Comparison of the Morphology of the Limbs of Juvenile and Adult Horses (*Equus caballus*) and Their Implications on the Locomotor Biomechanics

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ABSTRACT
We analyzed the morphology and the walk–trot and trot–gallop transition velocities of nine juvenile horses and compared them with their mothers. We also compared the relative stride length and the duty factor of the juveniles with respect to adults at three equivalent trotting speeds (Froude numbers 0.5, 0.75, and 1.0), to determine dynamic similarity. Juveniles had a negative allometry in their leg bones, mainly because of little size changes of the distal portions. The negative allometry of extremities allows juveniles to increase stride length without increasing step frequency, which can be biomechanically advantageous. The Froude number during the walk–trot velocity transition of juveniles was similar to that of adult horses, but walk–trot transition velocity in juveniles was greater than expected for their mass. However, during the change trot–gallop, the trot–gallop velocity transition was conserved, but the Froude number was lower. Thus, juvenile horses did not move in a manner that was dynamically similar to the adult horses. At low speed (walk–trot), the gait approaches the behavior predicted by the inverted pendulum model, but at high speed (trot–gallop) dominates the inertial forces. The trot–gallop gait change would be conducted at speeds that would minimize energy costs of transport owing to collisions and changes in the trajectory of the center of mass. *J. Exp. Zool. 313A:292–300, 2010.* © 2010 Wiley-Liss, Inc.

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Animals of different sizes can use the same patterns of locomotion. For example, Artiodactyls (Alexander and Jayes, '83) and different breeds of horses conserve the principle of dynamic similarity (Griffin et al., 2004; Bullimore and Burn, 2006). This means that they maintain geometric similarity over a range of body mass and the ratio of all the forces and time intervals that operate in the animal dynamic are similar. The principle of dynamic similarity allows us to determine relations among velocities, frequencies, and periods of an animal in movement, with the size of structures that move at equal relative velocities (i.e. equivalent velocities). For example, the movement of two pendulums of different lengths that oscillate through the same angle shows dynamic similarity, because the ratio between the forces those act

on each is the same (i.e. inertial force/gravitational force). This ratio of forces for terrestrial systems is called the Froude number (*Fr*): $Fr = F_{\text{Inertial}}/F_{\text{Gravity}}$; $Fr = (mv^2/L)/mg$; $Fr = v^2/gL$, where v is the absolute velocity (distance from the center of mass moved in one

unit of time), L is the length of the oscillator, and g is the acceleration due to gravity (Alexander, '76).

Equal Froude number is a requirement for dynamically similar locomotion in animals and if that requirement is satisfied they are said to use the same gait patterns. But, this would only be true up to a certain size, because the effect of mechanical advantage larger animals would lose acceleration capacity and maneuverability (Biewener, '89). Quadrupeds use different transport velocities as well as different gaits depending on the velocity at which they move. Because of the latter, to compare the dynamic similarity of animals of different size, it is necessary to use the velocity at which the animals are performing equivalent movements; thus, it is usual to occupy transition velocities between gaits, for example, between walk and trot ($V_{\text{W-T}}$) or between trot and gallop ($V_{\text{T-G}}$), the latter has been used more frequently (Heglund et al., '74).

Studies have determined the Froude number and studied different morphological and kinematic variables in adult horses of different-sized breeds (Heglund and Taylor, '88; Bullimore and Burn, 2004), and the allometric coefficients of these variables have been determined, thus establishing the locomotor mechanics of this species (Griffin et al., 2004; Bullimore and Burn, 2006). As in the case of other ungulates (Alexander and Jayes, '83), different breeds of horses conserve the principle of dynamic similarity (Griffin et al., 2004; Bullimore and Burn, 2006). However, few studies have examined the principle of dynamic similarity during ontogeny, during which there are changes in both size and form.

In one of the few studies of ontogenetic changes in ungulates, a morphological and kinematic study in the Goat *Capra hircus*, a negative allometry of the transverse section of the radius, the second moment of area during ontogeny, as well a positive allometry of the levels of bone tension and pressure were reported (Main and Biewener, 2004). This showed that limb skeleton must grow to accommodate the increases in body weight and the resulting locomotor forces placed on the limbs and even though bone strains also increases with growth and age younger goats maintain safety factors similar to adults. Also, it has been shown that the rigidity (i.e. elastic modulus) of the tendon of the superficial digital flexor of horses increases during ontogeny (Gillis et al., '95). These results are relevant for the inference of the kinematic locomotion of juvenile animals.

