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I, Lisa M. Day ,

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Approved by:

Dr. Bruce C. Jayne

Dr. Rebecca Z. German

Dr. William F. Swanson

How size affects limb posture in cats

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Lisa Marie Day

B.S., University of Cincinnati, 2001

Committee Chair: Bruce C. Jayne, Ph.D.

Abstract

Previous studies of phylogenetically diverse mammals suggest that size-related differences in the scaling of mammals result from increasingly erect limbs in larger taxa. However, whether limb erectness changes with increased size during locomotion of animals within a lineage is poorly understood. To better establish the correlation between size and posture of mammalian limbs, I quantified the joint angles, orientation of limb segments, and tested for correlations with size within the felid (cat) clade, which has qualitatively similar limb bones. If size alone is the causal basis for different limb posture, then erectness of limb should be positively and highly correlated with increased size within an individual clade. I videotaped and performed kinematic analyses of the walking of nine felid species (domestic cat, serval, ocelot, lynx, leopard, cheetah, cougar, lion and tiger) with masses ranging from less than 4 to nearly 200 kg. Twenty one out of a total of twenty four angular variables at footfall and midstance did not vary significantly ($P = 0.05$) with mass and if corrections were made for multiple comparisons, none of the kinematic variables change significantly with size. Thus, larger species did not have more upright limbs than smaller species, and size did not appear to affect either limb posture or kinematics during walking within the cat clade.

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Introduction

Limb posture is the position of the limbs relative to the body and ground. Bakker (1971) and Charig (1972) grouped categorized extant tetrapodal vertebrates into three main categories based on limb postures: sprawling, semi-erect, and erect (Gatesy, 1991). Endothermic vertebrates have erect posture where the limbs are confined primarily in a parasaggital plane such that the limbs appears directly beneath the shoulder and hip when seen in an anterior view (Jenkins, 1971). Crouched erect limbs characterize birds and many mammals, whereas straight or upright and column-like limbs are typical of some mammals, particularly ungulates. More recently, Gatesy (1991) emphasized that rather than being discrete categories, these terms reflect a continuum of variation from sprawling to erect and crouched to upright.

Body size and locomotion play key roles in the evolution of mammalian skeletal structure and function (Biewener, 1983a; 1983b). For all mammals, the mass of the whole skeleton is proportional to $(\text{body mass})^{1.1}$, a relationship that holds for the traditional mouse to elephant curve (Alexander et al., 1979; Biewener, 1983a; 1983b; Schmidt-Nielsen, 1984). As terrestrial mammalian body size increases, the mechanical requirements for support and locomotion change as well (Bertram and Biewener, 1990). Although the material strength and functional capacity of mammalian limb bones and skeletons appear uniform (Bennett et al., 1986; Biewener and Blickhan, 1988) changes in body size likely determine skeletal forms influencing limb bone shape and posture (Bertram and Biewener, 1990; Biewener, 1983a; 1989a; 1990). Several studies propose that size-dependent changes in limb posture facilitate decreasing the stresses on the bones (McMahon, 1975; Biewener, 1983a; 1983b; 1989; 1990; Bertram and Biewener, 1990).

A theoretical potential advantage of upright limbs is the weight being borne through the bones rather than muscles (Gray, 1968; Biewener, 1989) and loading the bones in compression (Biewener, 1983b). This posture permits maintenance of similar safety factors (ratio of fracture stress to peak functional stress (Biewener, 1983b) as smaller mammals by aligning the limb segments and joints with the ground reaction force, thus reducing bending of bones (Biewener, 1983b; Rubin and Lanyon, 1984; Biewener,1990). A greater force acting to load bones in compression exerts a lesser amount of stress than a small force that loads bones in bending (Biewener, 1983a).

Alexander (1985) describes the impact of size on the scaling of limb architecture (how limbs are structured) scales from shrews to elephants. He emphasizes the importance of body size for understanding how the body is supported. Geometric similarity and isometry occur if the scaling exponent between any two linear measurements is one, which, would describe a situation where a small animal could be made identical to the large one simply by multiplying all linear dimensions by a constant factor (Alexander, 1985; La Barbera, 1989; Hildebrand and Goslow, 2001). Alexander et al. (1979) found that terrestrial mammals, with the exception of bovids, scale close to geometric similarity.

Unfortunately, Alexander et al. (1979) and other studies on the effects of size and scaling compare phylogenetically diverse mammals with qualitative differences in skeletal structure rather than making comparisons within one clade with fundamentally similar limb architecture. Such generalizations regarding size based on interclade comparisons can be problematic if different lineages have different ranges of size. In such a case, a variable of interest could be unrelated to size within a clade but highly correlated with size for a sample including several clades of different sizes (Fig. 1). For example, most ungulates are relatively large and have fairly straight upright limbs, whereas most rodents are quite small and have crouched limbs. However, if size alone is a causal factor underlying erect limb posture, then limbs should become increasingly erect with increased size within a clade as well as with increased size among clades. Previous studies have not systematically determined whether size affects posture within one taxonomic group.

