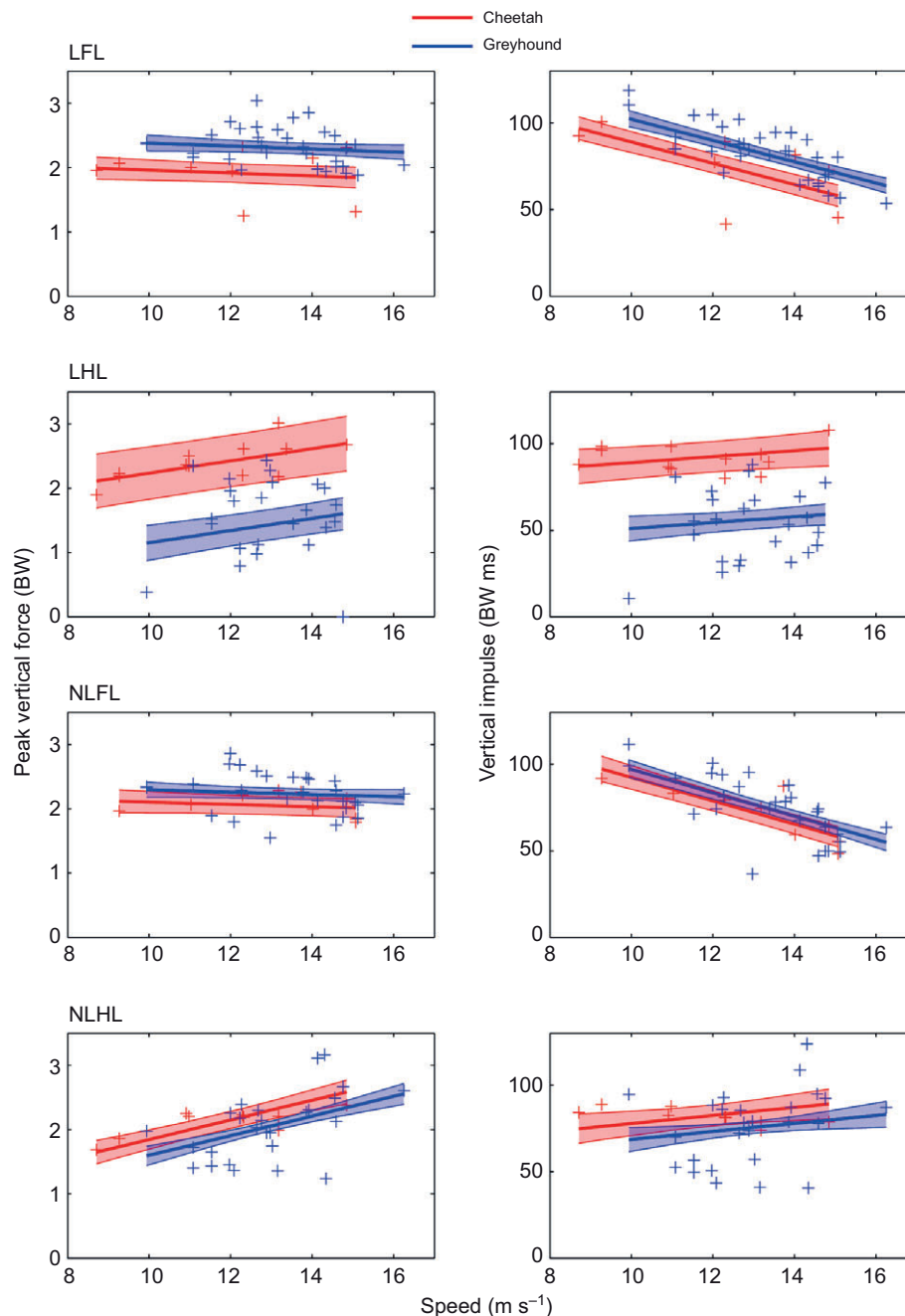
Fig. 6. Variations in limb peak vertical force (BW, body weight) and limb vertical impulse with increasing speed in the cheetah (red +) and greyhound (blue x). Variations are shown for each of the limbs, whereby lines represent predicted means from the LMM ± s.e.m. Both forelimbs showed a significant decrease in vertical impulse with increasing speed ($P<0.01$), and the vertical impulse applied by the cheetah's LHL was significantly larger than that applied by the greyhound's. The NLHL showed a significant increase in peak vertical force with speed ($P<0.01$), but no significant species variation in peak force was apparent.

significant change in weight distribution with increasing speed and changing gait, with 57% of their body weight being supported on their forelimbs (Witte et al., 2004); however, both cheetahs and greyhounds appear to support body weight differently whilst galloping. As for most other quadrupeds, greyhounds support more of their body weight (56%) on their forelimbs, but the division of weight on the two hindlimbs is very asymmetrical, with 27% of body weight supported by the NLHL and only 17% by the LHL. This fore–hind weight distribution is similar to that observed in galloping dogs (various breeds) (Walter and Carrier, 2007); however,

at the lower speeds examined ($9.2\pm0.3\,\mathrm{m\,s^{-1}}$), these researchers observed the hindlimbs contributing equally.