In the case of horses, because leg length in relation to mass seems to be greater in juveniles with respect to adults, we may expect that this length would increase less than expected during growth, that is, a negative allometry of legs during growth. We would expect to find differences in the walk–trot ($V_{\text{W-T}}$) and trot–gallop ($V_{\text{T-G}}$) transition velocities between horses in early stages of ontogeny and adult horses. Alexander and Jayes ('83) formulated the hypothesis that quadrupeds tend, where possible, to move in dynamically similar ways, which implies that they will change gaits at equal Froude numbers, i.e. about 0.2 walk to trot and about 1.25 from trot to gallop, reflecting the fact that kinetic energy fluctuations of an animal's body become important at faster speed (Biewener, 2003). But in juvenile animals, body mass, the relationship between the parts, resistance and stress in bones and muscles, and the stiffness of the tendons are not the same as in adult animal, which may result in a biomechanical performance different to that of adults. This may affect the fitness in ungulates whose survival depends on its ability to move and escape predators.

In this study we address two questions: (i) are juvenile horses geometrically similar to adults? and (ii) do juvenile horses move in a manner that is dynamically similar to the locomotion of adult horses?

METHODS

Animals
Morphological variables were studied in 9 adult mares of *Equus caballus* (Mb = 492.4 ± 38.2 kg) and morphological and kinematic variables in 9 of their offspring (6 fillies and 3 colts; (Mb = 105.6 ± 12.0 kg). Juveniles were studied between ages 43 and 54 days (46.3 ± 3.9 days; mean ± SD). The animals were kindly provided by Haras Santa Mónica (Linderos, Buín, Chile). Trials were performed in this company's ranch, and each process of data collection was approved by their veterinary team. All animals were weighed on a platform scale (± 1 kg).

Morphological Measures of Adults and Juveniles
We measured 13 lengths and calculated 2 derived variables from them. Segments were measured using the methodology of Griffin et al. (2004) by means of palpations when animals were at rest: (1) trunk length (LT), (2) foreleg length or distance ground-shoulder (DGS), (3) hind leg length or distance ground-hip (DGH), (4) length of scapula (LE), (5) humerus (LH), (6) ulna (LU), (7) third metacarpal (LMC), (8) phalanx of the fore leg, (9) distance ground-dorsal scapula (DGD), (10) femur (LF), (11) tibia (LTB), (12) third metatarsal (LMT), (13) phalanx of the hind leg (PHL) (Fig. 1). Trunk length was measured as the craneocaudal distance between the anterior aspect of the scapulohumeral articulation and the ischion. Foreleg length was measured in two ways: as the vertical distance between (i) the shoulder (scapulohumeral articulation) and the ground, and (ii) the dorsal border of the scapula and the ground. The effective length of the foreleg is probably between these two lengths, owing to the rotational movement of the scapula during movement. Hind leg length was measured from the ground to the greater trochanter of the femur, a bone prominence slightly dorsal to the acetabulum (articulation of the femur with the hip). This height was used to calculate the Froude number (Fr) and the relative step length (RSL). To estimate the posture of the hind leg and foreleg of the animals (PHL and PFL, respectively), we calculated the ratio between the height of the leg at rest and the sum of the lengths of all the bones that compose it. This index indicates the orientation of the segments of each leg with respect to the vertical axis from the articulation
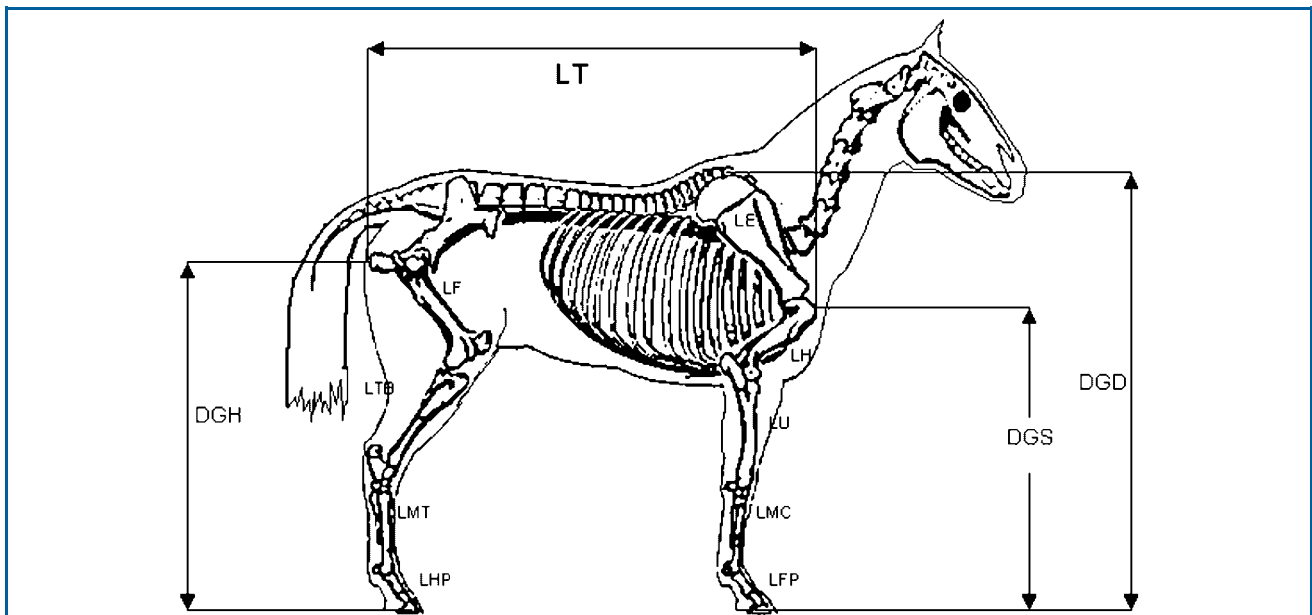
Figure 1. Morphological measures and relative morphological measures of adult mares and juveniles horses. LT, length of trunk; LE, length of the scapula; LH, length of humerus; LU, length of ulna; LMC, length of metacarpals; LFP, length of foreleg phalanges; DGD, distance ground-dorsal scapula; DGS, distance ground-shoulder; LF, length of femur; LTB, length of tibia; LMT, length of metatarsals; LHP, length of hind limb phalanges; DGH, distance ground-hip.

