

Temporal gait parameters in the alpaca and the evolution of pacing and trotting locomotion in the Camelidae

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Abstract

Alpacas are increasingly popular as domesticated companion and commercial animals. Their footfall patterns, however, are not well documented. It would be fascinating to know if artificial selection has changed alpacas' locomotor patterns from the ancestral condition in the vicuña. Some members of the Camelidae pace rather than trot, but the gaits of most species have not been studied quantitatively. Thus, investigating alpacas' gaits might contribute to understanding the factors influencing gait choice and evolution. We aimed to quantify the temporal footfall patterns of alpacas to determine observed gaits and to describe gait parameters as a function of speed. Kinematic data (3D motion capture) of locomotor patterns over a range of speeds were collected from four alpacas. We quantified the influence of speed on stance time, swing time, stride time (and frequency), duty factor and stride length, and created gait diagrams for symmetrical and asymmetrical gaits. Alpacas moved using lateral sequence walks, mainly lateral couplets walks and runs with some lateral sequence, singlefoot footfall patterns. Remarkably, the alpacas never truly paced or trotted. At faster speeds, they switched to asymmetrical gaits, predominantly transverse gallops. With increasing speed, stance and stride times decreased, and stride frequencies and stride length increased. Swing times decreased slightly with speed for symmetrical gaits, and a tendency towards an increasing swing time was evident in asymmetrical gaits. It is still uncertain why quadrupeds choose particular gaits and intriguingly, extant camelids (alpacas, dromedary camels) do not trot. The apparent absence of pacing in alpacas deserves further investigation in an experimental and comparative framework. Yet, this absence seems inherited from their vicuña ancestors, indicating that pacing gaits may not be ancestral or common for Camelidae. Future studies should include kinetic and anatomical data to provide insight into whole-body mechanics, and include other unstudied species such as guanacos and vicuñas.

Introduction

Alpacas are a domesticated descendant of the wild vicuña (*Vicugna pacos*) (Kadwell *et al.*, 2001) and a member of the artiodactyl clade Camelidae, which comprises the New World (wild guanaco and vicuña; domestic llama and alpaca) and Old World (bactrian and dromedary camels) subclades. They were domesticated in Pre-Columbian South America, around 6000–7000 years ago (Kadwell *et al.*, 2001), mainly for fleece production (Hoffman, 2006). It is commonly assumed that all extant members of the Camelidae have the natural ability to pace (moving ipsilateral limbs in near-synchronicity) and prefer this footfall pattern over others, particularly at slower to moderate speeds (Webb, 1972; Hildebrand, 1976, 1989; Fowler, 1998; Janis, Theodor & Boisvert, 2002; Hoffman, 2006). Webb (1972) even linked the success of camelid species to their pacing adaptation and

open habitats. However, Dagg (1974) has questioned the assumption that all camelids emphasize the usage of pacing gaits, contending that only camels routinely pace. Yet, there is almost no reliable empirical documentation of footfall patterns in camelid species to rigorously test her assertion (partly founded on anecdotal observations by Koford, 1957). This is a major focus of our study. Alpacas are slightly larger than vicuña and more amenable to handling. They thus make superb subjects for locomotor studies. Here, we present a kinematic (motion-based) analysis of footfall patterns and gaits in alpacas to quantify how they move and how their locomotion compares with that of other wild and domestic Camelidae.

An understanding of the basic locomotor dynamics of animals permits investigations into why animals select particular gaits (Heglund & Taylor, 1988; Farley & Taylor,

1991; Iriate-Díaz, Bozinovic & Vásquez, 2006), and how mechanics and energy expenditure vary between gaits (Cavagna, Heglund & Taylor, 1976; Minetti *et al.*, 1999; Hoyt *et al.*, 2006). The movements of both clinically sound and unsound animals of a wide variety of species have been documented (e.g. Hildebrand, 1965, 1966, 1968, 1989), with some domestic animals, such as the dog and the horse having received particular attention (e.g. Kirpensteijn *et al.*, 2000; Khumsap, Clayton & Lanovaz, 2001; Owen *et al.*, 2004). Interesting questions are still unresolved, such as why animals of different species, sizes and body build or conformation alter their locomotor patterns due to factors such as altered substrates or inclination, load-bearing (Hoyt, Wickler & Cogger, 2000; Iriate-Díaz *et al.*, 2006; Schiffman *et al.*, 2006) or limb amputation (Kirpensteijn *et al.*, 2000).

Since the end of the 19th century, when Muybridge, in addition to Marey and others, pioneered the use of high-speed kinematic analysis to prove that horses have an aerial phase when trotting, kinematic analysis methods have been used extensively to investigate footfall patterns. A commonly used method to classify quadrupedal footfall patterns into different categories is based on the two gait diagrams (one for symmetrical and one for asymmetrical gaits) introduced by Hildebrand (1965, 1966, 1968, 1977, 1980, 1989).

First, for symmetrical gaits, such as the lateral sequence walk, trot and pace, where the footfalls of the pairs of fore or hind feet are evenly spaced in time, the gait formula incorporates two percentage figures. The first is what is termed the 'duty factor' (Alexander *et al.*, 1979), or the percentage of the stride time (the time from one foot contact to the next foot contact of the same limb) that a foot is in contact with the ground (contact time or stance time). The second is the percentage of the stride interval that the forefoot footfall lags behind the footfall of the ipsilateral hind foot (here referred to as the 'phase shift'). This gait formula can be plotted on a graph (duty factor on the *x*-axis, phase shift on the *y*-axis), and it is then possible to group footfall patterns into clusters (Hildebrand, 1965, 1966, 1968, 1977, 1980, 1989).

Second, for asymmetrical gaits such as the gallop or canter, where the footfalls of pairs of feet are unevenly spaced in time, the gait formula is slightly modified. Instead of considering pairs of ipsilateral legs, the forelegs are considered as a pair and the hind legs as a pair (Hildebrand, 1989). In asymmetrical gaits, the time lag between the fore and hind foot striking the ground often differs on the left and right. Therefore, instead of measuring the time lag between the hind foot and forefoot on the same side of the body (which might be different for the two sides), the time lag between the hind feet and the forefeet (each as a pair) is considered, again expressed as a percentage of the stride and plotted along the *y*-axis. Duty factor is also calculated for a pair of limbs, usually hind limbs (Hildebrand, 1989), and is plotted on the *x*-axis.

