The Journal of Experimental Biology 215, 4144-4156

doi:10.1242/jeb.073031

# RESEARCH ARTICLE

# Biomechanical determinants of transverse and rotary gallop in cursorial mammals

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## SUMMARY

**Transverse and rotary gallop differ in the placement of the leading hindfeet and forefeet: ipsilateral in the former gait, contralateral in the latter. We analysed 351 filmed sequences to assess the gallop type of 89 investigated mammalian species belonging to Carnivora, Artiodactyla and Perissodactyla orders. Twenty-three biometrical, ecological and physiological parameters were collected for each species both from literature data and from animal specimens. 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 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 distal and proximal limb segments. Large size and longer proximal limb segments were associated with transverse gallop, while rotary and speed-dependent species showed higher metacarpus/humerus and metatarsus/femur length ratio and faster relative speeds. The resulting limb excursion angles were proportional to the square-root of the Froude number, and significantly higher in rotary gallopers. The gait pattern analysis indicated significant differences between transverse and rotary gallop in forelimb and hindlimb duty factor (*t*-test; $P<0.001$), and in duration of the forelimb contact (*t*-test; $P=0.045$). Our results show that an exclusive gallop gait is adopted by a large number of mammalian species, and indicate that the gallop pattern depends on diverse environmental, morphometrical and biomechanical characters.**

Key words: transverse gallop, rotary gallop, cursorial mammals, biomechanics, gait.

Received 13 April 2012; Accepted 15 August 2012

## INTRODUCTION

Quadrupedal mammals move using sharply distinct speed-dependent gaits (Alexander, 1989). Gaits are commonly identified by their footfall patterns (Muybridge, 1957). Symmetrical gaits, such as trot, are characterised by the alternating footfalls of the two feet of the same pair (forefeet or hindfeet) being evenly spaced in time. In asymmetrical gaits, such as the two forms of gallop, this is not the case for at least one of the two pairs of feet (Hildebrand, 1965; Hildebrand, 1977). 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 hindfoot' (Hildebrand, 1966; Hildebrand, 1977). Limb phase is particularly important to distinguish lateral gait sequences (limb phase <50%) from diagonal gait sequences (limb phase >50%) (Renous et al., 2004). A new approach to gait analysis, still based on quantitative analysis of gait variables, has recently been provided by Abourachid, who introduced the concept of antero-posterior sequence (Abourachid, 2003).

There are two distinct forms of gallop, known as transverse and rotary. In transverse gallop the two hindfeet are placed in sequence. The placement of the second hindfoot is followed by that of the contralateral forefoot and then by the remaining forefoot. The right–left or right–left sequence is the same in forelimbs and hindlimbs 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 may then be a second suspended phase, known as the 'extended flight phase' (often found in paintings from the 15th to 18th century), after the lifting of the hindfeet and before the placement of the first forefoot. In rotary gallop, the placement of the second hindfoot 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 (Fig. 1).

Gallop has been widely considered to be one gait (e.g. Alexander, 2006). However, transverse and rotary gallop can be distinguished by some of the variables commonly used to separate different gaits (Abourachid, 2003; Hildebrand, 1959; Hildebrand, 1977; Renous et al., 2004). Galloping gaits have been modelled by Minetti as a combination of two bipedal skipping gaits (Minetti, 1998). The resulting transverse or rotary gallop depends on whether the two bipeds employ the same unilateral or opposite (counter-lateral) skipping gaits (Minetti, 1998).

Although gallop is well understood in terms of footfall pattern and gait quantities, it is still argued whether a quadrupedal animal species

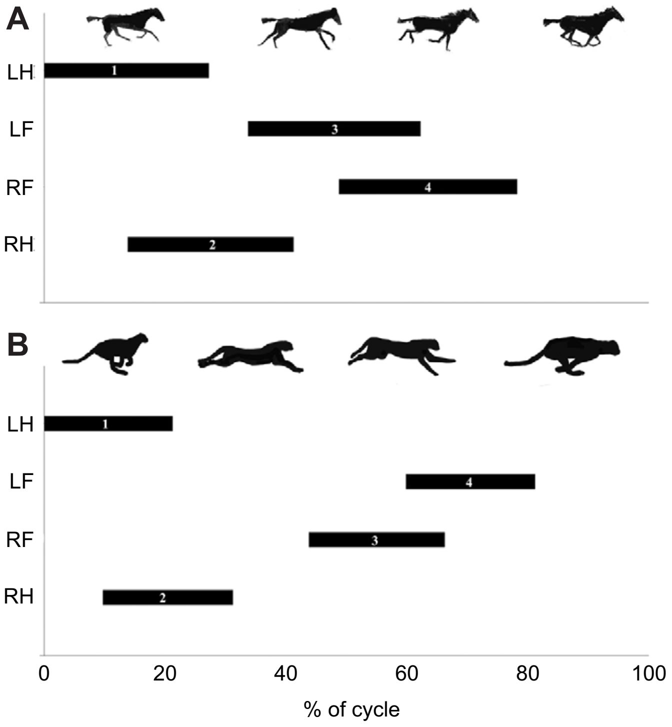

Fig. 1. Gait diagrams of transverse (A) and rotary (B) gallop. LH, eft hindfoot; LF, left forefoot; RF, right forefoot; RH, right hindfoot. The pictures above the diagrams explain the corresponding stride phase.

can perform transverse or rotary gallop equally well, which species only show one of the two patterns, and whether there are constraints on/biomechanical determinants 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 clearly been associated with cheetahs and racing dogs (Hildebrand, 1977). Some dogs are known to use rotary gallop at high speed and transverse gallop at lower speed (Walter and Carrier, 2007).

Contrary to the static ‘bridge’ model described by Thompson (Thompson, 1917), the mammalian spine is known to be actively involved in locomotion. The mechanism suggested consists of a spring system where part of the kinetic energy associated with limb swing is stored as elastic strain energy in the stretched aponeurosis of the longissimus dorsii muscle. The subsequent spinal extension restores part of the energy to reaccelerate the limbs in the opposite direction (Alexander, 1988; Alexander et al., 1985). The recruitment of this elastic spinal mechanism makes galloping the most economical gait at higher speeds (Alexander, 1988).

Based on the above, we made the following initial hypotheses about the determinants of transverse or rotary gallop. (1) Species specificity: by analysing different filmed sequences of gallop for as many species as possible, it should be possible to reliably assess whether they employ only one galloping gait or both. (2) Speed dependency: assessed by collecting, for each investigated species, the maximum speed and average limb and body length, and obtaining the Froude number and the relative speed in body lengths per second. (3) Limb length and limb segment ratio: obtained by collecting average limb segment length and circumference. (4) Spine bending characteristics: determined by collecting morphometric measurements of thoraco-lumbar vertebrae and calculating the ‘moment of resistance’ (see Materials and methods). (5) Gait characteristics: obtained by analysing duty factor and phase shifts from filmed sequences. (6) Behaviour and environment: collecting categorical parameters such as habitat type, sociality, feeding behaviour and activity pattern.