of the leg to the ground; it may be used as a measure of effective mechanical advantage of limb muscles (Biewener, 2003).

The scapula was measured from its dorsal edge to the scapulohumeral articulation (shoulder). The humerus was measured from the shoulder articulation to the humeroradial (elbow) articulation. The third metacarpal was measured from the anterior articulation to the proximal articulation with the first phalanx. The last segment of the foreleg was measured from the last-mentioned articulation to the end of the hoof in the same angle as the phalanges. The femur was measured from the greater trochanter to the patella (knee). The tibia was measured from the patella to the ankle. The third metatarsal and phalanges were measured as described for the foreleg. The posture of the leg during rest is an indicator of the relative position of the segments of the leg. The posture of the foreleg (PFL) was calculated dividing the vertical distance shoulder-ground by the sum of the segments of the leg. The posture of the hind leg (PHL) was calculated by dividing the hip-ground distance by the sum of the segments inferior to this articulation.

Kinematic Analysis

Only juvenile animals were measured in this analysis, because adults have transition velocities greater than those which can be measured by the methods we used. We used a digital video camera of 30 frames per second (SONY, DCR-DVD92 NTSC) coupled to a chronometer, which indicated hundredths of seconds. This assured a minimum of 15 frames per step, which

is adequate for kinematic analysis (Alexander, 2003). The camera was installed at a height of horizontally 1 m from the ground and perpendicularly 10 m from the route of the animals. The camera field width corresponded to 10 m of the route. Juveniles were induced to traverse the route at different velocities using their spontaneous following behavior, by leading the mother with reins at different velocities. Using different guides, juveniles were made to walk, trot, and gallop, at different velocities within each gait. Three to four trials were performed at each gait for each animal. Velocities (v), stride length (sl), limb contact time (t_c), and stride period (T_s) were measured in each trial. To avoid sub-estimations of velocity, trials in which the animal deviated more than 1 m from the perpendicular to the focal plane were eliminated (deviations of <1 m produce errors in velocity estimation of $<0.5\%$). To calculate movement velocities, first stride time was measured (one complete gait cycle, e.g. from ground contact of a leg to the next contact of the same leg) and then stride length was estimated by direct measurement in a flat monitor (LG, FLATRON 29 inches). We used the hind leg closest to the camera to determine the beginning (contact of the hind leg with the ground) and end (when the hind leg leaves the ground) of each step. We used only observations in which the juvenile maintained a constant velocity. This was done by calculating the velocity of two successive steps, considering as valid only those steps in which the difference was less than 5%. Transition velocities (walk–trot V_{W-T} and trot–gallop V_{T-G} velocities) were calculated using the intersections of regression lines between the

stride length and the velocity of each gait (following Heglund and Taylor, '88).

We estimate relative stride length and duty factors ($\beta = t_c/T_s$) at different Froude numbers. To calculate the relative stride length at given Froude (Fr) numbers, first, we estimated the velocity that corresponds to each Fr value (0.5, 0.75, and 1.0) for each juvenile ($v_f = \sqrt{Fr \cdot g \cdot l}$) and linear regression between the measured velocities and stride length in each horse were used to estimate the stride length associated with the calculated velocity. These stride lengths were then divided by the leg length of each juvenile, yielding the relative stride length at particular Fr numbers. The duty factor for the Fr values was calculated in the same way using v_f but performing a linear regression between duty factor and the measured velocities in each juvenile for the estimation (Fig. 2).