The gaits of alpacas are not very well documented quantitatively; however, alpacas are commonly said to show four different gaits: lateral sequence walk, pace, trot and

gallop (Fowler, 1998), although some studies contradict this (e.g. Koford, 1957; Dagg, 1973, 1974). A previous study of the locomotion of the dromedary camel (Dagg, 1974) found that camels paced routinely but never trotted, only used lateral sequence locomotion, and rarely galloped, but instead tended to use the pace as the main method for covering distance at speed. The pace is speculated to be more unstable than the trot, being a lateral rather than diagonal sequence gait, but which may be slightly faster [pacing horses tend to run marginally faster than trotters (Hildebrand, 1965, 1980; Webb, 1972; Robilliard, Pfau & Wilson, 2007)]. This might be related to the pace's decreased risk of limb interference when taking longer strides, relative to the trot. This decreased risk might be very important in long-legged animals such as camelids (Webb, 1972). Hildebrand (1980), depicting the guanaco, noted how this benefit may also apply to the transverse (as opposed to rotary) gallop. Unfortunately, the current understanding of locomotor biomechanics and stability leaves these speculations as quite uncertain.

All camelids seem anatomically well adapted to pacing (Janis *et al.*, 2002). They have a very narrow chest and hips for their size, and a narrow, dorsally tapering abdomen, much narrower than the abdomen of other ungulate species such as cattle, deer or horses (Hoffman, 2006). Finally, camelids have a padded, digitigrade foot with two main supportive toes that might help with ipsilateral stability (Webb, 1972; Janis *et al.*, 2002). All these factors mean that the animals have a very narrow-based stance, with the legs very close to the midline (Webb, 1972), perhaps making them more stable when supported only by ipsilateral limbs. The narrow, evenly contoured trunk also allows the limbs to swing freely forwards and backwards. The relatively long limbs [the limbs of the vicuña are two-thirds of the length of its back, (Hoffman, 2006)] allow for a long stride. The hind feet of dromedary camels normally strike the ground well in front of the ipsilateral forefeet, as opposed to the pattern in cows, deer and horses, where the forefeet are superimposed over the hind footprints, and giraffes, where the forefeet strike the ground slightly in front of the hind feet (Dagg, 1974). Few animals other than camelids naturally pace, but some horses and dogs do. A study of locomotor patterns in dogs (Hildebrand, 1968) found that of the dogs observed to pace, all were long-legged breeds.

Our study aims to classify the footfall patterns of alpacas and to quantitatively document their basic stride parameters [stance time, swing time, stride time (and frequency), duty factor and stride length] as a function of speed, and to use gait diagrams (Hildebrand, 1965, 1966, 1968, 1977, 1980, 1989) to identify the different types of gaits used. We will then compare our results with previous studies of other species, especially Camelidae.

Materials and methods

Animal selection and preparation

Four alpacas (see Table 1 for details) were selected from a group of nine animals owned by The Royal Veterinary

College. None of the animals were well halter-trained previously, and hence the most cooperative animals were chosen and underwent 1 week of halter training before the study. Ethics approval for the use of these alpacas had been granted and animals were assessed by a qualified veterinarian (C. W.) to be sound and not suffering from any orthopaedic disease. One of the alpacas used had an extra digit associated with the fetlock of each forelimb that did not appear to have any effect on overall limb conformation or locomotor kinematics. All alpacas were female and of the Huacaya breed. The fleece was clipped (by the same handler) at sites where infrared-reflective markers would be placed on the body and limbs. Each site was clipped enough to allow the markers to be seen by most cameras throughout the capture area.

The majority of markers were placed on the right lateral side of the alpacas over the following anatomical landmarks (Fig. 1): dorsal scapular spine, midway between acromium and head of humerus, greater tubercle of humerus, olecranon, carpus, fetlock (metacarpophalangeal joint) and lateral toe on the forelimb, and on the iliac crest, greater trochanter of femur, stifle (knee) joint, point of the hock (tarsus), fetlock (metatarsophalangeal joint) and lateral toe on the hind limb. Fetlock and lateral toe markers were also placed on the left fore and hind limb and further two markers were placed on the fleece of each animal over the point of the withers and the sacro-iliac joint (to calculate average speed for each trial), and another on the head just ventro-rostral to the base of the ear. Here, only the most distal markers (on the toenails and on the fetlocks of all four legs) (Fig. 1) were used to calculate footfall patterns; the other markers will be used in subsequent studies.

Data collection

Each alpaca was led in front of 10 infrared cameras (Oqus Series 300/500, Qualisys AB, Gothenburg, Sweden), placed

Table 1 Age, mass and height of the four alpacas used in this study

	Age (years)	Mass (kg)	Height (m)	Gender
1	5	67	0.85	Female
2	6	70	0.91	Female
3	11	72.5	0.96	Female
4	7	68.5	0.85	Female

c. 3 m away from a main runway, with a calibrated area of *c.* 5 m length and 2 m width (Fig. 2). Alpacas were either led on a lead rope, or at faster speeds encouraged to run (either by chasing the alpaca from behind or by using food rewards at the end of the run) while being led. Each alpaca was led through the calibrated area until at least six good trials had been achieved (each set of ~ 6 trials at different speeds) or until the behaviour of the alpaca prevented the collection of more data. Barriers were created at either side of the runway using thin strips of tape running at approximately the alpacas' chest height to restrict sideways movement. The flooring was non-slip coated, level concrete.

Data processing and analysis

Data were processed using Qualisys Track Manager (Qualisys AB) motion-analysis software for tracking and labelling marker coordinates, which were then exported into text files and subsequently imported into MATLAB (The MathWorks Inc., Natick, MA, USA). Speed was calculated from the withers marker. The velocities of the fetlock markers were used to determine the times when the individual feet contacted the ground and left the ground (simplified from Peham, Scheidl & Licka, 1999). Here, a user-defined threshold (rather than a histogram) was chosen interactively based on the velocity graphs of all four feet: then, we derived foot on and foot off times, which were exported into text files together with the speed values (average speed for each stride, no more than 20% difference between initial and end speed allowed). Stance time, swing time, stride time, stride



Figure 2 Data collection set-up showing 10 camera optical motion capture system, animal on lead rope and handler in the gait laboratory.