Despite this, the impulse records indicate that the proportion of body weight supported by each limb changed considerably with increasing speed (Fig. 6). The LMM fits of speed against impulse for each individual limb were used to calculate how body weight support is distributed across the limbs with increasing speed (Fig. 7). In both species, the forelimbs tend to support a greater proportion of the body weight than the hindlimbs at low speed; however, as speed increases this changes such that the hindlimbs
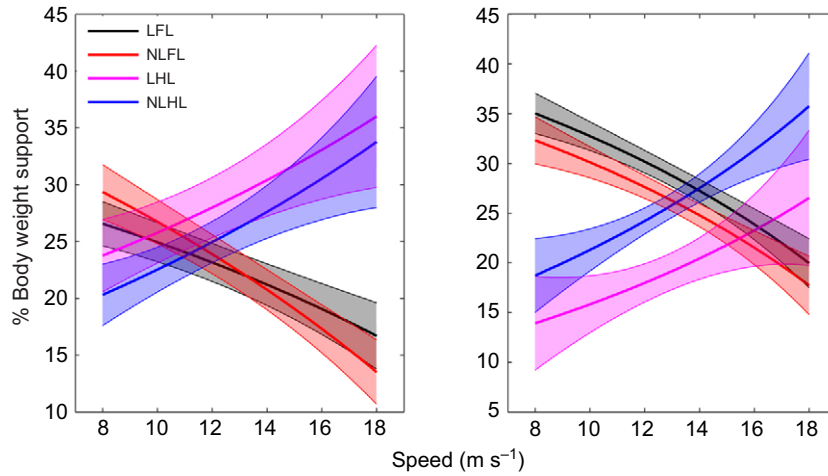
Fig. 7. Percentage of body weight support on each limb of the cheetah (left) and greyhound (right), as calculated from the LMM fits to speed against impulse for each individual limb (Fig. 6).

deliver the majority of the vertical impulse. At $18\,m\,s^{-1}$ (the fastest speeds for which data could be collected), the cheetah supports 70% of its body weight on its hindlimbs, and the greyhound's hindlimbs support 62% of its body weight. This difference may be due to the highly flexible back of the cheetah enabling it to position its hindlimbs further forward, and therefore more directly under its CoM than the greyhound can. Supporting more body weight on its hindlimbs will enhance the cheetah's grip for acceleration and manoeuvring using the hindlimb musculature, thereby reducing the risk of slipping. This may also increase the capacity for using the forelimbs for prey capture and not solely weight support.

The smaller proportion of body weight supported by the LHL of the greyhound may be due to the forelimbs and NLHL having deflected the CoM to such a height, that the LHL simply cannot apply a large impulse (Bertram and Gutmann, 2009). In such a case the limb would be extended throughout stance, and therefore would have a limited role to exert force on the CoM at these straight line speeds. This is also reflected in the lower accelerative and deccelerative impulses that the greyhound's LHL applies to its CoM when compared with the cheetah.

Finally, we also note that the cheetah and greyhound are able to apply large accelerative impulses, at the end of stance, whilst

supporting minimal body weight (Fig. 8). We believe this is made possible by their substantial claws (Gonyea and Ashworth, 1975; Gorman and Londei, 2000; Russell and Bryant, 2001). The artificial grass surface that the cheetahs and greyhounds ran over allowed their claws to dig in and deliver high levels of grip. On some preliminary trials, whilst galloping on a roughened concrete surface, the greyhound's feet slipped forward on touchdown, and backwards as the greyhound attempted to push off. We believe this is because the greyhounds were unable to use the additional traction of digging their claws into the ground. The use of claws will allow both species to apply larger propulsive forces, potentially enabling them to accelerate more rapidly (Fig. 8).