Statistical Treatment

To compare morphological data of juveniles with adults, we normalized the morphological variables by dividing by trunk length (LT) and performed a discriminant analysis. Univariate approaches for each variable using Student's t-test for dependent samples were performed. The morphological measures LT, DGS, and DGH were compared with those expected from allometric relationships (Griffin et al., 2004) with Student's t-test for independent samples. The walk–trot– transition velocity was compared with reported data in adults using Student's t-tests, and the trot–gallop transition velocity, relative stride length, and duty factors were compared with expected values from allometric relationships using Student's t-tests.

RESULTS

Morphology

The multivariate response of morphological variables showed differences between mares and juvenile groups in the discriminant analysis (Willks-$\Lambda = 0.01224$; $F_{12,5} = 33.36$; $P = 0.0006$).

As expected, juveniles differed from adults in body mass and all the relative morphological measures (Table 1) and all the absolute measures excepting length of forelimb phalanges (LFP), ground-dorsal scapula distance (DGD) and length of metatarsals (LMT). The posture of the forelimb (PFL) did not show differences with respect to adults ($t_8 = 0.85$, $P = 0.42$). By contrast, the posture of the hind limb (PHL) in juveniles was significantly less erect than in adult horses (0.83 ± 0.03 and 0.92 ± 0.04, respectively; $t_8 = 4.67$, $P = 0.002$).

The body mass of adult horses was about 3.7 times that of the juveniles. When comparing juveniles with their mothers, the trunk was the measure that showed the largest juvenile–adult change, both in relative (68.8%) and absolute (0.64 m) terms, whereas the measures with the least change were the distal segments (Table 1).

Allometry

For the relationship between LT and Mb in our horses, we found $LT = 0.188 \, Mb^{0.34 \pm 0.01}$ ($F_{1,16} = 628,9$ $P \ll 0.001$, $R^2 = 0.97$) and
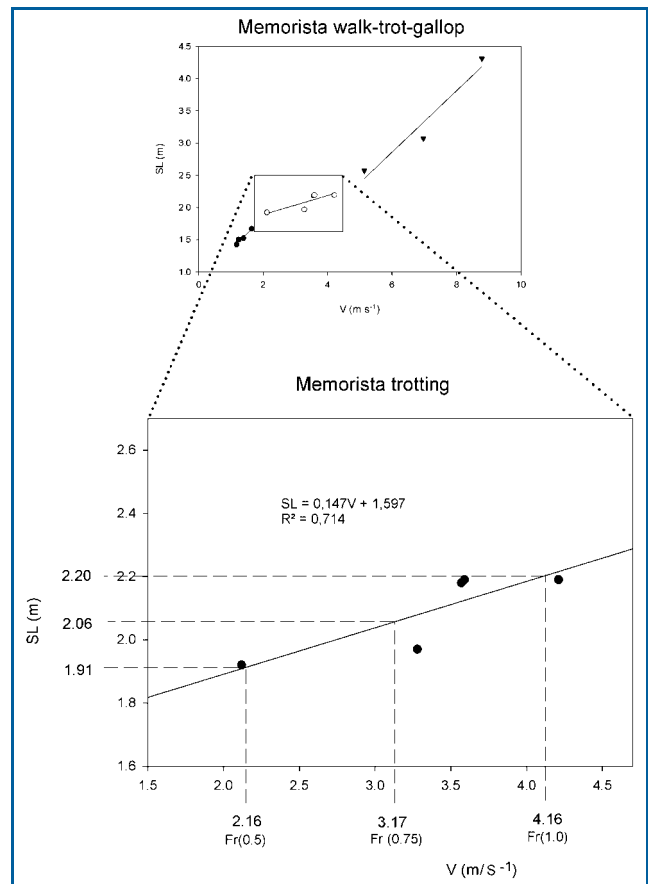

Figure 2. Step length as a function of velocity for one juvenile "Memorista". Black circles are step length values while the colt walked, open circles to values while trotting, and triangles to values while galloping. The transition velocities were obtained from the intersection of the linear functions of each pace. The zoom shows the method used to estimate stride length at different velocities resulting from different Froude numbers characteristics of trot gait.

