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Biomechanics of terrestrial locomotion: asymmetric octopedal and quadrupedal gaits

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PhD Student: **Dott. Carlo M. Biancardi**
Matricola: **R08161**

Tutor: **Prof. Alberto E. Minetti**
Coordinatore: **Prof. Paolo Cavallari**

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"If you really want something, and really work hard, and take advantage of opportunities, and never give up, you will find a way"
Jane Goodall

"Quadrupedante putrem sonitu quatit ungula campum"
Publius Vergilius Maro - Aeneis

"Ci sono adolescenze che si innescano a novanta anni"
Alda Merini - La vita facile

Abstract

The main goal of this dissertation is to investigate the biomechanics of octopedal and quadrupedal locomotion in terrestrial animals, common determinants, advantages and limits, in particular of the asymmetric gaits. Two different approach have been chosen: i) a kinematic study of a terrestrial spider, the Brazilian giant tawny-red tarantula, an octopods predator species that hide in burrows, ambush and rapidly bounce the prey with a sprint, and ii) a comparative study of the two types of gallop of the cursorial terrestrial mammals.

Eight-legs locomotion has been one of the first travelling modes on land, and spiders display one of the most versatile locomotor repertoire: they move at slow and fast speed, forward-backward-sideways, they climb and even jump, both on firm terrain and from the water surface. Spiders can walk in the two senses at the same speed, just by reversing their diagonal footfall scheme. They turn on the spot like an armoured tank, with opposite direction of the two treads of limbs. Also, the high number of limbs ensures an increased locomotor versatility on uneven and rough terrains, particularly in the likely unawareness of each endpoint location on the ground.

The aims of this first part were: i) identifying the principal octopod gaits, ii) calculating the mechanical external and internal work at the different speeds/gaits, iii) assessing any tendency to exchange potential and kinetic energy of the body centre of mass, as in pendulum-like gaits, and iv) evaluating how spiders' mechanical performance and variables allometrically compare to other species. Another question was: can the octopod gaits be considered as different combinations of two quadrupeds' locomotion?

In this investigation we used inverse dynamics to study the locomotor performance of a terrestrial spider. 9 reflective markers have been placed on the tip of the 8 legs and on the cephalothorax, and their position recorded at a frequency of 50 Hz and digitized through a motion analysis system. Data have been processed using LabView (National Instruments, USA) specific development. The 3D trajectories of the body centre of mass in local coordinates, as during locomotion on a treadmill, have been calculated by applying a mathematical method based on the Fourier analysis of the three coordinates of the centre of mass (COM) over time. Two main gaits, a slow and a fast one characterised by distinctive 3D trajectories of COM, have been identified.

The calculated total mechanical work (= external+internal) and metabolic data from the literature allowed estimating the locomotion efficiency of this species, which resulted less than 4%. Octopod gait pattern due to alternating limb support, which generates asymmetrical COM trajectories and a small but consistent energy transfer between potential and kinetic energies of COM, can be considered as formed by two subsequent quadrupeds, where the first two pairs of feet (1 and 2) are the fore and the hind feet of the first quadruped, and the third and fourth pairs are the fore and hind feet of the second quadruped. The two quadrupeds are almost in phase, being the first and third pairs synchronised in their movements as well as the second and fourth.

Octopedal locomotion exhibits two main gaits, neither of which incorporating a flight phase, characterised by a consistent limb pattern and a small but remarkable energy recovery index.

Gallop has been chosen as model of asymmetric cursorial locomotion in quadrupeds. In transverse gallop the placement of the second hind foot is followed by that of the contralateral forefoot, while in rotary gallop is followed by the ipsilateral forefoot, and the sequence of footfalls appears to rotate around the body. The question are: why two models of gallop? Are they specie-specific? Which are the biomechanical determinants of the choice between transverse and rotary gallop?

Aims of this part of the research were: i) assess, when possible, the specie-specificity of the gallop type in different cursorial mammal species, ii) phylogenetically classify the investigated species, iii) Made a comparative analysis based on morphological, physiological and environmental differences.

351 filmed sequences have been analysed to assess the gallop type of 89 investigated mammal species belonging to Carnivora, Artiodactyla and Perissodactyla orders. 23 biometrical, ecological and physiological parameters have been collected for each species both from literature data and from experimental measures. Most of the species showed only one kind of gallop: transverse (42%) or rotary (39%), while some species performed rotary gallop only at high speed (19%).

In a multivariate factorial analysis the first principal component (PC), which accounted for 40% of the total variance, was positively correlated to the relative speed and negatively correlated to size and body mass. The second PC was correlated to the ratio between autopodial and zygopodial limb segments. Large size and longer proximal limb segments resulted associated to transverse gallop, while rotary and speed dependent species showed higher metacarpus/humerus and metatarsus/femur length ratio and faster relative speeds. The maximum angular excursion resulted proportional to the maximum Froude number, and significantly higher in rotary galloper. The gait pattern analysis provided significant differences between transverse and rotary gallop in fore and hind duty factor, and in duration of the fore contact. Our results assessed that a typical gallop gait is adopted by a large number of mammal species, and indicated that the gallop pattern depends on diverse environmental, morphometrical and biomechanical characters.

Even if mammals and spiders can be considered far and different worlds, we can recognize common pattern of locomotion. The quadruped gaits have been modelled as the combination of two biped gaits with some difference in the phase-cycle, in the same way, we described the octopods gaits as the combination of two quadruped gaits in series.

In conclusion, this work shed light on some aspects of octopedal and quadrupedal asymmetric gaits, opening to the raising of new questions and new perspective of research.

1. Introduction

1.1. Foreword

The evolution of terrestrial multi-legged locomotion moved towards two main models: the 8-6 legged terrestrial arthropods and the 4-2 legged terrestrial vertebrates. Speed is indeed one important pressure factor in evolution of animal locomotion: it is important for prey to escape the predators and to predator as well to catch the prey. The inverted pendular paradigm of walking gaits has been proved to be shared by bipeds, quadrupeds, hexapods and octopods. However, as soon as the number of locomotive limbs increases, the multiple support reduces the vertical excursions of the body centre of mass, limiting the possibilities of energy exchange between gravitational potential energy and kinetic energy.

1.2. Objectives

The main goal of this dissertation is to investigate the biomechanical determinants, advantages and limits of octopedal and quadrupedal locomotion in terrestrial animals. Two different approaches have been chosen and developed as independent projects: i) a kinematic study of a terrestrial spider, the Brazilian giant tawny-red tarantula (*Grammostola mollicoma*), an octopedal predator species that hide in burrows, ambush and rapidly bounce the prey with a sprint, and ii) a comparative study of the two models of gallop, transverse and rotary, of the cursorial terrestrial mammals, orders of Perissodactyla, Artiodactyla and Carnivora.

1.3. Thesis structure

This thesis is composed by an introductive overview on terrestrial legged locomotion (Chap. 2), followed by two chapters, one for each of the mentioned project, structured as standalone scientific papers (with introduction, methods, results and discussion). The first one (Chap. 3) has been already published on the *Journal of Experimental Biology* (IF 2010: 3.040), while the second (Chap. 4) is in the submission process on the same journal. Conclusions with future perspectives are discussed in Chapter 5.

In order to ease the reading and the consultation of the thesis, the references are listed at the end of each chapter.

2. Terrestrial legged locomotion

2.1. Introduction

Moving on the Earth surface requires a mechanical device to overcome gravity and accommodate to changes in substrate.

Wheels, which are man's own devices for efficient land transport, have hardly evolved as a means of terrestrial locomotion in living organisms (Biewener, 2003). This is partially due to the difficulties of building a biological rotary engine, at least beyond the bounds of the microscopic dimension of the bacterial flagellum (Dawkins, Nov. 24, 1996). However, the simple main reason is that wheels are not a good device for movements over rough and uneven terrain (Biewener, 2003). Wheel-based transport requires expensive and inevitably wearing infrastructures and, during the course of human history, the wheel has not been universally preferred as a mode of transportation (Gould, 1983; LaBarbera, 1983). For instance, between the second and the sixth centuries, as a result of the degradation of Roman roads, the wheeled vehicles were replaced by camels in all the Middle East and Northern Africa (Bulliet, 1975).

Instead of wheels, natural selection has leaned towards the evolution of limbs to exert forces on the ground, support and move their weight and negotiate uneven surfaces (Biewener, 2003; Walker, 1991). Besides the possibility to efficiently clear hurdles and proceed over rough terrains, limbs permit a high level of manoeuvrability around obstacles, by far unparalleled by wheeled vehicles and, owing to it, recent progresses in robotics have been focused to the development of multilegged robotic vehicles (Krasny and Orin, 2010; Lee and Biewener, 2011; Nagatani et al., 2011; Raibert, 1986; Wang et al., 2011).

Terrestrial animals rely primarily on legs for movement, but there is indeed an alternative technique for locomotion on land that relies on contraction of the axial musculature. Crawling, based on body undulations, is nearly always associated to burrowing habits (Alexander, 2006b; Biewener, 2003). Maggots, larval Diptera, use a kind of two-anchor crawling (Berrigan and Pepin, 1995), while many other worms, like earthworms, crawl by peristalsis (Alexander, 2006b). Worms never evolved limbs, but other animals, like reptiles (i.e., snakes and some lizards) and amphibians (i.e., caecilians), disposed of them (Zaher et al., 2009).

2.2. Energetics and mechanics of terrestrial legged locomotion

2.2.1. Limbs mechanics

Terrestrial locomotion is powered by muscles, namely striated muscles, which convert metabolic energy into mechanical work with a maximal efficiency around 25% (Margaria, 1976; McMahon, 1984).

Locomotor movement requires that forces generated by muscles be transmitted to the external environment. This is achieved by muscles attaching to rigid elements that form a skeleton. The most familiar skeletons are the vertebrates' endoskeleton and the invertebrates' exoskeleton. Hydrostatic skeleton, which use the fluid contained in an internal body cavity, the coelom, as a compression-resistant element, is a common solution among crawling invertebrates (Alexander, 1968). Pressurized fluid is used also in combination to a rigid exoskeleton, like in arachnids (Barth and Biedermann-Thorson, 2001; Foelix, 1996) and hydrostatic components, the intervertebral discs, are even present in the vertebrate endoskeleton (Biewener, 2003).

Terrestrial arthropods exoskeleton is formed by rigid elements made by chitin fibres embedded in a protein matrix. Joints within the exoskeleton elements are made by more flexible chitinous cuticle. Chitin fibres form also apodemes, functional like vertebrate tendons. Apodemes and muscles necessarily attach to the inside of the skeleton (Biewener, 2003). The skeleton of vertebrates is formed by internal bony elements. Bone, like many biological materials, is a complex composition of basic elements, in this case collagen (a protein), fibres and mineral (hydroxiapatite). Bone provides stiffness to effectively transmit forces, but it is also capable of absorbing a considerable amount of energy before failing. Such mechanical properties of bones depend on the mineralization level, which is maintained within a narrow range (63-70%) (Biewener, 2003).

Skeleton works like a jointed lever system, where muscles produce movements and transmit force by developing moments at joints (torque). Flexion and extension of a

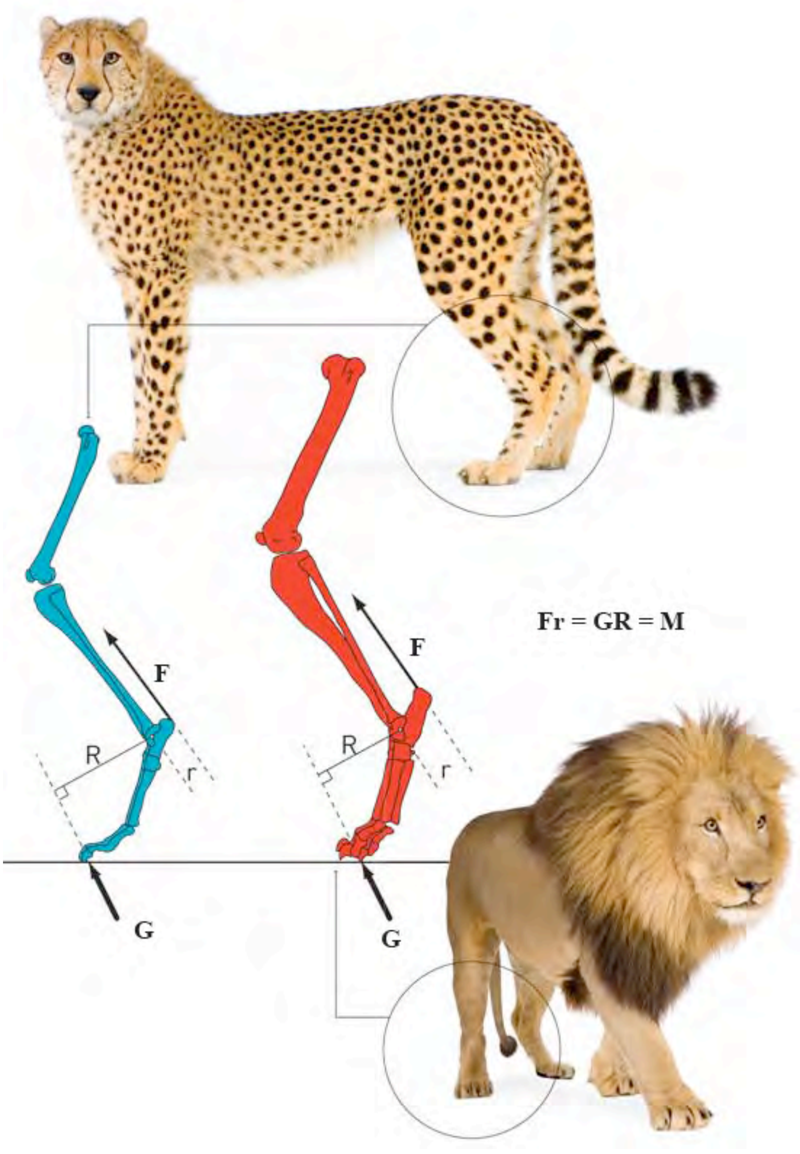

Fig. 2.1. Schematic diagram of the ankle joint, showing the moment (*M*) balance of the extensor muscle force (*F*) relative to the ground reaction force (*G*), which depends on the moment arms (*r* and *R*). Cheetah and lion joints show different mechanical advantages. The long forefoot and short heel of the cheetah give it a very high "gear ratio" (R/r). The lion, with a smaller gear ratio, is less effective at achieving rapid acceleration.

Adapted from S.J. Piazza - "The sprinter's foot" - American Society for Mechanical Engineering Magazine (October 2009) www.memagazine.asme.org

joint are provided by antagonistic sets of muscles, as they only can generate tensile forces (McMahon, 1984). The torque exerted by a muscle depend on the force *F* and the moment arm *r,* that is the perpendicular distance from the vector of the force to the rotational axis of the joint (Fig. 2.1):

$$M = F \cdot r \qquad (1.1)$$

However, the angular velocity ω varies inversely with the moment arm:

$$\omega = v_s \cdot r^{-1} \qquad (1.2)$$

being v_s the rate of shortening of the muscular fibres. Consequently, the moment that a muscle can develop varies inversely with the range and speed of joint motion that it can produce (Fig. 2.1), and the trade-off in force versus speed of movement acts at two levels:

i. the force-velocity relationship within the muscle itself (Alexander, 2006b; Margaria, 1976; McMahon, 1984);
ii. the force-velocity relationship resulting from the lever mechanism (Alexander, 2006b; Biewener, 2003; McMahon, 1984).

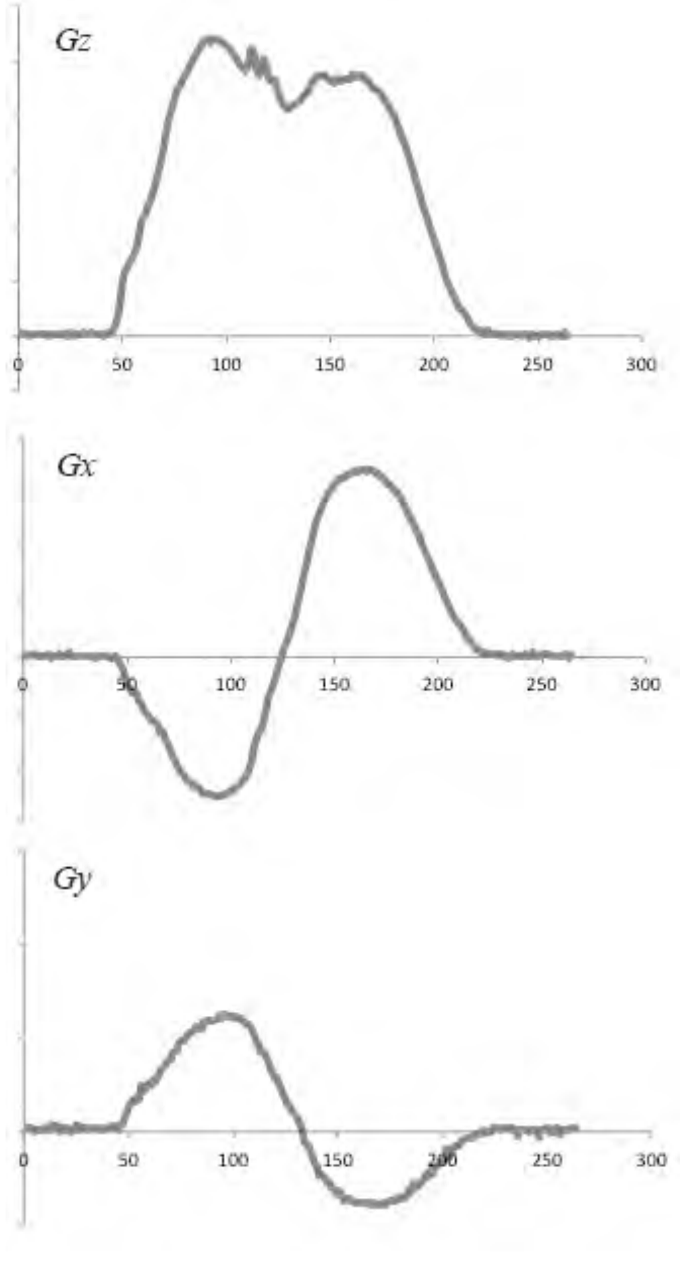

Fig. 2.2. Vertical (G_z), horizontal (G_x) and medio-lateral (G_y) components of the ground reaction force exerted by the forelimbs of a dog during gallop. On abscissa time in ms, on ordinates the force.

When a terrestrial animal limb contacts the ground it exerts a ground reaction force (*G*; fig. 2.1). The vertical component G_z supports the animal's weight, while the horizontal and medio-lateral G_x and G_y allow the animal to accelerate, decelerate, manoeuvre and balance (Fig. 2.2). At rest, the force G_z acting on a limb is approximately equal to $Wg \cdot n^{-1}$, where *n* is the number of limbs supporting the body weight. When an animal moves, independently from the gait and speed, the limbs push on the ground accelerating the body in the desired direction, during the so called stance phase, then the limbs must be repositioned to take a step forward, leaving the ground and accelerating with respect to the body, in the course of the swing phase. During locomotion, the forces exerted by one limb on the ground rise and fall during the stance phase (when the foot is on the ground), and are zero when the limb is in the swing phase, but the average vertical force exerted by the sum of the limb over a complete locomotor cycle (stride) must be equal to the body weight. It follows that if the limbs are kept on the ground for a shorter period of time, larger forces will be exerted on each limb (Alexander, 2006b; Biewener, 2003).

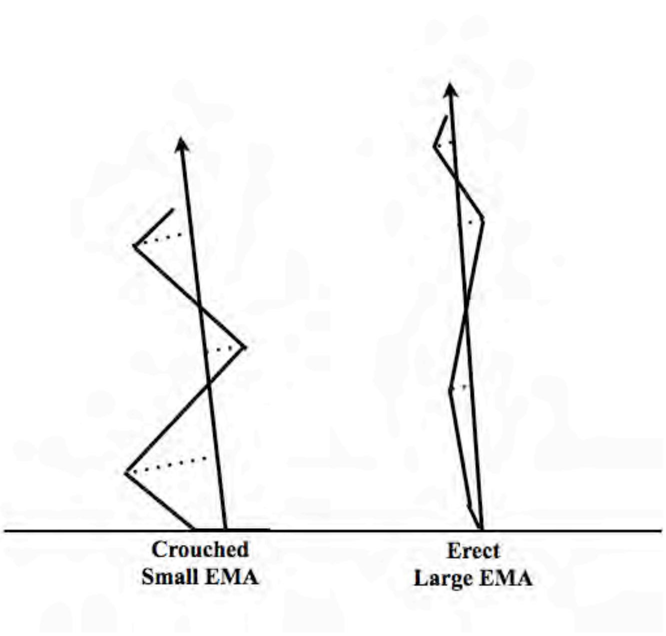

Fig. 2.3. Changes in effective mechanical advantage (EMA) according to the limb posture.
Redrawn from Biewener (2005)

The relative fraction of a stride period when a particular limb is in the stance phase is defined as the limb's duty factor (*Df*). To move faster, an animal has to move its limbs more rapidly, increasing the stride frequency (*Sf*), and/or has to take longer steps, increasing the stride length (*Sl*), eventually engaging one or more flight phases - whenever no limbs are on the ground. In any case, the increase of locomotion speed is achieved by reducing the duty factor, and thereby increasing the magnitude of force exerted against the ground. Because the moments acting at a joint must balance (Fig. 2.1):

$$F \cdot r = G \cdot R \qquad (1.3)$$

Rearranging the equation 1.3:

$$r/R = G/F \qquad (1.4)$$

These moment arm and force ratios provide a measure of the effective mechanical advantage (EMA) of limb muscles. The alignment of the joints in the direction of the ground reaction force changes the mechanical advantage, reducing the muscular force (Biewener, 1989). Such a changes in limb EMA are important for allowing different sized mammals to maintain the peak muscle and bone stresses within a narrow range, and thus having a similar safety factor. Bone and muscle stress depend on bones and muscle fibres cross sectional area, which scale proportionally to (body mass)$^{0.8}$

(Alexander et al., 1981). Thus, the mass-specific reduction in peak musculoskeletal forces is achieved, in large size animals, by adopting a more upright posture, which changes the EMA (Fig. 2.3) (Biewener, 1989). Consequences of size differences will be further discussed.

2.2.2. Size differences

Living organisms are very different in size. Such an enormous difference can be resumed by the exponential value of 10^{21} (Schmidt-Nielsen, 1984). Only among mammals, the smallest shrew (Soricomorpha) is one-millionth the size of an elephant (Proboscidea). Scaling deals with the structural and functional consequences of changing in size or scales among otherwise similar organisms (Schmidt-Nielsen, 1984). For a comprehensive introduction to scaling I refer to the following references (Biewener, 2005; Pennycuick, 1992; Schmidt-Nielsen, 1984).

For the purpose of this dissertation, I would like to resume the main model that have been proposed to describe and deal with the changing in size of animals:

Geometric similarity

Two animals are geometrically similar when one is a precise scale of the other. In other words, when all the length dimensions of one animal can be obtained multiplying the correspondent measure of the other by a fixed factor (Alexander, 2006b). Therefore, geometrically similar structures have areas proportional to $(\text{length})^2$ and volumes proportional to $(\text{length})^3$. Considering that similar animals, being constituted by near the same proportion of the same materials, have near the same density, also the body mass is proportional to $(\text{length})^3$.

Some of the allometric equations, built analysing real values from different species, show relationship between biological measures that are in agreement with that predicted by the geometric similarity model (Alexander, 2006b; West et al., 1997). As an example, the relationship between body mass and body length of the 89 species of cursorial mammals analysed in chapter 4 is shown in fig. 2.4.

Dynamic similarity

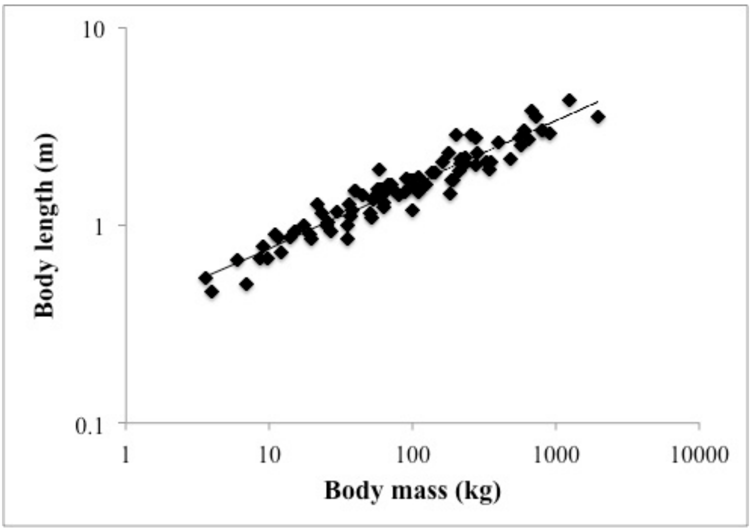

Fig 2.4. Geometric similarity: scaling of body length versus body mass in cursorial mammals (data of the 89 species analysed in chapter 4). The slope of the regression line is actually 0.323, very close to the predicted value (1/3).

Dynamic similarity is an extension of geometric similarity to compare the movements of animals of different size (Alexander, 2006b). Two motions are dynamically similar if one could be described by multiplying all lengths of the other by a factor λ, all times by a factor τ and all forces by a factor ϕ. Two pendulum of different lengths swinging through the same angle is an example of dynamically similar motion (Alexander, 2006b).

Dynamic similarity applies to all the kind of motions (Alexander, 2001; Alexander, 2002a; Minetti et al., 2009). The most important application to terrestrial locomotion is represented by the concept of Froude number, a dimensionless quantity defined as:

$$Fr = v^2 \cdot g^{-1} \cdot l^{-1} \qquad (1.5)$$

Where *v* is the velocity of locomotion, *g* the gravity acceleration and *l* the leg length (Alexander and Jayes, 1983) or the height of the hip joint from the ground in normal standing (Alexander, 2006b; Irschick and Jayne, 2000).