Figure 1 Position of markers on the left side (left panel) and the right side (right panel) of one individual alpaca used in this study.

frequency and stride length were then calculated based on these data. Duty factor was calculated from stance time and stride time, and phase shift as the time a forefoot placement follows the placement of the ipsilateral hind foot, as a percentage of the stride time. We followed the methodology of Hildebrand (1965, 1966, 1968, 1977, 1980, 1989) to construct gait diagrams and classify footfall patterns (also see Biknevicius & Reilly, 2006). We inferred Hildebrand's diagram to have boundaries for pacing of 0–6.25 and 93.75–100% phase shift (i.e. eight symmetrical gait patterns each should occupy 12.5% of the diagram; Hildebrand, 1965, 1966, 1976, 1980). For asymmetrical gaits, in order to distinguish between transverse and rotary gallops, front lag, hind lag and pair lag were calculated for each stride following the method described by Abourachid (2003).

Speed was normalized and expressed as Froude number [$v^2/(gl)$, with v , speed; g , acceleration due to gravity; l , leg length, expressed as withers height from the ground] to compensate for differences in height between alpacas (Alexander, Langman & Jayes, 1977; Biewener, 2003). Linear or power curves were fitted (using the best fit equation judged by the R^2 value in MATLAB) to the data to express the change of stride parameters as a function of speed (Froude number) because of their suitability for representing scaling effects (Alexander & Jayes, 1983; Alexander, 1985).

Results

The majority of the data we collected came from two of the four alpacas (the most amenable to being led), allowing data to be collected for a wider range of gaits and speeds. Over a period of 4 days, 310 recordings were made (between 27 and 183 per animal).

Symmetrical gaits

Speeds ranged from 0.47 to 2.01 m s^{-1} (Froude number between 0.02 and 0.5). Figure 3 shows the change of temporal locomotor parameters with an increasing speed in symmetrical gaits of alpacas (see Table 2 for regression equations of fitted curves). As observed in other animals (Cavagna *et al.*, 1976; Hoyt *et al.*, 2006), stance time decreased curvilinearly with increasing speed. Stride time also decreased with increasing speed, while stride frequency increased linearly with speed again agreeing with published data (Heglund & Taylor, 1988; Hoyt *et al.*, 2006; Witte, Hirst & Wilson, 2006). Swing time decreased linearly with the increasing speed, with a relatively shallow slope. Hence, duty factor decreased curvilinearly with maximal values of 0.75 and minimal values around 0.35 at maximal speed in symmetrical gaits. No symmetrical gaits involved an aerial

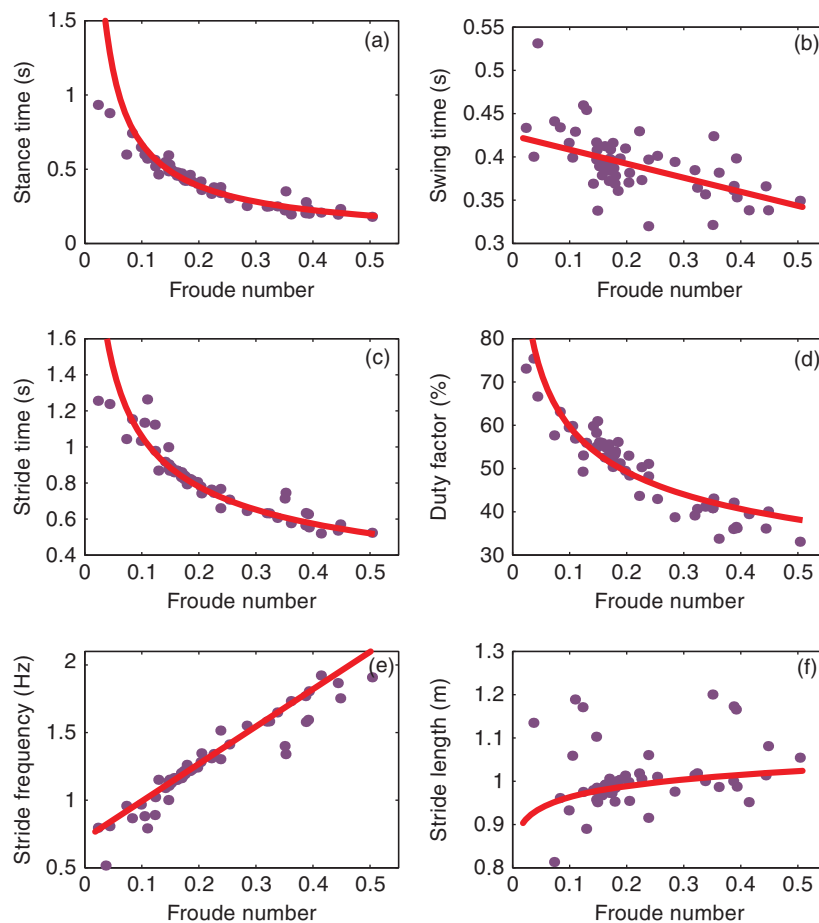


Figure 3 Basic stride parameters as a function of speed (Froude number) in alpacas for symmetrical gaits, (a) stance time (s), (b) swing time (s), (c) stride time (s), (d) duty factor (%), (e) stride frequency (Hz) and (f) stride length (m). Graphs include individual data points as well as regression lines (linear or power curves, see Table 2 for details).

Table 2 Regression equations (coefficients a and b with 95% confidence intervals) for linear (lin: $y = a \times x + b$) respectively power (pow: $y = a \times x^b$) curves and R^2 values for stance time (staT), swing time (swT), stride time (strT), duty factor (DF), stride frequency (SF) and stride length (SL) for symmetrical (Fig. 3) and asymmetrical gaits (Fig. 5) in the alpaca as a function of speed

	Symmetrical gaits				Asymmetrical gaits			
	Fit	a	b	R^2	Fit	a	b	R^2
staT (s)	pow	0.11 [0.102; 0.115]	-0.79 [-0.81; -0.77]	0.97	pow	0.12 [0.111; 0.135]	-0.63 [-0.87; -0.38]	0.69
swT (s)	lin	-0.16 [-0.224; -0.098]	0.424 [0.410; 0.440]	0.70	lin	0.029 [0.009; 0.048]	0.322 [0.300; 0.344]	0.25
strT (s)	pow	0.38 [0.371; 0.396]	-0.44 [-0.451; -0.420]	0.97	pow	0.46 [0.462; 0.473]	-0.11 [-0.142; -0.086]	0.88
DF (%)	pow	31.6 [29.79; 33.3]	-0.27 [-0.303; -0.249]	0.82	pow	25.9 [23.8; 28.06]	-0.54 [-0.749; -0.331]	0.65
SF (Hz)	lin	2.76 [2.659; 2.862]	0.72 [0.692; 0.741]	0.98	pow	2.14 [2.118; 2.159]	0.12 [0.091; 0.139]	0.89
SL (m)	pow	1.154 [1.069; 1.239]	0.084 [0.041; 0.126]	0.24	pow	1.342 [1.316; 1.369]	0.370 [0.325; 0.416]	0.92

Linear or power curves are chosen based on the R^2 value and regression equations were fitted in MATLAB.