the exponent was similar to that expected by isometry (0.33; $t_{16} = 1.0$, $P = 0.49$). That relationship was similar to $LT = 0.19 \, Mb^{0.33 \pm 0.02}$ reported for adult horses by Griffin et al. (2004). The lengths of the forelimbs (1.06 ± 0.03) and hind limbs (0.95 ± 0.04) of juveniles were greater than those expected for adult horses (0.56 ± 0.02 and 0.67 ± 0.03, respectively), from $DGS = 0.1 \, Mb^{0.37 \pm 0.031}$ and $DGH = 0.12 \, Mb^{0.37 \pm 0.02}$ (Griffin et al., 2004) ($t_{16} = 36.9$ and $t_{16} = 18.9$ respectively, $P \ll 0.001$, Fig. 3). The calculated allometric relationships of foreleg and hind leg length with the data of juveniles and their dams were $DGS = 0.4 \, Mb^{0.209 \pm 0.02}$ ($F_{1,16} = 556.5$, $P \ll 0.01$, $R^2 = 0.97$) and $DGH = 0.42 \, Mb^{0.177 \pm 0.01}$ ($F_{1,16} = 273.0$, $P \ll 0.01$, $R^2 = 0.94$), respectively. Both exponents differed to 0.33 ($t_{16} = 6.05$ and $t_{16} = 15.3$, $P \ll 0.001$). Thus, it is clear that there is a negative allometry of horse limbs during growth, because the exponent is much less than the 0.33 expected from isometry.

Table 1. Body mass (Mb), absolute morphological measures (in m), relative morphological measures and postural indexes (PHL and PFL) of adult mares and juveniles horses.

	Absolute measures		Relative measures	
	Adults mares	Juveniles	Adult mares	Juveniles
Mb (kg)	492.44±38.24*	105.67±12.00		
LT	1.58±0.07*	0.93±0.07		
LE	0.54±0.04*	0.36±0.04	0.37±0.07*	0.40±0.06
LH	0.36±0.02*	0.26±0.02	0.23±0.02*	0.28±0.03
LU	0.42±0.02*	0.32±0.04	0.27±0.01*	0.36±0.07
LMC	0.28±0.02*	0.26±0.03	0.19±0.03*	0.29±0.05
LFP	0.17±0.01	0.15±0.02	0.11±0.01*	0.17±0.04
DGD	1.0±0.04	0.82±0.02	0.63±0.04*	0.82±0.19
DGS	1.46±0.06*	1.06±0.03	0.92±0.04*	1.07±0.22
LF	0.32±0.02*	0.28±0.02	0.21±0.03*	0.29±0.02
LTB	0.47±0.03*	0.37±0.03	0.31±0.05*	0.40±0.03
LMT	0.39±0.04	0.34±0.03	0.28±0.10*	0.37±0.04
LPH	0.18±0.01*	0.15±0.02	0.11±0.01*	0.17±0.04
DGH	1.25±0.04*	0.95±0.04	0.77±0.07*	0.97±0.15
PFL	0.81±0.03	0.83±0.07		
PHL	0.92±0.04*	0.84±0.03		

Relative measures correspond to absolute measures divided by LT. Abbreviations as in Figure 1. (*) represents significative differences between adults and juveniles of this study, respectively, using $\alpha = 0.05$, with Bonferroni's correction. LT, length of trunk; LE, length of the scapula; LH, length of humerus; LU, length of ulna; LMC, length of metacarpals; LFP, length of foreleg phalanges; DGD, ground-dorsal scapula distance; DGS, ground-shoulder distance; LF, length of femur; LTB, length of tibia; LMT, length of metatarsals; LHP, length of hind limb phalanges; DGH, ground-hip distance. The calculation to determine the posture of the forelimb (PFL) was DGH/(LH+LU+LMC+LFP), and for the hind limb (PHL), DGH/(LF+LTB+LMT+LHP).

Walk–Trot Transition Velocity

Juveniles walked at velocities that ranged from 0.87 to 1.75 m s^{-1} and trotted between 1.86 and 4.21 m s^{-1}. The walk–trot transition velocity for the 9 juveniles was 2.01±0.42 m s^{-1} (Table 2, Fig. 2). This V_{W-T} value was significantly greater from values expected for adult miniature horses (1.63±0.1 m s^{-1}) of similar body mass (112±21 kg) (Griffin et al., 2004) ($t_8 = 2.71$, $P = 0.027$) but similar to that of arabian adults (1.91±0.14 m s^{-1} and 448±22 kg) ($t_8 = 0.71$, $P = 0.49$).

The Froude number associated with this V_{W-T} for juveniles was 0.45±0.21 similar to the Fr numbers observed in adults of other breeds of horses: 0.347±0.0283 ($t_8 = 1.47$, $P = 0.18$).

Trot–Gallop Transition Velocity

Gallop velocities fluctuated between 3.2 and 10.7 m s^{-1}; the V_{T-G} transition velocity (Fig. 2) was 4.05±0.65 m s^{-1}, which was not different from, the expected value for adult animals of the same body mass as the juveniles (4.21±0.099 m s^{-1}), according to Heglund and Taylor ('88) $V_{T-G} = 1.54 \cdot Mb^{0.216}$ (Mb in kg and V_{W-T} in m s^{-1}; $t_{16} = 0.73$, $P = 0.48$).