Further hypotheses, such as the role of intervertebral discs, the different relative width of the girdles and the relative leg masses could not be investigated because of a lack of data. Nonetheless, the present results should help to infer the gait types in extinct quadrupeds.

## MATERIALS AND METHODS

### Movies

A total of 1650 films and videoclips of free-ranging mammals, from different origins, were analysed in order to assess the spontaneous chosen gallop type. The analysed footage included commercial documentary films, clips from on-line resources (YouTube, Arkive, BBC Motion Gallery), movies from private collections (see Acknowledgements) and original footage recorded by one of the authors (C.M.B.). Galloping animals were filmed by means of a high-speed camera (Casio Exlim EX-FH20, Casio Europe GmbH, Norderstedt, Germany) at 210 frames $s^{-1}$.

A first classification of transverse and rotary galloper species, made by R. McNeill Alexander (personal communication), was used as a starting point. The list was integrated with data from the literature (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, if possible on the level or on a mild gradient; (ii) a stepping pattern clearly detectable in a consistent number of strides.

After a preliminary screening, 351 clips were selected and the stride sequences assigned to one of the three defined categories: transverse, rotary and speed-dependent gallop. The number of filmed sequences used to assign a species to each category ranged from 1 to 17 (mean 3.9). However, one sequence could include more than one individual (e.g. bisons, gazelles) over several strides. The final criteria used to assign a species to each category were as follows. (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 after several observations (e.g. transverse in wildebeests and rotary in buffalos). (iv) Pattern observed a few times but confirmed by observation of very similar species (e.g. mule deer compared with white-tailed deer; dama gazelle compared with Grant’s gazelle). (v) Pattern observed a few times but confirmed by literature data (e.g. chinese water deer, striped hyaena).

### Gait and limb angle analysis

In gallop, as in other asymmetrical gaits, the footfalls of a pair of feet are unevenly spaced in time: the first foot of a couplet, forefoot or hindfoot, 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 trailing hindfoot as the starting point of the stride cycle (Alexander, 2006; Hildebrand, 1977). Recently, a new method based on the 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, hindfeet lag and pair lag.

The gait parameters were collected by counting the frames of the best filmed motion sequences, according to Biewener (Biewener, 1983). The maximum angular excursion of a line drawn from the head of the femur (hip joint) to the toe of the foot was measured by tracing frames from available movies of animals running at high speed. This parameter has been proved to scale in inverse proportion to body mass, according to the elastic similarity hypothesis (McMahon, 1975). In our hypothesis it should also be positively correlated to actual and relative speed.

### Classification of the species

A phylogenetic tree of the classified species was built following previous studies (Carroll, 1987; Wyss and Flynn, 1993; McKenna and Bell, 1997; Froehlich, 1999; Hu et al., 2010). Species were named as previously (Wilson and Reeder, 2005).

### Data collection

Maximal running speed was taken from data in two comprehensive reviews (Garland, 1983; Christiansen, 2002a), based on other literature sources. Averaged body mass, body length, forelimb and hindlimb measurements, averaged limb length and height at the shoulder, as well as other behavioural and ecological data, were taken from previous studies (Egorov, 1965; Spinage, 1968; Groves, 1974; Spinage, 1986; Putman, 1988; Churcher, 1993; Bennett and Hoffmann, 1999; Nowak, 1999; Mitchell and Skinner, 2003).

Bones mass data (Christiansen, 2002b) and bone and spine measurements (Biella, 1998; Christiansen, 1999a; Christiansen, 1999b; Gargantini, 1997; Wroe et al., 2008) were similarly obtained. Further measurements were taken by one of the authors (C.M.B.) on specimens housed in the Natural History Museum of Florence and Milan. A digital calliper was used for lengths up to 220 mm, and an analogic calliper for greater lengths.

Vertebral body width ($w_b$) and vertebral body height ($h_b$) were measured for each single vertebra. During locomotion in 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, thoracic and lumbar) as well as among different species. A value of the 'moment of resistance' of any single vertebra ($S$) was calculated after Slijper (Slijper, 1946):

$$S = w_b h_b \ , \tag{1}$$

derived from structural mechanics and similar to the first moment of area of rectangular section logs (Zotti et al., 2011). Spine stiffness indices ($k_1$, $k_2$) were calculated as follows:

$$k_1 = \frac{S_{\max}}{S_{\min}} \ , \tag{2}$$

$$k_2 = \frac{S_{\mathrm{TL,max}}}{l_{\mathrm{TL}}} \ , \tag{3}$$

where $S_{\max}$ and $S_{\min}$ are the maximum and the minimum values of $S$, respectively, $S_{\mathrm{TL,max}}$ is the maximum value of the thoracic–lumbar region and $l_{\mathrm{TL}}$ is the length of the thoracic–lumbar region.

The dimensionless Froude number:

$$Fr = v^2 / \boldsymbol{g} l_{\mathrm{limb}} \ , \tag{4}$$

where $v$ is speed, $\boldsymbol{g}$ is gravitational acceleration and $l_{\mathrm{limb}}$ is limb length, was calculated from the maximum running speed and average limb length. Dynamic similarity between two different-sized animals is possible when their speeds are such that they 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). Moment of inertia and radius of gyration of the body and of the long bones have been also calculated.

The following ecological and behavioural traits of the species were collected from the literature: habits, habitat coverage, habitat type, social behaviour, feeding behaviour, strategies and ecological role (Nowak, 1999).

### Comparative and statistical analyses

Data and phylogeny were used to perform species-level analysis and phylogenetically independent contrasts (Felsenstein, 1985; Garland et al., 2005). Categorical data were analysed using a non-parametric $\chi^2$ test with Monte-Carlo simulation.

ANOVA was performed under a general linear model (GLM). Contrasts were preferred to *post hoc* multiple comparison (e.g. with Bonferroni correction) because they allow pooling and assigning of specific weight to any group. Pearson's correlation among continuous variables was carried out.

After a selection to avoid high co-linearity and data deficiency, a principal component analysis (PCA) was performed, considering 15 log-transformed measures on 46 species (18 transverse, 20 rotary and 8 speed-dependent gallopers). The results of traditional and comparative analyses are compared and discussed below.

Statistical analyses were performed using the following softwares: SPSS, ver. 19.0 (IBM Inc.); Mesquite, ver. 2.74.550 (Maddison and Maddison, 2010) with extra package PDAP, ver. 1.15 (Midford et al., 2010); LabView, ver. 2009 (National Instruments Inc.).