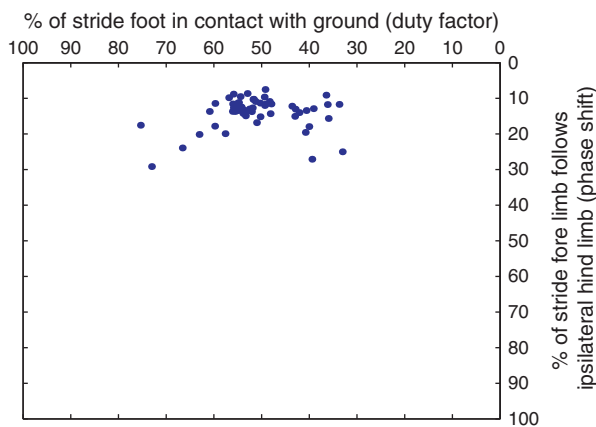


Figure 4 Gait diagram (Hildebrand, 1965, 1966, 1968) of the symmetrical gaits of alpacas. Comparing with published data, it is evident that alpacas prefer phase shifts of just below 10% to just above 20%, thus being categorized as either lateral couplet walks (phase shift $\sim 15\%$), lateral – sequence single footfall walks (duty factor above 50%) and single footfall runs (duty factor below 50%).

phase. Stride length varied from 0.59 to 1.32 m with substantial variation at any one speed, and showed a slight curvilinear increase with increasing Froude number (Fig. 3) with a steeper slope at lower speeds again agreeing with previous studies in other animals (Hoyt *et al.*, 2000).

The gait graph (Fig. 4) for symmetrical gaits of alpacas shows the animals mainly using a lateral sequence footfall pattern with the phase shift typically between 10 and 20% (total range: 7–29%). Thus, the symmetrical gaits can all be classified as lateral sequence gaits, mostly using lateral couplets (phase shift $\sim 15\%$). No strides showed phase shifts below 6.25%, which would be classified as pacing (see ‘Materials and methods’). Limb phase also did not show a pronounced increase with speed (or any trend towards a

pace) as it does in dromedary camels (Alexander & Jayes, 1983).

Asymmetrical gaits

At speeds faster than about 2 m s^{-1} (Froude number 0.5), the alpacas did not continue to use lateral sequence footfall patterns but rather switched to asymmetrical gaits. Speed values for asymmetrical gaits ranged from 2.1 to 4.5 m s^{-1} (Froude number between 0.53 and 2.51). The faster speeds were slow in comparison with many other animals (e.g. Alexander *et al.*, 1977) but are not deemed to be near-maximal because we sought to avoid causing the animals excessive stress. Koford (1957: p. 173) quoted studies suggesting top speeds of $> 20\text{--}30 \text{ mph}$ ($> 9\text{--}13 \text{ m s}^{-1}$).

Using asymmetrical gaits, alpacas are able to achieve an increase in speed by decreasing the amount of time each foot spends in contact with the ground (Fig. 5) and decreasing the amount of time taken to complete a stride (Fig. 5). Because stance time dropped more rapidly with speed than stride time, a reduction in relative stance time (duty factor) was observed (Fig. 5). Duty factor was lower than for symmetrical gaits, varying between 0.35 (at a Froude number of 0.53) and 0.12 (at a Froude number of 2.5). Stride length for asymmetrical gaits (Fig. 5) was longer than for symmetrical gaits (as expected for higher speeds), ranging from 1.04 to 1.89 m, and stride frequency increased with Froude number, peaking at 2.4 Hz.

The gait graph (Fig. 6a) reveals that alpacas prefer to gallop using a phase shift of *c.* 0.3 (30%) and analysing front lag, hind lag and pair lag (Abourachid, 2003) shows that the transverse gallop was the only asymmetrical gait used (see Table 3 for mean values). All asymmetrical strides had either no suspension phase or a very short gathered suspension phase (cf. Hildebrand, 1977: fig. 7). Figure 6b shows a ‘typical’ gait plot drawn using mean values of all

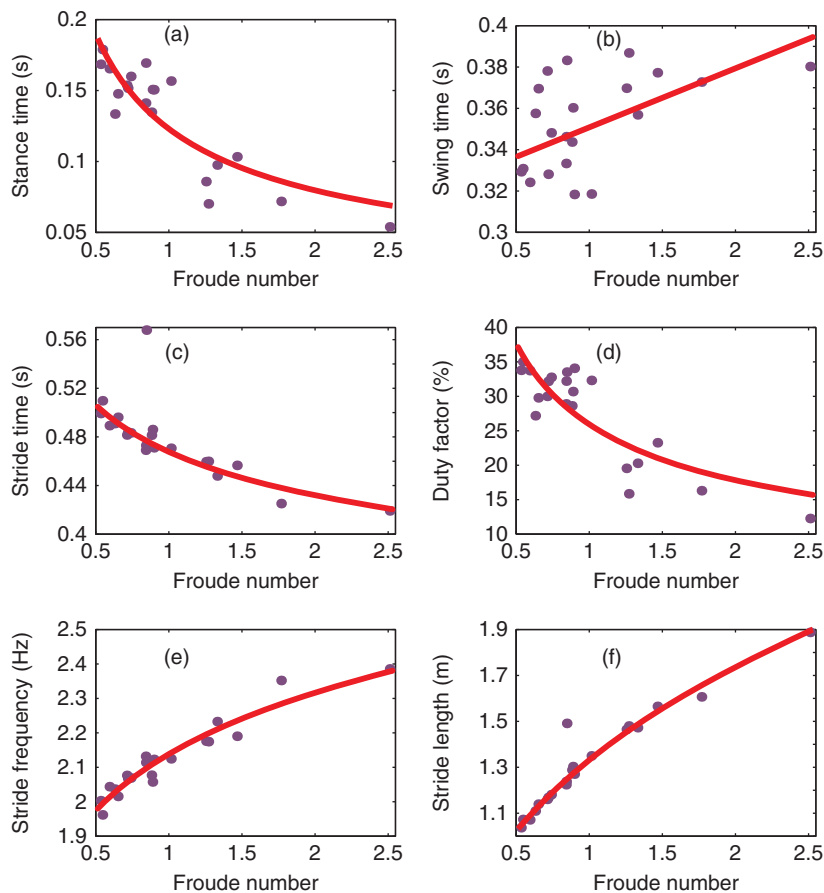


Figure 5 Basic stride parameters as a function of speed in alpacas for asymmetrical gaits; (a) stance time (s), (b) swing time (s), (c) stride time (s), (d) duty factor (%), (e) stride frequency (Hz) and (f) stride length (m). Graphs include individual data points as well as regression lines (linear or power curves, see Table 2 for details).