Alexander and Jayes (1983) hypothesized that all quadrupeds would tend to move in dynamic similar way, thus that they would change gait at equal Froude number. From their and other experimental results, it is now commonly accepted that quadrupeds switch from walk to trot at $Fr \approx 0.5$, and from trot to gallop at $Fr \approx 2.5$.

The relative stride length (*Rsl*) is stride length divided by *l* (as defined above). Animal of different size moving in dynamically similar way would have equal *Rsl* (Alexander, 2006b)

Elastic similarity

Biological structures, like limbs, tendons, bones or exoskeletons, are subjected to external forces. According to the elastic similarity model the response, in terms of strain, of biological components of different size, should be the same (McMahon, 1973). According to elastic similarity predictions, leg bones length should scale proportionally to (body mass)$^{1/4}$, and diameters proportionally to (body mass)$^{3/8}$, instead of the geometric similarity predicted common proportion of (body mass)$^{1/3}$. Good agreement with elastic similarity predictions have been found for the leg bones of bovids (McMahon, 1975) and of the cursorial mammals analysed in chapter 4 (e.g., humerus: Fig. 2.5), but not for other groups of mammals (Alexander et al., 1979a), where leg bones scaled more nearly as predicted for geometric similarity.

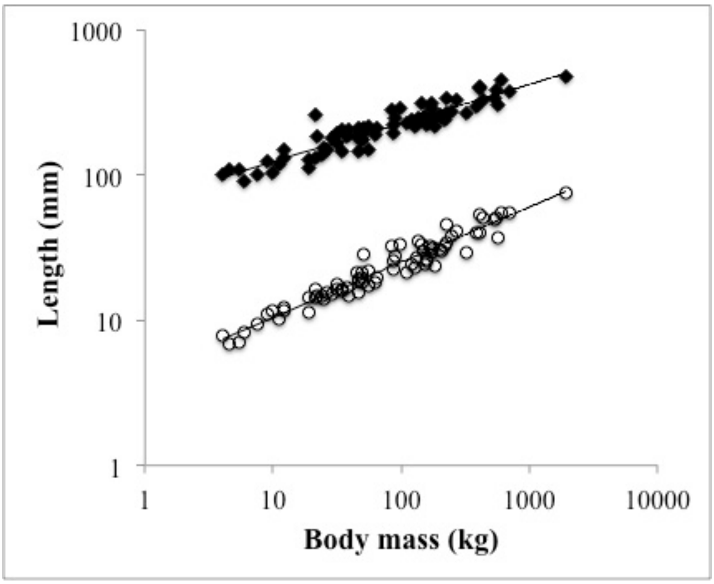

Fig. 2.5. Different scaling of humerus length (filled diamonds) and humerus diameter (open circles) versus body mass. Bone length slope is 0.27 and diameter slope is 0.38, both very close to the values predicted by the elastic similarity model. Data from the 89 cursorial mammal species analysed in chapter 4.

Stress similarity

Stress similarity and elastic similarity are two aspects of the same model design; nevertheless, the difference of viewpoint is important. In fact, while it would be difficult to explain why we would expect structures of different size having the same strain, there are clear reasons why we would expect them supporting the same stress (Alexander, 2006b). Leg bones of different sized animals, for instances, are of the same material with the same stress resistance characteristics. Thus, as previously explained (Chap. 1.2.1), their length and diameter, their joint angles and the position of their muscular insertions must be dimensioned in a way to maintain a good safety factor (Biewener, 1989; Biewener, 1990; Biewener, 2003).

2.2.3. Speed

The speed of an animal, as previously mentioned, is stride length times the stride frequency, and therefore it can be increased by taking longer strides, by moving the limbs more rapidly, or by a combination of the two strategies (Alexander, 2006b).

Legged animals can move faster than legless animals of similar size, and, as a general rule, larger animals can run faster than small ones (Alexander, 2006b). However, very large animals, like the largest terrestrial mammals, are relatively slow (Alexander and Pond, 1992; Genin et al., 2010; Hutchinson et al., 2006; Ren et al., 2008; Ren and Hutchinson, 2008).

To get a reliable measure of the maximum sprint speed is a difficult task, because it has to be measured in the field, except for small animals, arthropods and small vertebrates, for which a more accurate measure can be easily set up in laboratory (Alexander, 2006b; Farley, 1997). Most of the speeds found in scientific literature are estimates (eg: Garland, 1983; Pennycuick, 1975), even so, they have been commonly accepted (eg: Christiansen, 2002). The fastest of all terrestrial runners on sprint is considered the cheetah (Fig. 2.6), with a reliable measured speed of 105 $km \cdot h^{-1}$ (29.2 $m \cdot s^{-1}$) (Sharp, 1997).

Fig. 2.6. Cheetah (*Acinonyx jubatus*)
Fig. 2.7. Pronghorn (*Antilocapra americana*)
Photos by Carlo Biancardi

Maximum sprint speed is largely powered by anaerobic metabolism (Margaria, 1976); hence it can only be sustained on short tracks and largely depends on the mass of muscles in the body. Speeds sustainable by aerobic metabolism are generally much lower, and depend on the capacity of the lungs and blood system to supply oxygen to the muscles (Alexander, 2006b). Although maximum aerobic speeds are generally higher for larger animals, there is a huge variability among species of similar size. The American pronghorn (Fig. 2.7) is by far the fastest long-distance runner species, being able to maintain a maximum aerobic speed of 72 $km \cdot h^{-1}$ (20 $m \cdot s^{-1}$) (Lindstedt et al., 1988; Lindstedt et al., 1991). If we compare a pronghorn to a goat of the same mass, we would find that pronghorns present a maximum rate of oxygen consumption five times higher than the goat. Moreover, pronghorns have lungs more than twice the volume of those of a goat of the same mass, the heart pumps faster and the haemoglobin concentration in the pronghorn blood is higher than in goat blood (Carlton and McKean, 1977; Dhindsa et al., 1974; McKean and Walker, 1974). The legendary endurance characteristics of the pronghorn have been defined a ghost of predator past, as the late Pleistocene extinction decimated the North American fauna, including big predators, causing a great relaxation of the predatory selection pressure on preys (Byers, 1998).

Among invertebrates, small animals that use hexapod or octopod locomotion, ghost crabs (*Ocypode quadrata*) – 50 g of body mass - can sprint up to 1.6 $m \cdot s^{-1}$, employing a sideways octopedal running gait (Blickhan and Full, 1987), while cockroaches (*Periplaneta americana*) can even rise their 0.8 g weigh body switching from six- to four- and two-legs running gait, reaching a speed of 1.5 $m \cdot s^{-1}$ (Full and Tu, 1991). Their maximum aerobic speed are in the order of one-tenth or less of their maximum sprinting speed (Full, 1987).

2.2.4. Gaits

Locomotor gaits are generally defined by the footfalls sequences and by the relative timing of support among the limbs of the animal during the stride. The first foot of a pair in contact with the ground is called the “trailing” foot, while the second one is called the “leading” foot. Gait transitions involve a discontinuous change of one or more of the characteristic quantities, like the already described progression speed, duty factor, stride length and stride frequency, or the combination of time lags (phase shifts) between the footfalls (Alexander, 1989; Biewener, 2003; Hildebrand, 1962; Hildebrand, 1966; Hildebrand, 1977). The stride parameters described by Hildebrand (1966; 1977) were based on the convention to take the footfall of the first hind foot as the starting point of a stride, and consequently as the starting position for calculating the phase shifts among the footfalls. However, Abourachid (2003) introduced the antero-posterior sequence (APS) model, based on three new gait parameters: the time lag between the movements of the two pairs (Pair lag) and the time lag between the movements of the two feet inside each pair (Fore lag and Hind lag) (Fig. 2.8).

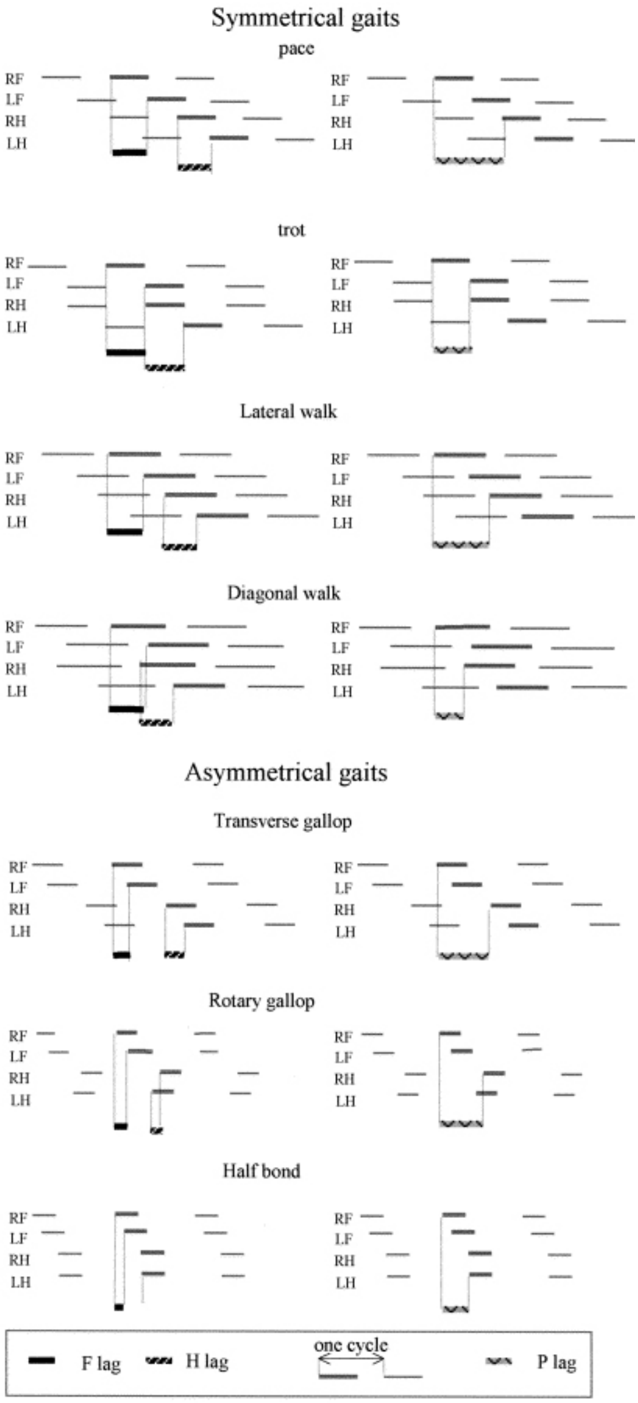

Fig. 2.8. Gait diagrams of the principal symmetrical and asymmetrical gaits and APS model parameters. Black lines represent the stance phase of the right forefoot (RF), left forefoot (LF), right hind foot (RH) and left hind foot (LH).

Adapted from Abourachid (2003)

Walking

Walking gaits are characterized by overlapping periods of stance among the limbs, with a duty factor generally > 0.5. For quadrupedal, hexapedal and octopedal animals this means that during walking there are periods where three or more feet are contemporary in contact with the ground (Fig. 2.8). For this reason walking is defined a statically stable gait. On contrary, bipedal walking must rely on dynamic equilibrium to achieve balance and stability (Biewener, 2003; Blickhan and Full, 1987; Wilson, 1967).

The range of speeds of walking gaits is limited by the absence of an unsupported phase. Therefore, any increase of speed can be achieved by taking longer steps, with the limit imposed by the limbs length, or by increasing the step frequency and consequently reduce the duty factor until the limit of no more overlapping period (Biewener, 2003).

The mechanics and energetics of walking gaits have been described using the inverted pendulum (IP) model (Margaria, 1976; Saibene and Minetti, 2003), in which the gravitational potential energy and the forward kinetic energy varies out-of-phase stride by stride (Fig. 2.9 a).

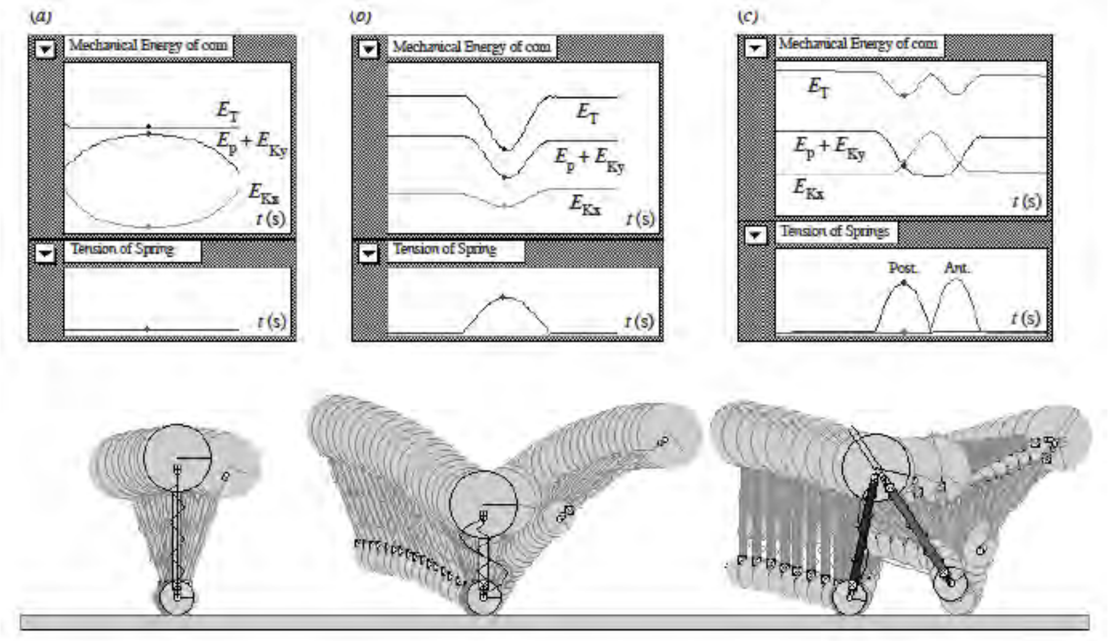

Fig. 2.9. (a) Inverted pendulum model (walking); (b) pogo-stick model (running and trotting); (c) double pogo-stick model (skipping and galloping). E_T total energy, E_P potential energy, E_{Ky} vertical kinetic energy, E_{Kx} horizontal kinetic energy

From Minetti (1998b)

Trotting and running

Running gaits are characterized by a duty factor < 0.5, that means no overlapping support periods between alternating support limbs. Bipedal running gait is considered homologous to the quadrupedal trot, where the diagonal forelimb and hind limb move in phase (Fig. 2.10). Although avian bipeds can run maintaining an overlap between the stance phases, in human run is always characterized by an unsupported flying phase (Fig. 2.8) (Biewener, 2003).

Running insects use a gait pattern similar to quadrupedal trot, in which an alternating tripod of limbs supports the body (Full et al., 1991; Full and Tu, 1990; Full and Tu, 1991; Ting et al., 1994). Similarly, running arachnids use an alternating tetrapod gait that can include, at high speeds, an aerial phase (Spagna et al., 2011; Wu et al., 2010).

Sideways running crustaceans, functionally octopedal, also adopt an alternating tetrapod strategy (Blickhan et al., 1993).

In pacing, differently from trot, the ipsilateral fore- and hind limbs move in phase. This cause a rocking motion of the body, which results in a less stable gait with respect to the trot. However, few quadrupeds, such as camels, normally pace instead of trotting (Parsons et al., 2006). Probably because of the less dynamic stability, there are not hexapedal or octopedal gaits similar to pace.

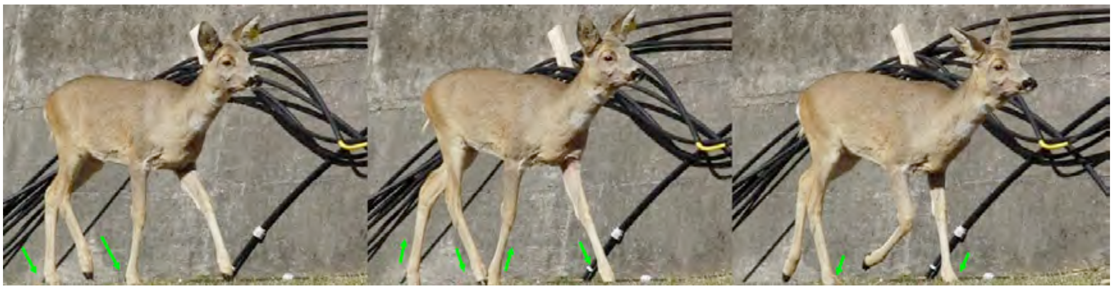

Fig. 2.10. Trot sequence in a roe deer (*Capreolus capreolus*)

From Biancardi and Minetti (2010)

Trotting and running animals generally use gaits in agreement with the bouncing-ball or pogo-stick model (Blickhan, 1989; Margaria, 1976; Minetti et al., 1994; Saibene and Minetti, 2003), in which the animal moves with gravitational potential energy and forward kinetic energy of the body in-phase, exploiting part of the energy temporary stored in elastic structures, such as tendons (Fig. 2.9). However, for sprawled-postured running animals, whose motion occurs primarily in the horizontal plane, a similar but simplified model called “lateral leg-spring” have been proposed (Kukillaya and Holmes, 2007; Lee et al., 2006; Schmitt et al., 2002; Schmitt and Holmes, 2000)

Other bouncing gaits

This is a large family of gaits, which each other similarity could be not immediately obvious. It comprehends hopping, skipping, pronk, bound, half bound, transverse and rotary gallop. All of these gaits are characterized by a jumping phase, which involves a spring-like action of the tendons, and a more or less extended aerial phase. In the energetics of bouncing gaits elastic energy, stored during the tendon stretching and released during recoil, plays a leading role. In hopping, pronk, bound and half bound at least two limbs of a pair move in phase, while in skipping and galloping gaits the two limbs of a pair are always slightly out of phase.

Fig. 2.11. Transverse gallop in a mounted horse (*Equus caballus*)
From Biancardi and Minetti (2010)

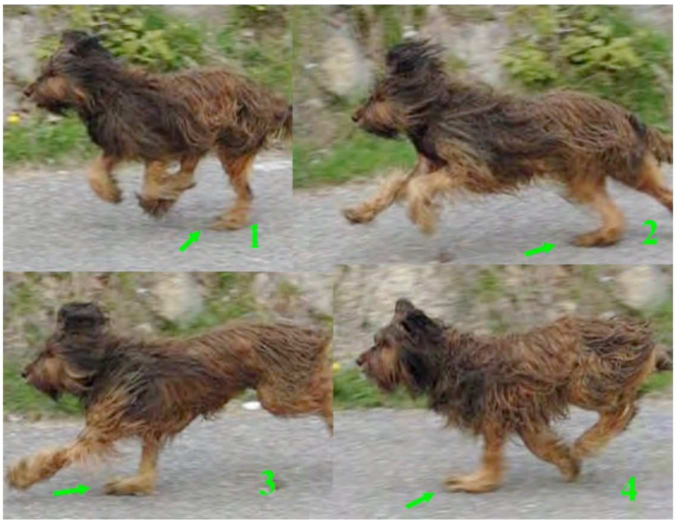

Fig. 2.12. Rotary gallop in *Nuvola,* a Briard dog (*Canis familiaris*)
From Biancardi and Minetti (2010)

Hopping is used by several marsupial and few rodent species, being kangaroos and wallabies the most famous, and is characterized by the in-phase movement of the hind limbs accompanied by no forelimb contact. Therefore, hopping species can be considered functionally monopedal.

Pronk is used by some antelopes, gazelles and deers, which jump with all the limbs together. In pronk all the limbs move in phase. This gait is not functional to speed, but is used by the mentioned species as a fitness proof, to damp predators from catching them (Spinage, 1986).

In bound the two hind limbs and the two forelimbs move in phase, and are separated by an aerial phase between the hind detach and the fore contact. Differently, in half bound the forelimbs are slightly out of phase. Small running mammals, like weasels, stoats, martens, rabbits and hares, usually employ these gaits.

Skipping is a bipedal asymmetric gait - normally used by some lemur species, like the sifakas (*Propithecus* sp.) - which is strictly linked to the quadrupedal gallop (Minetti, 1998b). Among humans, skipping is commonly displayed by children but not by adults. However, in conditions of low gravity, like that experienced by astronauts during the Apollo missions on the Moon's surface, skipping was the "natural" gait choice (Minetti, 1998b). In skipping the footfalls of the two limbs, with a double support phase, is followed by an aerial phase. When the first foot in contact with the ground (trailing foot) is always the same, the skipping is unilateral, otherwise, when trailing and leading feet change stride by stride, the skipping is called bilateral. In both skipping and gallop there is a simultaneous use of inverted pendulum and elastic structures to save energy (Fig. 2.9). Their reference model is a combination of two linked pogo-stick (Minetti, 1998b).

Galloping gaits are used by quadrupeds at high speed. During the stride, galloping animals start to arch their backs when the forefeet are on the ground. It follow an aerial phase, with all the limbs grouped under the body (grouped flight phase), and then the hind limbs contacts with a contemporary stretching of the backs. A second aerial phase can occur between the hind- and the forelimbs contact (extended flight phase). The flight phases contribute to increase the stride length, and then the speed. The elastic role played by the spine will be later explained. As already mentioned, two different galloping gaits can be displayed: transverse or diagonal (Fig. 2.11), when the leading feet of hind- and forelimbs are on the same side (ipsilateral), and rotary or lateral (Fig. 2.12), when the leading feet of hind- and forelimbs are counterlateral (Fig. 2.8).

2.2.5. Biomechanics of the spine

'Standing four square upon its fore-legs and hind-legs, with the weight of the body suspended between, the quadruped at once suggests to us the analogy of a bridge, carried by its two piers.' (Thompson, 1917)

This statement was taken from the famous treatise "*On Growth and Form*", written by D'Arcy Thompson at the beginning of the twentieth century. However, the static view of a bridge-like spine is not realistic, and the importance of spinal mobility has been focused in many subsequent works (Alexander, 1988; Alexander et al., 1985; Hildebrand, 1959). The mechanism suggested by these authors consists in a spring system where part of the kinetic energy associated to limb swing is stored as elastic strain energy in the stretched aponeurosis of the *longissimus dorsii* muscle. The subsequent spinal extension restores some of the kinetic energy to reaccelerate the limbs in the opposite direction. The recruitment of this elastic spinal mechanism makes galloping the most economical gait at higher speeds (Alexander, 1988).

As observed by Smeathers (1981), the spine flexibility differs among mammals, and the differences can be observed in the lumbar region. Smaller animals tend to have more flexible lumbar column than larger ones.

2.2.6. Forces and energy

A standing animal generates forces against the ground to support its weight. During locomotion it must also exert forces to support the changes in potential (PE) and kinetic (KE) energy associated to movements. Among terrestrial animals, independently from the number of limbs, there are common patterns of energy fluctuation occurring during legged locomotion (Cavagna et al., 1977).

PE variations occur when the body centre of mass (bCOM) raise or lower during every step. KE is associated to accelerations, hence it can be separated into three components: fore-aft, medio-lateral and vertical and, furthermore, not only applied to the bCOM, but also to the body segments which accelerate or decelerate with respect to the bCOM.

Variations in total energy (TE), the algebric sum of PE + KE of bCOM, must be supplied by muscle work. The mechanical external work (W_{EXT}) associated to locomotion is defined as the sum of all the positive variation in TE, generally standardized on body mass and distance ($J \cdot kg^{-1} \cdot m^{-1}$). However, muscles have to supply power also to re-accelerate the limbs with respect to the bCOM. The mechanical work associated to such limbs movements is defined as internal (W_{INT}). The total mechanical work (W_{TOT}) is given by the sum of $W_{EXT} + W_{INT}$ (Heglund et al., 1982; Minetti, 1998a; Willems et al., 1995).

Animals have evolved mechanisms either to minimize the oscillations of PE and KE of bCOM, or to efficiently recover energy by exchanging PE and KE and/or by elastic energy storage and recovery (Biewener, 2003).

The inverted pendulum model, which applies to walking gaits, is based on the out of phase fluctuation of PE and KE over a stride. PE is maximal at mid-support, when the supporting limb (or limbs) is perpendicular to the ground, and falls as the animal shifts to the next supporting limbs. Loss in PE is partially transformed in KE, which increase as the animal falls. Similarly, approaching the next support phase, KE decreases and PE rises (Fig. 2.9). The exchange between PE and KE of bCOM during walking gaits occur in a similar fashion from bipeds to octopods, with an energy recovery percentage up to 70% (maximum in walking bipeds) (Cavagna et al., 1977; Cavagna and Kaneko, 1977; Cavagna and Margaria, 1966; Cavagna et al., 1963; Heglund et al., 1982).

In bouncing gaits the PE and KE of bCOM fluctuate in phase, therefore an efficient energy exchange like in walking is not possible. The mechanism to save energy in these gaits involve the elastic structures, tendons or ligaments, which absorb part of the energy released when landing on the ground, and restore part of it when the limb rebounds off the ground (Alexander, 1998; Alexander, 2002b; Alexander et al., 1982; Alexander et al., 1979b; Cavagna and Kaneko, 1977; Cavagna et al., 1976; Dimery et al., 1986; Kaneko, 1990). As mentioned above, elastic structures in the back of mammals are involved as well (Alexander et al., 1985). Although present, the amount of elastic energy storage in invertebrates is still not well known (Blickhan et al., 1993; Dudek and Full, 2006).

2.3. Instruments of investigation

Photo and video recording

Before the introduction of photo and video recording it was almost impossible to analyse and study animal locomotion. The possibility to freeze movements in a single or in a series of frames was really a revolution, and the potentialities of cinematography and photography have been well understood by Edward Muybridge in his milestones studies (Muybridge, 1957).

Standard videos are recorded at 25 (Europe) or 30 (USA) frames per second and, if played in slow motion, can help to recognize pattern of movements otherwise difficult to appreciate. However, fast animal movements can be only (or better) analysed taking high-speed recordings, usually 200 to 500 fps and more in case of very fast movements, like the wing movements of insects (Weis-Fogh, 1975).