## RESULTS

A total of 89 species belonging to three mammal orders were analysed and classified in three groups (Table 1): (i) rotary (R): 35 species performing rotary gallop at any speed; (ii) transverse (T): 37 species performing transverse gallop at any speed; and (iii) speed dependent (S): 17 species performing rotary gallop at high speed and transverse gallop at lower speed. The phylogenetic relationships among these species are shown in the cladogram (Fig. 2).

A wide range of data was collected (see Materials and methods), and ratios between morphometric measurements were computed to reduce the size effect. Both measurements and ratios were log transformed in order to improve normality and allow comparisons among different variables.

### ANOVA

Significant differences between the gallop categories were found for almost all the investigated variables (Table 2). The estimated Froude number at maximum speed was significantly higher in rotary and speed-dependent gallopers. The cheetah, a rotary galloper, records both the highest absolute ($29.2\,\mathrm{m\,s^{-1}}$) and relative speed ($Fr$=149.6), while the highest speed in body lengths per second ($l\,\mathrm{s}^{-1}$) belongs to the goitered gazelle ($26.3\,l\,\mathrm{s}^{-1}$) (Fig. 3A,B). The aspect ratio (height/body length), an index of the general shape of a vertebrate, was significantly lower in rotary than in transverse gallopers, while speed-dependent species data were more variable (Fig. 3C). Body mass index (BMI) was significantly lower in rotary and speed-dependent species (Fig. 3D). In contrast, lower values of the limb bones index of aspect ratio (bone length/bone circumference) were observed in transverse species (Fig. 3E–H). The ratios between the distal and proximal limb segments (metacarpus/humerus and metatarsus/femur) reached the highest values in rotary gallopers and the lowest values in speed-dependent gallopers, while transverse gallopers were in between the two (Fig. 3I,J). To summarise, transverse galloper species resulted

Table 1. List and classification of the analysed species

| 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 |
| | *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 |
| | *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 |
| Carnivora (cont.) | *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 |

Gallop type is listed as rotary (R), speed dependent (S) or transverse (T).

significantly slower and heavier than rotary and speed-dependent ones, and had proportionally thicker bones.

### Non-parametric tests

Non-parametric $\chi^2$ tests, using 10,000 sampled tables with Monte Carlo simulation, were performed to test for differences in the frequency of occurrence of the categorical variables and the gallop types (Tables 3, 4). Transverse gallop was significantly more frequent in diurnal gregarious species that live in open habitat (grassland and plains). Species performing rotary or speed-dependent gallop were more likely to be those in mixed habitats and with crepuscular behaviour. Rotary gallopers were significantly more frequent among solitary predator species.

### Multivariate and comparative analyses

Four principal components were extracted by PCA, explaining 84.3% of the total variance (Table 5). The first component, explaining 37.2% 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, BMI and radius of gyration of the body (Table 6). For the second component (27.0% of the variance), the ratio between the most distal and the most proximal segments of both the forelimb and hindlimb had the major weight, while the ratio between forelimb and hindlimb length was negatively correlated. The third and fourth components account for a minor percentage of the total variance (Tables 5, 6). PCA score means of gallop categories were significantly different on the first two axes (ANOVA: PC1, $F_{2,43}$=7.45, *P*=0.002; PC2, $F_{2,43}$=5.11, *P*=0.010).

Analysing the position of the centroid for each of the three groups (Fig. 4), we observed, in the first PC, an increasing trend from transverse, located on the negative side of the axis (larger relative size), to rotary, not far from zero, to speed dependent, centred on the positive side (larger relative speed and thinner limbs). The differences between transverse and rotary were statistically significant (ANOVA contrast test: $t_{43}$=–2.43, *P*=0.019), but not the differences between rotary and speed dependent (ANOVA contrast

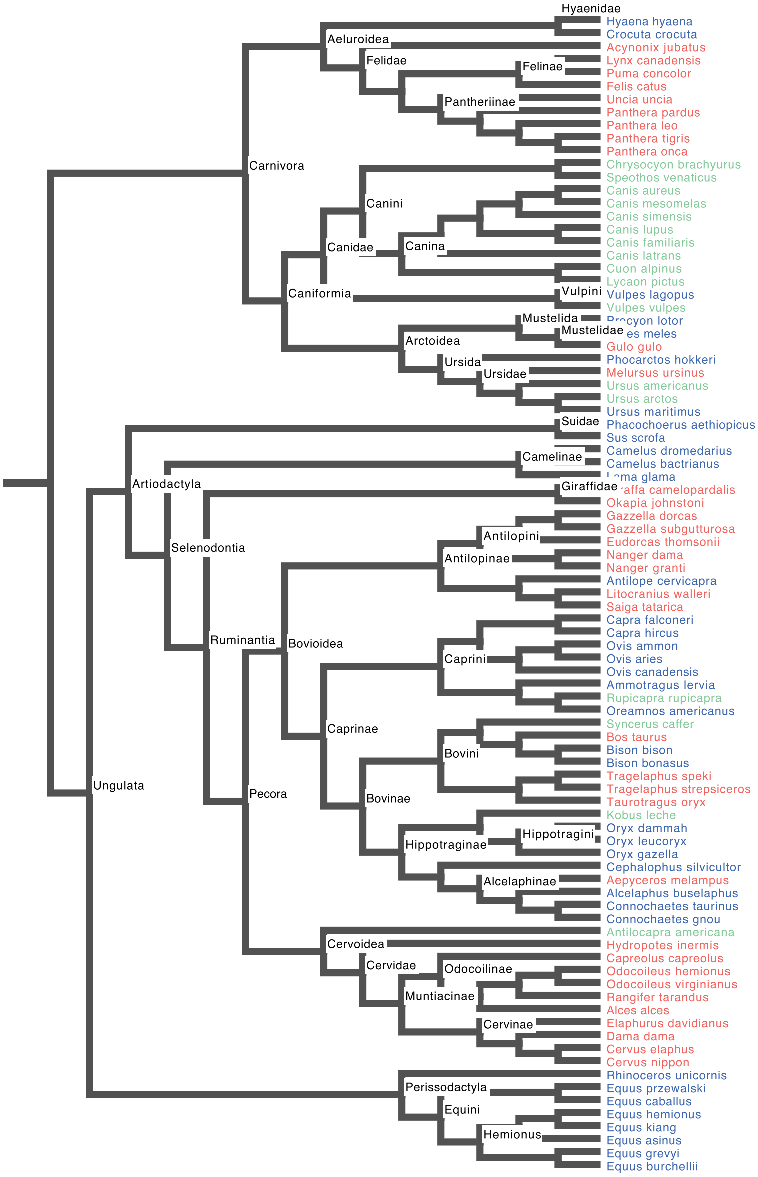

Fig. 2. Phylogenetic tree. Blue, transverse species; red, rotary species; green, speed-dependent species.

test: $t_{43}$=–1.89, $P$=0.065). The centroid position for the second PC indicated a different trend, with speed dependent and transverse located not far from each other on the negative side, indicative of relatively long forelimbs (ANOVA contrast test: $t_{43}$=0.64, $P$=0.524), and the rotary group, with relatively long feet, significantly separated on the positive side of the axis (ANOVA contrast test: $t_{43}$=–3.19, $P$=0.003). A further discriminant analysis was performed considering the four principal components; 61% of original grouped cases were correctly classified through the discriminant function (Wilk's lambda=0.498, $\chi^2_8$=28.91, $P$<0.001).