asymmetrical strides for duty factor and individual limb phase lag; this shows no period of whole body suspension.

Discussion

Gait parameters and speed

Speed range and transition from symmetrical to asymmetrical gaits

The alpacas in this study exhibited symmetrical gaits (lateral sequence) for slower speeds and asymmetrical gaits for faster speeds. Although this study was not designed to investigate gait transitions and animals were encouraged to show steady-state locomotion, it is interesting to note that the speed ranges of symmetrical and asymmetrical gaits reported in this study do not overlap. While symmetrical gaits are reported with a Froude number ≤ 0.5 , the minimum Froude number recorded for a stride of an asymmetrical gait was 0.53, supporting the inference that the gait transition speed in alpacas is near a Froude number of 0.5, similar to that observed in other animals (0.4–0.6; Alexander & Jayes, 1983). Dromedary camels appear to prefer to switch from lateral sequence walking to pacing at around

this speed (Alexander & Jayes, 1983; Maloiy, Rugangazi & Rowe, 2009), but our alpacas never switched to pacing.

However, duty factor values for the faster symmetrical gaits were well below 50% (as low as 33%, Fig. 3, mid right) and some gait definitions would classify these as running gaits. A considerable number of symmetrical strides showed duty factors to be higher for the fore than for hind limbs, a slightly unusual finding for quadrupeds (e.g. Hildebrand, 1965, 1989). Here, 43 out of 57 symmetrical gait trials had a greater forelimb duty factor while in asymmetrical gaits only eight out of 21 strides showed higher forelimb duty factors. Some other animals, such as elephants, exhibit this behaviour as well (Hutchinson *et al.*, 2006); it is opposite the pattern observed in horses (Robilliard *et al.*, 2007; Witte *et al.*, 2006) and as yet unexplained.

When comparing the relationship of the gait parameters with speed between symmetrical and asymmetrical gaits, it can be observed that some parameters (except swing time, stride length and stride frequency) show similar trends with speed (Figs 3 and 5). Stance time, stride time and duty factor decreased curvilinearly with speed and stride length increased curvilinearly with speed. Swing time decreased linearly for symmetrical gaits (-0.16 s Fr^{-1} , Table 2) and increased slightly for asymmetrical gaits (0.029 s Fr^{-1} , Table 2). Stride frequency increased linearly with speed for

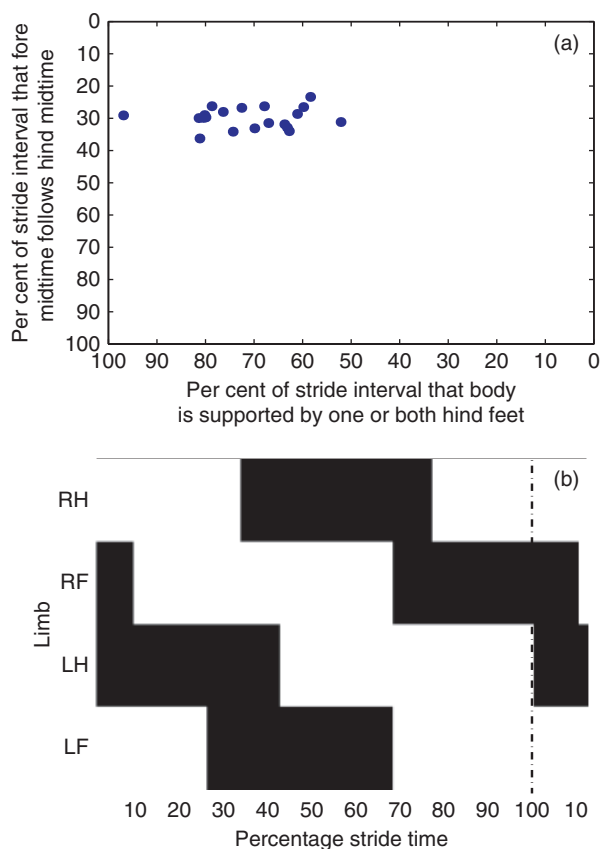


Figure 6 (a) Gait graph for asymmetrical gaits of alpacas. During faster locomotion, the animals are seen to mainly use the transverse gallop and seem to prefer a phase shift of $\sim 50\%$. (b) Typical footfall pattern of an alpaca using an asymmetrical gait. Black bars represent stance phases of individual limbs (LF, left front; RF, right front; LH, left hind; RH: right hind).

Table 3 Mean, standard deviation (SD) and number of strides (N) for front lag (FL), hind lag (HL) and pair lag (PL) for strides of asymmetrical gaits calculated following the method described in Abourachid (2003)

	FL	HL	PL
Mean	39%	31%	74%
SD	4.3%	6.2%	4.4%
N	40	40	40

Values are expressed as a percentage of stride time and positive values for hind lag confirm that alpacas use the transverse gallop.

symmetrical gaits (2.8 Hz Fr^{-1} , Table 2) but curvilinearly and less prominently for asymmetrical gaits. Stride length on the other hand increased more rapidly with speed for asymmetrical gaits than for symmetrical gaits indicating that alpacas use a different strategy for increasing speed at higher speeds, in which they prefer to increase stride length rather than stride frequency. This is common to many animals (Heglund & Taylor, 1988). Indeed, generally the stride parameters of alpacas match patterns observed in

many other ungulates (Alexander *et al.*, 1977; Alexander & Jayes, 1983).