Three-dimensional movements can be analysed using two or more synchronized cameras and putting marks on the point of interests of the body, like joints and segments. The progresses of computer aided digital imaging gave new fuel to the studies on locomotion, speeding up some phases of image and data processing.

An opto-electronic systems for motion analysis is composed by a series of digital cameras equipped with stroboscopic infra-red flashes, a set of reflecting markers, a control unit, a computer to receive and store data and a software to analyse data. These systems are able to detect and store the 3D-coordinates, in a previously calibrated space, of the reflecting markers at a chosen frequency of acquisition (the same as the recording speed). The positions of the markers on reference points of the body segments are chosen consistently to the movements to analyse.

The data obtained can be used to calculate the centre of mass of any single segment and, by knowing the segment mass, the moment of inertia. The joint coordinates can be used to calculate the velocity, angular velocity and kinetic energy of each body segment. Accelerations can be derived and then forces can be calculated. The process to calculate forces starting from velocities is defined as inverse dynamic.

An opto-electronic system can only be used in equipped laboratories, usually in conditions of stationary locomotion (on a treadmill). Therefore, a large amount of data on locomotion of free ranging wild animals can be obtained using standard or high-speed video cameras in the field. Footage from scientific documentaries, digital libraries or nowadays also from on-line resources (YouTube), can also be a source of useful data.

Energy consumption

The mechanical work produced by muscles to sustain locomotion corresponds to some metabolic energy used. The metabolic cost of transport and the efficiency of locomotion can be calculated if we know the metabolic energy expenditure and the mechanical work done.

Fig. 2.14. Cosmed K4 metabolimeter set
Fig. 2.15. Horse mask for Cosmed K4

The most common way to estimate the amount of energy used by a subject for steady-state locomotion is by measuring the rate of oxygen consumption, but this works only when the activity is powered by aerobic metabolism. Closed-circuit calorimetric setups can be used, especially for small animals (Herreid et al., 1981; Herreid and Full, 1980; Stock, 1975; Stock, 1979). Indirect calorimetric measurements in humans and large animals can be obtained by means of different apparatus, from Douglas bags to various metabographic devices, which use a facemask or a mouthpiece to collect and analyse expiratory gases (Segal, 1987; Smithies et al., 1991). Douglas bags and metabolic systems are generally large and intrusive devices, useful when used in stationary locomotion on a treadmill but difficult to use in the field. However, portable devices, like the Cosmed® K4, are available both for laboratory and field experiments (McLaughlin et al., 2001). When used on animals, metabolic systems must be opportunely calibrated, especially turbines measuring expiratory flow, and specific masks should be used (Schmidt-Nielsen et al., 1981).

Force plates

The forces that animals exert on the ground can be measured by means of force plates. These are instrumented platforms, with force transducers under each corner. Transducers can be either piezoelectric devices or strain gauges, and should be able to detect and record the three components of a force vector (parallel to the direction of locomotion, transverse and vertical).

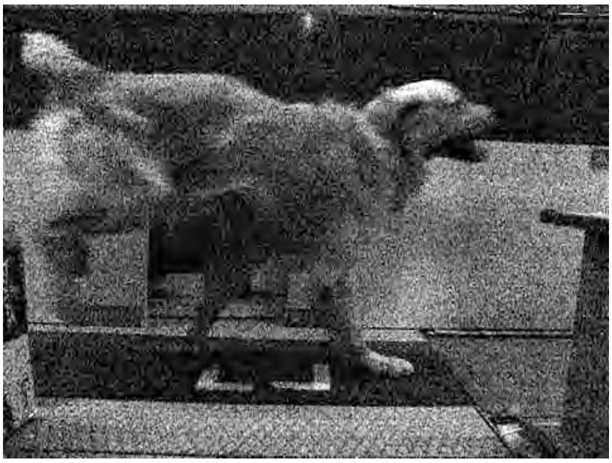

Fig. 2.16. *Hobbes,* a Labrador Retriever, while galloping over a force plate. Frame taken from a high speed video

The analog electric output of transducer must be sampled at a chosen frequency and digitized. The output generally gives the three components of force and the three moments. From forces and moment, combined with information about the subject mass and acquisition frequency, accelerations, velocities, bCOM positions and, at the end, mechanical work and power can be calculated.

Multiple force plates can be used to record one or more strides of medium-size to large animals, like dogs (Walter and Carrier, 2007), horses (Bertram and Gutmann, 2009) and even elephants (Genin et al., 2010). On the other hand, miniaturized force plates are available for small and light animals (Biewener and Blickhan, 1988; Biewener et al., 1988; Blickhan and Full, 1987).

2.4. Evolution of terrestrial locomotion

The first terrestrial animals emerged from the water during the late Silurian, they were similar to the extant Arachnida (Coddington and Levi, 1991; Dunlop and Webster, 1999). Therefore the first kind of terrestrial legged locomotion was octopedal. During the adaptive radiation of terrestrial animals, different solutions have been experienced. Diplopoda (Myriapods), with their multilegged body, also were among the first colonizer of the terrestrial habitats. Many other groups of arthropods, with different locomotion solutions, became terrestrial, and the most successful in terms of number

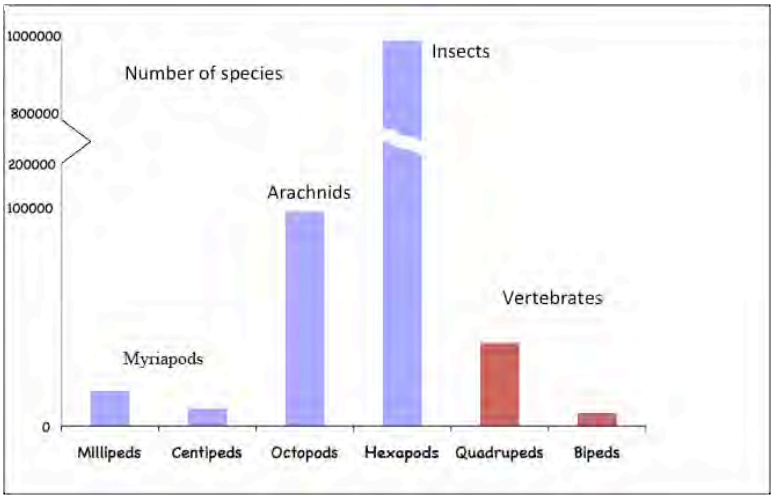

Fig. 2.17. Approximate number of species for terrestrial locomotor pattern

of species was the insects' hexapedal model (Fig. 2.17) (Full, 1989). Vertebrates evolved in water, where the tetrapod model appeared for the first time in fish (Boisvert, 2005; Coates, 1993; Coates, 1994; Shubin et al., 2006; Wagner and Chiu, 2001). The first terrestrial tetrapod were primitive and now extinct amphibians, with elongated body, sprawled limbs and finned tail (Ahlberg et al., 2005).

Myriapods terrestrial locomotion is characterized by posteriorly propagated waves of bending. However, Manton (1977) argued that the lateral bending was energetically inefficient and imposed on the body as it pivots around each supporting leg. More recent studies on treadmill at different speed and contemporary electromyograms indicated an active bending of the axial segments, which can enhance locomotion similarly to what happen in vertebrates (Anderson et al., 1995).

Octopedal locomotion, in spite of the high number of true or functional octopods, has not been deeply investigated. The first studies were focused on the characterization of the leg kinematics and the energetics in stationary locomotion (Bowerman, 1981; Herreid and Full, 1980; Wilson, 1967). Sideways locomotion of crabs, functionally octopods, has been widely investigated between the '80s and '90s (Blickhan and Full, 1987; Blickhan et al., 1993; Weinstein, 1995). Only recently, thanks also to the methodological improvements, major focus has been given to speeds and gaits (Schmitz, 2005; Spagna et al., 2011).

A comprehensive study on kinematics, gait patterns, mechanical external and internal work, mechanical power and efficiency of locomotion of terrestrial spiders will be a consistent part of this dissertation, and will be treated in chapter 3 (Biancardi et al., 2011).

More efforts have been spent over hexapedal species. Although many of them are able to fly, there are so many species of insects that they are still the large majority of terrestrial species. Hexapod locomotion of insects is the end-product of a process of limb reduction among terrestrial Arthropoda (Hughes, 1952). Six limbs can guarantee static stability during locomotion, also at relatively high speed (Hughes, 1952), and a good level of manoeuvrability (Hughes, 1952; Jindrich and Full, 1999). Insects employ different gaits, not completely analysed and described, yet (Full and Tu, 1990; Full and Tu, 1991). Arthropods are the most successful members of the animal kingdom largely because of their ability to move efficiently through a range of environments. These characteristics have been taken into account by engineers seeking to design agile legged robots (Beer et al., 1997; Delcomyn, 2004; Wang et al., 2011), and particular emphasis has been given to the control mechanisms (Ghigliazza and Holmes, 2004; Kukillaya et al., 2009).

Arthropods and vertebrates evolved legged locomotion independently. However, many neural control properties and mechanical schemes are remarkably similar (Ritzmann et al., 2004).

Vertebrate quadrupedal locomotion evolved from a re-adaptation of structures, girdles and limbs, developed for movements under water, an evolutionary mechanism called exaptation (Gould and Vrba, 1982). The locomotion of the first tetrapods resembled

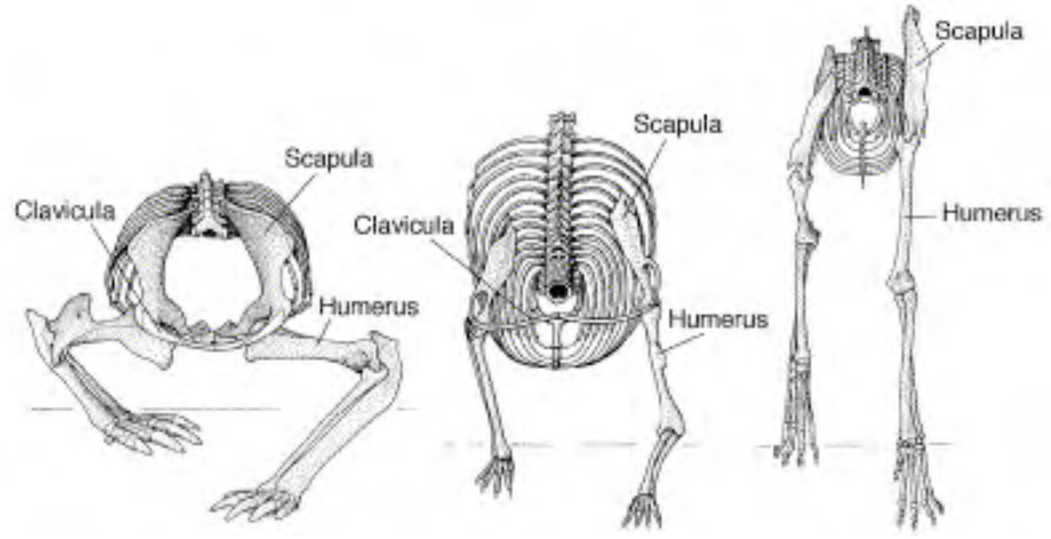

Fig. 2.18. (Left) Sprawling posture of the first vertebrates. (Middle) Erected posture. (Right) Pillar-erected posture.

that of extant salamander (Bennett et al., 2001; Wake, 1997), with pronounced lateral movements of the spine aiding locomotion. The same pattern characterizes lizard-like reptiles and alligators (Reilly et al., 2005; Ritter, 1992).

The shift of the limbs under the animal body already occurred in reptiles, in particular dinosaurs, with the main purpose of better sustain the increasing body mass (Yates and Kitching, 2003). Nevertheless, the new graviportal quadrupedalism made also possible to develop new gaits and reach higher speeds (Alexander, 2006a). Graviportal posture evolved again in mammals, as soon as they started to increase their dimensions (Gasc, 2001). Bipedalism also appeared first in reptiles (Hutchinson, 2004), and consequently in birds (Farke and Alicea, 2009), only later, bipedalism appeared in mammals (Schmitt, 2003).

Both quadrupedal and bipedal locomotion have been largely analysed, as already mentioned in this chapter. Nevertheless, large parts of the studies have been carried out on few species, on artificial substratum (laboratories or treadmills) and in conditions of straight level locomotion. Standard conditions are of course necessary to get metabolic and mechanics comparable data along different speeds. On the other hand, during free range in environmental conditions, animals must deal with irregular terrains, gradients, obstacles and maybe prey-predator interactions, which conditions speed, gaits, direction changes.

Speed, acceleration and manoeuvrability are crucial factors for many animals. The natural selection may tend to favor pattern of movements and biomechanical solutions that increase one or more of them (Alexander, 2006b). A wide comparative investigation on the biomechanical, morphological and environmental determinants of the two type of gallop, the faster gait among quadrupeds, will be treated in chapter 4, as second main topic of this dissertation.

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3. Biomechanics of octopedal locomotion

The content of this chapter has been presented as oral communication at the Society for Experimental Biology Annual Main Meeting, Prague 30th June - 3rd July 2010 (Biancardi et al., 2010) and published as:

Biancardi, C. M., Fabrica, C. G., Polero, P., Loss, J. F. and Minetti, A. E. (2011).
Biomechanics of octopedal locomotion: kinematic and kinetic analysis of the spider
Grammostola mollicoma. *J. Exp. Biol.* 214 (20): 3433-3442.
(Biancardi et al., 2011)

3.1.Introduction

Partially because of the anthropocentric attitude and the tendency towards a manageable simplification, it is intuitive to consider the locomotion of multi-legged species as the result of combining gaits of fewer-leg organisms. For example, quadrupedal trot can be regarded as the combination of a front and a rear bipeds running half a cycle out of phase, and similar analogies can be done for many other gaits (gallop is the combination of two bipedal skipping strides). This seems a useful approach when we need to understand the mechanics of complex gaits by starting to analyse simpler ones (Minetti, 1998b). To push this strategy to the limit, monopods have been theoretically analysed (Blickhan and Full, 1993) and successfully designed (Raibert, 1986) in the early stages of locomotion research. Another potential benefit of this approach is in motor control investigations, which could seek simpler central pattern generators and hypothesize a modular control of more complex locomotion forms.

But evolution moved the other way round: the first multi-legged terrestrial animals presumably had 8 limbs, lately radiating both towards more complex locomotor organisms (myriapods) (Wilson and Anderson, 2004) and to larger size –lower number of limbs species. Six-legged insects appeared later on the terrestrial surface, then vertebrates, down to quadrupeds, bipeds and even to substantially 'monopodal' species as jumping kangaroos (Carroll, 1987).

Eight-legs locomotion has been one of the first travelling modes on land, and an extinct group of terrestrial arachnids related to modern day spiders, the Trigonotarbids, are among the most ancient arthropod groups (Upper Silurian, about 444-428 Myrs) (Jeram et al., 1990). Spiders display the most versatile locomotor repertoire: they move at slow and fast speed, forward-backward-sideways, they climb and even jump, both on firm terrain and from the water surface. Even humans, despite of the inherent bipedal instability, can walk (Minetti and Ardigò, 2001) and run (Cavagna et al., 2010) backwards, but the performance and the related cost of transport are quite penalized. Spiders can walk in the two senses at the same speed, just by reversing their diagonal footfall scheme. They turn on the spot like an armoured tank, with opposite direction of the two treads of limbs. When a spider loses one (or even two) of its legs, it is still capable of comfortably moving around, differently from bipeds and quadrupeds, through a duty factor compensation and a reprogramming of the central patten generator (Foelix, 1996). Also, the high number of limbs ensures an increased locomotor versatility on uneven and rough terrains, particularly in the likely unawareness of each endpoint location on the ground (despite the up to 4 pairs of eyes!).

There is no surprise, then, to learn that the US Defence Advance Research Project Agency (DARPA) had in the past tactical interests in developing up to 8-leg robots capable to semi-automatically face various terrain roughness (Klaassen et al., 2002).

Despite of all those reasons, scientific research on 8-leg locomotion is rather scanty and only a few papers (Herreid and Full, 1980; Schmitz, 2005a; Schmitz, 2005b; Sensenig and Schultz, 2006; Ward and Humphreys, 1981a; Wilson, 1967) addressed the spider gaits in detail.

We had the opportunity to capture and analyse the locomotion biomechanics of large spiders in captivity. We aimed to apply to this animal the same methodology used in the past to obtain gait dynamics variables on bipeds (humans, e.g. (Minetti et al., 1993)) and quadrupeds (horses, (Minetti et al., 1999)). The interest was about: 1) identifying the principal gaits, 2) calculating the mechanical external and internal work at the different speeds/gaits, 3) assessing any tendency to exchange potential and kinetic energy of the body centre of mass, as in pendulum-like gaits, and 4) evaluating how spiders' mechanical performance and variables allometrically compare to other species.

Going back to the simplification approach mentioned above, another question was: can the octopedal gaits be considered as different combinations of two quadrupeds' locomotion?

3.2. Methods

Animals

All measurements were made in adult female specimens of *Grammostola mollicoma* (Ausserer, 1875) (Araneae, Theraphosidae) (n=3, mass 18.5 ± 3.7 SD g). The species were identified using the literature criteria (Costa and Pérez-Miles, 2002; Mello-

Leitao, 1923). Animals were collected in the region called "Sierra de Minas" (Department of Lavalleja, Uruguay), and were held in captivity with constant and optimum environmental conditions throughout the experimental period.

Experimental procedure

The position of the body centre of mass (COM) in the static posture, where the main body marker should have been placed, was independently determined in killed specimens (same species, similar sizes). COM coordinates were determined by suspending the legless spider body (cephalothorax) on a nylon fibre glued to the thorax and moving the point of attachment until the spider assumed a horizontal position.

Additional 8 markers were placed at the tips of the locomotive legs (Fig. 3.1). The experimental conditions used in this work were similar to those recently used to analyse locomotion in large mammals (Hutchinson et al., 2006; Wickler et al., 2002; Wickler et al., 2003), with the spiders filmed during free displacements.

Five fixed video cameras (JVC GR-DVL 9800) were simultaneously used. The recordings were made within a space of 60 x 30 x 15 cm, calibrated by using 20 markers evenly distributed in 3D. The frequency used for video recordings (50 frames per second) has been determined by others as suitable for this type of analyses (Ward and Humphreys, 1981b). The camera synchronization was done with a sound signal and all images were digitized. Each of these frames was later used to reconstruct the position of each marker. Orthogonal axes were defined by following the recommendations of the Biomechanics International Society (Wu and Cavanagh, 1995): the direction of the "X" axis agreed with the main displacement direction, the direction of the "Y" axis agreed with the height respect to the ground, and the direction of the "Z" axis was determined by the "right hand rule" (Meneghesso, 2002; Wu and Cavanagh, 1995).

Fig. 3.1. Position of the 9 reflective markers

The measurement error in the system was assessed according to Barros (Barros et al., 2006).

Data analysis

Only locomotors acts performed on a straight line were chosen. The frame-by-frame analysis was conducted using an image analysis program (Dvideow 6.3, Campinas University), (Barros et al., 1999; Figueroa, 1998; Figueroa et al., 2003). A series of programs written in LabView (ver. 8.6/MacOS, National Instruments, USA) were built to manage and process the kinematics/kinetics data of the legs and of the true centre of mass. Virtual markers corresponding to the *coxa* joint, i.e. the point of insertion of each leg on the *thorax* of the spider, were calculated according to mean angles of leg origin from the body on the coronal plane as obtained from the analysis of 'static' film frames and photographs, and by assuming that the sagittal plane of the body moves parallel to the progression axis.

Further, we had to consider the movement of the legs in term of segments and joints. Each spider leg is formed by seven segments: *coxa* and *trochanter*, which are very short and represent a kind of "shoulder/hip" joint, a long *femur* and a knee-like *patella*, long and thin *tibia* and *metatarsus* followed by a distal *tarsus* (Foelix, 1996). In order to manage such a complex structure and after inspection of locomotion footage of the spider, we decided to reduce the animal leg to just two segments connected by a "*knee*" joint between the *coxa* and the leg tip. Thus, we first clustered the 7 segments into a *Femur,* a *Tibia* and a *Metatarsus* (15.5, 15.2, 12.0 mm, respectively). Then, we decided to build four models, considering the 3D shape of the leg either as a cone or a frustum of cone (with diameters ranging from 6.4 mm at *coxa* to 4.0 mm at *metatarsus*) and the position of the knee either in the middle point between the leg extremes (equal-segment model) or at the end of the *femur* segment, corresponding to the *femur-patella* joint (*patella*-joint model). The positions of the virtual "*knee*" marker have been computed for each model and added to the data set (See movie in the electronic supplementary materials).

The 3D positions of the centres of mass of each leg segment (LCOM) and of the main body (BCOM), and the respective masses have been used to compute the 3D position of the 'true' Centre of Mass (tCOM).

The stride coordination was evaluated by means of the spatiotemporal sequence of support of the locomotive legs (gait diagram). The parameters were:

1) Duty Factor (Df), defined as the ratio between the duration of a foot contact interval and the stride duration.

2) Fore Lag (FL), defined as the time lag between the two fore feet footfalls (right first), which measures temporal coordination within the fore pair.

3) Hind Lag (HL), defined as the time lag between the hind feet footfalls (right first), which measures temporal coordination within the hind pair.

4) Pair Lag (PL), defined as the time lag between hind and fore feet footfalls (fore feet first), which measures temporal coordination within the two pairs.

The time lag can be expressed as a percentage of the cycle duration. The gait can be defined for the values of FL, HL and PL according to the Antero-Posterior Sequence (APS) method described by Abourachid (2003). According to Minetti (1999) who considered the horse like two consecutive bipeds in series, we looked at the spider as composed by two successive quadrupeds in series, being the first L1-R1-L2-R2 and the second L3-R3-L4-R4 (L/R stand for Left-Right and the numbers start from the first pair of feet in anterior-posterior sequence), and we calculated the gait parameters for each of them. Further, a new parameter, QL, representing the phase shift between the two quadrupeds and defined as the time lag between two homologous feet of them (e.g. R1 and R3), was calculated.

Due to the periodical characteristics of a gait, where a sequence of footfalls is repeated in time, the gait pattern is summarized by phase shifts of footfalls that can be plotted as points on a trigonometric circumference. Their mean according to circular statistics takes into account their position on the circumference – e.g. two phase shifts, 1° and 359°, results with a value of 0° rather than 180° (the arithmetic linear mean).

Let θ be the position on a trigonometric circumference for n observations, we can define $S = (\Sigma \sin\theta)/n$, $C = (\Sigma \cos\theta)/n$, and the circular mean $\bar{\theta} = \arctan(S/C)$ (Batschelet, 1981). The mean resultant length: $r = \sqrt{S^2 + C^2}$, is a measure of dispersion of data. However, since r decreases from 1 to 0 while the dispersion increases, an index of variability equivalent to the standard deviation in linear statistics is calculated as mean angular deviation: $s = \sqrt{2(1-r)}$ (Batschelet, 1981).

The circular mean and mean angular deviation, in radians, have been transformed as fraction of the stride cycle.

Biomechanical analysis

The 3D trajectories of the body centre of mass in local coordinates, as during locomotion on a treadmill, have been calculated by applying a mathematical method based on the Fourier analysis of the three coordinates of tCOM over time (Minetti, 2009; Minetti et al., 2011). The analysis is truncated to the 6th harmonic, because further harmonics addition did not enhance the description power of the result (Perseval's theorem). The final outcome, for each analysed stride, is a system of three parametric equations with a total of 18 amplitude, 18 phase coefficients and a vertical translation constant, which describes a 3D closed loop (Lissajous contour). The dynamics of tCOM movement is linked to the mechanical external work and is proven to reflect the metabolic energy needed in many locomotor conditions (Minetti et al., 1993).

Values for the segment mass (as a fraction of body mass) were obtained from average measurements, while the radii of gyration were calculated by assuming a cone frustum or conical shape of segments, according to the mentioned models. Positive internal and external work (W_{INT} and W_{EXT}, respectively) were computed using the method of Cavagna and Kaneko (Cavagna and Kaneko, 1977), who used König's theorem to account for the changes in the kinetic energy of segments whose movements do not affect the position of the overall centre of mass (e.g. symmetrical limbs displacements). This theorem states that the total kinetic energy of a multi-link system can be divided into two parts: (a) the kinetic energy increases of the segments arising from their change of speed with respect to the overall centre of mass, and (b) the kinetic energy increases of the overall centre of mass with respect to the environment. The first term constitutes the positive W_{INT}, while the second is included in the positive external work, W_{EXT}, defined as the work necessary to raise and accelerate the centre of mass of the body with respect to the environment.

The positive work (W_{EXT}) was obtained by summing the increments of the total energy (TE) with respect to time: $TE=PE+KEx+KEy$ (where PE is the potential energy of the centre of mass of the body and KEx and KEy are the horizontal and vertical components, respectively, of the kinetic energy of the body's centre of mass).

The total mechanical work (W_{TOT}) was computed as the sum of W_{EXT} and W_{INT}. Mechanical work was expressed as the (mechanical) cost of transport, i.e. per kilogram of body mass and per unit distance (i.e. J $kg^{-1}m^{-1}$).

The peak mechanical power, due to sudden acceleration from rest, was estimated from the maximum acceleration recorded during the first strides of the faster filmed sequences.

The ‘energy recovery’, an index of the ability of a system to save mechanical energy through the interchange between PE and KE (equal to 100 % in an ideal pendulum), was obtained according to Cavagna et al. (1976).