The Froude number associated with this velocity was 1.81±0.61 for animals with an effective limb length of 0.95±0.04 m (hind leg). This value is less than that observed
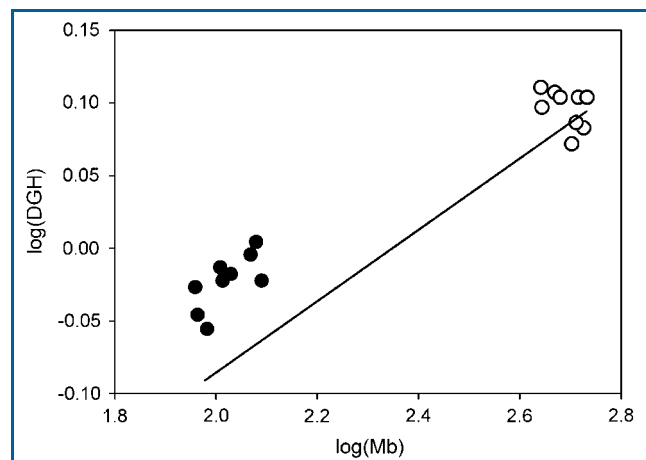

Figure 3. Log–log graph of DGH and Mb. Black circles are juvenile horses and white circles are adults. The line correspond to the expected values for adult horses DGH = 0.12Mb0.37 (Griffin et al., 2004).

for cursorial mammals, which change from trot to gallop in Fr values between 2 and 3 (Alexander and Jayes, '83), and also less than the expected values from the definition of the Froude

Table 2. Relative step length (LRS) and duty factor (β) for different Froude numbers (*Fr*) during the trot of juvenile horses.

Fr	LRS	β
0.5	1.567 ± 0.241 (1.43) ($t_8 = 1.71$; $P = 0.062$)	0.490 ± 0.027 (0.47) ($t_8 = 2.22$; $P = 0.028$)
0.75	1.868 ± 0.186 (1.49) ($t_8 = 6.094$; $P < 0.001$)	0.447 ± 0.043 (0.44) ($t_8 = 0.46$; $P = 0.328$)
1.0	2.307 ± 0.275 (1.66) ($t_8 = 7.072$; $P < 0.001$)	0.408 ± 0.029 (0.39) ($t_8 = 1.96$; $P = 0.043$)

The expected values from Bullimore and Burn (2006) and Student's *t*-test and *P* values are given in parentheses.

number and the allometric relationships for DGH and $V_{\text{T-G}}$ in adult horses: 2.69 ± 0.09 ($t_{16} = 4.37$, $P = 0.0004$).

The stride frequency during this gait transition was lower than the expected, sf $= 0.623 + 0.25$ Mb, according to Heglund and Taylor ('88), $1.92 \pm 0.2\,\text{s}^{-1}$, and $2.08 \pm 0.03\,\text{s}^{-1}$, respectively ($t_{16} = 2.37$, $P = 0.03$).

Dynamic Similarity

The RSL values of the juveniles at three different trot velocities corresponding to the three different *Fr* numbers described by Bullimore and Burn (2006) in adult horses were different at the three *Fr* values (Table 2) ($t_8 = 1.71$, $P = 0.062$; $t_8 = 6.09$, $P \ll 0.01$, $t_8 = 7.07$, $P \ll 0.01$ for $Fr = 0.5$, $Fr = 0.75$ and $Fr = 1$, respectively). Duty factors were linearly correlated with *v*: $\beta = 0.561 - 0.0337\,v$; $F_{1,24} = 19.51$, $P \ll 0.001$). Comparing with values from Bullimore and Burn (2006), in adult horses, we found differences at $Fr = 0.5$ and $Fr = 1$ ($t_8 = 2.22$, $P = 0.028$ and $t_8 = 1,96$, $P = 0.043$, respectively but not at $Fr = 0.75$ ($t_8 = 0.46$, $P = 0.328$; Table 2).

DISCUSSION

Horses are born with disproportionately long limbs with respect to adults; the negative allometry is because of only a few bone segments. In the forelegs, the segments that differed least from those of adults were the metacarpals and phalanges; for the hind legs, they were the metatarsals and phalanges. Thus, it is clear that distal segments of extremities are that grow least during ontogeny (i.e. with the greatest degree of negative allometry). The majority of the musculature of an adult horse is practically at the level of the trunk, that is, above the articulations of the elbow and knee, thus it is the tendons that reach the more distant areas and transmit the forces. This permits having longer limbs with more proximal centers of mass, which results in less force required to overcome the inertia of the appendicular structure. It is interesting that it is precisely the structures which have less musculature and that collaborate in the length of the limb, which are those that have the least change in the index and in relative

and absolute length. In contrast, the allometric coefficient of trunk length fully adjusted to the expected from isometry, which indicates that the juveniles have a trunk length in agreement with their body mass but not the length of their extremities.