Analysis of the independent contrasts (IC) showed a phylogenetic signal affecting the morphometric measurements of the limb segments. However, a PCA performed on IC gave the same composition for PC1, maintaining statistically significant differences (ANOVA: PC1, $F_{2,42}$=3.72, $P$=0.033). The Pearson's correlations were statistically significant comparing both the speed-related variables (*Fr* and body lengths per second) with some morphometric measurements [positive correlation: humerus ratio, radius ratio, femur ratio and tibia ratio (ratio of length to circumference), tibia/femur length], and to relative size indices (negative correlation: BMI, radius of gyration), also taking into account phylogeny.

### Gait analysis

We analysed 152 strides (121 rotary and 31 transverse) of 15 species, from original (filmed by C.M.B.) and commercial slow motion footage. The average results are shown in Table 7.

Duty factor is known to be inversely proportional to cursoriality, the ability of different animals to reach high maximum speed (Hildebrand, 1977). Both forelimb and hindlimb duty factor values were significantly different between rotary and transverse strides. Moreover, in rotary gallopers the duration of the forefoot contact was significantly lower than that of the hindfoot (Table 7, Fig. 5).

The combination of hindfoot ratio and midtime lag provided information about the number and type of suspension phase(s) (Hildebrand, 1977). If we plot hindlimb ratio on the 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 western section represents gaits with no suspension period, like in slow gallop (canter). The southern section includes gaits with one flight phase in extended suspension (legs extended forward and backward). The northern section of the graph shows gaits with one flight phase with the legs gathered under the body, like in horse gallop. Finally, in the eastern section we found

Table 2. Results of ANOVA with contrasts

| Description | Gallop | | | ANOVA *P* | Contrasts | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Transverse | Speed dependent | Rotary | | T *vs* RS | R *vs* TS | S *vs* TR | T *vs* R | T *vs* S | R *vs* S |
| Froude no. | 38.20±20.96 | 54.52±21.73 | 56.89±30.75 | 0.003 | <0.001 | 0.089 | 0.147 | 0.002 | 0.009 | 0.987 |
| Stride length (m) | 3.46±1.15 | 2.87±0.81 | 3.94±1.03 | 0.009 | 0.921 | 0.003 | 0.015 | 0.051 | 0.147 | 0.003 |
| Forelimb/hindlimb ratio | 0.87±0.07 | 0.86±0.06 | 0.83±0.06 | 0.049 | 0.126 | 0.021 | 0.489 | 0.019 | 0.706 | 0.106 |
| Limb/body ratio | 0.40±0.05 | 0.45±0.06 | 0.43±0.09 | 0.042 | 0.004 | 0.985 | 0.018 | 0.147 | 0.002 | 0.193 |
| Aspect ratio | 0.60±0.08 | 0.66±0.17 | 0.57±0.12 | 0.044 | 0.650 | 0.024 | 0.025 | 0.250 | 0.108 | 0.013 |
| BMI | 46.1±25.3 | 29.5±17.3 | 29.4±16.4 | 0.002 | 0.001 | 0.083 | 0.153 | 0.001 | 0.010 | 0.997 |
| Humerus ratio | 2.75±0.59 | 3.64±0.81 | 3.06±0.45 | <0.001 | <0.001 | 0.639 | <0.001 | 0.014 | <0.001 | 0.012 |
| Radius ratio | 3.55±0.83 | 4.63±1.25 | 4.00±0.71 | 0.002 | <0.001 | 0.968 | 0.006 | 0.022 | <0.001 | 0.090 |
| Femur ratio | 3.31±0.56 | 4.19±0.76 | 3.68±0.37 | <0.001 | <0.001 | 0.963 | 0.008 | 0.003 | 0.001 | 0.058 |
| Tibia ratio | 3.74±0.85 | 4.78±0.93 | 4.25±0.72 | 0.001 | <0.001 | 0.837 | 0.006 | 0.012 | <0.001 | 0.107 |
| Radius/humerus ratio | 1.06±0.16 | 0.98±0.07 | 1.06±0.16 | 0.203 | 0.284 | 0.228 | 0.009 | 0.952 | 0.037 | 0.027 |
| Metacarpus/humerus ratio | 0.71±0.29 | 0.48±0.24 | 0.92±0.35 | <0.001 | 0.747 | <0.001 | <0.001 | 0.035 | 0.023 | <0.001 |
| Tibia/femur ratio | 1.00±0.14 | 1.04±0.12 | 1.06±0.16 | 0.219 | 0.146 | 0.188 | 0.902 | 0.083 | 0.416 | 0.554 |
| Metatarsus/femur ratio | 0.63±0.22 | 0.48±0.21 | 0.83±0.31 | 0.002 | 0.804 | <0.001 | 0.005 | 0.018 | 0.100 | <0.001 |
| Radius of gyration (m) | 0.56±0.23 | 0.33±0.15 | 0.50±0.23 | 0.003 | 0.003 | 0.263 | 0.001 | 0.227 | <0.001 | 0.010 |
| Relative speed ($s^{-1}$) | 9.10±3.85 | 15.38±5.18 | 12.24±5.72 | <0.001 | <0.001 | 0.960 | 0.002 | 0.019 | <0.001 | 0.052 |

R, rotary; S, speed dependent; T, transverse. For full definitions, see Glossary.

the gaits with two suspended phases, one gathered and one extended. Plotting our data, we can see how rotary gallop strides are generally associated with the eastern triangle (two flight phases) and transverse gallop strides with the northern one (Table 7, Fig. 6).

Significant differences were also found in other gait parameters (Table 7). In rotary gallop, the contact time of the trailing hindfoot was significantly longer than that of the leading foot (paired *t*-test: $t_{103}$=4.348, *P*<0.001). In contrast, for forefeet, leading foot contact was longer than trailing foot contact (paired *t*-test: $t_{103}$=–2.166, *P*=0.033). In transverse gallop, no significant differences occurred.

### Maximum limb excursion angles

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

The maximum limb excursion angles were positively correlated to the relative speed, expressed by the Froude number (angle$\propto Fr^{0.46}$, $R^2$=0.517, $F_{1,20}$=21.370, *P*<0.001), and negatively to the body mass (angle$\propto m_b^{-0.19}$, $R^2$=0.324, $F_{1,21}$=11.539, *P*=0.003).