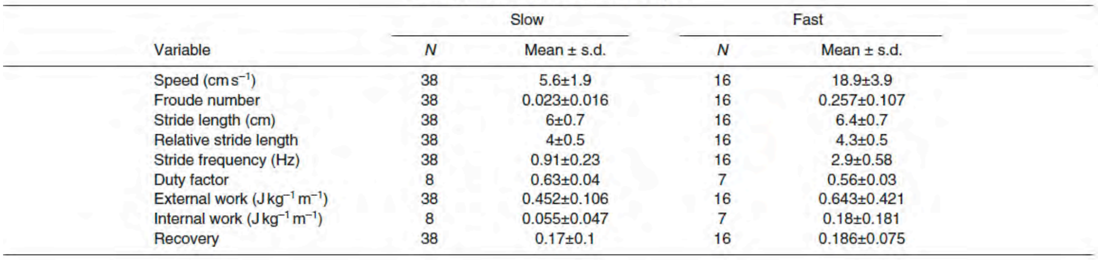
All the data-processing and statistics were performed on an Apple iMac computer, using: LabView (ver. 8.6, National Instruments, USA), MS-Excel (ver. 2008, Microsoft, USA) and SPSS (ver. 17.0, SPSS Inc., USA).

3.3. Results

We analysed a total of 54 strides, distributed in 13 different sequences of 3 to 5 strides each. The overall results are shown in Table 3.1.

Speed, Gaits and tCOM trajectory

During the experiments we observed “slow” and “fast” displacements. In order to assess the consistency of these two categories, we considered the following variables: speed, relative stride length, stride frequency, mechanical external work, and energy recovery. A preliminary cluster analysis permitted to identify two main groups with a cut-off speed that ranged from 8.7 to 14 $cm \cdot s^{-1}$, according to the clustering method. In order to choose a reliable boundary speed and define the slow and sprint groups, a set of five multivariate analyses of variance (MANOVA) have been performed. All the models were highly significant ($p < 0.001$), but the Wilks’ F value and the Partial eta



	Slow		Fast	
Variable	*N*	Mean ± s.d.	*N*	Mean ± s.d.
Speed (cm s^{-1})	38	5.6±1.9	16	18.9±3.9
Froude number	38	0.023±0.016	16	0.257±0.107
Stride length (cm)	38	6±0.7	16	6.4±0.7
Relative stride length	38	4±0.5	16	4.3±0.5
Stride frequency (Hz)	38	0.91±0.23	16	2.9±0.58
Duty factor	8	0.63±0.04	7	0.56±0.03
External work (J kg^{-1} m^{-1})	38	0.452±0.106	16	0.643±0.421
Internal work (J kg^{-1} m^{-1})	8	0.055±0.047	7	0.18±0.181
Recovery	38	0.17±0.1	16	0.186±0.075

Table 3.1. Results of the gait analysis

square, an effect size estimator, reached a maximum for a cut-off speed of 11 cm·s^{-1} (Fig. 3.2), which corresponds to a Froude number of 0.08.

For slow displacements gait diagrams (Fig. 3.3a and 3.3b) show a four-legged alternation (R1, R3, L2, L4 - L1, L3, R2, R4). This pattern is summarized by two walking quadrupeds, with almost no phase delay between them. During fast movements, a similar alternation of tetrapods occurs, although with a more variable pattern (Fig. 3.3c).

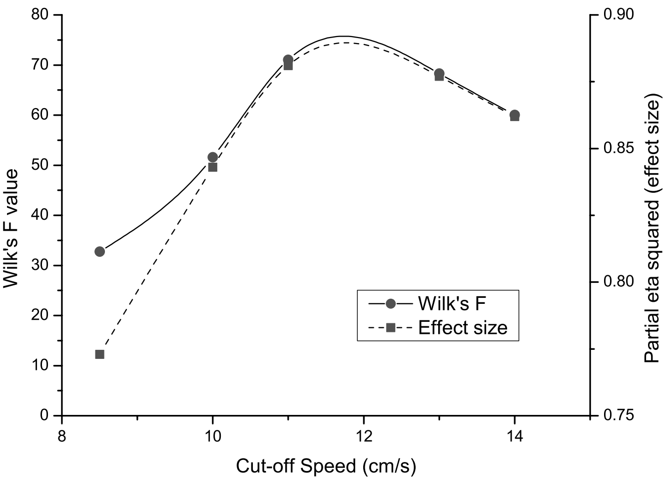


Fig. 3.2. Compound results of five MANOVA analyses (see text for details). Boundary speed between slow and sprint displacements has been set to 11 cm·s^{-1}. In this case we obtained the largest separation of the two groups: both highest Wilks F value and highest estimator of effect size.

The visual analysis of diagrams shows that two anterior pairs of legs (1st quadruped) and two posteriors pairs (2nd quadruped) have the same pattern for slow displacements, whereas during faster gait the pattern is different for both groups of legs, being the phase shift between legs of the pairs 3 and 4 more irregular. However the values of the parameters FL, HL, and PL (Table 3.2), correspond to a quadruped walk for slow displacements and to a variant walk sequence for fast ones, as witnessed by the greater variability of values for the second quadruped.

The second quadruped anticipated the first one with average shifts of 16% (slow) and 8% (fast).

Speed (s, m·s^{-1}) and duty factor d varied inversely according to the equation:

$$d = -0.531s + 0.666 \quad (R^2 = 0.71;\ p < 0.001) \tag{1}$$

with d always greater than 50%.

In both gaits the stride frequency f increases proportionally to the speed (Fig. 3.4). Separate linear regressions slopes for slow and fast displacements did not significantly differed (p = 0.88), and the fitting for the pooled data produced the following equation:

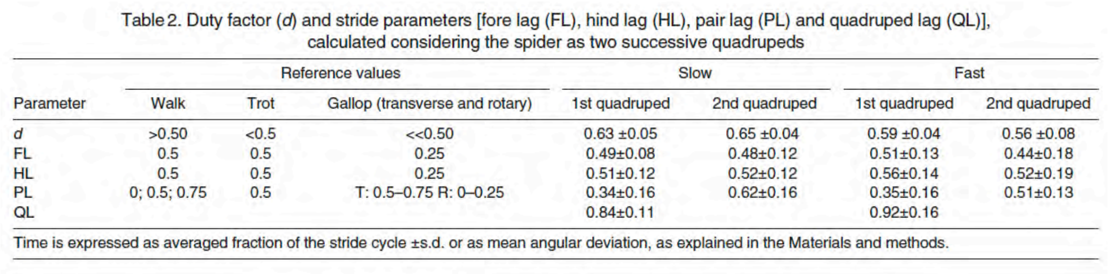


Table 2. Duty factor (*d*) and stride parameters [fore lag (FL), hind lag (HL), pair lag (PL) and quadruped lag (QL)], calculated considering the spider as two successive quadrupeds

	Reference values			Slow		Fast	
Parameter	Walk	Trot	Gallop (transverse and rotary)	1st quadruped	2nd quadruped	1st quadruped	2nd quadruped
d	>0.50	<0.5	<<0.50	0.63 ±0.05	0.65 ±0.04	0.59 ±0.04	0.56 ±0.08
FL	0.5	0.5	0.25	0.49±0.08	0.48±0.12	0.51±0.13	0.44±0.18
HL	0.5	0.5	0.25	0.51±0.12	0.52±0.12	0.56±0.14	0.52±0.19
PL	0; 0.5; 0.75	0.5	T: 0.5–0.75 R: 0–0.25	0.34±0.16	0.62±0.16	0.35±0.16	0.51±0.13
QL				0.84±0.11		0.92±0.16	

Time is expressed as averaged fraction of the stride cycle ±s.d. or as mean angular deviation, as explained in the Materials and methods.

$$f = 14.4\ s + 0.14 \quad (R^2 = 0.92;\ p < 0.001) \qquad (2)$$

The linear regression of stride length *l* vs speed is significantly increasing only for slow speeds:

$$l = 28.37s + 4.43 \quad (R^2 = 0.61;\ p < 0.001) \qquad (3)$$

For the fast locomotion the stride length is almost constant ($R^2 = 0.21$; $p = 0.08$) at a mean value of 6.14 ± 0.71cm.

The geometry described by the legs on the ground (support area) is plotted together with energies and gait diagrams in fig. 3.3 (a, b, c). The time course of the support area seems quite irregular during the stride, although a quite distinctive pattern is shown particularly during the slow movement. The average support area at all speeds was 56.3 ± 4.1 cm^2.

Three examples of Lissajous contour of the centre of mass, at different speeds, are shown in fig. 3.5 (movies showing the dynamics of tCOM trajectory are available in the Electronic Supplementary Materials). The spider's tCOM has little lateral oscillations while proceeding at slow speed (*a*) (about 0.5 cm, when compared to roughly 8 cm of support area diameter), with a more diagonal pattern at higher speeds (*b*, *c*).

Mechanical work

Despite the 5-fold increase in speed, the external work per unit distance is almost constant with a tendency to increase as the spider proceeds faster (Fig. 3.6).

The sum of forward and lateral kinetic energy (KE = KE*x* + KE*z*) changes was lower than the sum of vertical kinetic and potential energy (PE = PE + KE*y*) changes at slow speeds (KE = 0.022 ± 0.016 mJ; PE = 0.150 ± 0.052 mJ). At higher speeds PE changes maintained almost the same values, while KE changes reached and overlapped PE (KE = 0.255 ± 0.203 mJ; PE = 0.183 ± 0.123 mJ). The energy

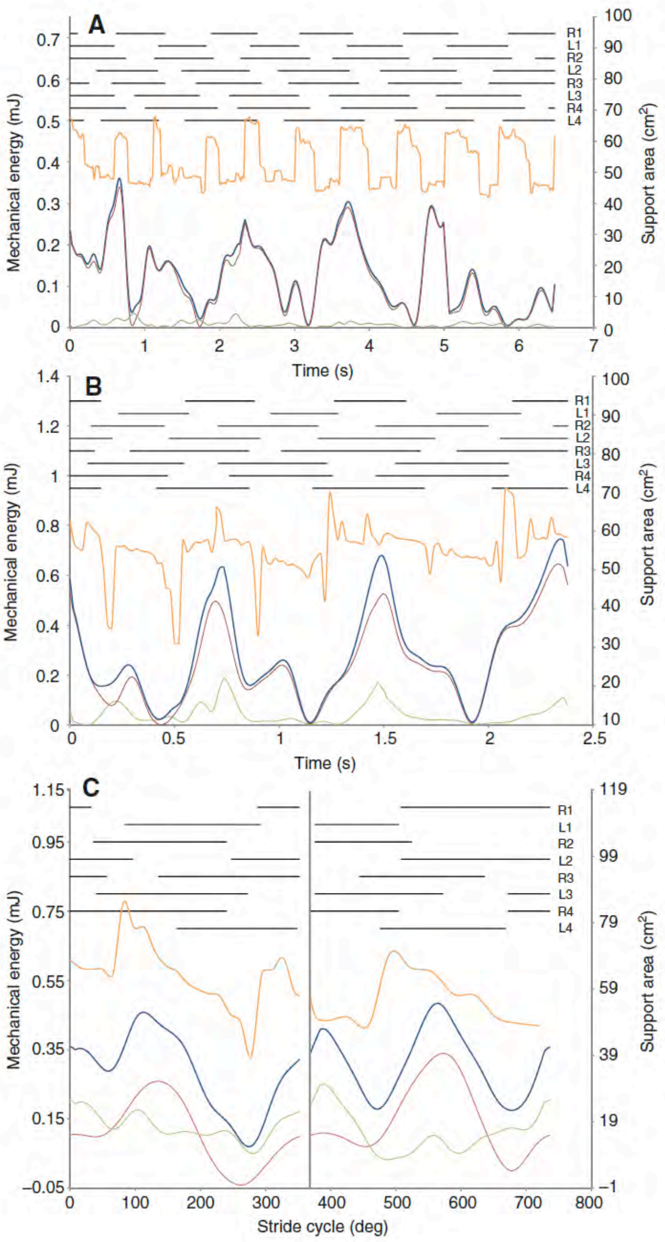


Fig. 3. Main characteristics of typical *Grammostola mollicoma* strides at different speeds. Top: gait diagram of the footfall pattern. Horizontal bars represent the time the foot is on the ground. Each line represents one foot (R and L indicate the legs of the right and left sides, respectively; numbers 1 to 4 indicate the sequence of legs from the head backwards). Middle: support area (cm^2), right ordinate. Bottom: mechanical energies (mJ). The blue line represents total energy (E_{tot}), the red line vertical energy ($E_{pot} + E_{kin,y}$) and the green line kinetic horizontal energy ($E_{kin,x} + E_{kin,z}$). See Mechanical work in the Results for further explanation. (A) Sequence of five slow strides (5.5, 4.7, 4.2, 3.9 and 3.8 cm s^{-1}). Potential energy, changes in which are tenfold the kinetic energy span, accounts for almost all the changes in total energy. Duty factor=65–69%. (B) Sequence of three strides at medium speed (10.4, 8.7 and 7.5 cm s^{-1}). Changes in kinetic and potential energy are approximately in phase. Duty factor=58–59%. (C) Sequence of two mean fast strides (13.4 to 23.6 cm s^{-1}). Time has been standardised in degrees (1 stride=360 deg). Kinetic energy values are comparable to those of potential energy; a slight phase shift between potential and kinetic energy diagrams accounts for an average 12% of recovery. Duty factor=55–57%.

recovery, an index of the exchange between KE and PE that occur when their time-courses are out of phase, did not significantly change as the speed increased (*t*-test, p = 0.57, see also table 3.1 and fig. 3.3).

The sum of the leg's masses was approximately 13% of the total mass of the spider. The mechanical internal work (W_{INT}), estimated for each leg model (see methods), ranged from 0.021 to 0.328 J·kg^{-1}m^{-1} (average 0.113 ± 0.083 SD). Internal work values resulted significantly lower in the conical shape models versus the frustum shape models (paired *t*-test: p < 0.001), and in the asymmetrical *patella*-joint vs the equal-segments models (paired *t*-test: p = 0.004). However, we observed a similar pattern of variation of W_{INT} as a function of speed (Fig. 3.7), independently from the adopted limb model.

According to Fedak et al. (1981), who considered intra- and interspecific differences in species that ranged from 44 g to almost 100 kg in mass, W_{INT} should scale as:

$$W_{INT} = 0.478 \times s^{0.53} \tag{4}$$

where s is the average progression speed ($m \cdot s^{-1}$).

In our 18.5 g spiders we observed an almost linear relationship between W_{INT} and speed ($W_{INT}\ \alpha\ s^{1.05}$), with measured values lower than predicted by (4) at slow speeds, and comparable values at higher speeds. However both the slopes ($p < 0.001$) and the intercepts ($p = 0.002$) of the regression lines significantly differed.

The mechanical internal work rate has been modeled for bipeds by Minetti and Saibene (1992), and then extended to quadrupeds (Minetti, 1998a). The model links the internal work to: 1) the stride frequency (f, Hz), 2) the average progression speed (s, as in eq. 4), 3) a term related to duty factor (d)), and 4) a compound dimensionless term accounting for limb geometry and fractional mass (q), which should be almost constant throughout all the speeds and gaits if the geometry of the oscillated limb

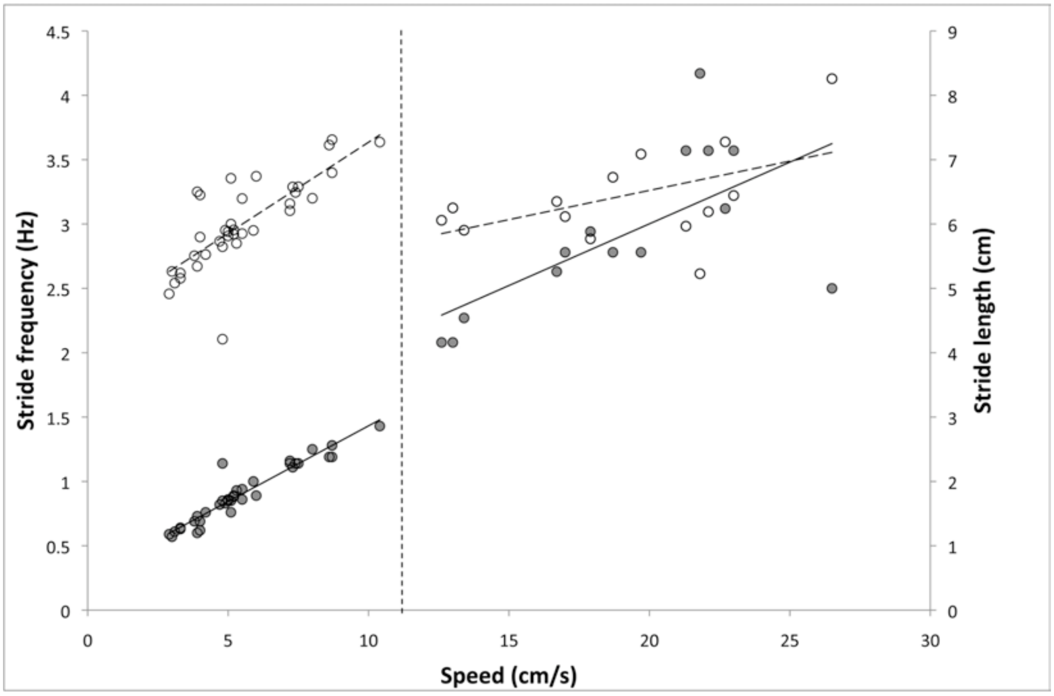
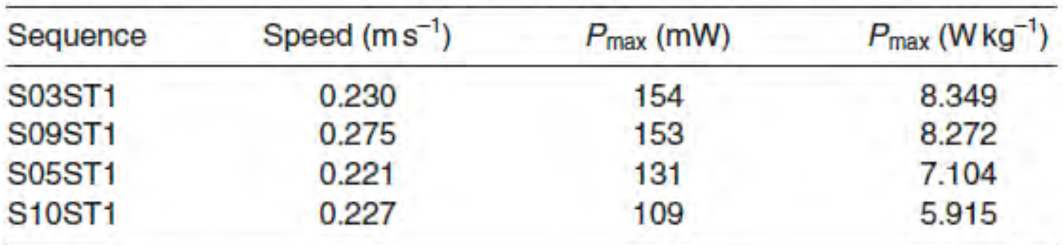


Fig. 3.4. Stride length (open circles) and stride frequency (filled circles) versus speed in *Grammostola mollicoma*.

remains the same. The value of q for the investigated species can be estimated (Minetti, 1998a) by the equation

$$\frac{W_{INT}}{fs\left(1+\left(\frac{d}{1-d}\right)^{2}\right)}=q \tag{5}$$

The actual and the mean values of q calculated for *Grammostola mollicoma* from our experimental data are compared to the mean values for humans and horses in figure 8.



Sequence	Speed ($\mathrm{m\,s^{-1}}$)	P_{max} (mW)	P_{max} ($\mathrm{W\,kg^{-1}}$)
S03ST1	0.230	154	8.349
S09ST1	0.275	153	8.272
S05ST1	0.221	131	7.104
S10ST1	0.227	109	5.915

Table 3.3. Maximum power (*Pmax*) values at fast gait

Maximum power

In our experimental design the spiders were filmed during free displacements starting from rest. In fast performances they showed a rapid acceleration and reached a high speed during the first stride of each sequence. We could therefore estimate the maximum positive power exerted by the spider during acceleration from rest, which was about 8.3 W/kg (Table 3.3).

3.4.Discussion

Gait pattern

The stride-based analysis shows contact sequences that were described in previous works (Bowerman, 1981; Wilson, 1967), which observed that the anterior legs pairs have a strong tendency to be used alternately, but the posterior pairs do not. Our data concur with this view, but only in fast sequences (FL and HL, Table 3.2).

The four-legged alternation associated with those unilateral sequences in slow displacements can be interpreted as alternating tetrapods stepping pattern, similar to the symmetrical trot gait of four-legged vertebrates, but with interfaces longer than the time of quadrupedal support. This is currently accepted as a general model of spider locomotion (Barth and Biedermann-Thorson, 2001; Ward and Humphreys, 1981a), except for a group of functional exapod harvestmen (Opiliones), their antenniform second pair of leg being used as tactile organs, which display an alternating tripod gait (Sensenig and Schultz, 2006).

Alternating tripod gait is a widespread interleg coordination pattern for insects walking at moderate to high speed, and is generally lacking during slow walking (Full and Tu, 1990; Hughes, 1952; Kukillaya and Holmes, 2007; Zollikofer, 1994). Our results showed that an inverse situation could happen for this species of vagrant spider, as the general model of tetrapod alternation is not observed in fast displacements.

We can consider the octopod as formed by two subsequent quadrupeds, where the first two pairs of feet (1 and 2) are the fore and the hind feet of the first quadruped, and the third and fourth pairs are the fore and hind feet of the second quadruped. The

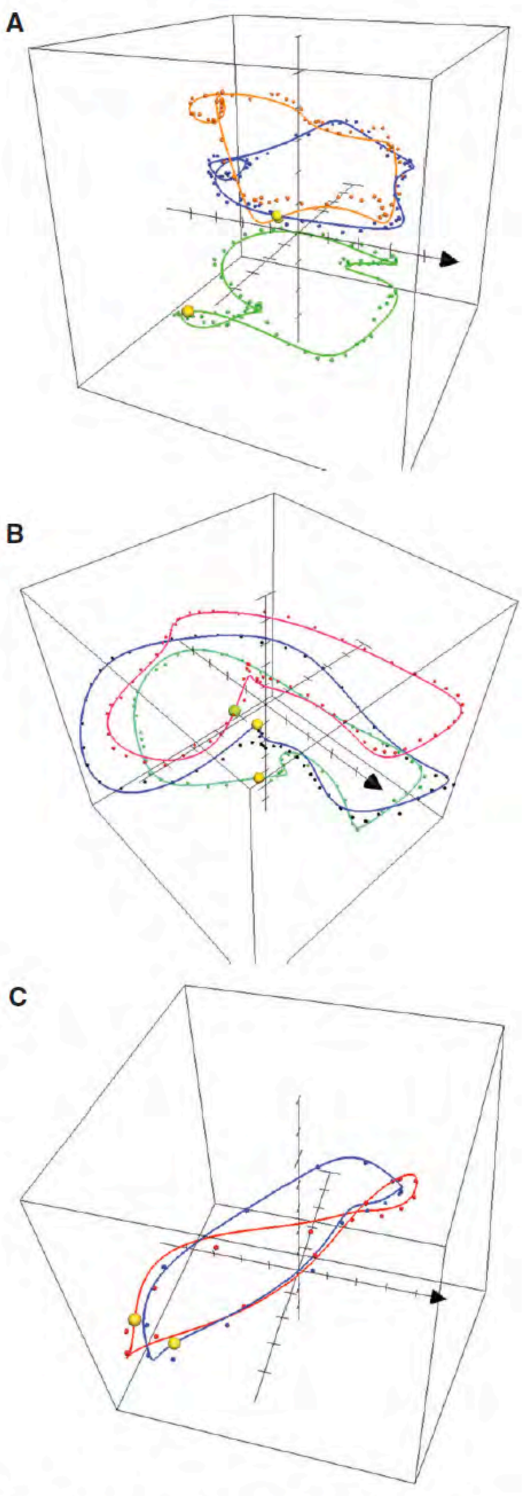


Fig. 5. Trajectory of the centre of mass of *G. mollicoma* in local coordinates. The axis with an arrow indicates progression direction. The side length of the represented cubes is 5 mm. Each loop corresponds to one stride. Small dots represent the observed positions of the tCOM, lines represent the calculated Lissajous contour, and larger dots represent the actual position of the tCOM during the animated simulations (see supplementary material Movie 2). (A) Slow: 2.9–4.2 cm s^{-1} (right side view), three strides. (B) Slow: 5.0–6.0 cm s^{-1} (dorsal view), three strides. (C) Fast: 19.7–23.0 cm s^{-1} (dorso-lateral view), two strides.

two quadrupeds are almost in phase, being the first and third pairs synchronised in their movements as well as the second and fourth (QL, Table 3.2).

The gait parameters of the first quadruped are more consistent with a kind of diagonal walk (i.e. a trot wih no flight phase). The diagonal feet are not moving in phase, as the hind foot of a pair slightly anticipates the controlateral forefoot (PL, Table 3.2). This could be due to the unusual high trajectory of the first pair of feet, probably used also as helper "probes" to detect obstacles. Their suspended "swing" phase is longer than any other and the second pair of footfalls appear to be anticipated.

The second quadruped shows a similar symmetrical stepping pattern with a the duty factor of about 60% (PL, Table 3.2), with a tendency towards symmetry at high speeds, probably due to the rhythmic "pushing" role of the fourth pair of leg.

During fast displacements spiders did not maintain a constant speed. An explosive acceleration usually characterise the first stride, with the speed constantly decreasing thereafter. The stepping pattern observed during these sprints was very variable and irregular. The third pair of feet (the forefeet of the second quadruped) was prone to

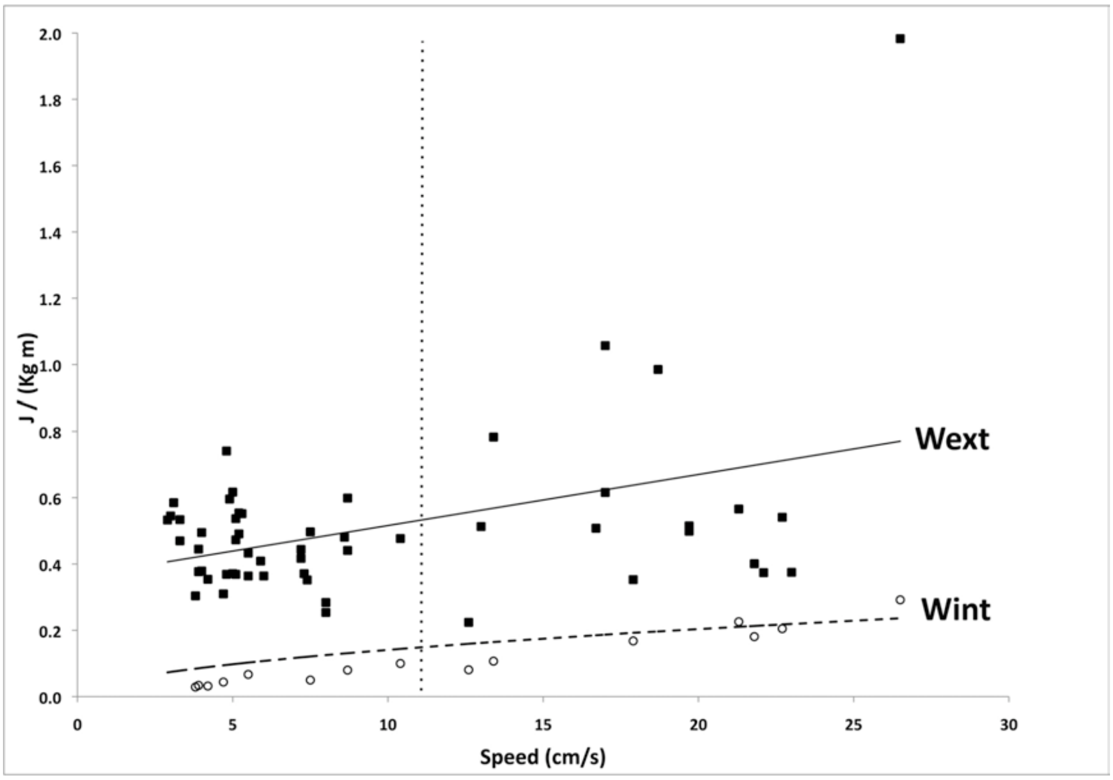


Fig. 3.6. Mechanical work at different speeds. External work (squares) with regression lines and Internal work (circles). The W_{INT} line refers to the Fedak et al. (1982) predicted values of internal work.

move in phase during the acceleration of the first stride, probably to boost the propulsion (FL 2nd quadruped, fast, Table 3.2).