The posture of the foreleg of the juveniles was similar to that of adults; thus, the greater distance between the shoulder and the ground is only because of an increase in length of the individual bones and not to a more erect posture of the limb. The segments of the hind leg were individually larger, but in contrast to the posture of the foreleg, the posture of the hind leg was significantly less erect. This suggests an extremity with less effective mechanical advantage, because the forces of reaction of the ground are projected more perpendicularly to the longitudinal axis of the bone segment, thus producing greater muscle-skeletal force (Biewener, '89, 2005). However, the degree of effective mechanical advantage is not only because of the direction of the forces of reaction from the ground and the orientation of the muscle-skeletal structures, but also because of the relative distances of the arms of the lever that acts on the articulation, which was not considered in this study. Also, a reduction from 0.90 to 0.83 in the posture index of the hind limb ($< 10\%$) indicates only a small change in the angles of the segments of the limb and a small effect in the effective mechanical advantage, because the variation in this index indicates how much the arms of the lever change. For example, if the extremity was only composed of two segments, then an index of 0.9 would indicate an angle of $128.3°$ between the segments, and an index of 0.82 would indicate an angle of $112.2°$. Because effective mechanical advantage is a function of body mass and juveniles had a lower mass than that expected for their limb lengths, the lever forces would not increase greatly with a change of 10% in the posture index.

Tendons are very important for the elastic energy, which they accumulate during locomotion; thus, modification of the elastic properties of the tendon (Bullimore and Burn, 2004) may also be involved in the change of posture of the hind leg, as a compensatory modification to conserve dynamic similarity. Gillis et al. ('95) observed that the superficial digital flexor of juvenile horses has a lower elastic modulus than adult horses and that the tendon becomes more rigid with age but not related to the increase in mass. This may also be related to locomotor ability because juvenile flexible tendons have also been observed in the rabbit, an animal with clear adaptations for jumping (Yamamoto et al., 2004).

The morphological differences of juvenile conditioned the movements during gait changes. The juvenile horses did not move in a manner that was dynamically similar to the adult horses. While during walk–trot transition, $V_{\text{W-T}}$ was higher than the expected, but with similar Froude number, during the trot–gallop transition, $V_{\text{T-G}}$ was similar but the Froude number was lower than the expected value. Also, differences in relative stride length and in duty factors between juveniles and adults

horses were found at similar Froude number (usually found during trot gait in horses).

To increase gait speed requires an increase in the energy expenditure per unit of time, at least in horses (Hoyt and Taylor, '81), because this increase is associated with an increase in the length or in frequency of steps (or both). Heglund and Taylor ('88) showed that increasing step length without changes in stride frequency increases the energy expenditure per unit of time.

Juveniles had RSLs larger than the expected values at equivalent velocities (between 10 and 39% for Fr numbers between 0.5 and 1), that is, the limb follows larger relative trajectories than adult horses; thus, they should have a greater energy expenditure owing to length. But, because the length of the limb is also significantly greater than expected ($\approx 41\%$), juveniles cover greater distances per step probably without greater cost of transport, at least because of the trajectory of the limb.

Heglund and Taylor ('88) also showed that there is an increase in the energy expenditure per unit of time owing to step frequency, which is because of the fact that in a step, at least 30% of the energy is used in the muscular activation associated with the calcium pump to the sarcoplasmic reticulum, and the other 70% is used in the contraction and performance of work. This would explain the decrease in cost of transport for larger animals (Heglund et al., '74; Kram and Taylor, '90), because smaller animals have greater frequencies or take more steps to move a given absolute distance. This implies that a greater number of steps in a given time produces a greater total energetic cost due to loss of energy without performing work. However, the step length of juveniles was about 1.3 times longer than for adult horses of the same mass, from which, if the increase in velocity is due only to step length (i.e. equal frequencies), then the walk–trot transition velocity would be 1.3 times greater, taking into account that the RSL is constant for a given equivalent velocity. The mean V_{WT} of juveniles ($2.01 \pm 0.42\,\mathrm{m\,s^{-1}}$) with respect to adults ($1.64 \pm 0.09\,\mathrm{m\,s^{-1}}$) was 1.23 times greater; thus, the increase in velocity is probably mainly because of the longer step length and not to the changes in step frequency. Increases in step length may be important in reducing cost of transport because they allow covering a greater distance in less time and using fewer steps. By increasing their V_{W-T}, juveniles could stay in an energetically more economical pace than adult horses of the same mass because trotting increases step frequency.