In addition, all parameters showed a relatively smooth transition (no obvious step change) when changing from symmetrical to asymmetrical gaits. More data including whole body mechanics and limb forces (e.g. using force platform data) would be useful to provide further interesting insights into why alpacas switch between symmetrical and asymmetrical gaits, in particular because other quadrupeds (e.g. horses) have clearly overlapping speed ranges between symmetrical and asymmetrical gaits (Robilliard *et al.*, 2007). However, the non-overlapping speed range should not be overemphasized due to the limited amount of data (with animals on a lead rope) and the study design aiming at capturing steady state locomotion.

Choice of gait

Symmetrical gaits

Using the gait graphs proposed by Hildebrand (1965, 1966, 1968, 1977, 1980, 1989) to analyse motion capture data recorded from the four alpacas in this study, we found that the preferred (symmetrical) gaits of these animals are in a range of phase shifts of just under 10% to just over 20%, both for duty factors below and above 50% (a cut-off value sometimes used to discriminate between walking and running). Previous research gives no conclusive classification for phase shifts in this area of the gait graph. Although gaits with a 0–6.25% phase shift are categorized as pacing (walking or running paces depending on duty factor), gaits with an approximate phase shift of 20–30% are described as having a singlefoot in lateral sequence (Hildebrand, 1989) or simply as lateral sequence walks (Biknevicius & Reilly, 2006). In addition, diagonal sequence gaits with *c.* 45–55% phase shift are labelled as trots, and gaits with 75–80% phase shift are singlefoot in diagonal sequence gaits. In addition, Hildebrand (1965) argued that, for pacing horses, not only is it rare to have the fore and hind foot on the same side strike exactly at the same time (a phase shift of zero) but also rare for the fore foot to follow the hind foot by as much as 12%, although examples of horses moving using this gait had been recorded. The majority of data for pacing horses fall within an area covering phase shift values somewhere between 3 and 10% (Hildebrand, 1965); however, pace strides with higher values have been reported in in Icelandic horses (Robilliard *et al.*, 2007). Note that some of these values exceed our cut-off phase shift of 6.25%, even though this cutoff was somewhat explicit in Hildebrand's studies (see 'Materials and methods') and seems the most rational, non-arbitrary division of pacing from lateral sequence footfall patterns. If a higher phase shift such as 10% were allowed, then only seven out of 57 (12% of the total) symmetrical strides would have been classified as paces, and only barely so.

Compared with data from Hildebrand (1976, 1980), which have been nicely illustrated elsewhere (Biknevicius & Reilly, 2006), only a few animals have been reported to

move using phase shift values in the preferred range of the alpacas (10–20%) combined with duty factors of below 50%. These gaits are described as ‘lateral couplets’ walks or runs (Hildebrand, 1965); note that for vicuñas the confusing term ‘diagonal walk’ was used by Koford (1957). Recently, it has been argued (and confirmed using automated pattern recognition methods, Starke *et al.*, 2009) that duty factor should not be used to distinguish between walking and running and that gaits of this type should be termed lateral sequence singlefoot, or simply lateral sequence walks/runs (Biknevicius & Reilly, 2006).

Regardless, a persistent problem vexing studies of locomotion in the Camelidae has been gait terminology, which also plagues studies of many other groups (e.g. elephants; Hutchinson *et al.*, 2006). In particular, the term ‘pace’ has been used interchangeably with rack, amble, lateral walk, walking amble (Magne de la Croix, 1936), and other terms in reference to the gaits of alpacas and other camelids (Dagg, 1973). Like Biknevicius & Reilly (2006), we consider that Hildebrand’s (1965, 1966, 1968, 1976, 1980, 1989) terminology has become the jargon of consensus and future confusion would be prevented by using it – and by recognizing that gait terminology in past studies might not reflect current practice. By this consensus, pacing should be restricted to symmetrical footfall patterns with a phase shift $\leq 6.25\%$.

Following this convention, we recognize that alpacas (and presumably vicuñas; Koford, 1957; Dagg, 1973) do not routinely pace. Webb (1972) went so far as to claim that pacing was ancestral for all Camelidae (also presumed by Hildebrand, 1976, 1989; but for a different view, see Janis *et al.*, 2002), but used a broad definition of pacing that included lateral sequence walking (as demonstrated on his p. 101, which cites elephants as using pacing gaits, which they do not; Hutchinson *et al.*, 2006). Dagg (1974) also disputed Webb’s (1972) classifications. Our results favour the hypothesis intimated by Dagg (1974) that only camels routinely pace. We speculate that llamas and guanacos behave similarly to alpacas and prefer lateral sequence locomotion at slow to medium speeds. It is more conclusive that alpacas, like all other camelids studied to date, do not trot (*contra* Fowler, 1998).

Asymmetrical gaits

In this study, alpacas were found to use the transverse gallop as their most common asymmetrical gait. This is also the most usual asymmetrical gait of the camel and is described as the most commonly selected fast asymmetrical gait of large cursorial mammals such as vicuñas, horses and large antelopes, and presumed to be relatively stable and fairly energy efficient (Hildebrand, 1977, 1989). In addition, the transverse gallop is suggested to have less chance of interference between fore and hind limbs (Hildebrand, 1977, 1989), which seems important for an animal with long legs that can swing easily, unencumbered by a large chest or abdomen, and which lie quite close to the midline. Janis *et al.* (2002) followed previous studies in assigning a rotary

gallop to camelids, but the alpacas in this study did not use that form of gallop and Hildebrand (1977) found transverse gallops in his study of *Camelus* and *Lama*. Why giraffids seem to favour rotary gallops (Hildebrand, 1977) and camelids seem to favour transverse gallops remains unsolved.

Dagg (1973) noted that camels and llamas galloped but did not record this behaviour for vicuñas, although she cited a reference (Koford, 1957: fig. 14) depicting it. Dagg (1974) also empirically documented that dromedary camels seldom gallop. If this is correct, then perhaps alpacas have maintained the ancestral ungulate condition of using walking and galloping footfall patterns, but secondarily lost trotting along with other Camelidae, and camels separately evolved a stronger reliance on pacing over galloping. A more satisfying test of this hypothesis awaits further experimental documentation of camelid gait usage. Gait usage in llamas, guanacos and Bactrian camels remains almost unstudied.

Study limitations

Before this study, the animals had only had a very limited amount of halter training, and thus it is possible that the gaits shown in this study do not cover the whole ‘natural’ range these animals would display in their natural environment. Dagg (1974) speculated that the trot is as equally an energetically cheap and rapid method of travel as the pace (*vide* Maloiy *et al.*, 2009) but with the advantage of more stability in uneven terrain. Thus, the absence of trotting is not surprising and might only suggest a preference for lateral sequence walks on even terrain, although this speculation deserves empirical testing rather than being assumed to be correct.