Studies of gait pattern in insects have suggested that regularities in the support area are strongly influenced by central pattern generators (CPGs) under the influence of sensor input (Cruse and Muller, 1986; Delcomyn, 1985). Since sensory feedback seems to be essential for leg coordination during slow walking (Cruse and Muller, 1986; Delcomyn, 1985), the control operated by the CPGs actions become increasingly important with speed (Delcomyn, 1991). In a study made with different ant species it was proposed that the rigidity of their three-legged gait pattern regardless of changes in speed could reveal the prevailing of CPGs over sensory input (Zollikofer, 1994).

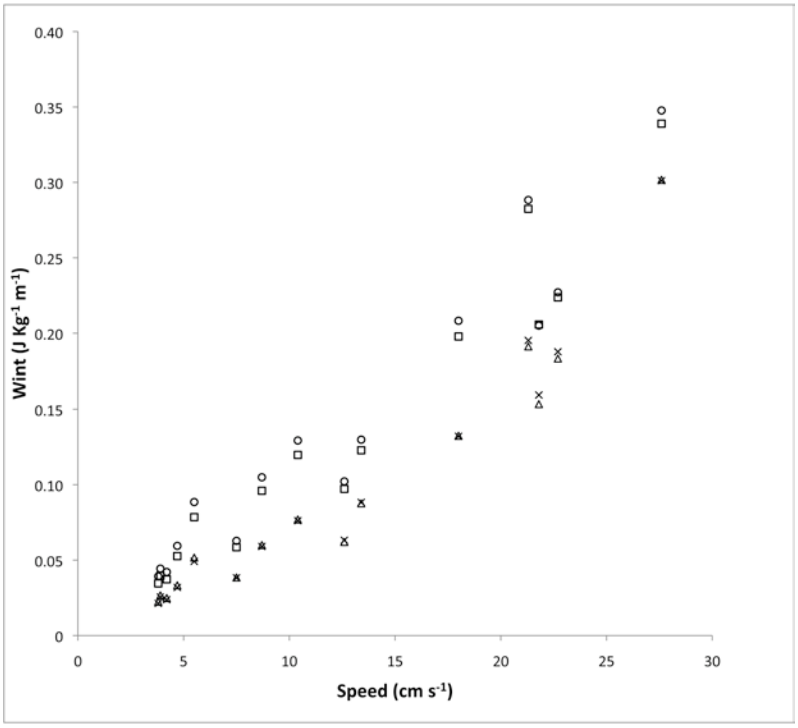


Fig. 3.7. Internal work (Wint) values at different speeds according to four leg models: (1) Open circle: Frustum of cone shape, two equal segments; (2) Open box: Frustum of cone shape, shorter proximal segment (*patella*-joint); (3) Open triangle: Cone shape, two equal segments; (4) X: Cone shape, shorter proximal segment (*patella*-joint)

Following this argument, the results of spatiotemporal coordination in the legs of *Grammostola mollicoma* during both regimes of displacement, could indicate that in this species there is no rigid neural control by CPGs. However, it may also indicate that locomotion patterns in spiders could be more complex and should be interpreted by means of other variables. In this respect the present data clearly show a pattern in the time-course of the support area and in stability during slow locomotion but not during faster gaits. That suggests a rigid neural control by CPGs during slow displacements to keep stability, but not at higher speed.

Speed and gaits

A gait transition can be determined by mechanical and energetic factors (Griffin et al., 2004), and can be recognised by an abrupt change in the speed-dependency of at least one mechanical or metabolic variable (Alexander, 1989).

In *Grammostola mollicoma* several variables showed significantly different speed-dependency behaviour between slow and fast gaits: stride frequency ($p < 0.001$), duty factor ($p = 0.003$), internal ($p < 0.001$) and external work ($p = 0.011$). The stride frequency increased linearly with speed in both gaits, which is typical for walk and run/trot (Heglund et al., 1974). The maximum stride frequency (4.55 Hz) and the maximum speed (0.275 $m \cdot s^{-1}$) recorded during our experiments are well below the predicted trot-gallop transition values for animals of the same mass (Heglund et al.,

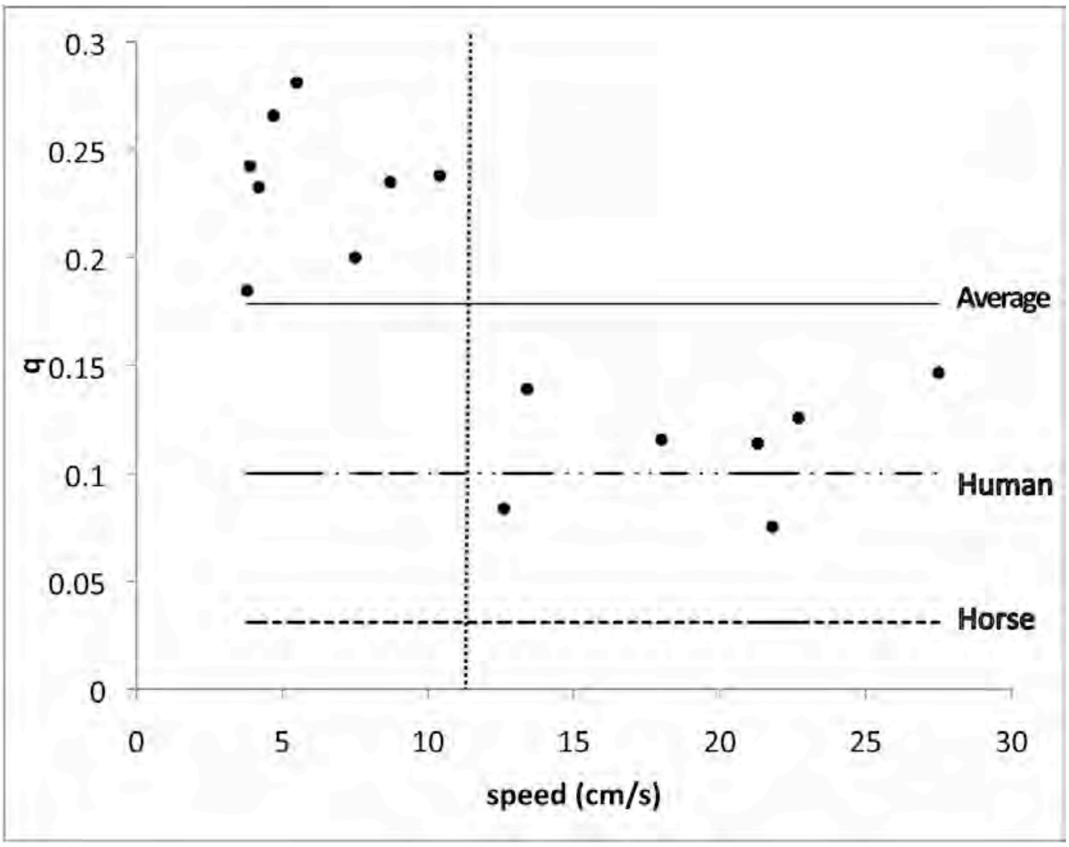


Fig. 3.8. Calculated variations of the dimensionless term q (Eqn 2). Dots represent the q-values as obtained from the experimental data. Lines represent the mean values of q in *G. mollicoma*, humans and horses. Data on humans and horses are from Minetti (Minetti, 1998a). The vertical dotted line represents the cut-off speed between slow and fast displacements.

1974), which should occur at 0.586 $m \cdot s^{-1}$. This comes with no surprise as spider slow and fast gaits are both similar to walking (Df > 0.5, Table 3.2).

Octopod locomotion in spiders appears to be completely different from the functional octopod sideways locomotion of crabs (Full, 1987; Weinstein, 1995), where the right and left legs act as leading or trailing ones, depending from the movement direction. Crabs show a walking gait with an inverted pendulum (IP) energy-conserving mechanism similar to the quadrupedal and bipedal walking (Cavagna et al., 1976; Margaria, 1976), a slow run and a fast run with an aerial phase similar to a gallop (Blickhan and Full, 1987; Blickhan et al., 1993).

The IP model (Margaria, 1976) applies to animals moving forward while vaulting over stiffened legs. Changes in potential and forward kinetic energy through time occur out of phase, with a consequently high value of energy recovery (Cavagna et al., 1976). Such behaviour has been observed in walking bipeds (Cavagna and Margaria, 1966), quadrupeds (Heglund et al., 1982; Minetti et al., 1999) and the mentioned crabs (Blickhan and Full, 1987; Blickhan et al., 1993), but it has never been observed in other Arthropods (Sensenig and Schultz, 2006).

During running gaits the potential and forward kinetic energy change in phase during the stride, therefore neither exchange nor recovery occurs. The bouncing ball model (Margaria, 1976) is consistent with vertebrate run/trot (Farley et al., 1993), insects locomotion (Full and Tu, 1990), and functional exapodal spiders (Sensenig and Schultz, 2006). Running insects can reach considerable high speed. The American cockroach *Periplaneta americana* can run up to 1.5 $m \cdot s^{-1}$ switching from exapodal to quadrupedal and bipedal running (Full and Tu, 1991).

A third paradigm has been proposed to model the skipping gaits (Minetti, 1998b). An analysis of human skipping and quadruped's gallop revealed that a combination of potential and forward kinetic pendulum-like exchange and elastic energy storage is responsible for the efficiency of this gait model (Saibene and Minetti, 2003).

The symmetrical gaits by definition are those in which the lag time of the two feet of the pairs (FL and HL) is the same (50% of the cycle duration) (Abourachid, 2003; Hildebrand, 1966; Hildebrand, 1977). Analysing our subject, *Grammostola mollicoma*, as a combination of two quadrupeds (Minetti, 2000), we observed that the gait parameters roughly represented symmetrical walk at low speed, while during fast locomotion we found a remarkable variability of such parameters and more asymmetric trajectories of the tCOM over a stride, although the duty factor remained above 0.5 and a flight phase was absent (Table 3.2, Fig. 3.5). The increase of asymmetry during faster gaits is consistent with the observation that asymmetrical gaits probably evolved, in amphibians and several times in reptiles, to benefit escape (Hildebrand, 1977).

Duty factor greater than 0.5 classically define the kinematics of walking gaits (Alexander, 1989). However, running gaits characterised by duty factor > 0.5 and stride frequency which proportionally increases with the progression speed have been also described for running frogs (Ahn et al., 2004), for terrestrial locomotion in bats (Riskin et al., 2006), and even in human race walking, where the flight phase is forbidden but the potential and kinetic energy curves of tCOM are in phase as during running.

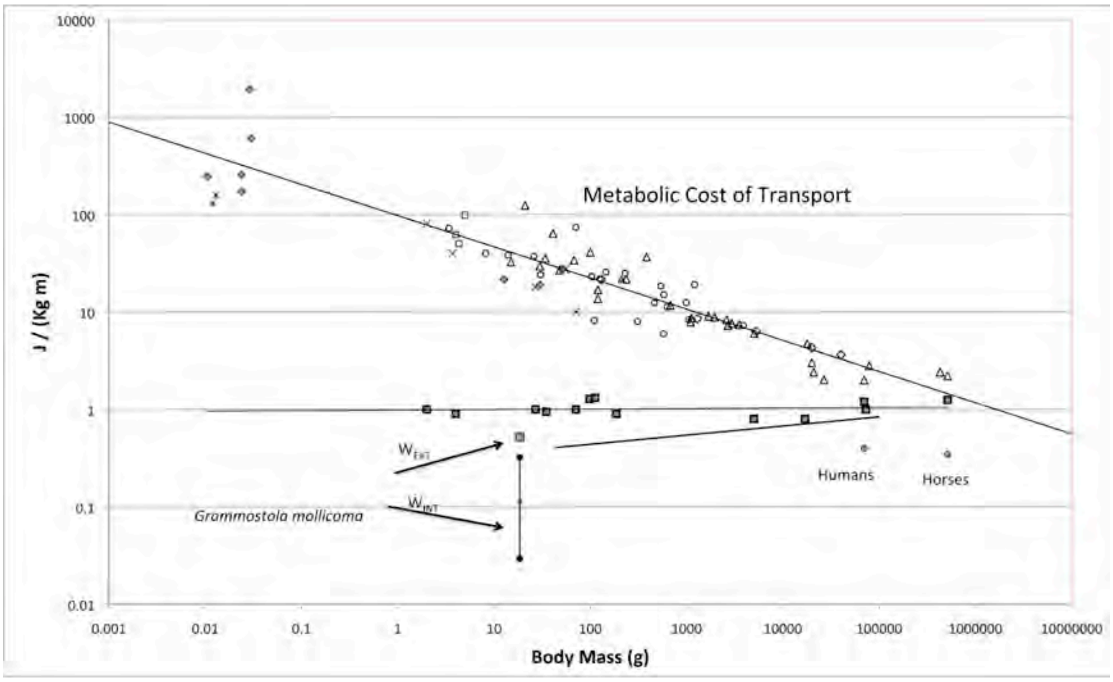


Fig. 3.9. Cost of transport versus body mass in animals. The upper line shows the allometric regression of the net metabolic cost, the middle line the almost constant mechanical cost (Wext, ignoring fluctuations of internal kinetic energy, and energy saving by elastic mechanisms) and the lower line the internal work (Wint) according to predicted values (Fedak et al., 1982). Asterisks, ants; filled diamonds, spiders; open squares, cockroaches; , crabs; open circles, reptiles; filled triangles, amphibians; open diamonds, birds; open triangles, mammals; filled squares, Wext; filled circles, Wint in G. mollicoma (present study, yellow circle represents the mean value), humans and horses. Data are from various sources [Full (Full, 1989) and Full and Tu (Full and Tu, 1991) and references therein] (Lighton and Gillespie, 1989; Steudel, 1990; Secor et al., 1992; Lighton et al., 1993; Minetti et al., 1999; Baudinette et al.,

In conclusion the locomotion of these spiders, analysed using stride-based analysis, shows significant differences from other arthropods, such insects. Changes in stability during each support situation, show an important difference with other animals, and are in agreement with a backward-forward activation sequence.

Mechanical work and efficiency

We did not find significant differences between the W_{EXT} estimated by using a single marker approximating BCOM and the W_{EXT} values based on the true COM position (9 measured + 16 virtual markers) for the complete strides (paired *t*-test: $p = 0.098$).

Spiders as a group have lower resting metabolic rates than other poikilothermic animals (Anderson, 1970; Greenstone and Bennett, 1980). However, there are only few available data about the metabolic cost of transport in tarantula spiders of the family *Theraphosidae* (Herreid and Full, 1980). As pointed out by Herreid (1981) in his review, the minimum cost of transport (Cmin) in spiders is subject to underestimation, due to the long recovery time after every performance, which is a characteristic of these animals (Herreid, 1981).

The adjusted Cmin for a 12.7 g *Theraphosidae* spider was 20.0 $J \cdot kg^{-1} \cdot m^{-1}$. The average mass-specific mechanical energy used to move the centre of mass a given distance (Fig. 3.6) was 0.52 $J \cdot kg^{-1} \cdot m^{-1}$, approximately one half the almost constant value detected in other arthropods, mammals and birds (see fig. 3.9 and caption for references).

The mechanical work expressed per kg of mass and per meter is almost constant in all the animals, independently of the body mass. A potential reason for the deviation from such a rule detected in spiders could be their particular femoropatellar (knee) extensor mechanism. In fact spiders, as many arachnids, lack extensor muscles at the femoropatellar joints, and extend them with hydraulic pressure generated by contraction of endosternal suspensor muscles (Shultz, 1991).

This work is the first attempt to calculate the internal mechanical work in spiders. Octopods have a multiple of eight segments moving with respect of the centre of mass. We would therefore expect a high fraction of the total work accounted as internal work. In fact, even if the arthropod legs are considerably lighter compared to vertebrate limbs, (i.e..: the fractional mass of the legs with respect to the body mass is lower in spiders than in vertebrates in spite of the higher number of segments), the calculated value of *q* (Minetti, 1998a), reflecting the inertial arrangement in leg dynamics, is higher in spiders than in human and horses, particularly at slow speeds (fig. 3.8).

According to that model (Minetti, 1998a; Minetti and Saibene, 1992), the internal work increases proportionally to the progression speed and the stride frequency. Our results are consistent with this prediction but suggest a difference between invertebrates and vertebrates, or between octopods and quadrupeds. The equation proposed by Fedak et al. (1982) was based on vertebrates between 0.044 and 98 kg. The spiders considered in the present work are out of this range, and the calculated internal work shows a linear proportionality to speed.

The "q" term depends on inertial characteristics of moving segments. Arthropod and tetrapod limbs are, from an evolutionary point of view, analogous and in many ways convergent structures, but their geometric and physical parameters can be very different. These peculiarities could account for a different relationship between the internal work and the progression speed and for a different average "q" parameter in arthropods. More data on octopods and invertebrates mechanical internal work could shed light on this issue.

The different behaviour of "q", higher during slow displacements than in faster gaits (Fig 8), could be explained also by different limb geometry and moving pattern. It has already been stressed the slow and high "exploratory" trajectory of the first pair of feet, which is expressed during walking in the range of slow speed. During fast movements this behaviour is lost in order to increase the stride frequency and speed. Another potential explanation for higher q values at slow speed could have been a wider base of support, which our data tend to exclude.

The estimated efficiency of locomotion in *Grammostola*, obtained by summing W_{INT} and W_{EXT} and dividing the result (W_{TOT}) by the estimated Cmin, ranged between 2.6 and 3.8%, a value comparable to the estimated efficiency in animals of the same mass.

Conclusions

Spiders locomotion, here studied in the *Grammostola mollicoma,* exhibits two main gaits, neither of which incorporating a flight phase, characterised by a consistent limb pattern and a small but remarkable energy recovery index. Both the mechanical internal and external work, never investigated previously, were found to be lower than the allometric predictions. By considering the total work done, the estimated efficiency of locomotion resulted no greater than 4%.

Further studies estimating the mechanical work through direct dynamics on a greater number of specimens and higher speeds, if available, could refine the present observations, although the very low mass of those spiders makes the ground reaction force measurement problematic. Also, new metabolic studies on steady state locomotion in spiders are necessary to detect the presence of optimal speeds within the two identified gaits.

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4. Biomechanical determinants of transverse and rotary gallop in cursorial mammals

The content of this chapter has been presented as oral communication at the Society for Experimental Biology Annual Main Meeting, Glasgow 1st - 4th July 2011 (Biancardi and Minetti, 2011) and in preparation for submission to the *Journal of Experimental Biology*.

4.1. Introduction

Quadrupedal mammals move using sharply distinct speed dependent gaits (Alexander, 1989). A part of the speed range, gaits are commonly identified by their footfall patterns (Muybridge, 1957). Symmetrical gaits, like trot, are characterized by the footfalls of the two feet of the same pair (fore or hind) evenly spaced in time. In asymmetrical gaits, like the two forms of gallop, this is not the case for at least one of the two pairs of feet (Hildebrand, 1965; Hildebrand, 1977). However, other variables, such as the duty factor (the fraction of the duration of the stride for which each foot is on the ground) and the pattern of force exerted on the ground, abruptly vary as the gait changes. Consequently, the definition of gait adopted by Alexander was: "*A pattern of locomotion characteristics of a limited range of speeds described by quantities of which one or more change discontinuously at transition to other gaits*" (Alexander, 1989).

In his milestone papers, Hildebrand provided a grid system for comparison of the gait performed by quadrupedal animals, introducing the concept of limb phase as "*percent of the stride interval that a footfall of a forefoot lags behind the strike of the ipsilateral hind foot*" (Hildebrand, 1966; Hildebrand, 1977). Limb phase is particularly important do distinguish lateral gait sequences (limb phase < 50%) by diagonal gait sequences (limb phase > 50%) (Renous et al., 2004). A new approach to gait analysis, yet based on quantitative analysis of gait variables, has been recently provided by Abourachid, who introduced the concept of antero-posterior sequence (APS) and the definitions of fore lag (the time lag between the footfalls of the forefeet), hind lag (the time lag between the footfalls of the hind feet) and pair lag (the time lag between the footfall of the first forefoot and the first hind foot) (Abourachid, 2003).

The two distinct forms of gallop are known as transverse and rotary. In high-speed transverse gallop the two hind feet are placed in sequence. The placement of the second hind foot is followed by that of the controlateral forefoot and then by the remaining forefoot. The right-left or vice-versa sequence is the same in fore and hind limbs and is generally conserved for several strides. There is a typical suspended phase after the lifting of the forefeet, with all the legs off the ground and gathered under the body: this is called the gathered flight phase. There could be a second suspended phase, known as the “extended flight phase” (often found in paintings from 15th to 18th century), after the lifting of the hind feet and before the placement of the first forefoot. In rotary gallop the placement of the second hind foot is followed by that of the ipsilateral forefoot, and the sequence of footfalls appears to rotate around the body. At high-speed both gathered and extended flight phases are present.

Gallop has been widely considered one gait (eg: Alexander, 2006). However, transverse and rotary gallop can be distinguished by some of the quantities commonly used to separate different gaits (Abourachid, 2003; Hildebrand, 1959; Hildebrand, 1977; Renous et al., 2004). According to the traditional Hildebrand’s method, rotary gallop has a lateral sequence (limb phase $< 50\%$), while transverse gallop has a diagonal one (Hildebrand, 1977; Renous et al., 2004). According to Abourachid, rotary gallop has a negative hind lag, while transverse gallop has a positive one (Abourachid, 2003).

Although well understood in terms of footfall pattern and gait quantities, it is still argued if a quadruped animal species can equally perform transverse or rotary gallop, which species only show one of the two patterns, if there are constraint or biomechanical determinant of the type of gallop (Bertram and Gutmann, 2009; Grillner, 1975; Hildebrand, 1959). It is known that horses only perform transverse gallop at any speed, while rotary gallop has been clearly associated to cheetah and racing dogs (ref). Some dogs are known to use rotary gallop at high speed and transverse gallop at lower speed (Walter and Carrier, 2007). Aims of this work are to assess the gallop form displayed by as much as possible cursorial mammal species and investigate the morphological, ecological and physiological differences among them, looking for biomechanical determinants of rotary and transverse gallop. Other tan shedding light on those aspects, the present results could help to infer the gait types in extinct quadrupeds.

4.2. Materials and methods

Movies

A total of 351 films and clips of free ranging mammals have been analysed in order to assess the gallop type of the investigated mammal species. A first classification made by Alexander (Personal obs.) was used as starting point. The list has been compared to literature data and integrated (Alexander et al., 1977; Egorov, 1965; Hildebrand, 1977; Muybridge, 1957).

The criteria used to select a videoclip were:

i) A clear sequence of straight linear galloping strides, possibly on level or on mild gradient

ii) A stepping pattern clearly detectable

After a first screening, it has been chosen to define three categories: transverse, rotary and speed dependent. The criteria used to assign a species to each category were:

i) Same pattern observed many times in different individuals, at different speeds (e.g.: transverse gallop in horses and camels; rotary gallop in cheetah, gazelles and roe deer)

ii) Same pattern observed in different individuals at different speeds. This is because some species adopt a slow gallop gait (canter), which frequently is transverse, and switch to a "true" rotary gallop at higher speeds. (e.g.: pronghorn, wolf and coyote)

iii) Pattern clearly more frequent on several observations. (e.g.: transverse in wildebeests and rotary in buffalos)

iv) Pattern observed few times but confirmed by comparative observation of very similar species. (e.g.: mule deer compared to white-tailed deer; dama gazelle compared to Grant's gazelle)

v) Pattern observed few times but confirmed by literature data. (e.g.: chinese water deer, striped hyaena)

Gait and joint angles analysis

Gallop, as other asymmetrical gaits, have the footfalls of a pair of feet unevenly spaced in time: the first foot of a couplet, fore or hind, to strike the ground is called the trailing foot, while the other is the leading foot (Hildebrand, 1977).

Stride based analysis generally considers the contact of the hind trailing foot as starting point of the stride cycle (Alexander, 2006; Hildebrand, 1977). Recently a new method based on antero-posterior sequence (APS) has been proposed (Abourachid, 2003; Abourachid et al., 2007). APS permits a gait classification based on the combination of three variables: forefeet lag, hind feet lag and pair lag.