### 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: $k_1$, $F_{2,17}$=1.000, *P*=0.388; $k_2$, $F_{2,18}$=0.063, *P*=0.939). *Post hoc* multiple comparisons gave the same results.

## DISCUSSION

Gallop is usually associated with 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 limb posture, like some crocodiles (Renous et al., 2002) and seals (A.E.M., personal observation). Nevertheless, in these species there is neither a clear relationship between the type of gallop and the speed, like we have observed in cursorial mammals, nor a difference 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 two galloping gaits, transverse and rotary, have been described since the pioneering work of Muybridge (Muybridge, 1957). However, until now, a documented survey assessing which species use which gait was not available (Bertram and Gutmann, 2009). We assessed that more than 80% of the analysed species used only 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.

### 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 into investigating the differentiation of forms, functions and gaits within cursorial species (Bertram and Gutmann, 2009; Hildebrand, 1962; Hildebrand, 1977; Hildebrand and Hurley, 1985).

Gambaryan (Gambaryan, 1974), Hildebrand (Hildebrand, 1977) and, more recently, Bertram and Gutmann (Bertram and Gutmann, 2009) have indicated a different role of hindlimbs and forelimbs in the two galloping gaits. In rotary gallopers the duration of forefoot contact was significantly lower than that of the hindfeet, but from Fig. 5, a kind of continuous gradient from transverse to speed-dependent to rotary species is quite evident. The phase shift within a pair of forefeet or hindfeet depends on the leg touchdown angle, the angle relative to the vertical of the trailing leg, smaller than the angle of the leading leg (Marhefka et al., 2003).

Our results indicate that slower and larger mammals, with relatively longer and thicker limbs, predominantly employ transverse gallop. In contrast, lighter and faster mammals, which have relatively shorter legs and longer body, were more likely to use rotary gallop. The rotary galloper had also relatively longer hindlimbs 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

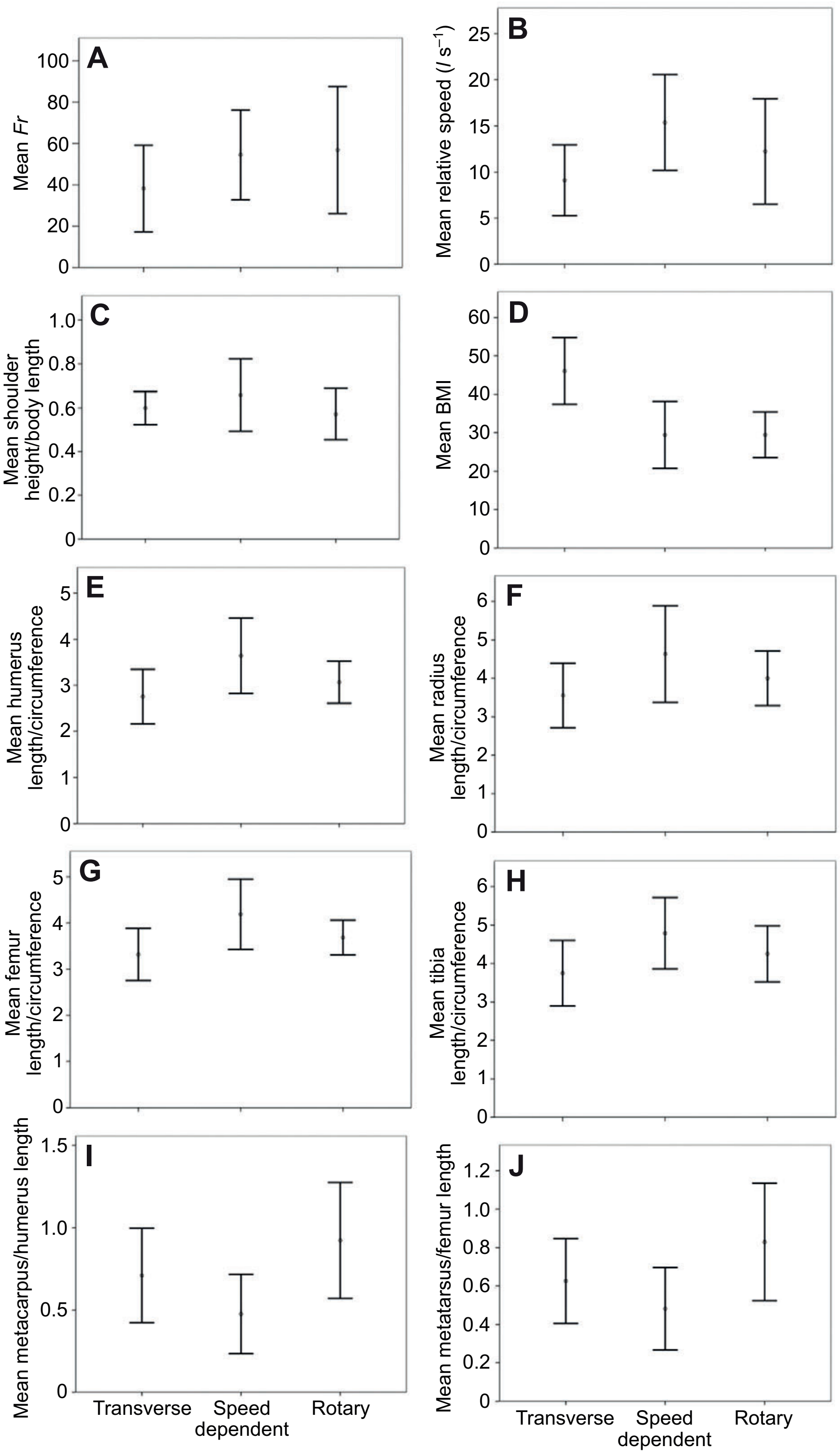

Fig. 3. ANOVA. Data are means ± s.d. BMI, body mass index.

ratio and the relative length of the metatarsal and metacarpal bones. However, they had thin and slender limb bones, relatively light body masses and high maximal relative speed.

Looking to the phylogenetic tree of the 89 analysed species (Fig. 2), we can recognise clusters of species showing a common gallop pattern. There is indeed a phylogenetic component in some of the typical characteristics of the three groups. Part of the correlation among the limb segment ratios and the gallop type, as stressed by the comparative analysis, was due to the relatedness of many species. For instance, all the Perissodactyla employed transverse gallop, all the Felidae used rotary gallop and most of the Canidae showed speed-dependent gallop. However, even taking this bias into account, the framework is still consistent.