The V_{T-G} was not different from the expected for adult animals of the same mass, but the Froude number associated with this value of V_{T-G} is less than the expected for animals with the leg length of the juvenile horses. This may not be contradictory with a good performance in the locomotor system of juveniles.

Solving for the velocity in the equation for the Froude number, velocity increases (for a given Fr) with an allometric exponent of 0.17 ($Mass^{0.166}$). Comparing this exponent with the observed for V_{W-T} and V_{T-G} (0.164 and 0.216, respectively), it is clear that V_{W-T} (at least in horses) is determined by similar principles to those of a kinematic pendulum. Because the Froude number may be interpreted as the quotient of the inertial force and the gravitational force of a pendulum, in the model of inverted pendulum (Alexander, 2003), this value has a maximum given by the force of gravity (at greater velocities the body loses contact with the ground); thus, the pendulum model is correctly applied during the V_{W-T} and the only way to increase velocity would be to increase leg length.

The explanation of the positive allometry of the V_{T-G} is less clear, which may indicate that for these velocities there is a greater participation of the capacity of storage of elastic energy (tendons and muscles). Thus, it is possible that V_{T-G} coincides with the expected for the muscular mass of an organism, that is, that the restrictions are not mechanical but rather physiological. According to our results, during the walk–trot transition, the inverted pendulum model seems to work relatively well, agreeing with the results of Griffin et al. (2004) with adult horses. However, during the trot and the transition trot–gallop, this model does not seem to apply. We found changes in duty factors and relative stride length for Froude numbers that are characteristics of the horse trot (Bullimore and Burn, 2006) and the trot–gallop transition speed was similar to that expected for a horse of similar mass, but with a lower Froude number. It indicates that during the trot and the transition trot–gallop (at higher speeds) the gait change is governed by inertial forces.

Many criteria have been proposed to determine a pace change using this as an *equivalent velocity*. However, deviations from these theoretical predictions are found when different species are compared (Griffin et al., 2004). Thus, instead of a universal criterion, different criteria have been developed (Day and Jane, 2007). It has also been suggested that certain variables should have a size-dependent interpretation (Iriarte-Diaz, 2002; Iriarte-Diaz et al., 2006). Several hypotheses different to the principle of dynamic similarity may help explain our results. (1) Gait changes would reduce the mechanical stress of the musculoskeletal system (Biewener and Taylor, '86; Farley and Taylor, '91), (2) gait changes would reduce metabolic costs (Hoyt and Taylor, '81; Alexander, '89), (3) gait changes could be associated with reduced energy costs because of collisions resulting from changes in the trajectory of the center of mass (Bertram and Ruina, 2001; Bertram et al., 2006). Effectively, Bertram and Ruina (2001) and Bertram (2002, 2005) in several experiments using human volunteers with speed, step length or frequency constraints, not only rejected the predictions of inverted pendulum model but also gave credit to the unnatural locomotory restrictions imposed to the subjects. They proposed the constrained optimization hypothesis, which predicts that locomotor variables used during a gait are those that minimize underlying functions related to metabolic costs of transport.

Our results were obtained without the use of a treadmill, obtaining the spontaneous march of juveniles, indicating that even in spontaneous movements at speed of trot–gallop

transition the inverted pendulum model does not explain the findings. The different morphology of juveniles should condition a different mechanical movement that becomes relevant at higher speeds, for example, collisions and changes in the center of mass trajectories that result in energetic costs increments.

Locomotor advantages that help juveniles stay with the herd (or at least close to the mother) during long migrations would be of great utility (Main and Biewener, 2004), as, because of their size, juveniles tend to move at lesser velocities than adults. The length of the limbs of juveniles with respect to adults described in this study may be one of these locomotor advantages, considering that in some juvenile ungulates these disproportionately long limbs are apparently disadvantageous because they cannot graze standing up but must "kneel" to eat (Pennycuick, '75). A good locomotive performance in juveniles would be a relative advantage compared with those which do not have it, taking into account that efficiency in the locomotor system may mean an energy savings, which would be available for growth and development of the reproductive system (Alexander, 2003).

ABBREVIATIONS

DGD: ground-dorsal scapula distance
DGH: ground-hip distance
DGS: ground-shoulder distance
Fr: Froude number
LE: length of scapula
LF: length of femur
LFP: length of foreleg phalanges
LH: length of humerus
LHP: length of hind limb phalanges
LMC: length of Metacarpals
LMT: length of metatarsals
LT: length of trunk
LTB: length of tibia
LU: length of ulna
PFL: posture of the forelimb
PHL: posture of the hind limb.
RSL: relative step length
SL: stride length
t_c: limb contact time
T_s: stride period
V_{T-G}: trot–gallop transition velocity
V_{W-T}: walk–trot transition velocity
β: duty factor

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