Name	Var	Dim	Description
Stride			Compete cycle of movement from the strike of a reference foot to the next strike of the same foot
Stride length	*Sl*	l	Distance travelled in one stride
Relative stride length	*Rsl*		SL divided by the height of the hip joint from the ground
Stride frequency	*Sf*	t^{-1}	Strides taken in unit time
Step length	*Step*	l	Distance travelled while a particular foot is on the ground
Duty factor	*Df*		Fraction of the duration of a stride for which a foot is on the ground. Can be applied to each foot, as average of fore or hind feet, as average of the four feet. The average Df is approx. = Step / Sl
Phase difference	*Ph*		Time of the first contact of a fore foot as percentage of the stride duration
Paired phase difference	*PPh*		Averaged phase difference of ipsilateral feet
Forefeet lag	*Flag*		Time lag between the footfalls of the forefeet as percentage of the cycle duration
Hind feet lag	*Hlag*		Time lag between the footfalls of the hind feet as percentage of the cycle duration
Pair lag	*Plag*		Time lag between the footfalls of the first fore foot and of the first hind foot, as percentage of the cycle duration
Fore midtime	*Fmid*		Instant in time half way the duration of contact by one or both forefeet
Hind midtime	*Hmid*		Instant in time half way the duration of contact by one or both hind feet
Midtime lag	*Mlag*		Time lag between Hmid and Fmid as percentage of the stride duration
Hind ratio	*Hr*		Percent of the stride interval that body is supported by one or both hind feet

Table 4.1. Abbreviations and descriptions of the gait parameters

The gait parameters (Tab. 4.1) have been collected by counting the frames of the best filmed motion sequences, according to Biewener (1983).

The maximum angular excursion of a line drawn from the head of the femur (hip joint) to the toe of the foot has been measured, tracing frames of motion pictures of animals running at high speed, taken from the available footage (McMahon, 1975).

Classification of the species

A phylogenetic tree of the classified species has been built after Carroll (1987), Wyss and Flynn (1993), McKenna and Bell (1997), Froelich (1999), Hu et al (2010). Species have been named after Wilson and Reeder (2005).

Data collection

Maximal running speed has been taken after the comprehensive papers of Garland (1983) and Christiansen (2002a), based on other literature sources. Averaged body masses, body length, fore and hind limb measures, averaged limb length and height at shoulder have been taken from Egorov (1965), Groves (1974), Spinage (1986), Putman (1988), Churcher (1993), Bennett & Hoffmann (1999) and Nowak (1999), as well as other behavioural and ecological data.

Bones masses have been taken from Christiansen (2002b), while bones and spine measures came from different sources: literature (Christiansen, 1999a; Christiansen, 1999b; Wroe et al., 2008) or specimens housed either in the Natural History Museum of Milan, measured by Gargantini (1997) and Biella (1998), or in the Natural History Museum "La Specola" of Florence, measured by one of the authors (CMB). Digital calliper has been used for lengths up to 220 mm, normal calliper for longer measures.

The following measures have been taken for each single vertebra: vertebral body length (vbl), measured between the edges of the ventral epyfisae; vertebral body width (*b*), as the average of the measured width of the cranial and caudal faces; vertebral body height (*h*) as the vertical diameter of the caudal face of the vertebral body. During locomotion of mammals the spine is subject to sagittal bending movements (Hildebrand, 1974). The resistance of the spine to flexion varies along the different column regions (cervical, toracic and lumbar) as well as among different species. A value of the moment of resistance of any single vertebra has been calculated after Slijper (1946). The formula is:

$$S = bh^2 \qquad (1)$$

derived from structural mechanics and similar to the first moment of area of rectangular section logs. Spine stiffness indices (St_1, St_2) were calculated as following:

$$St_1 = \frac{S_{MAX}}{S_{MIN}} \qquad (2)$$

$$St_2 = \frac{S_{TLMAX}}{L_{TL}} \tag{3}$$

where S_{MAX} and S_{MIN} are the maximum and the minimum values of S, S_{TLMAX} is the maximum value of the toracic-lumbar region and L_{TL} is the length of the toracic-lumbar region.

The dimensionless Froude number:

$$Fr = v^2 / gL \tag{4}$$

where v = speed, g = gravitational acceleration, L = leg length, has been calculated from the maximum running speed and average limb length. Dynamic similarity between two different sized animals is possible when their speeds are such to give them equal values of Fr (Alexander, 2006; Alexander and Jayes, 1983). Relative stride length and stride length were estimated from Fr and average limb length (Jayes and Alexander, 1978). Momentum of inertia and radius of gyration of the body and of the long bones have been also calculated.

Statistical analyses

Statistical analyses were performed using the following softwares: SPSS, ver. 19.0 (IBM Inc., USA); Mesquite, ver. 2.74.550 (Maddison W. and Maddison D., 1997-2010) with extra package PDAP, ver. 1.15 (Midford P.E., Garland T. and Maddison W., 2010); LabView, ver. 2009 (National Instruments Inc., USA).

Order	species	common name	Gallop
Artiodactyla	*Aepyceros melampus*	Impala	R
	Alcelaphus buselaphus	Hartebeest	T
	Alces alces	Eurasian Elk	R
	Ammotragus lervia	Barbary sheep	T
	Antilocapra americana	Pronghorn	S
	Antilope cervicapra	Blackbuck	T
	Bison bison	American Bison	T
	Bison bonasus	European Bison	T
	Bos taurus	Aurochs	R
	Camelus bactrianus	Bachtrian camel	T
	Camelus dromedarius	One-humped camel	T
	Capra falconeri	Markhor	T
	Capra hircus	Goat	T
	Capreolus capreolus	Roe deer	R
	Cephalophus silvicultor	Yellow-backed duiker	T

Order	species	common name	Gallop
Artiodactyla	*Cervus elaphus*	Red Deer	R
	Cervus nippon	Sika deer	R
	Connochaetes taurinus	Blue wildebeest	T
	Connochaetes gnou	Black wildebeest	T
	Dama dama	Fallow deer	R
	Elaphurus davidianus	Pere David's deer	R
	Eudorcas thomsonii	Thomson's Gazelle	R
	Gazella dorcas	Dorcas gazelle	R
	Gazella subgutturosa	Goitered gazelle	R
	Giraffa camelopardalis	Giraffe	R
	Hydropotes inermis	Chinese water deer	R
	Kobus leche	Lechwe	S
	Lama glama	Guanaco	T
	Litocranius walleri	Gerenuk	R
	Nanger dama	Dama gazelle	R
	Nanger granti	Grant's gazelle	R
	Odocoileus hemionus	Mule deer	R
	Odocoileus virginianus	White-tailed deer	R
	Okapia johnstoni	Okapi	R
	Oreamnos americanus	Mountain goat	T
	Oryx dammah	Scimitar-horned oryx	T
	Oryx gazella	Gemsbok	T
	Oryx leucoryx	white oryx	T
	Ovis ammon	Argali	T
	Ovis aries	Red sheep	T
	Ovis canadensis	Bighorn sheep	T
	Phacochoerus aethiopicus	Warthog	T
	Rangifer tarandus	Reindeer	R
	Rupicapra rupicapra	Chamois	S
	Saiga tatarica	Steppe saiga	R
	Sus scrofa	Wild boar	T
	Syncerus caffer	Buffalo	S
	Taurotragus orix	Eland	R
	Tragelaphus spekei	Sitatunga	R
	Tragelaphus strepsiceros	Greater Kudu	R
Carnivora	*Acinonyx jubatus*	Cheetah	R
	Canis aureus	Golden jackal	S
	Canis familiaris	Dog	S
	Canis latrans	Coyote	S

Order	species	common name	Gallop
Carnivora	*Canis lupus*	Wolf	S
	Canis mesomelas	Black-backed jackal	S
	Canis simensis	Ethiopian wolf	S
	Chrysocyon brachiurus	chrysocyon	S
	Crocuta crocuta	Spotted hyena	T
	Cuon alpinus	Dhole	S
	Eumetopias jubatus	Steller sea lion	T
	Felis catus	Cat	R
	Gulo gulo	Wolverine	R
	Hyaena hyaena	Striped Hyena	T
	Lycaon pictus	African wild dog	S
	Lynx canadensis	Canadian lynx	R
	Meles meles	Badger	T
	Melursus ursinus	Sloth bear	R
	Panthera leo	Lion	R
	Panthera onca	Jaguar	R
	Panthera pardus	Leopard	R
	Panthera tigris	Tiger	R
	Procyon lotor	Racoon	T
	Puma concolor	Coguar	R
	Speothos venaticus	Bush dog	S
	Uncia uncia	Snow leopard	R
	Ursus arctos	Brown bear	S
	Ursus americanus	Black bear	S
	Ursus maritimus	Polar bear	T
	Vulpes lagopus	Arctic fox	T
	Vulpes vulpes	Red Fox	S
Perissodactyla	*Equus asinus*	African wild ass	T
	Equus burchellii	Burchell zebra	T
	Equus caballus	Horse	T
	Equus caballus przewalskii	Przewalski horse	T
	Equus grevyi	Grevy's zebra	T
	Equus hemionus	Onager	T
	Equus kiang	Asian wild ass	T
	Rhinoceros unicornis	Indian Rhinoceros	T

Table 4.2. List and classification of the analysed species

4.3. Results

A total of 89 species belonging to 3 mammal orders have been analysed and classified in three groups (Table 4.2):

i) Rotary (R): 35 species performing rotary gallop at any speed
ii) Transverse (T): 37 species performing transverse gallop at any speed
iii) Speed dependant (S): 17 species performing rotary gallop at high speed and transverse gallop at lower speed

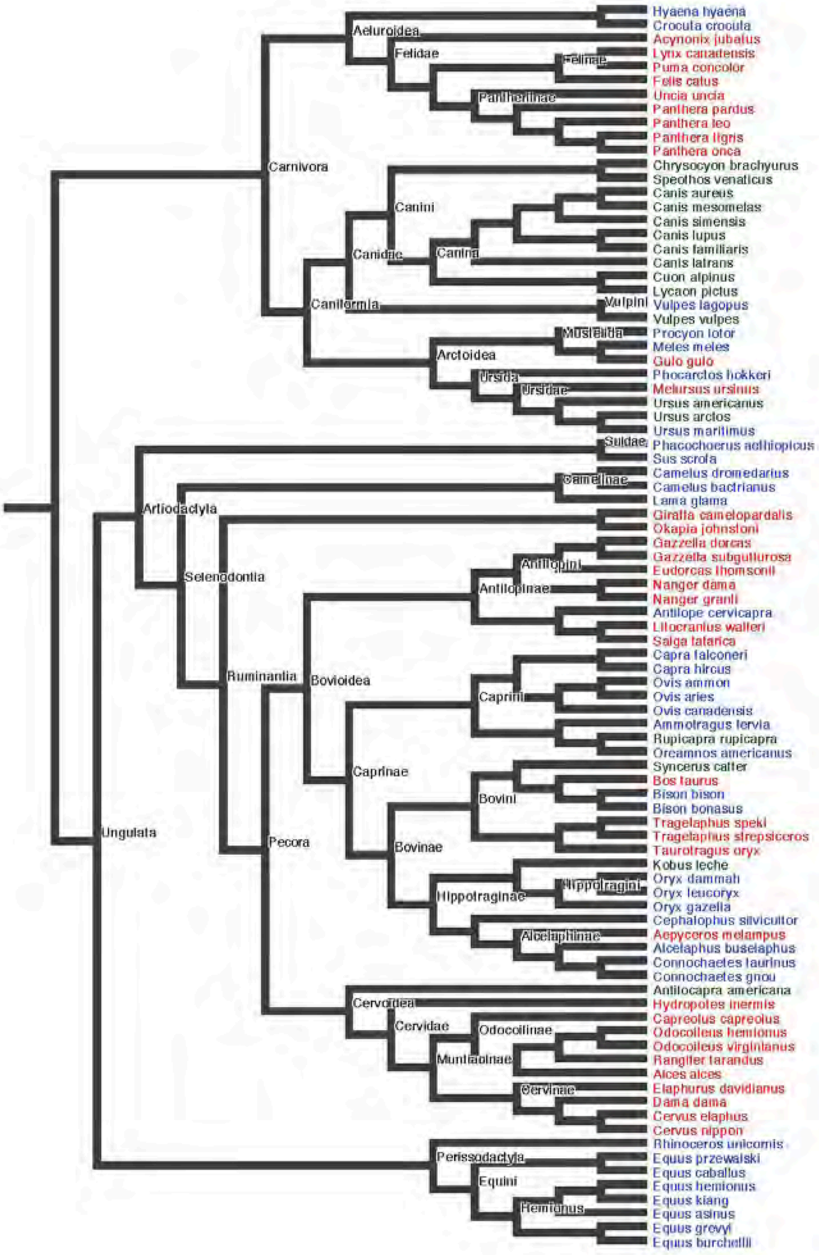
The phylogenetic relationships among them are shown in the cladogram (Fig. 4.1).

A wide range of data have been collected (see methods), ratio between morphometric measures have been computed to reduce the size effect. Their descriptive statistics are reported in table 4.3. Both measures and ratios have been log transformed, in order to correct for allometric distribution and improve the comparisons among different variables.

Analysis of variance

A first analysis of variance has been performed under a general linear model (glm). Significant differences between the gallop categories have been found for almost all the investigate variables (Table 4.4). More interesting were the results obtained applying contrasts (Table 4.5). Contrasts have been preferred to post-hoc multiple comparison (e.g. with Bonferroni correction), because they allow pool and assign specific weight to any group.

The estimated Froude number at maximum speed was significantly higher in rotary and speed dependent galloper, while cheetah, a rotary galloper, records both the highest absolute (29.2 $m \cdot s^{-1}$) and relative speed (Fr = 149.6). However, while the highest speed in body length per second is in charge to a rotary species, the goitered gazelle (26.3 $bl \cdot s^{-1}$), the higher mean value belongs to the speed dependent group (Fig. 4.2a-b). The aspect ratio (height / body length), an index of general shape of a vertebrate, was significantly lower in rotary than in transverse galloper, while speed dependent species data were more variable (Fig. 4.2c). Standardized mass per body length showed a decreasing trend from transverse to rotary and finally to speed dependent species (Fig. 4.2d). Consistent to the decreasing trend of body mass was the observed opposite



Modified from tree 1

Fig. 4.1. Phylogenetic tree. Blue: Transverse; Red: Rotary; Green: Speed dependent species

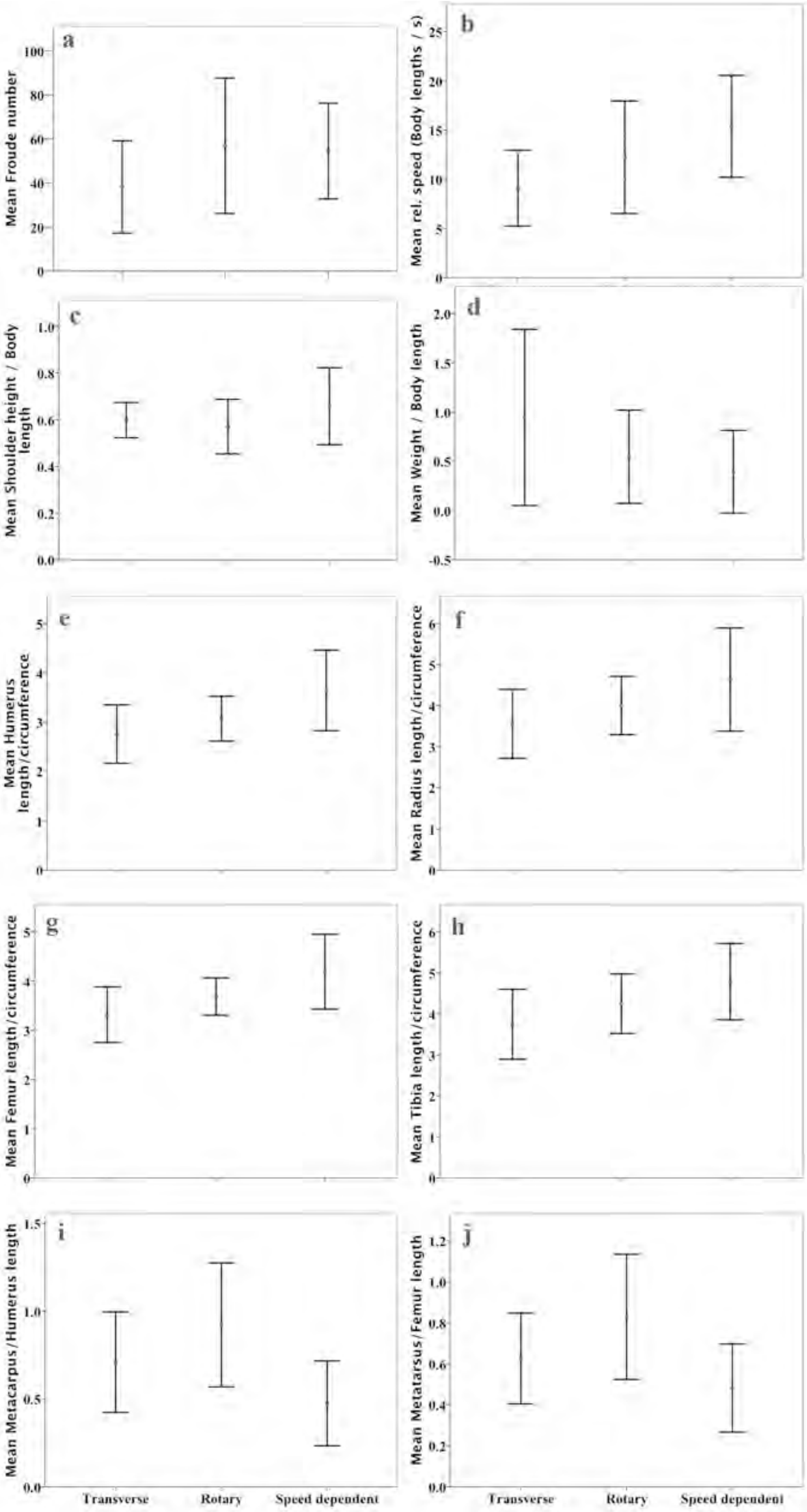


Fig. 4.2. ANOVA. Mean ± SD

increasing trend of the limb bones index of aspect ratio (bone length / bone circumference) (Fig. 4.2e-h). The ratios between the distal and prossimal limb segment (metacarpus / humerus and metatarsus / femur) reached the highest values in rotary and the lowest ones in speed dependent, while transverse galloper were in between the two (Fig. 4.2i-j). To resume, transverse galloper species resulted significantly slower and heavier than rotary and speed dependent ones, and had proportionally thicker bones.

Gallop			**N**	**Min**	**Max**	**Mean**	**SD**
Transverse	Rsl	Relative Stride Length	35	1.64	8.97	4.89	1.28
	Sl	Stride Length (m)	35	0.84	5.28	3.46	1.15
	Fr	Froude number	35	4.04	120.62	38.20	20.96
	V	Maximum speed (m/s)	35	6.67	26.39	15.51	4.02
	Fll	Fore Limb length (mm)	26	212	1216	683.8	231.3
	Hll	Hind Limb length (mm)	26	258	1265	787.0	248.1
	Ll	Average limb length (m)	35	0.22	1.42	0.74	0.27
	M	Mass (Kg)	37	5.0	1900.0	226.50	324.69
	Hl	Humerus length (mm)	29	100.5	479.0	245.60	91.73
	Hc	Humerus circumference (mm)	29	21.6	235.5	96.44	48.60
	Rl	Radius length (mm)	29	87.2	504.5	261.58	106.18
	Rc	Radius circumgerence (mm)	29	17.3	159.5	80.83	42.01
	Mcl	Metacarpus length (mm)	9	29.0	313.3	132.73	89.86
	Mcc	Metacarpus circumference (mm)	2	19.5	26.0	22.75	4.60
	Fl	Femur length (mm)	30	106.7	552.0	297.50	117.27

Gallop			N	Min	Max	Mean	SD
Transverse	Fc	Femur circumference (mm)	29	23.0	231.0	96.06	48.36
	Tl	Tibia length (mm)	29	99.3	460.5	286.21	97.13
	Tc	Tibia circumference (mm)	29	20.4	203.0	83.97	42.60
	Mtl	Metatarsus length (mm)	9	33.1	329.8	142.13	94.54
	Mtc	Metatarsus circumference (mm)	2	19.0	26.0	22.50	4.95
	Bl	Body length (m)	37	0.51	3.80	1.91	0.77
	Sh	Shoulder height (cm)	36	26.6	205.0	113.27	46.53
	Tal	Tail length (cm)	26	10.0	90.0	43.50	25.50
	I	Body moment of Inertia (Kg m^2)	34	0.09	1990.63	193.91	381.15
	Rgyr	Body radius of gyration (m)	34	0.15	1.10	0.56	0.23
	Spi	Spine stiffness index (mm^2)	8	6.50	128.79	42.30	46.80
	Bls	Speed Body length ratio (s^{-1})	34	2.14	24.69	9.10	3.85
	FHr	Fore/Hind limb ratio	26	0.75	1.04	0.87	0.07
	Hr	Humerus ratio (Hl/Hc)	29	2.03	5.08	2.75	0.59
	Rr	Radius ratio (Rl/Rc)	29	2.20	5.73	3.55	0.83
	Fr	Femur ratio (Fl/Fc)	29	2.39	4.64	3.31	0.56
	Tr	Tibia ratio (Tl/Tc)	29	2.01	5.96	3.74	0.85
	RHr	Radius Humerus ratio	31	0.75	1.31	1.06	0.16
	McHr	Metacarpus Humerus ratio	24	0.15	1.31	0.71	0.29
	TFr	Tibia Femur ratio	31	0.74	1.25	1.00	0.14

Gallop			N	Min	Max	Mean	SD
Transverse	MtFr	Metatarsus Femur ratio	24	0.15	1.02	0.63	0.22
	ShBlr	Aspect ratio (Shoulder/Body length)	36	0.41	0.74	0.60	0.08
	MBlr	Mass Body length ratio	37	0.09	5.43	0.95	0.90
Rotary	Rsl	Relative Stride Length	34	3.11	9.99	5.97	1.55
	Sl	Stride Length (m)	34	1.74	5.79	3.94	1.03
	Fr	Froude number	34	14.50	149.64	56.89	30.75
	V	Maximum speed (m/s)	34	13.30	29.17	18.34	3.84
	Fll	Fore Limb length (mm)	23	385	1746	680.0	288.9
	Hll	Hind Limb length (mm)	23	480	1656	815.4	279.2
	Ll	Average limb length (m)	26	0.73	1.05	0.83	0.06
	M	Mass (Kg)	35	4.0	600.0	118.95	148.99
	Hl	Humerus length (mm)	31	99.3	444.4	221.16	83.79
	Hc	Humerus circumference (mm)	31	24.7	173.1	75.26	34.25
	Rl	Radius length (mm)	31	93.8	704.3	236.06	113.32
	Rc	Radius circumgerence (mm)	31	15.0	161.7	61.75	31.20
	Mcl	Metacarpus length (mm)	11	68.2	667.5	195.95	166.64
	Mcc	Metacarpus circumference (mm)	5	25.0	52.0	37.04	10.85
	Fl	Femur length (mm)	31	106.7	481.8	267.26	93.29
	Fc	Femur circumference (mm)	31	26.0	157.6	74.51	31.04
	Tl	Tibia length (mm)	31	111.5	566.1	279.43	100.25

Gallop			**N**	**Min**	**Max**	**Mean**	**SD**
Rotary	Tc	Tibia circumference (mm)	31	23.0	159.1	68.80	30.44
	Mtl	Metatarsus length (mm)	10	83.8	701.5	223.60	181.14
	Mtc	Metatarsus circumference (mm)	5	27.0	52.5	39.98	10.65
	Bl	Body length (m)	35	0.46	4.25	1.72	0.81
	Sh	Shoulder height (cm)	35	28.00	310.00	96.29	50.68
	Tal	Tail length (cm)	31	6.75	140.00	43.36	34.41
	I	Body moment of Inertia (Kg m^2)	34	0.25	1.70	0.70	0.28
	Rgyr	Body radius of gyration (m)	35	0.07	1881.51	123.80	342.60
	Spi	Spine stiffness index (mm^2)	35	0.13	1.23	0.50	0.23
	Bls	Speed Body length ratio (s^{-1})	11	7.17	475.94	77.42	139.52
	FHr	Fore/Hind limb ratio	30	3.66	26.29	12.24	5.72
	Hr	Humerus ratio (Hl/Hc)	31	2.32	4.40	3.06	0.45
	Rr	Radius ratio (Rl/Rc)	31	2.86	6.25	4.00	0.71
	Fr	Femur ratio (Fl/Fc)	31	2.76	4.69	3.68	0.37
	Tr	Tibia ratio (Tl/Tc)	31	2.95	5.62	4.25	0.72
	RHr	Radius Humerus ratio	32	0.81	1.58	1.06	0.16
	McHr	Metacarpus Humerus ratio	21	0.33	1.50	0.92	0.35
	TFr	Tibia Femur ratio	32	0.69	1.30	1.06	0.16
	MtFr	Metatarsus Femur ratio	21	0.25	1.46	0.83	0.31
	ShBlr	Aspect ratio (Shoulder/Body length)	35	0.29	0.78	0.57	0.12

Gallop			**N**	**Min**	**Max**	**Mean**	**SD**
Rotary	MBlr	Mass Body length ratio	35	0.09	2.06	0.55	0.47
Speed	Rsl	Relative Stride Length	17	4.18	7.80	5.91	1.23
	Sl	Stride Length (m)	17	1.77	5.22	2.87	0.81
	Fr	Froude number	17	26.21	91.34	54.52	21.73
	V	Maximum speed (m/s)	17	13.33	24.17	15.56	2.72
	Fll	Fore Limb length (mm)	13	281.00	820.00	489.37	168.40
	Hll	Hind Limb length (mm)	13	329.00	991.00	570.15	202.81
	Ll	Average limb length (m)	17	0.26	0.91	0.51	0.18
	M	Mass (Kg)	17	5.50	440.00	64.27	106.67
	Hl	Humerus length (mm)	12	89.50	332.00	192.98	67.67
	Hc	Humerus circumference (mm)	12	22.00	157.50	58.18	35.24
	Rl	Radius length (mm)	12	73.30	306.00	190.53	66.63
	Rc	Radius circumgerence (mm)	12	17.80	131.00	45.97	29.80
	Mcl	Metacarpus length (mm)	4	36.00	140.00	74.65	47.63
	Mcc	Metacarpus circumference (mm)	0				
	Fl	Femur length (mm)	12	92.80	396.30	219.52	83.10
	Fc	Femur circumference (mm)	12	23.70	146.80	55.98	32.57
	Tl	Tibia length (mm)	12	85.50	394.50	227.47	86.96
	Tc	Tibia circumference (mm)	12	21.80	129.80	50.37	28.58
	Mtl	Metatarsus length (mm)	4	46.40	160.00	85.80	53.58