There are at least two other factors affecting the gait choice: the type of activity and the terrain structure (Goldenberg et al., 2008). For instance, the locomotion of the extant Camelidae, llamas and

Table 3. Results of non-parametric tests

| Variable | d.f. | Monte Carlo $\chi^2$ *P* |
|---|---|---|
| Habit | 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 |

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 locomotion on flat and soft terrains (Janis et al., 2002). Indeed, living in forest or mixed, open and closed, habitats benefits nimble animals, capable of dexterous manoeuvres to bypass obstacles. When they need sudden sprints and sharp turns, rotary gallop is largely preferred. Conversely, living in wide-open spaces, such as grasslands or deserts, for many reasons favours large-sized animals. Capability to reach high running speed is also a strong stimulus, but this goal is accomplished by longer limbs to increase the stride length, the angular excursion of the limbs constrained by size. Of course, evolution provided many different solutions and answers to the environmental questions, and in savannahs there are species that perform rotary, transverse or both gallop types. For example, gazelles employ rotary gallop and maintain agile and quite light forms in open habitats. Antelopes and gazelles rely on speed and manoeuvrability to escape predators, cheetahs above all (Alexander, 1977; Alexander, 2006; Alexander et al., 1977; Spinage, 1986).

However, when there are 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, they need to maintain running speed as long as possible. In species that can use both gallop gaits, rotary gallop is strongly associated with flat plain terrains where the animals can run faster (Goldenberg et al., 2008).

Table 4. Ecological and behavioural traits

| | Transverse | Rotary | Speed dependent |
|---|---|---|---|
| Habit | | | |
| Diurnal | 25 | 14 | 4 |
| Nocturnal | 3 | 4 | 1 |
| Crepuscular | 4 | 13 | 9 |
| Always active | 4 | 4 | 3 |
| Habitat coverage | | | |
| Open | 27 | 14 | 8 |
| Closed | 1 | 2 | 0 |
| Mixed | 8 | 19 | 9 |
| 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 5. Principal components

| | | Extraction sums of squared loadings | |
|---|---|---|---|
| Component | Total | % Variance | Cumulative % |
| 1 | 5.584 | 37.229 | 37.229 |
| 2 | 4.048 | 26.990 | 64.219 |
| 3 | 1.781 | 11.871 | 76.091 |
| 4 | 1.235 | 8.235 | 84.326 |

In gallop, faster speeds are achieved by taking longer strides, with stride frequency almost constant, and the development of longer legs is one of the ways to get it (Biewener, 2003). However, in cursorial species, the distal segments of a leg usually lengthen more than the proximal (Hildebrand, 1974), giving not only longer legs but also a longer moment arm of the distal segments. In this way, relatively larger ground forces can be applied, reducing the limb contact time (duty factor) and increasing the flight time (Weyand et al., 2000). This is particularly evident in species that employ rotary gallop (Figs 5, 6, Table 7).

During high speed strides, species of both rotary and speed-dependent groups employed a rotary pattern with significantly larger hindlimb excursion angles than the transverse species; this is also related to speed (Biewener, 1983; Pike and Alexander, 2002). The hindlimb 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 hindlimb excursions.

### Centre of mass position

In almost all mammals the centre of mass is closer to the shoulder than to the hips, at nearly 1/3 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)

Table 6. Principal component matrix

| | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| *Fr* | 0.624 | 0.442 | –0.123 | 0.437 |
| Stride length | –0.400 | 0.543 | 0.268 | 0.479 |
| Forelimb/hindlimb ratio | 0.004 | –0.402 | 0.797 | 0.256 |
| Aspect ratio | 0.171 | 0.169 | 0.717 | –0.451 |
| BMI | –0.597 | –0.149 | 0.390 | –0.468 |
| Humerus ratio | 0.890 | –0.221 | 0.143 | –0.073 |
| Radius ratio | 0.859 | –0.114 | 0.326 | 0.156 |
| Femur ratio | 0.841 | –0.293 | 0.193 | 0.118 |
| Tibia ratio | 0.843 | 0.370 | –0.006 | –0.256 |
| Radius/humerus ratio | –0.206 | 0.689 | 0.428 | 0.233 |
| Metacarpus/humerus ratio | –0.179 | 0.949 | 0.075 | –0.008 |
| Tibia/femur ratio | 0.257 | 0.834 | –0.145 | –0.323 |
| Metatarsus/femur ratio | –0.190 | 0.938 | 0.065 | –0.113 |
| Radius of gyration | –0.887 | –0.055 | 0.119 | 0.206 |
| Relative speed | 0.859 | 0.328 | –0.020 | 0.064 |

For full definitions, see Glossary.

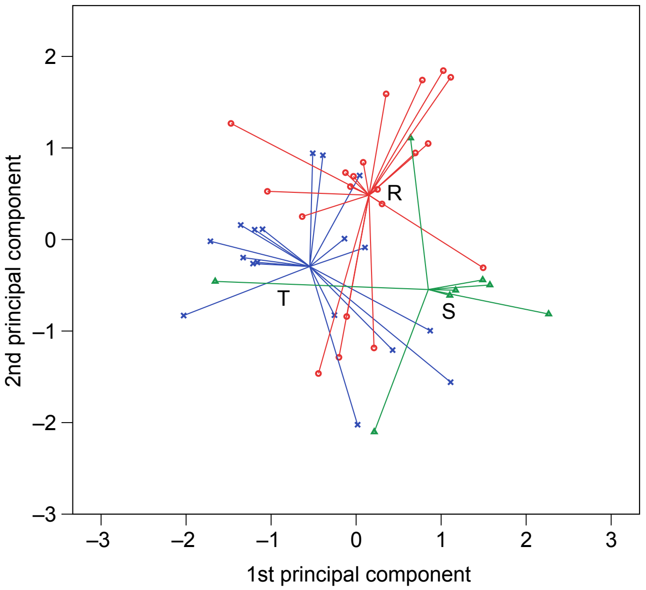

Fig. 4. Principal component analysis. Blue crosses, transverse; red circles, rotary; green triangles, speed dependent.

to 57% in dynamic conditions (Walter and Carrier, 2007). Using simple models, it has been demonstrated that it is beneficial to a galloping system to have the centre of mass closer to the shoulder than to the hips. In this scenario, the forelegs must support a larger fraction of body weight. Thus, the vertical component of the foreleg thrust is higher and the resultant force vector nearly vertical as well (Waldron et al., 2009).

However, these 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 hindlimbs would elevate 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 questionable: 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 represents a particular point of weakness, as it has been widely underlined that the role of spinal flexure in the sagittal plane is 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 movements 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), 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 and colleagues (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 some 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, at certain speeds, make galloping more economical than trotting, because of the lower internal work, 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, lying between the shoulder and the pelvic girdle, is involved in back bending during locomotion (Grasse, 1972). While the lumbar stretch in all three groups is composed of 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). The lumbar spine of cursorial mammals is known to show particular adaptation to the specific biomechanical demands for locomotion, like the presence/absence and 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 gallopers and cursorial transverse gallopers. This was probably due to the support provided by the 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 capacity and compliance, depend on intervertebral joint complexes, intervertebral discs and interlocking processes (Gál, 1993a; Gál, 1993b).