Furthermore, one should be hesitant to dismiss the gait of alpacas as irrelevant to ‘normal’ locomotor evolution just because the animals have been domesticated. Following Dagg’s (1973, 1974) observation that camelids tend never to trot, this may still be a peculiar feature of this clade, probably indicating secondary loss at some point in their evolutionary history. This would be a remarkably fertile area for evolutionary and biomechanical research but it hinges on the basic scientific understanding of (1) why animals choose certain footfall patterns over others, which is an active area of current research in comparative biomechanics (e.g. Biknevicius & Reilly, 2006); (2) how musculoskeletal morphology (e.g. leg length and features noted in the Introduction) relates to these patterns (e.g. Webb, 1972; Janis *et al.*, 2002). We have contributed towards the first of these two priorities but the second deserves more intensive biomechanical and experimental study, which could reduce the speculation involved in interpreting fossil anatomies as well as footprints.

Van der Sluijs, Gerken & Preuschoft (2010) presented a study of New World camelid symmetrical gait kinematics that came to very similar overall conclusions as our study. In particular, they provide wonderful confirmation that pacing is largely unique to Old World taxa (i.e. camels) among extant Camelidae, although our data show that pacing is

still occasionally used at least in alpacas. Furthermore, our study agrees with their findings that camelids in general do not normally trot. Their quantitative kinematic results also match ours reasonably well where an overlap in data format exists.

Future work

Recently, different methods have been investigated providing alternative methods to analyse temporal (and spatial) gait parameters (Abourachid, 2003; Robilliard *et al.*, 2007) and to automatically distinguish between walking and running (Starke *et al.*, 2009). Certainly, force platform analysis of alpaca (and other camelid) gaits is essential to determine which footfall patterns use vaulting or bouncing mechanisms and at what speeds such mechanical gait transitions actually occur (Biknevicius & Reilly, 2006). It would be interesting to add more data, preferably representing 'field locomotion', to the database of alpaca gaits and then thoroughly compare the different approaches and to make a more robust comparison with better-studied mammals. Our results indicate that although alpacas move in a similar fashion to other animals at faster speeds, at slower speeds and on flat terrain, they tend to move somewhat differently to animals such as horses, deer and cattle, moving using only lateral sequence walks. Indeed, we never saw true pacing (with highly synchronized ipsilateral limbs) in alpacas. It would be interesting to extend the study to involve other New World camelids such as the llama (although slightly larger than the alpaca, relatively similar in body build) in order to investigate whether these similar animals adhere to the dynamic similarity principle (Alexander & Jayes, 1983) and whether all of them do or do not use the same gaits. This would help to illuminate how pacing (as opposed to trotting) evolved in mammals, especially camelids (e.g. the hypothesis of locomotor homoplasy in Camelidae from Janis *et al.*, 2002), and would constrain identifications of putative pacing trackmakers from the fossil record (Webb, 1972; Thompson, White & Morgan, 2007; Pérez-Lorente *et al.*, 2009).

Conclusion and potential relevance

We have provided important new basic measurements of the footfall patterns, stance, stride and swing times, stride length and frequency and speed of four alpacas, and used these to generate gait diagrams (Hildebrand, 1965) for alpacas moving at both symmetrical and asymmetrical gaits. These graphs showed alpacas used lateral sequence, lateral couplets and singlefoot in lateral sequence walks and runs, but never the pace. At faster speeds they mainly used the transverse gallop. Gait parameters such as stance and stride times, and stride length and frequency, changed with speed in a manner consistent with data reported for other species. With the increasing popularity of alpacas as pets and commercial animals, the data presented here provide a baseline for normal locomotor patterns seen in these animals, which might provide useful in the framework of

clinical investigations of locomotor deficits. Furthermore, these data will be crucial for reconstructing the evolution of locomotion in camelids and other artiodactyls, including the influence of domestication on their gait. Why might true pacing be absent or less frequently used in New World camelids, especially considering their anatomical specializations that might enhance pacing (Webb, 1972; Fowler, 1998; Janis *et al.*, 2002; Hoffman, 2006)? A lack of empirical studies of these species means that this curious result cannot yet be explained as an effect of breeding, terrain, anatomy or other influences, but we have provided one step towards solving this mystery.

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References

- Abourachid, A. (2003). A new way of analysing symmetrical and asymmetrical gaits in quadrupeds. *C. R. Biol.* **326**, 625–630.
- Alexander, R.McN. (1985). Body support, scaling, and allometry. In *Functional vertebrate morphology*: 26–37. Hildebrand, M., Bramble, D.M., Liem, K.F. & Wake, D.B. (Eds). Cambridge: The Belknap Press of Harvard University Press.
- Alexander, R.McN. & Jayes, A.S. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool. (Lond.)* **201**, 135–152.
- Alexander, R.McN., Langman, V.A. & Jayes, A.S. (1977). Fast locomotion of some African ungulates. *J. Zool. (Lond.)* **183**, 291–300.
- Alexander, R.McN., Maloiy, G.M.O., Hunter, B., Jayes, A.S. & Nturibi, J. (1979). Mechanical stresses during fast locomotion of buffalo (*Syncerus caffer*) and elephant (*Loxodonta Africana*). *J. Zool. (Lond.)* **189**, 135–144.
- Biewener, A.A. (2003). *Animal locomotion*: 65–66. Oxford: Oxford University Press.
- Biknevicius, A.R. & Reilly, S.M. (2006). Correlation of symmetrical gaits and whole body mechanics: debunking myths in locomotor biodynamics. *J. Exp. Zool.* **305A**, 923–934.
- Cavagna, G.A., Heglund, N.C. & Taylor, C.R. (1976). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.
- Dagg, A.I. (1973). Gaits in mammals. *Mammal. Rev.* **3**, 135–154.