Gallop			N	Min	Max	Mean	SD
Speed	Mtc	Metatarsus circumference (mm)	0				
	Bl	Body length (m)	17	66.25	255.00	116.07	50.65
	Sh	Shoulder height (cm)	17	30.00	135.00	75.56	31.02
	Tal	Tail length (cm)	15	3.50	80.00	33.24	17.81
	I	Body moment of Inertia (Kg m^2)	14	0.73	0.95	0.86	0.06
	Rgyr	Body radius of gyration (m)	15	0.22	311.58	30.46	81.98
	Spi	Spine stiffness index (mm^2)	15	0.19	0.74	0.33	0.15
	Bls	Speed Body length ratio (s^{-1})	3	4.32	17.25	10.31	6.52
	FHr	Fore/Hind limb ratio	15	6.21	24.69	15.38	5.18
	Hr	Humerus ratio (Hl/Hc)	12	2.11	5.08	3.64	0.81
	Rr	Radius ratio (Rl/Rc)	12	2.34	7.51	4.63	1.25
	Fr	Femur ratio (Fl/Fc)	12	2.70	5.79	4.19	0.76
	Tr	Tibia ratio (Tl/Tc)	12	3.04	6.59	4.78	0.93
	RHr	Radius Humerus ratio	14	0.82	1.09	0.98	0.07
	McHr	Metacarpus Humerus ratio	11	0.17	1.07	0.48	0.24
	TFr	Tibia Femur ratio	14	0.76	1.26	1.04	0.12
	MtFr	Metatarsus Femur ratio	11	0.16	0.96	0.48	0.21
	ShBlr	Aspect ratio (Shoulder/Body length)	17	0.45	1.20	0.66	0.17
	MBlr	Mass Body length ratio	17	0.08	1.73	0.39	0.42

Table 4.3. Descriptive statistics

	Sum of Squares	df	Mean Square	F	P	sig.
Fr	0.657	2	0.328	6.406	0.0026	**
Sl	0.225	2	0.113	5.001	0.0089	**
FHr	0.001	2	0.001	3.159	0.0493	*
LBr	0.003	2	0.002	3.296	0.0421	*
ShBlr	0.006	2	0.003	3.252	0.0436	*
MBlr	0.247	2	0.124	7.656	0.0009	***
Hr	0.124	2	0.062	10.302	0.0001	***
Rr	0.115	2	0.057	6.592	0.0024	**
Fr	0.094	2	0.047	11.220	0.0001	***
Tr	0.114	2	0.057	7.300	0.0013	**
RHr	0.003	2	0.002	1.631	0.2027	ns
McHr	0.098	2	0.049	8.345	0.0007	***
TFr	0.003	2	0.001	1.551	0.2187	ns
MtFr	0.064	2	0.032	7.059	0.0019	**
Rgyr	0.047	2	0.023	6.351	0.0027	**
Bls	0.501	2	0.251	8.263	0.0006	***

Table 4.4. ANOVA

ANOVA	**Contrasts**						**Post-hoc**		
	T-RS	R-TS	S-TR	T-R	T-S	R-S	T-R	T-S	R-S
Fr	***	ns	ns	**	**	ns	**	*	ns
Sl	ns	**	*	ns	ns	**	ns	ns	**
FHr	ns	*	ns	*	ns	ns	ns	ns	ns
LBr	**	ns	*	ns	**	ns	ns	ns	*
ShBlr	ns	*	*	ns	ns	*	ns	ns	*
MBlr	***	ns	*	**	***	ns	*	**	ns
Hr	***	ns	***	*	***	*	*	***	*
Rr	***	ns	**	*	***	ns	ns	**	ns
Fr	***	ns	**	**	**	ns	*	***	ns
Tr	***	ns	**	*	***	ns	*	**	ns

ANOVA	Contrasts						Post-hoc		
RHr	ns	ns	**	ns	*	*	ns	ns	ns
McHr	ns	***	***	*	*	***	ns	ns	***
TFr	ns	ns	ns	ns	ns	ns	ns	ns	ns
MtFr	ns	***	**	*	ns	***	ns	ns	**
Rgyr	**	ns	**	ns	***	*	ns	**	*
Bls	***	ns	**	*	***	ns	ns	**	ns

Table 4.5. Results of applied contrasts and post-hoc (Bonferroni)

Non-parametric tests

Non-parametric Chi-square tests, using 10000 sampled tables with Monte Carlo simulation, have been performed to investigate for differences among the frequency of occurrence of the categorical variables and the gallop types (Tables 4.6-4.7). Transverse gallop was significantly more frequent in diurnal gregarious species that live in open habitat (grassland and plains). Species performing rotary gallop or speed dependent were more likely related to mixed habitats and crepuscular behaviour. Rotary gallopers resulted significantly more frequent among solitary predator species.

		Species
	df	Monte Carlo X^2 P
Activity pattern	6	0.025 (0.021-0.029)
Habitat coverage	2	0.010 (0.008-0.013)
Habitat type	4	0.027 (0.023-0.031)
Social behaviour	2	< 0.001
Feeding behaviour	2	0.017 (0.013-0.020)
Strategies		NA
Ecological role	2	< 0.001

Table 4.6. Results of non-parametric tests

	Transverse	**Rotary**	**Speed dependent**
Activity pattern			
Diurnal	25	14	4
Nocturnal	3	4	1
Crepuscolar	4	13	9
Always active	4	4	3
Habitat coverage			
Open	27	14	8
Closed	1	2	0
Mixed	8	19	9

	Transverse	Rotary	Speed dependent
Habitat type			
Grasslands and plains	24	16	7
Broken cover	11	13	4
Mixed and forest	1	6	6
Social behaviour			
Solitary	2	14	3
Gregarious	34	20	14
Feeding behaviour			
Generalist	9	3	8
Specialist	27	31	9
Strategies			
Scavenger	1	0	0
Cryptic	1	1	0
Run to cover	9	10	2
Stalking and pouncing	1	6	5
Cooperative hunting	1	0	4
Solitary hunting	0	4	0
Flight	16	13	2
Ecological role			
Predator	4	11	13
Prey	29	24	4

Table 4.7. Ecological and behavioural traits

Multivariate analyses

Several variables have been discarded because of data deficiency or to avoid high colinearity. Finally, 15 log-transformed variables have been selected for multivariate analyses.

First a Principal Component Analysis on 46 species (18 transverse, 20 rotary and 8 speed dependent galloper) has been performed. Four principal components were extracted explaining 85.5% of the total variance (Table 4.8). The first component, explaining 39.7% of the variance, was positively correlated to relative speed, in body-lengths per second and Froude number, and thinner limb bones, while it was inversely correlated to relative size, as mass per body length and radius of gyration of the body (Table 4.9). In the second component (26.9% of the variance), the ratio between the distal and the proximal sections of both fore and hind limb had the major weight, while the ratio between fore and hind limb length was negatively correlated. Third and fourth components account for minor percentage of the total variance. Third component in particular was positively connected to fore/hind limb length and to the aspect ratio, while the fourth component was related to relative speed and stride length. PCA score means of gallop categories were significantly different on the first two axes (ANOVA: PC1, $F_{2,43} = 6.75$, $P = 0.003$; PC2, $F_{2,43} = 4.86$, $P = 0.012$).

Component	**Extraction Sums of Squared Loadings**		
	Total	% of Variance	Cumulative %
1	5.962	39.748	39.748
2	4.038	26.917	66.665
3	1.734	11.559	78.224
4	1.097	7.315	85.539

Table 4.8. Principal components

	Component			
	1	2	3	4
Froude number	0.619	0.439	-0.075	0.605
Stride length	-0.418	0.540	0.328	0.507
Fore/hind ratio	-0.001	-0.398	0.842	0.038
Aspect ratio	0.189	0.186	0.609	-0.376
Mass/Body length	-0.853	-0.090	0.219	-0.145
Humerus l/c ratio	0.883	-0.218	0.148	-0.109
Radius l/c ratio	0.849	-0.113	0.366	0.030
Femur l/c ratio	0.827	-0.293	0.234	0.033
Tibia l/c ratio	0.840	0.374	-0.031	-0.287
Radius / Humerus length	-0.209	0.690	0.457	0.089
Metacarpus / Humerus length	-0.181	0.948	0.070	-0.053
Tibia / Femur length	0.255	0.835	-0.184	-0.350
Metatarsus / Femur length	-0.193	0.939	0.048	-0.170
Body radius of gyration	-0.907	-0.062	0.174	0.061
Relative speed (Bl/s)	0.866	0.332	-0.035	0.220

Table 4.9. Component matrix

Analysing the position of the three groups centroids (fig. 4.3), we observed, in the first PC, an increasing trend from transverse, located on the negative side of the axis, to rotary, not far from zero, to speed dependent, centred on the positive side. The differences between T and R were statistically significant (ANOVA contrast test: t_{43} = -2.23, P = 0.031), not the differences between R and S (ANOVA contrast test: t_{43} = -1.90, P = 0.064). The centroid position on the second PC indicated a different trend, from S and T, located not far each other on the negative side (ANOVA contrast test: t_{43} = 0.64, P = 0.536), to R, significantly separated on the positive side of the axis (ANOVA contrast test: t_{43} = 3.11, P = 0.003).

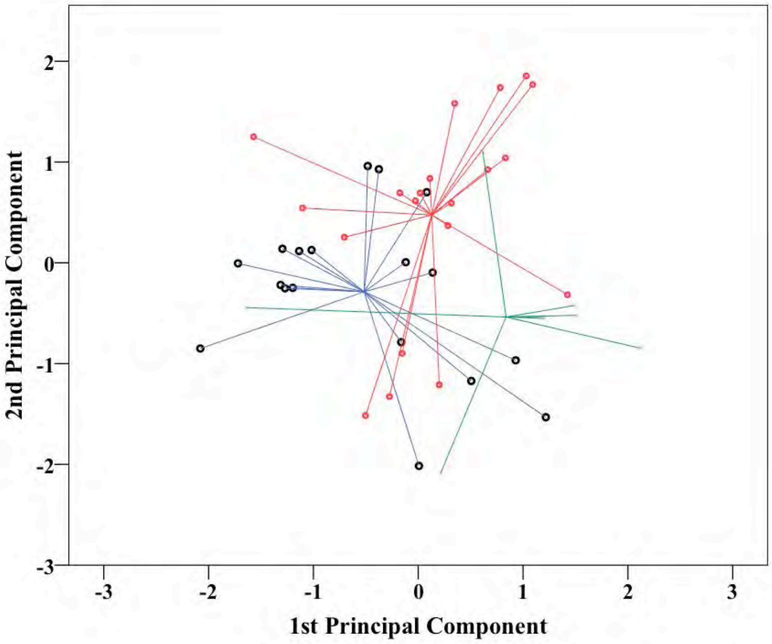


Fig. 4.3. Principal component analysis. Blue: Transverse; Red: Rotary; Green: Speed dependent

A further Discriminant analysis has been performed considering the four principal components. Two discriminant functions were calculated as a weighted combination of the four principal components. The first canonical discriminant function (CD1) combined with almost the same weight PC1, PC2 and PC4, all well correlated to speed. On the other hand, the second canonical discriminant function (CD2) resulted by a combination of PC2 on the axis negative side and PC1 on the positive side, with a maximum separation of the speed dependent group from the other two. The 63% of original grouped cases were correctly classified through the discriminant function (Wilk's lambda = 0.556, X^2_8 = 24.33, P = 0.002).

Gait analysis

152 rotary or transverse gallop strides of 15 species, from original (filmed by CMB) and commercial slow motion footages, were analysed. The average results are shown in table 4.10.

Species	Gallop	F lag (%)	H lag (%)	P lag (%)	Duty Factor	Phase shift F/H	Phase shift F/F	DF Ratio F/H	DF Ratio L/NL Fore	DF Ratio L/NL Hind
Roe deer	Rotary	15.3	-8.8	60.3	0.24	0.52	0.19	0.88	0.99	0.97
Tiger	Rotary	16.0	-13.3	73.3	0.32	0.41	0.16	1.38	1.12	1
Lion	Rotary	17.8	-8.7	59.5	0.18	0.54	0.18	0.83	1.08	0.98
Cheetah	Rotary	13	-15.3	68.8	0.16	0.45	0.12	0.82	0.85	1
Cat	Rotary	11.7	-7.7	72.8	0.32	0.38	0.16	1.01	0.95	0.94
Giraffe	Rotary	27.3	-13.6	81.8	0.34	0.39	0.27	1.03	1.14	0.93
Caribou	Rotary	15.0	-20.0	70.0	0.16	0.48	0.15	0.63	0.67	1
Dog	Rotary	8.2	-7.0	62.7	0.26	0.45	0.08	1.04	1.01	0.98
Dog	Transverse	22.7	18.5	70.0	0.31	0.32	0.23	1.14	1.05	0.89
Spotted hyaena	Transverse	24.1	22.2	64.8	0.33	0.36	0.24	0.89	1	1
Onager	Transverse	12.9	19.4	77.4	0.23	0.19	0.13	0.93	1.33	1.5
Horse	Transverse	28.3	15	85	0.35	0.22	0.28	1.04	0.85	0.91
Burchel zebra	Transverse	16.7	12.7	78.4	0.21	0.25	0.17	1.07	1.14	0.83
Bighorn sheep	Transverse	22.2	11.1	77.8	0.32	0.28	0.22	0.92	1.2	1
Markhor	Transverse	31.2	18.1	68.6	0.35	0.38	0.31	1.14	0.97	0.98
Gemsbock	Transverse	na	na	na	0.25	0.25	na	na	na	na

Table 4.10. Results of the gait analysis

Duty factor is known to be inverse proportional to cursoriality, the attitude of different animals to reach high maximum speed (Hildebrand, 1977). Both, fore and hind Duty factor values were significantly different between rotary and transverse strides (*t*-test: Fore *DF*, $t_{150} = -4.875$, $P < 0.001$; Hind *DF*, $t_{150} = -4.611$, $P < 0.001$). Moreover, in rotary galloper the duration of the fore contact was significantly lower than that of the hind (*t*-test: Fore/Hind *DF*, $t_{150} = -2.019$, $P = 0.045$, fig. 4.4).

The combination of hind ratio and midtime lag provided information about the number and the kind of suspension phase(s) (Hildebrand, 1977). If we plot hind ratio on abscissa against midtime lag on a square grid, the diagonal lines divide the graph into four triangular sections. As explained by Hildebrand (Hildebrand, 1977), the left section represents gaits with no suspension period, like in slow gallop (canter). In the lower section are gaits with one flight phase in extended suspension (legs extended forward and backward). The upper section of the graph shows gaits with one flight phase with the legs gathered under the body, like in horse gallop. Finally, on the right

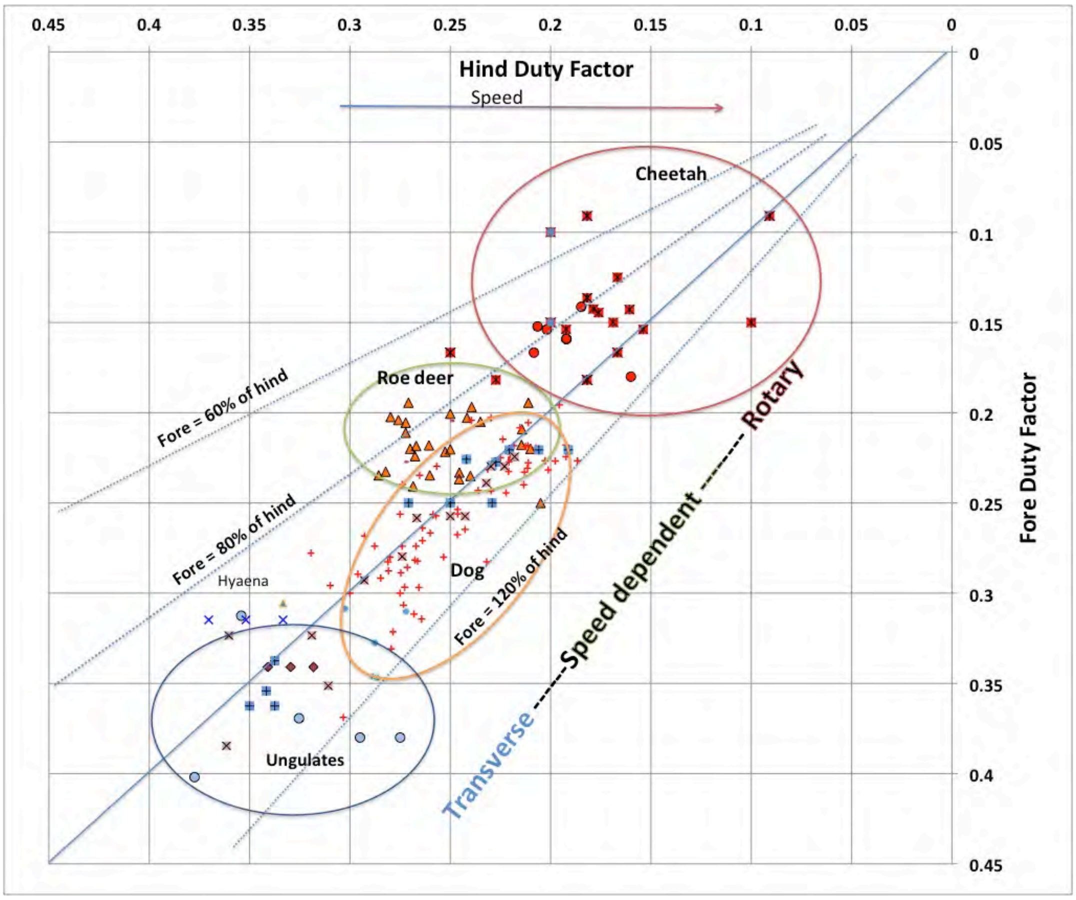


Fig. 4.4. . Hind versus Fore Duty Factor. Analysis of 152 strides of 15 species at different speed.

we can found the gaits with two suspended phases, one gathered and one extended. Plotting our data we can see how rotary gallop strides are generally associated to the right triangle (two flight phases) and transverse gallop strides to the upper triangle (*t*-test: *Mlag*, $t_{148} = 10.133$, $P < 0.001$; *Hr*, $t_{148} = -5.215$, $P < 0.001$; fig. 4.5).

Significant differences have been found also among the APS gait parameters (*t*-test: *Flag*, $t_{150} = -3.808$, $P < 0.001$; *Hlag*, $t_{150} = -32.794$, $P < 0.001$; *Plag*, $t_{150} = -2.034$, $P = 0.044$).

Maximum angular excursion

The hind limb maximum excursion angle has been calculated in 23 species, from high-speed transverse or rotary gallop sequences. In rotary strides the average angle was 91.1 ± 29.7 degrees, while in transverse it was 65.7 ± 7.7 degrees. The difference was statistically significant (t-test: $t_{15.6} = 3.05$, $P = 0.008$).

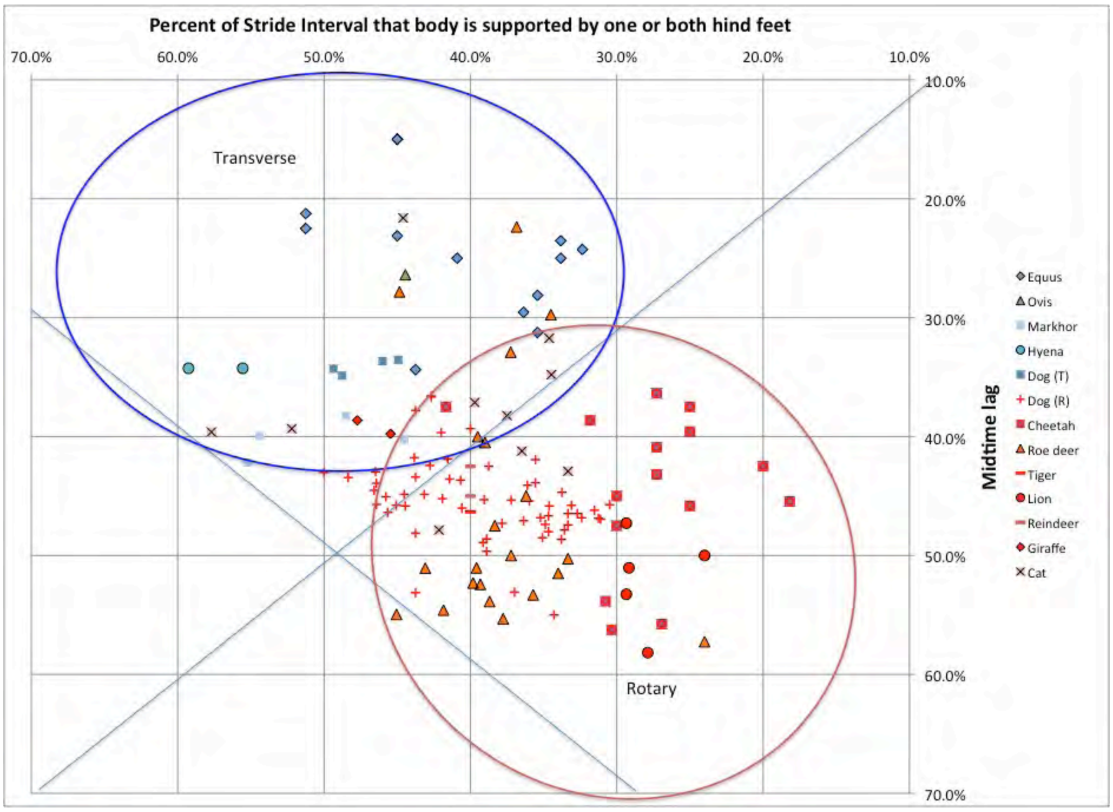


Fig. 4.5. . Hind feet ratio versus midtime lag. Analysis of 152 strides of 15 species at different speed.

The maximum angular excursion at the maximum speed is proportional to the square root of the relative speed, expressed by the Froude number (Angle (degrees) = 12.8 * $Fr^{0.5}$, $R^2 = 0.517$, $F_{1,20} = 21.370$, $P < 0.001$).

Spine

The spine stiffness indices, computed from the analysis of vertebral bodies of 21 species, and grouped per gallop type, were not significantly different (ANOVA: *St1*, $F_{2,17} = 1.000$, $P = 0.388$; *St2*, $F_{2,18} = 0.063$, $P = 0.939$). Post-hoc multiple comparisons gave the same results.

However, the Slijper diagrams showed a nearly common pattern related to cursoriality, where the moment of resistance is higher in the vertebral bodies of the lumbar section, connected to the pelvic girdle, than in the thoracic section, thus the forelimb generally supports great part of the body weight (Fig. 4.6).

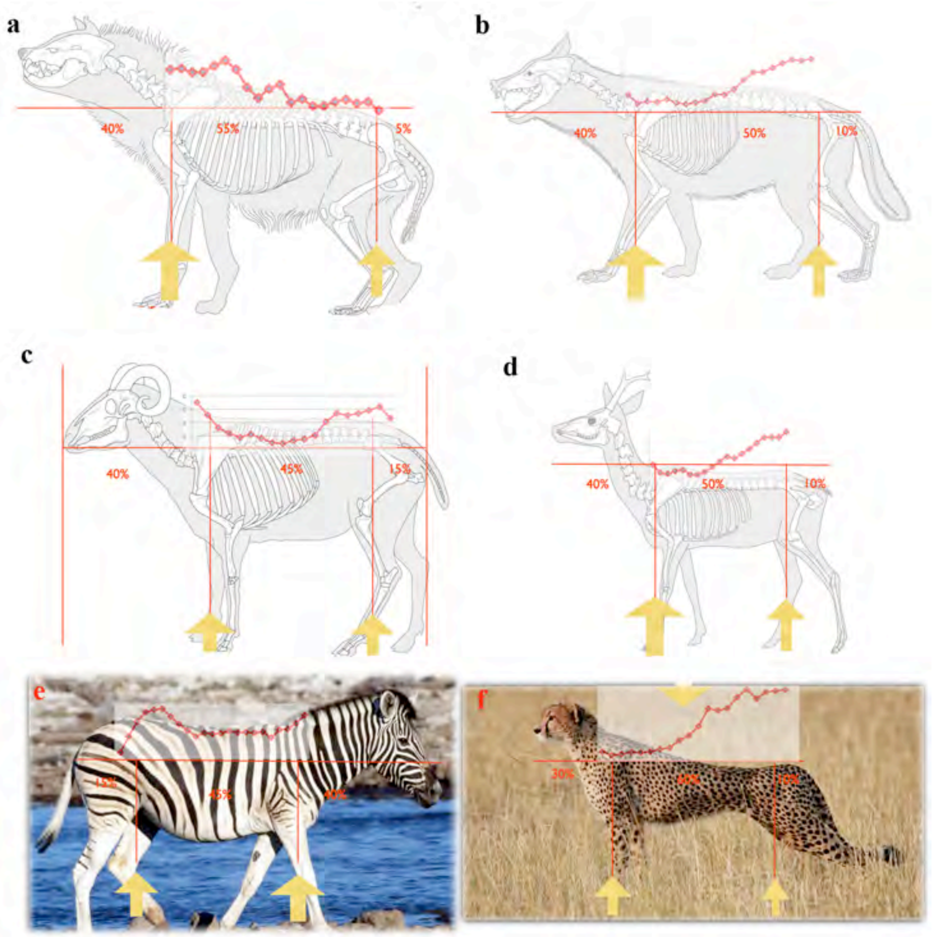


Fig. 4.6. Slijpeer spondilometric charts. a) Hyaena; b) Wolf; c) Bighorn sheep; d) Roe deer; e) Burchel zebra; f) Cheetah

4.4. Discussion

There are two well-recognized galloping gaits, the transverse and the rotary gallop, commonly referred respectively to the horse and to the cheetah. However, since today, a documented survey assessing which species use one or the other gait was not available (Bertram and Gutmann, 2009). The two galloping gaits have been described since the pioneering work of Muybridge, published for the first time at the end of the nineteenth century and successively reprinted many times (Muybridge, 1957).