## Quadruped gallop control

Quadrupedal locomotion is generated by an intraspinal network of neurons called the central pattern generator (CPG), capable of producing the rhythms associated with 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;

Table 7. Results of gait analysis (*t*-test)

| | Transverse (mean ± s.d.) | Rotary (mean ± s.d.) | *t*-value | d.f. | *P* |
|---|---|---|---|---|---|
| Duty factor (%) | 29.1±5.5 | 23.3±5.2 | –5.023 | 150 | <0.001 |
| Forelimb duty factor (%) | 29.6±6.1 | 22.9±6.3 | –4.875 | 150 | <0.001 |
| Hindlimb duty factor (%) | 28.6±5.5 | 23.6±4.8 | –4.611 | 150 | <0.001 |
| Forelimb/hindlimb ratio duty factor | 1.04±0.14 | 0.96±0.17 | –2.019 | 150 | 0.045 |
| Forefeet lag (%) | 22.2±6.6 | 17.6±5.2 | –3.808 | 150 | <0.001 |
| Hindfeet lag (%) | 16.4±3.7 | –12.9±4.2 | –32.794 | 150 | <0.001 |
| Hindfeet ratio (%) | 45.0±7.6 | 36.7±7.1 | –5.215 | 148 | <0.001 |
| Midtime lag (%) | 29.6±7.6 | 44.6±6.4 | 10.133 | 148 | <0.001 |
| Pair lag (%) | 73.9±6.8 | 70.3±8.3 | –2.034 | 150 | 0.044 |
| Vertical force | 1.20±0.16 | 1.28±0.19 | 2.009 | 133 | 0.047 |

For full definitions, see Glossary.

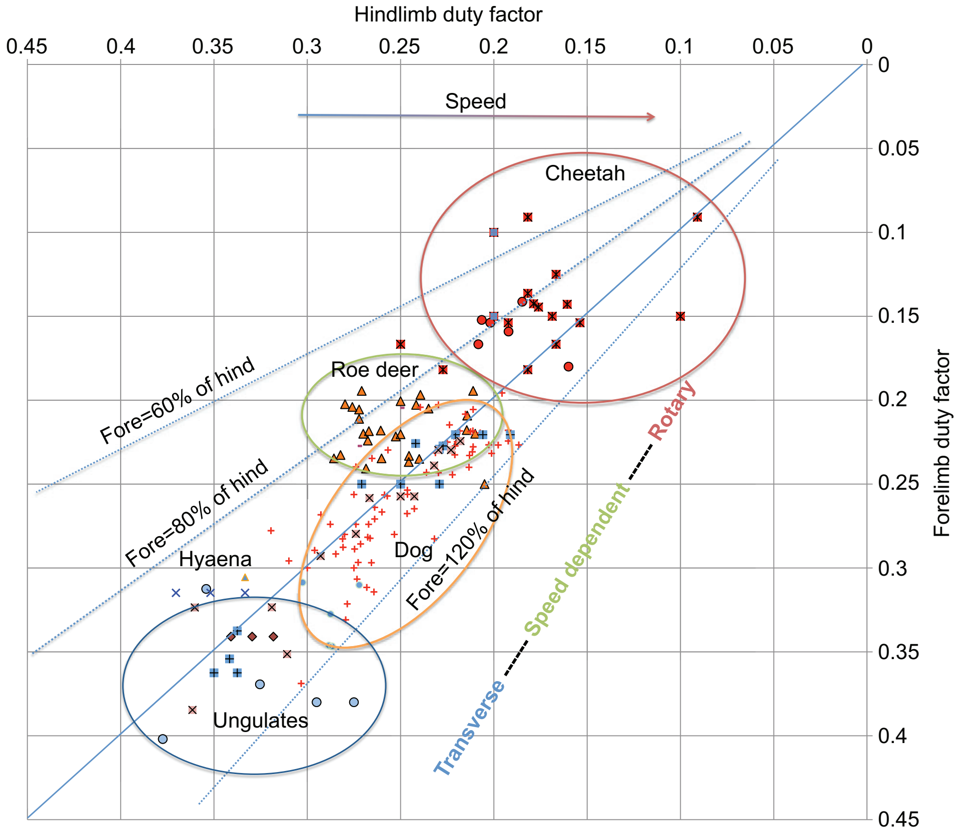

Fig. 5. Hindlimb *versus* forelimb duty factor. Analysis of 152 strides of 12 species at different speeds.

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 emergence of research into the development and production

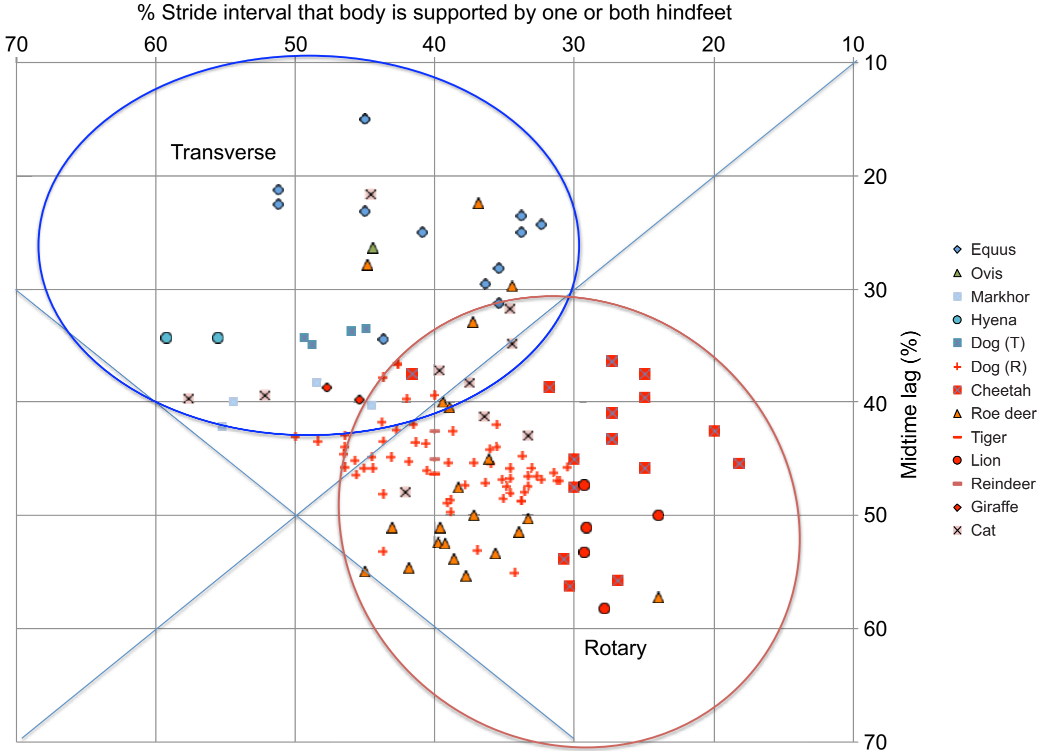

Fig. 6. Hindfoot ratio *versus* midtime lag. Analysis of 152 strides of 12 species at different speeds. T, transverse gallop; R, rotary gallop.