- Dagg, A.I. (1974). The locomotion of the camel (*Camelus dromedarius*). *J. Zool. (Lond.)* **174**, 67–78.
- Farley, C.T. & Taylor, C.R. (1991). A mechanical trigger for the trot–gallop transition in horses. *Science* **19**, 306–308.
- Fowler, M.E. (1998). Conformation and gaits. In *Medicine and surgery of South American Camelids: llama, alpaca, vicuña, guanaco*, 2nd edn: 517–530. Fowler, M. (Ed.). Ames: Blackwell Publishing.
- Heglund, N.C. & 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. (1965). Symmetrical gaits of horses. *Science* **191**, 701–708.
- Hildebrand, M. (1966). Analysis of the symmetrical gaits of tetrapods. *Folia Biotheor.* **6**, 9–22.
- Hildebrand, M. (1968). Symmetrical gaits of dogs in relation to body build. *J. Morphol.* **124**, 353–360.
- Hildebrand, M. (1976). Analysis of tetrapod gaits: general considerations and symmetrical gaits. In *Neural control of locomotion*: 203–236. Herman, R.M., Grillner, S., Stein, P.S.G. & Stuart, D.G. (Eds). New York: Plenum Press.
- Hildebrand, M. (1977). Analysis of asymmetrical gaits. *J. Mammal.* **58**, 131–156.
- Hildebrand, M. (1980). The adaptive significance of tetrapod gait selection. *Am. Zool.* **20**, 255–267.
- Hildebrand, M. (1989). The quadrupedal gaits of vertebrates. *Bioscience* **39**, 766–775.
- Hoffman, E. (2006). *The complete alpaca book*, 2nd edn. Santa Cruz: Bonny Doon Press.
- Hoyt, D.F., Wickler, S.J. & Cogger, E.A. (2000). Time of contact and step length: the effect of limb length, running speed, load carrying and incline. *J. Exp. Biol.* **203**, 221–227.
- Hoyt, D.F., Wickler, S.J., Dutto, D.J., Catterfield, G.E. & Johnsen, D. (2006). What are the relations between mechanics, gait parameters, and energetics in terrestrial locomotion? *J. Exp. Zool.* **305A**, 912–922.
- Hutchinson, J.R., Schwerda, D., Famini, D.J., Dale, R.H.I., Fischer, M.S. & Kram, R. (2006). The locomotor kinetics of Asian and African elephants: changes with speed and size. *J. Exp. Biol.* **209**, 3812–3827.
- Iriate-Díaz, J., Bozinovic, F. & Vásquez, R.A. (2006). What explains the trot–gallop transition in small mammals? *J. Exp. Biol.* **209**, 4061–4066.
- Janis, C.M., Theodor, J.M. & Boisvert, B. (2002). Locomotor evolution in camels revisited: a quantitative analysis of pedal anatomy and the acquisition of the pacing gait. *J. Vertebr. Paleontol.* **22**, 110–121.
- Kadwell, M., Fernandez, M., Stanley, H.F., Baldi, R., Wheeler, J.C., Rosadio, R. & Bruford, M.W. (2001). Genetic analysis reveals the wild ancestors of the llama and the alpaca. *Proc. Roy. Soc. Lond. B* **268**, 2575–2584.
- Khumsap, S., Clayton, H.M. & Lanovaz, J.L. (2001). Effect of walking velocity on ground reaction force variables in the hind limb of clinically normal horses. *Am. J. Vet. Res.* **62**, 901–906.
- Kirpensteijn, J., van den Bos, R., van den Brom, W.E. & Hazewinkel, H.A.W. (2000). Ground reaction force analysis of large breed dogs when walking after the amputation of a limb. *Vet. Rec.* **146**, 155–159.
- Koford, C.B. (1957). The vicuña and the puna. *Ecol. Monogr.* **27**, 153–219.
- Magne de la Croix, P. (1936). The evolution of locomotion in mammals. *J. Mammal.* **17**, 51–54.
- Maloiy, G.M.O., Rugangazi, B.M. & Rowe, M.F. (2009). Energy expenditure during level locomotion in large desert ungulates: the one-humped camel and the domestic donkey. *J. Zool. (Lond.)* **277**, 248–255.
- Minetti, A.E., Ardigo, L.P., Reinach, E. & Saibene, F. (1999). The relationship between mechanical work and energy expenditure of locomotion in horses. *J. Exp. Biol.* **202**, 2329–2338.
- Owen, M.R., Richards, J., Clements, D.N., Drew, S.T., Bennett, D. & Carmichael, S. (2004). Kinematics of the elbow and stifle joints in greyhounds during treadmill trotting – an investigation of familiarisation. *Vet. Comp. Orthop. Traumatol.* **17**, 141–145.
- Peham, C., Scheidl, M. & Licka, T. (1999). Limb locomotion-speed distribution analysis as a new method for stance phase detection. *J. Biomech.* **32**, 1119–1124.
- Pérez-Lorente, F., Herrero, C., Herrero, E. & Montoya, P. (2009). *Paracamelichnum jumillensis* n. ichnogen. n. ichnosp., Upper Miocene Camelidae ichnites from the Hoya de la Sima site (Murcia, Spain). *Ichnos* **16**, 208–219.
- Robilliard, J.J., Pfau, T. & Wilson, A.M. (2007). Gait characterisation and classification in horses. *J. Exp. Biol.* **210**, 187–197.
- Schiffman, J.M., Bense, C.K., Hasselquist, L., Greorczyk, K.N. & Piscitelle, L. (2006). Effects of carried weight on random motion and traditional measures of postural sway. *Appl. Ergon.* **31**, 607–614.
- Starke, S.D., Robilliard, J.J., Weller, R., Wilson, A.M. & Pfau, T. (2009). Walk-run classification of symmetrical gaits in the horse: a multidimensional approach. *J. Roy. Soc. Interface* **6**, 335–342.
- Thompson, M.E., White, R.S. Jr & Morgan, G.S. (2007). Pace versus trot: can medium speed gait be determined from fossil trackways? In *Cenozoic tracks and traces*: 309–314. Lucas, S.G., Spielmann, J.A. & Lockley, M.G. (Eds). Albuquerque: New Mexico Museum of Natural History and Science Bulletin.
- Van der Sluijs, L., Gerken, M. & Preuschoft, H. (2010). Comparative analysis of walking gaits in South American camelids. *J. Zool. (Lond.)*. (Online DOI: 10.1111/j.1469-7998.2010.00739.x).
- Webb, S.D. (1972). Locomotor evolution in camels. *Forma Functio* **5**, 99–112.
- Witte, T.H., Hirst, C.V. & Wilson, A.M. (2006). Effect of speed on stride parameters in racehorses at gallop in field conditions. *J. Exp. Biol.* **209**, 4389–4397.