Most of the studies on the gallop have been performed using the horse as model (Herr and McMahon, 2001; Hildebrand, 1965; Minetti et al., 1999; Parsons et al., 2008). The main reasons are because it is an animal relatively easy to train for experiments, it is a domesticated species commonly bred, and because there are many interests in studying horses performances (for horse-races). Therefore, mechanics and energetics of transverse gallop has been particularly well studied (Minetti et al., 1999).

On the other hand a few works have been produced specifically on rotary galloper species, and always compared to the transverse (Bertram and Gutmann, 2009; Hildebrand, 1959). Being difficult to employ a cheetah as experimental subject, greyhound dogs have been used instead (Bertram and Gutmann, 2009). Greyhounds have been chosen because they were considered a good model for the cheetah-like gallop, even if it was well known that many dogs were able to perform both transverse and rotary gallop (Walter and Carrier, 2007).

The first question addressed by our survey was if, within a species, there was a unique or prevalent kind of gallop. More than 80% of the analysed species used one kind of gallop at any speed, above the trot-gallop transition. The remaining 20% showed a preference for transverse canter or gallop at slow speed, and rotary gallop at higher travel speeds.

Evolution and phylogenesis of gallop

Gallop is usually associated to cursorial animals, which are commonly defined as "those terrestrial quadrupeds that possess vertically-oriented limbs which move in a parasagittal plane" (Stein and Casinos, 1997). However, both transverse and rotary gallop patterns can be displayed by species that have a sprawling limbs posture, like some crocodiles (Renous et al., 2002). Nevertheless, in these species there is neither a clear relationship between the type of gallop and the speed, like we have observed in mammals, nor differences in gait parameters other than the footfall pattern (Renous et al., 2002). Indeed, cursoriality and asymmetrical patterns of limb coordination seem to have appeared in different lineages of terrestrial vertebrates (Carrano, 1999; Renous et al., 2002; Stein and Casinos, 1997). The first mammals were small insectivorous animals that looked like the extant common treeshrews, and cursoriality in this group have arisen later, during the adaptive radiation of mammals, with the evolution of larger bodies and the realignment of the limbs (Stein and Casinos, 1997)

Looking to the phylogenetic tree of the 89 analysed species (Fig. 4.1), we can recognize clusters of species showing a common gallop pattern. Hyaenidae, one of the most primitive clades of carnivores, displayed a transverse pattern at any speed, as it was already annotated by Hildebrand (1977).

The evolution of Felidae, the “cats”, coupled with rotary gallop, performed by all the investigated species. The other carnivores are separated into the clade of Canidae, where all the analysed species displayed a speed dependent pattern, with the exception of the always-transverse galloper arctic fox. This could be due to the particular habitat type, the frozen territories of Arctic. Thus, the gait choice most likely depends on two main factors: the type of activity and the terrain structure (Goldenberg et al., 2008). In species that can use both gallop gaits, like many canids, rotary gallop is strongly associated to flat plain terrains where the animals can run faster (Goldenberg et al., 2008).

The Arctoidea clade, which comprehend the procyonids, mustelids and bears, presented a more heterogeneous scenario: the transverse pattern was performed by mustelids, with the exception of the wolverine, a rapid and fierce predator living in mixed habitat of the Nearctic, and by the arctic bear. The other bears displayed, like canids, a speed dependent pattern, but the relatively small sloth bear use a rotary pattern. It is noticeable, among pinnipeds, the transverse gallop pattern displayed by the steller sea lion.

All the Perissodactyla, horses and asses, and the primitive Artiodactyla, such as Suidae and Camelidae, employed transverse gallop. The locomotion of the extant Camelidae, llamas and camels, is unique among ungulate mammals in their regular use of the pacing gait. Their particular morphology of the foot is considered an adaptation to the locomotion on flat and soft terrains (Janis et al., 2002). Among the even-toed ungulate mammals, rotary pattern appeared in Giraffidae, a group of herbivores that evolved in mixed forestal environments of Palaeotropics, where speed and manoeuvrability were of particularly importance, with features close to that of the modern okapi (Spinage, 1968). The rotary gallop, observed in *Okapia johnstonii*, has been conserved also in *Giraffa camelopardalis*, the other living member of this family. Giraffes are the tallest of all extant land-living species. The extremely long neck, evolved to reach the canopies of savannah trees but constrained by the mammal anatomical limit of seven cervical vertebrae, makes challenging some movements, like bending down to drink, as well as physiological functions like the blood circulation. In spite of their disproportionate body shape, giraffes are able to reach the considerable speed of 56 kmh^{-1} (Mitchell and Skinner, 2003).

Rotary gallop at any speed is characteristics of Cervidae, the deers. These ungulates live in forests or mixed habitat and rely on sprints and run to cover to get rid of predators (Dimery et al., 1986; Putman, 1988). The rotary pattern has been more deeply analysed in roe deers, filmed in slow motion during free ranging in a natural restocking area. At trot-gallop transition the animals exhibited a rotary canter, which became a twice flights rotary gallop as the speed increased. The pronghorn (*Antilocapra americana*), the only extant species of Antilocapridae, a sister group of Cervidae, lives in North-American Great Plains. Pronghorns are the fastest terrestrial animals on long distances: they are able to maintain a speed around 70 kmh^{-1} for long time (Byers, 1998; Hildebrand and Hurley, 1985). Another group of slender and fast-running ungulates displaying rotary gallop are gazelles. Antilopes and gazelles rely on speed and manoeuvrability to escape the predators, cheetah above all (Alexander, 1977; Alexander, 2006; Alexander et al., 1977; Spinage, 1986). Among the analysed bovids and goats species, the majority presented a transverse gallop pattern. With the remarkable exception of the African buffalo and the aurochs, only those species with a slender and lighter body display a speed dependent or rotary pattern.

Biomechanical determinants of transverse and rotary gallop

Although the morphometrical and mechanical differences of the body structure between cursorial and non-cursorial animals have been well analysed and explained (Carrano, 1999; Hildebrand, 1974; Stein and Casinos, 1997), less effort has been put investigating the differentiation of forms, functions and gaits within cursorial species (Bertram and Gutmann, 2009; Hildebrand, 1962; Hildebrand, 1977; Hildebrand and Hurley, 1985).

Gambaryan (1974), Hildebrand (1977) and, more recently, Bertram and Gutmann (2009) indicated a different role of hind and forelimbs in the two galloping gaits. In rotary galloper the duration of fore contact was significantly lower than that of the hind feet, but from the chart (Fig. 4.4) a kind of continuous gradient from transverse to speed dependent to rotary species appear quite evident. The phase shift within a pair, fore or hind feet, depends on the leg touchdown angles, being the angle relatives to the vertical of the trailing leg smaller than the angle of the leading leg (Marhefka et al., 2003).

Our results indicated that slower and larger mammals, with relatively longer and thicker limbs, predominantly employed transverse gallop. On the other hand, lighter and faster mammals with relatively shorter legs and longer body more likely used rotary gallop. The rotary galloper had also relatively longer hind limbs with respect to the forelimbs, and relatively longer metacarpal and metatarsal bones, another feature related to the maximal running speed (Garland and Janis, 1993). The species that showed a transition from transverse to rotary gallop at high speed presented some features more similar to the transverse group, such as the aspect ratio and the relative length of metatarsal and metacarpal bones. However, they had thin and slender limb bones, relatively light body weights and high maximal relative speed. Lengthening the legs is one of the way to get longer strides, and therefore higher speeds (Hildebrand, 1974), but the limb segments do not uniformly lengthen. In cursorial species, the distal segments of a leg usually lengthen more than the proximal (Hildebrand, 1974), obtaining not only longer legs, but also longer moment arm of the distal segments.

During high speed strides, the species of both rotary and speed dependent groups employed a rotary pattern with significantly larger hind limb excursion angles than the transverse species, this is also related to speed (Biewener, 1983; Pike and Alexander, 2002). The hind limb excursion angle is known to scale with body mass according to the elastic similarity model (Herr et al., 2002; McMahon, 1975), therefore it is expected that smaller animals are capable of larger hind limb excursions. The capacity of exploiting larger maximum angular excursion is indeed one of the fundamental biomechanical determinants of rotary gallop.

The roles of body mass distribution and of spine bending will be discussed below, in separated paragraphs.

Centre of mass position

In almost all mammals the centre of mass is closer to the shoulder than to the hips, nearly at 2/3 the shoulder-hip distance, ahead of the hip (Waldron et al., 2009). Therefore, the forelimb supports the majority of the body weight, in a variable percentage. In dogs, for instance, the fraction of body weight supported by the front legs varied from 61% in static conditions (Jayes and Alexander, 1978) to 57% in dynamic conditions (Walter and Carrier, 2007). Using simple models, it has been demonstrated that, being the vertical component of the leg thrust in inverse proportion to the distance between its girdle and the body centre of mass, it is beneficial to a galloping system to have the centre of mass closer to the shoulder than to the hips (Waldron et al., 2009).

However, those results point to a major role of the rear legs in the forward thrust for both, transverse and rotary gallop, in contrast to the model proposed by Bertram and Gutmann, where in rotary gallop the role of the hind limbs would be the elevation of the centre of mass, while the forelimbs would provide the main forward thrust (Bertram and Gutmann, 2009). The simple mathematical model of Waldron and collaborators, even if substantially correct, is based on several assumptions that, as recognised by the authors themselves, are questionables: the assumpion that the principal moments of inertia are constant during the stride cycle and, even more important, the assumption that the body is rigid (Waldron et al., 2009). The latter assumption represent a particular point of weakness, as it has been widely underlined the role of spinal flexure in the sagittal plane to lengthen the flight phase and to store and release elastic energy, specially in fast runner animals (Minetti et al., 1999; Schilling and Hackert, 2006).

Spine bending

Although trunk motions in mammals are often less apparent than limb movements, they play a central role in locomotion (Schilling and Carrier, 2010). Sagittal spine movements are important during asymmetrical gaits, such as the two forms of gallop (Minetti et al., 1999; Schilling and Hackert, 2006), and particularly in small mammals and in larger cursorial species, where cyclic flexion and extension of the spine help to increase the stride length (Hildebrand, 1959; Schilling and Hackert, 2006). The mechanism discussed by Alexander et al. (1985) involved the recruitment of dorsal musculature in a kind of dorsal spring system. In this scenario, the kinetic energy produced by the limb swing is stored as elastic strain energy mainly in the stretched aponeurosis of the longissimus dorsii muscle. The subsequent recoil restores part of the energy during the extension of the spine, reaccelerating the limbs in the opposite direction. The energy recovery allowed by the recruitment of such a spring system would make, at certain speed, galloping more economical than trotting, because of the lower internal work (W_{INT}), promoting the transition from trot to gallop (Alexander, 1988).

The mammalian vertebral column consists of morphologically differentiated groups of vertebrae: cervical, thoracic, lumbar, sacral and caudal. The thoraco-lumbar (TL) segment, laying between the shoulder and the pelvic girdle, is involved in the back bending during locomotion (Grasse, 1972). While the lumbar stretch is composed by four to seven elements (usually 5-6), the thoracic segment is longer in Perissodactyla (18-19 vertebrae) than in Artiodactyla and Carnivora (13-15 vertebrae) (Narita and Kuratani, 2005). Lumbar spine of cursorial mammals is known to present particular adaptation to the specific biomechanical demands for locomotion, like the presence/absence and, when present, the shape of the zygapophyseal joints (Boszczyk et al., 2001).

The spine stiffness index used in our analyses did not discriminate between high-speed rotary galloper and cursorial transverse galloper. This was probably due to the role of support exerted by quadrupedal spine, which has similar demands in term of stiffness of the vertebral bodies (Stokes and Gardner-Morse, 2003), while most of the spinal mobility characteristics, like extension and flexion capacities and compliance, depend on intervertebral joints complex, intervertebral discs and interlocking processes (Gal, 1993a; Gal, 1993b).

Other determinant of the gallop type

During the evolutionary and phylogenetic part of the discussion it has been already underlined the role of some environmental, behavioural and ecological factors affecting the locomotor performances and the gait choice.

Indeed, living in forestal or mixed, open and closed, habitats benefits nimble animals, capable to dexterous manoeuvre to bypass obstacles. When they need violent sprints and sharp turns, rotary gallop is largely preferred. On the other hand, living in wide-open spaces, such as grasslands or deserts, for many reasons favours large size animals. Capability to reach high running speed is also a strong pushing stimulus, but this goal is accomplished by longer limbs to increase the stride length, being the angular excursion of the limbs constrained by size. Of course evolution provided many different solutions and answers to the environmental questions, and we can find in savannahs species that perform rotary, transverse or both gallop types. For example gazelles employ rotary gallop and maintained agile and quite light forms in open habitats. Here, the competition with the cheetah, in a classic prey-predator relationship, certainly plays an important role. Predators that rely on explosive accelerations and high speed on short distance, like the medium and big cats, employ rotary gallop.

However, when we have conflicting evolutionary pressures, different or intermediary solutions may arise. Several gregarious predators, like canids, and other fast herbivores, like the pronghorn and some antelopes, need high endurance, that is to maintain the running speed as long as possible. These species generally show a transition between a slow transverse gallop to a faster rotary one.

Quadruped gallop control

Quadrupedal locomotion is generated by an intraspinal network of neurons called central pattern generator (CPG), capable of producing the rhythms associated to different gaits (Collins and Richmond, 1994; Pinto and Golubitsky, 2006). The CPG network structure has only been inferred from observable gait features, as its real architecture in vivo has not been observed, yet (Buono, 2001; Buono and Golubitsky, 2001; Golubitsky et al., 1998; Golubitsky et al., 1999). According to a recent review (Ijspeert, 2008), in the vertebrate locomotor system the spinal CPGs are responsible for producing the basic rhythmic patterns, while the high-level motor cortex, cerebellum and basal ganglia centres are responsible for modulating these patterns according to environmental conditions.

The control of locomotion has been a great challenge in robotics, since the researches for development and production of legged robots emerged from the very first steps (Fukuoka et al., 2003; Tsujita et al., 2009). Several simulation models have been developed, based on mathematical models used for tuning different parameters (Herr and McMahon, 2000; Herr and McMahon, 2001; Krasny and Orin, 2004; Marhefka et al., 2003). Galloping robot have been recently developed, demonstrating that small changes in control parameters can give as results all the combination of biological gaits. In particular, bound can easily converted to half-bound and rotary or transverse gallop. The experiments with galloping robots demonstrated an emergent stability as a characteristic of gallop, thus constrained to the sagittal plane in transverse gallop. These researches also confirmed the simulation findings that the rotary gallop has a tendency to drive towards circular trajectories (Poulakakis et al., 2006; Smith and Poulakakis, 2004). From these results we can argue that CPGs of cursorial mammals could potentially produce all the running gaits, from bound, half-bound to rotary and transverse gallop. The specie-specific use of only part of the available gaits is probably the result of a combination of morphological and environmental features.

Change of lead

Rotary gallop is clockwise when the right forefoot leads and consequently, counter-clockwise when the left forefoot leads. In the same way, transverse gallop can be right or left, according to which is the leading foot. Further, while transverse galloping, the animal is slightly bent in the direction of the leading legs. The asymmetric characteristics of gallop include also the different stress experienced by the two limbs of a pair, particularly by the forelimbs, due to the different geometry and timing of their support phase (Walter and Carrier, 2007; Witte et al., 2004).

Even if the use of right or left transverse gallop and clockwise or counter-clockwise rotary gallop can be partially explained by individual preferences and lateralities (McGreevy and Thomson, 2006), a periodical change of lead during long runs may be necessary to equilibrate the stress on both sides of the body, and of the rib cage in particular (Bramble and Carrier, 1983). The lead change usually starts from the forelimbs, entailing one transition stride, which is transverse during a rotary lead change and, vice-versa, rotary during a transverse lead change.

The lead choice is also influenced by changes of direction. It is in fact known that, during galloping, turns are facilitated when the inside leg is leading (Hildebrand, 1959). Horse-keepers and trainers know that during races, horses always approach a right turn with right-lead gallop and vice-versa. From our observations on free ranging animals, we noticed that both, transverse and rotary galloper, follow the rule. Fast predators rapidly change the lead limb, according to sharply changes of direction, during a chase.

Conclusions

This broad analysis of transverse and rotary gallop among the three main orders of cursorial mammals allowed us to make the following conclusions:

i. The gait choice is not a simple question of speed, gradient and terrain structure, but depends also on body proportions, environmental characteristics and ecological behaviour of the species. A good example of how these parameters are interrelated is given by three groups of carnivores: Hyaenidae, Felidae and Canidae. Peculiar body proportions in Hyaenidae, with long neck and long forelimb, have been put in relation to the attitude of carrying large and heavy preys (Spoor, 1985). Their proportion of hindlimb segments are different from that of canids, which have shorter os femoris (higher tibia/ femur ratio), and their running gait is transverse gallop. Canids are gregarious predators that rely on speed and endurance. They use transverse and rotary gallop at different speed. Felids, on the other hand, are solitary ambushing predators that rely on acceleration and manoeuvrability. They have longer autopodia and large angular excursion of the limbs and, like canids, they make use of the dorsal spring system at high speed. They gallop using exclusively a rotary pattern.

ii. Although some cluster of species using the same galloping pattern are identifiable, this is more often related to morphological and ecological similarities among strictly related species than to a phylogenetic inheritance of the galloping gait. This is quite evident in sister species, like the red and the arctic fox, which employ different gallop types because of the different environmental conditions.

iii. The most important biomechanical determinants of gallop type are the body mass, the relative length of the limb segments, the aspect ratio - the proportion of body height and body length – and the angular excursion of the limbs.

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5. Conclusions

5.1. Final remarks

Quoting Robert McNeill Alexander: "*Evolution by natural selection favours those animals that are best adapted to their environment, whether in structure or in behaviour.*" (Alexander, 1996). There is a network of tight relationships among what animals would be able to do, what they actually do and which are their morphological, physiological, environmental and behavioural constraints. Optimization is a process of finding the best possible solutions, which minimize the costs and maximize the benefit. Evolution by natural selection is a process of optimization (Alexander, 1996).

Evolutionary convergences occur when similar solutions to the same problem independently evolved along distant phylogenetic groups. For instance, the problem of minimizes the costs of legged locomotion, which involve multilegged invertebrates as well as quadrupeds and bipeds. Finding similar solutions means sometimes the possibility to rearrange or reuse structures evolved for other purposes. This is the concept of exaptation (Gould and Vrba, 1982). A suitable example of exaptation is the development of locomotive limbs from structure, the fins, evolved to assist locomotion in water (Wagner and Chiu, 2001).

Locomotive legs of arthropods and vertebrates are analogous structures, but not homologous (i.e. the jointed three-segment legs of vertebrates and the jointed multi-segment leg of arthropods originated from phylogenetically different and far structures). There are indeed many convergent, though scaled, features and solutions to optimize the cost of walking and running in animals sharing similar equipments (jointed legs) and facing the same physical laws (sustain the body against gravity and move it on different terrains), but different in size and shape (Alexander, 2006; Biewener, 2003).

In my dissertation the focus was the research of further common, or different pattern of locomotion and on the aspects that determine the choice of a particular pattern.

A terrestrial spider has been a good model to complete a lacking scenario. We know that the inverted pendulum mechanism allows a walking animal to recover a variable amount of energy, which is exchanged between potential and kinetic. In bipeds the energy recovery can reach 65% (Humans: Cavagna et al., 1976), and in quadrupeds it can exceed 40% (Horses: Minetti et al., 1999), but in some hexapods is less than 10% (Cockroaches: Full and Tu, 1991). The energy recovery of spiders, exposed in chapter 3, resulted around 17%, and was the first measurement obtained for terrestrial octopods. The pendular exchange seems to work well with two oscillating limbs, but when the number of legs increases, and three or more of them are contemporary on the ground in a different stage of stance, the amount of energy recovery decreases. One may think some of the difference being due to the sprawling posture of invertebrates compared to the erect posture of horses and humans. However, the calculated energy recovery during walking in lizards, a sprawling-postured quadruped, was 51%, thus not far and comparable to the recovery percentages of horses (Farley and Ko, 1997).

The transition between walking and running gaits is less pronounced in arthropods (Biewener, 2003). Nevertheless, a clear transition between a slow and a fast gait has been detected, and statistically confirmed, in *Grammostola mollicoma*, our model for terrestrial spiders. Fast locomotion in spiders cannot be aerobically sustained, because of the inefficient system of oxygen delivery (Foelix, 1996), but fast gait are used by these spiders to stalk and catch their preys with sudden and rapid sprints (Barth and Biedermann-Thorson, 2001).

The asymmetry of octopod gaits has been demonstrated, and for the first time modelled and showed, by the analysis of the 3D trajectory of the centre of mass (Minetti et al., 2011). Furthermore, the calculation, from kinematics data, of the mechanical external and internal work at different speed are among the relevant results exposed in chapter 3.

In chapter 4 the focus moved to cursorial mammals, a perfect group for investigating the factors determining the choice between two patterns of an asymmetric fast gait: the transverse and the rotary gallop. The first question addressed was which species employ one or the other (or both) pattern. Then, the purpose was to obtain quantitative and not anecdotal evidences of a choice based on the assumptions explained at the beginning of this chapter.

A series of questions and hypothesis have been put on the table and analysed. For some of them had not been possible to collect enough data, for instance a measure of spine bending during locomotion, the average transversal distance between the forefeet and between the hind feet, and the distance between the humerus heads and between the femur heads (a measure of the width of the girdles). In the following chapter I will discuss the chances to fill these gaps.

The results achieved indicate that several factors, physiological, environmental, behavioural, drove the evolution of cursoriality. The necessity to reach higher and higher sprint speeds pushed for longer limbs to get longer strides, with the trade-off of the stride frequency. Another solution to get longer strides was to lengthen the distal segments of the limbs, increase the maximum angular excursion of humerus and femur, and increase the flexibility of the spine while maintaining the ratio body mass/ body length at low values. This second solution gave the advantage of high level of manoeuvrability, and determined the employment of rotary gallop at any speed.

Even if mammals and spiders can be considered far and different worlds, we can recognize common pattern of locomotion. The quadruped gaits have been modelled as the combination of two biped gaits with some difference in the phase-cycle (Minetti, 1998), in the same way, we described the octopods gaits as the combination of two quadruped gaits in series.

5.2. Perspectives

The questions raised during the researches herewith discussed opened new perspectives for in-depth examinations and further researches.

In which measure are the spine bending and the girdles width determinant of the gallop type?

More can be done to achieve quantitative data on the role of spine bending in gallop. The amount of bending can be measured putting markers on the back of an animal running on a treadmill and recorded by an opto-electronic system (Minetti et al., 1999). It is of course difficult, or quite impossible, to put at least one species for each representative clade of cursorial mammals on a treadmill. However, it may be possible to estimate the amount of bending from high quality video recording.

The distance between the femur heads is not particularly difficult to take, on museum specimens, because the pelvic girdle is welded to the lumbar vertebrae of the spine. More difficult is the assessment of the distance between the humerus heads. This measurement is never possible on disarticulated bones, and even if the skeleton is mounted, it can be in some case unreliable, due to inaccurate reconstructions.

Which are the dynamic and kinematic differences between transverse and rotary gallop?

Dogs are able to use both, transverse and rotary gallop. Therefore it should be possible to train some dogs to perform transverse and rotary gallop in the same range of speeds.

Using force plates and opto-electronic system, the two type of gallop could be compared taking kinematic and dynamic data.

A first preliminary experiment have been carried out, recording the ground reaction forces of two dogs, one performing rotary gallop and the other transverse and rotary, at their preferred speed. The outcome will be useful to build an appropriate experimental protocol.

Which is the best gait to use on small radius circles, at different speeds?

Does counter gallop on a circle cost more than usual inside-lead gallop?

As explained in chapter 4, when galloping on a circle, quadrupeds lead with their inside foot. This asymmetry could represent:

i) an advantage of gallop on trot when moving on circles, lowering the transition speed;
ii) a dis-advantage of leading with the outside transverse leg, in the so-called counter-gallop.

Horse is a good model because it can be easily trained to perform the desired gait, even unnatural ones. Moreover, counter-gallop is already used as training gait for dressage and polo.

The experimental design includes:

i) measurement of the hearth rate (HR), with Polar-equine equipment;
ii) measurement of the metabolic cost, with portable Cosmed K4 equipment and an equine-mask;
iii) a 10 m radius circular track;
iv) three different speeds, each to be performed at trot, gallop and counter-gallop

Some preliminary experiments have been carried out, with two subjects and only taking the HR parameter, with encouraging first results.

Is there a preferred number of stride before a lead change?

While on turns the leading foot is determined by the direction, on straight ways it makes no difference which foot is leading. The change of lead foot introduces a little discontinuity in the rhythm of gallop, which could be unfavourable, particularly in races. On the other hand, for reasons of differential stress and fatigue, during long straight ways it could be necessary to change gallop lead limb. But how many strides can be covered before to change lead?

One approach to this question is the analysis of horse races, where lead changes usually occur approaching a turn, but sometimes also during long straights.

This approach may have some drawbacks. For instance, in mounted horses the starting lead and the lead change can be driven by the rider. However, in the middle of a straight there would be no reason for a rider to call for a lead change. In those cases it should be a “decision” of the animal itself.

In conclusion, this work shed light on some aspects of octopedal and quadrupedal asymmetric gaits, opening to the raising of new questions and new perspective of research.

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"Decaffeinato, Carmé???"

Antonio e Francesco
"Perchè non ti fermi a mangiare qui da noi, abbiamo... Fra, cos'abbiamo?"
"Vino bianco e vodka!"

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