Table 8. Identity cards of transverse and rotary galloper mammals

| | Transverse galloper | Rotary galloper |
|---|---|---|
| Mass | Heavy | Light |
| BMI | Higher | Lower |
| Habit | Diurnal | Crepuscular |
| Social behaviour | Gregarious | Solitary |
| Ecological role | Prey | Predator/Prey |
| Habitat coverage | Open | Mixed |
| Legs | Shorter | Longer |

of legged robots (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 robots have recently been developed, demonstrating that small changes in control parameters can produce all combinations of biological gaits. In particular, bound can easily be converted to half-bound and rotary gallop or transverse gallop. The experiments with galloping robots demonstrate an emergent stability as a characteristic of gallop, which is thus constrained to the sagittal plane in transverse gallop. This research has also confirmed findings from simulations that rotary gallop has a tendency to generate circular trajectories (Poulakakis et al., 2006; Smith and Poulakakis, 2004). From these results, we argue that CPGs of cursorial mammals could potentially produce all the running gaits, from bound and half-bound to rotary gallop and transverse gallop. The species-specific use of only some of the available gaits is probably the result of a combination of morphological and environmental features.

## CONCLUSIONS

To summarise, from our findings, we can now answer the question: who has a lean body, long legs and operates as a solitary predator/prey at dusk in mixed habitats? It is most probably a rotary galloper mammal, according to the outcome of our analyses (Table 8). In fact, this broad investigation of transverse and rotary gallop among the three main orders of cursorial mammals allowed us to make the following conclusions.

First, gait choice is not a simple question of speed, gradient and terrain structure, but also depends on the 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 a long neck and long forelimbs, have been linked to their practice of carrying large and heavy prey (Spoor, 1985). The proportions of their hindlimb segments are different from those of canids, which have a 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 speeds. Felids, in contrast, are solitary ambush 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 a rotary pattern exclusively.

Second, although some clusters 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 fox and the arctic fox, which employ different gallop types because of the different environmental conditions.

Third, the most important biomechanical determinants of gallop type are 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.

## GLOSSARY

Aspect ratio
Ratio of shoulder height to body length.

Body length ($l_b$)
Linear distance from the tip of the nose to the tail insertion (tail excluded). Whole body, not mounted skeleton.

Body mass ($m_b$)
Average mass of the adult.

Body mass index (BMI)
The ratio between the body mass (in kg) and the square of the body length (in m).

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 an average of forefeet or hindfeet, and as an average of the four feet. The average Df$\approx l_{\mathrm{step}}/l_{\mathrm{stride}}$.

Femur circumference
Minimum circumference of the femur.

Femur length
Maximum linear distance from the proximal to the distal epiphysis.

Femur ratio
Femur length/femur circumference.

Flight time
Fraction of the stride interval that the body is not supported.

Forefeet lag ($F_{\mathrm{lag}}$)
Time lag between the footfalls of the forefeet as a percentage of cycle duration.

Forefeet midtime
Half the duration of contact by one or both forefeet.

Forelimb/hindlimb ratio
Forelimb length/hindlimb length.

Hindfeet lag ($H_{\mathrm{lag}}$)
Time lag between the footfalls of the hindfeet as percentage of cycle duration.

Hindfeet midtime
Half the duration of contact by one or both hindfeet.

Hindfeet ratio
Fraction of the stride interval that the body is supported by one or both hindfeet.

Humerus circumference
Minimum circumference of the humerus.

Humerus length
Maximum linear distance from the proximal to the distal epiphysis.

Humerus ratio
Humerus length/humerus circumference.

Limb length
Maximum linear distance from the humerus head or the femur head to the ground. Leg fully extended.

Metacarpus length
Maximum linear distance from the proximal to the distal epiphysis of the longer metacarpal bone.

Metacarpus/humerus ratio
Ratio of metacarpus length to humerus length.

Metatarsus length
Maximum linear distance from the proximal to the distal epiphysis of the longer metatarsal bone.

Metatarsus/femur ratio
Ratio of metatarsus length to femur length.

Midtime lag
Time lag between hindfeet midtime and forefeet midtime as a percentage of stride duration.

Pair lag
Time lag between the footfalls of the first forefoot and the first hindfoot, as a percentage of cycle duration.

Paired phase difference
Averaged phase difference of ipsilateral feet.

Phase difference
Time of the first contact of a forefoot as a percentage of stride duration.

Radius circumference
Minimum circumference of the radius.

Radius length
Maximum linear distance from the proximal to the distal epiphysis.

Radius of gyration
The radius of gyration of the body, approximated as a cylinder.

Radius ratio
Ratio of radius length to radius circumference.

Radius/humerus ratio
Ratio of radius length to humerus length.

Relative speed
Ratio between the progression speed and body length.

Relative stride length
Stride length divided by the height of the hip joint from the ground.

Shoulder height
Maximum linear distance from the tip of the shoulder to the ground.

Slijper moment of resistance ($S$)
Defined as body width multiplied by body height squared ($w_bh^2$).

Step length ($l_{step}$)
Distance travelled (in m) while a particular foot is on the ground.

Stride frequency
Number of strides taken per unit time.

Stride length ($l_{stride}$)
Distance travelled (in m) in one stride.

Tibia circumference
Minimum circumference of the tibia.

Tibia length
Maximum linear distance from the proximal to the distal epiphysis.

Tibia ratio
Ratio of tibia length to tibia circumference.

Tibia/femur ratio
Ratio of tibia length to femur length.

Vertebral body height ($h_b$)
Vertical diameter of the caudal face of the vertebral body.

Vertebral body width
Average of the measured width of the cranial and caudal faces of the vertebral body.

Vertical force during contact
The average vertical ground reaction force during the contact phase, expressed in body mass ($m_b$) multiples and calculated as: $\mathbf{F}_{vert}=1/(1-T_{flight})$, where $T_{flight}$ is duration of flight.

## ACKNOWLEDGEMENTS

I would like to thank all the people who delivered information, comments, advice and original footage useful for our analyses: R. McNeill Alexander, F. Cagnacci, L. Cagnolaro, A. Cardini, C. Caslini, A. R. Di Cerbo, I. e D. Oliva; the Directors and the curators of the Natural History Museums of Florence and Milan, in particular P. Agnelli and G. Bardelli; and L. Marker, A. Schmidt-Kuntzel and P. Tricorache of the Cheetah Conservation Fund.

## FUNDING

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

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