In conclusion, we have described the galloping gait used by the cheetah and racing greyhound. We have obtained trials at near-maximal effort for the greyhound, and a comparable speed range for the cheetah, in which we collected temporal stride parameters and limb forces. Several differences were observed that may account for the large variation in their maximum speeds. The cheetah's longer limbs and back allow it to attain a longer stride at a given speed. This, coupled with the cheetah's ability to reduce its swing times to those used by the greyhound, should contribute to it achieving faster top speeds than the greyhound. The range of swing times used by both species indicates that the minimum possible
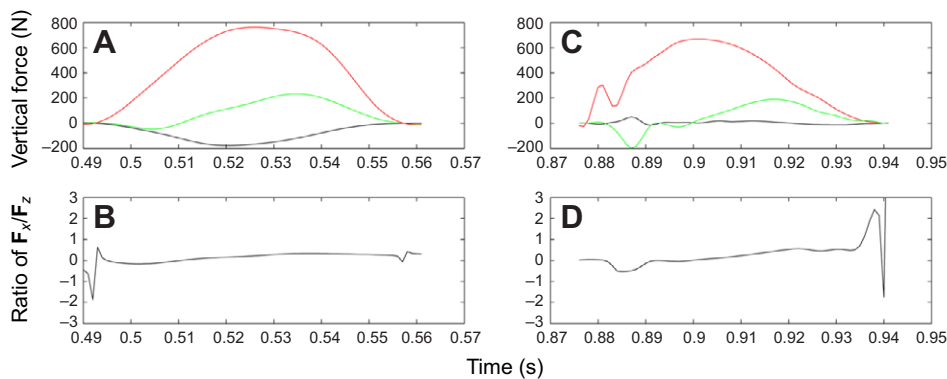

Fig. 8. GRF curves for the greyhound whilst on a concrete surface (A,B) and an artificial grass surface (C,D). Red line, vertical GRF; green line, cranio-caudal force; black line, medio-lateral force. When little body weight is being supported in the later part of stance, the greyhound is still able to apply large propulsive forces on the artificial grass, but not on the concrete surface. B and D represent the ratio of horizontal ($\mathbf{F}_x$) to vertical ($\mathbf{F}_z$) forces, providing an estimate of the coefficient of friction, which is large at the end of stance whilst on the artificial grass surface.

swing time was not often utilised and cheetahs in particular may attain even higher stride frequencies at greater speeds by reducing swing time. In both species we observed that the forelimbs maintain a constant peak force with increasing speed, reducing vertical impulse as stance time decreases. Despite this, it seems unlikely that a peak force limit has been reached as other locomotor tasks (turning, prey capture) are likely to require the forelimbs to resist higher peak limb forces than those during straight line steady-state galloping. The hindlimbs contributed a greater proportion of body weight support at higher speeds. Finally, we also observed the importance of claws for providing grip, enabling these animals to apply large propulsive forces.

LIST OF SYMBOLS AND ABBREVIATIONS

BW	body weight
CoM	centre of mass
GPS	global positioning system
GRF	ground reaction force
LFL	lead forelimb
LHL	lead hindlimb
LMM	linear mixed model
NLFL	non-lead forelimb
NLHL	non-lead hindlimb
SLC	single limb contact

REFERENCES

Alexander, R. M. (1988). Why mammals gallop. *Integr. Comp. Biol.* **28**, 237-245.

Bertram, J. E. and Gutmann, A. (2009). Motions of the running horse and cheetah revisited: fundamental mechanics of the transverse and rotary gallop. *J. R. Soc. Interface* **6**, 549-559.

Bowtell, M., Spence, A., Wilson, A., Kerwin, D., Irwin, G. and Bezodis, I. (2007). Limitation to maximal speed human sprinting-Insights from bend running and fatigue. *Comp. Biochem. Physiol.* **146A**, S109.

Bryant, J., Bennett, M., Brust, J. and Alexander, R. (1987). Forces exerted on the ground by galloping dogs (*Canis familiaris*). *J. Zool.* **213**, 193-203.

Gonyea, W. and Ashworth, R. (1975). The form and function of retractile claws in the felidae and other representative carnivorans. *J. Morphol.* **145**, 229-238.

Gorman, M. L. and Londei, T. (2000). The cheetah (*Acinonyx jubatus*) dewclaw: specialization overlooked. *J. Zool.* **251**, 535-537.

Heglund, N. C. and Taylor, C. R. (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301-318.

Hildebrand, M. (1959). Motions of the running cheetah and horse. *J. Mammology* **40**, 481-495.

Hildebrand, M. (1961). Further studies on locomotion of the cheetah. *J. Mammology* **42**, 84-91.

Hoyt, D. F. and Taylor, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239-240.

Hudson, P. E., Corr, S. A., Payne-Davis, R. C., Clancy, S. N., Lane, E. and Wilson, A. M. (2011a). Functional anatomy of the cheetah (*Acinonyx jubatus*) forelimb. *J. Anat.* **218**, 375-385.

Hudson, P. E., Corr, S. A., Payne-Davis, R. C., Clancy, S. N., Lane, E. and Wilson, A. M. (2011b). Functional anatomy of the cheetah (*Acinonyx jubatus*) hindlimb. *J. Anat.* **218**, 363-374.

Hunter, L. and Hamman, D. (2003). *Cheetah*. Cape Town: Struik Publishers.

Hyatt, J.-P. K., Roy, R. R., Rugg, S. and Talmadge, R. J. (2010). Myosin heavy chain composition of tiger (*Panthera tigris*) and cheetah (*Acinonyx jubatus*) hindlimb muscles. *J. Exp. Zool.* **313A**, 45-57.

Jayes, A. and Alexander, R. (1978). Mechanics of locomotion of dogs (*Canis familiaris*) and sheep (*Ovis aries*). *J. Zool.* **185**, 289-308.

Jayes, A. and Alexander, R. (1982). Estimates of mechanical stresses in leg muscles of galloping greyhounds (*Canis familiaris*). *J. Zool.* **198**, 315-328.

Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.

Lichtwark, G. A., Watson, J. C., Mavrommatis, S. and Wilson, A. M. (2009). Intensity of activation and timing of deactivation modulate elastic energy storage and release in a pennate muscle and account for gait-specific initiation of limb protraction in the horse. *J. Exp. Biol.* **212**, 2454-2463.

Maes, L. D., Herbin, M., Hackert, R., Bels, V. L. and Abourachid, A. (2008). Steady locomotion in dogs: temporal and associated spatial coordination patterns and the effect of speed. *J. Exp. Biol.* **211**, 138-149.

Minetti, A. E., Ardigo, L. and Saibene, F. (1994). Mechanical determinants of the minimum energy cost of gradient running in humans. *J. Exp. Biol.* **195**, 211-255.

Minetti, A. E., Ardigo, L., Reinach, E. and Saibene, F. (1999). The relationship between mechanical work and energy expenditure of locomotion in horses. *J. Exp. Biol.* **202**, 2329-2338.

Muybridge, E. (1957). *Animals in Motion*. New York: Dover Publications.

Pfau, T., Witte, T. H. and Wilson, A. M. (2006). Centre of mass movement and mechanical energy fluctuation during gallop locomotion in the Thoroughbred racehorse. *J. Exp. Biol.* **209**, 3742-3757.

Rodriguez-Barbudo, M., Vaamonde, R., Agueera, E. and Carpio, M. (1984). Histochemical and morphometric examination of the cranial tibial muscle of dogs with varying aptitudes (greyhound, German shepherd and fox terrier). *Zentralblatt fuer Veterinaermedizin, Reihe C* (Germany).

Russell, A. P. and Bryant, H. N. (2001). Claw retraction and protraction in the Carnivora: the cheetah (Acinonyx jubatus) as an atypical felid. *J. Zool.* **254**, 67-76.

Sharp, N. (1997). Timed running speed of a cheetah (*Acinonyx jubatus*). *J. Zool.* **241**, 493-494.

Tan, H. and Wilson, A. M. (2010). Grip and limb force limits to turning performance in competition horses. *Proc. R. Soc. Lond. B* **278**, 2105-2111.

Usherwood, J. R. and Wilson, A. M. (2005). Biomechanics: no force limit on greyhound sprint speed. *Nature* **438**, 753-754.

Usherwood, J. R. and Wilson, A. M. (2006). Accounting for elite indoor 200 m sprint results. *Biol. Lett.* **2**, 47-50.

Walter, R. M. and Carrier, D. R. (2007). Ground forces applied by galloping dogs. *J. Exp. Biol.* **210**, 208-216.

Weyand, P. G., Sternlight, D. B., Bellizzi, M. J. and Wright, S. (2000). Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J. Appl. Physiol.* **89**, 1991-1999.

Williams, S. B., Wilson, A. M., Daynes, J., Peckham, K. and Payne, R. C. (2008a). Functional anatomy and muscle moment arms of the thoracic limb of an elite sprinting athlete: the racing greyhound (*Canis familiaris*). *J. Anat.* **213**, 373-382.

Williams, S. B., Wilson, A. M., Rhodes, L., Andrews, J. and Payne, R. C. (2008b). Functional anatomy and muscle moment arms of the pelvic limb of an elite sprinting athlete: the racing greyhound (*Canis familiaris*). *J. Anat.* **213**, 361-372.

Williams, T. M., Dobson, G. P., Mathieu-Costello, O., Morsbach, D., Worley, M. B. and Phillips, J. A. (1997). Skeletal muscle histology and biochemistry of an elite sprinter, the African cheetah. *J. Comp. Physiol. B* **167**, 527-535.

Wilson, A. M., Watson, J. C. and Lichtwark, G. A. (2003). A catapult action for rapid limb protraction. *Nature* **421**, 35-36.

Witte, T. H., Knill, K. and Wilson, A. M. (2004). Determination of peak vertical ground reaction force from duty factor in the horse (*Equus caballus*). *J. Exp. Biol.* **207**, 3639-3648.

Witte, T. H., Hirst, C. V. and Wilson, A. M. (2006). Effect of speed on stride parameters in racehorses at gallop in field conditions. *J. Exp. Biol.* **209**, 4389-4397.