Cats are an excellent model system to use for studying limb kinematics and allometric relationships because they are a well-defined clade (Mattern and McLennan, 2000) with similar habitats and behaviors, but their sizes differ substantially (Sunquist and Sunquist, 2002). In this study, I used the Felidae to examine the correlation between limb posture and size. The two main questions I addressed are: does limb posture vary among felids, and if so, the erectness of limb increase with increased size? I predicted that if indeed limb posture is correlated with size, then there will be in increased erectness of limb with increased size within the Felidae.

Materials and Methods

Experimental subjects

I videotaped nine species of cats for this study including the domestic cat (*Felis catus*), ocelot (*Leopardus pardalis*), Canadian lynx (*Lynx canadensis*), serval (*Leptailarus serval*), cheetah (*Acinonyx jubatus*), cougar (*Puma concolor*), leopard (*Panthera pardus*), lion (*Panthera leo*) and tiger (*Panthera tigris*) (Table 1). I observed cats at the Cincinnati Zoo and Botanical Gardens (Cincinnati, OH) in the Cat Ambassador Program, the Columbus Zoo (Columbus, OH) The Exotic Feline Rescue Center (Center Point, IN), The Siberian Tiger Conservation Association (Gambier, OH) and A Zoo For You (Newark, OH). All cats were leash trained with the exception of those at The Exotic Feline Rescue Center. The twenty five individuals for final analysis were chosen according to the following criteria: similar duty factors (the duration of foot contact with the ground divided by stride duration) for both fore- and hindlimbs, continuous movement throughout the stride, and straightness of the path taken. I picked individuals based on statistical analysis of duty factors for both the fore- and hindlimbs to ensure the strides analyzed were walking (duty factors 0.54-0.73). The cats ranged in mass from less than 4 to nearly 200 kg (Table 1) and all individuals were within the normal body mass range for their species (Sunquist and Sunquist 2002).

Experimental protocol

I used a JVC digital camera (GR-DVL 9800) to videotape lateral views of the cats moving along a designated pathway. The cats walked on flat surfaces consisting of hard substrates including compact soil, short grass, concrete slabs, floors and table tops with rubber mats to prevent slipping. I placed temporary, non-invasive paper stickers on the shoulder, elbow, wrist, MCP (metacarpal-phalange), hip, knee, ankle, and MTP (metatarsal-phalange) joints to facilitate digitizing joint angles. The markers were placed on the fur of the cat after palpating the joint to find its exact location. The camera was perpendicular to the vertical plane contained the path traveled the path traveled by a cat. The x-axis of the two dimensional coordinate system was parallel to the overall direction of travel of the cat. To provide a distance scale a reference grid was placed in the field of view at the beginning of each filming session. Each cat was videotaped individually while walking along a pathway for several minutes to attempt to obtain at least four unobstructed strides of similar speeds of steady locomotion.

Anatomical measurements

I obtained masses of each cat from keeper records. I calculated the following anatomical lengths from the 2 dimensional analysis of the video footage: lengths of the humerus, radius/ulna, metacarpal, femur, tibia/fibula, metatarsal and phalanges and the intergirdle distance was the two-dimensional distance from the shoulder joint to the hip joint. Total limb lengths were calculated by summing the lengths of all limb segments for the fore- and hindlimbs separately. Relative distances were calculated by dividing a particular height or anatomical length by the total length of the appropriate limb and were expressed as %FLL (forelimb length) and %HLL (hindlimb length).

Kinematics

I performed frame-by-frame motion analysis with DgeeMe v1.0 (GeeWare.com) using at least 20 images per stride from footfall for one limb until a subsequent footfall of that same limb. Footfall is when the foot first contacts the ground. Within the stride cycle the stance and swing phases are when the foot is in contact with the ground and off of the ground, respectively. Midstance represents halfway through stance. Footfall and midstance were the two points in time analyzed in this study because they correspond to some of the largest forces experienced by a limb during locomotion. Duty factors, speed, relative stride length and relative speed were not highly correlated with size (Table 4). Stride frequency was negatively correlated with mass (Table 4). Stride length was determined from the difference in the x-coordinates of the most proximal joint at the times of successive footfalls. Shoulder and hip height were the vertical distances from the ground to the shoulder and hip joints, respectively. For each frame within a stride I measured the two linear variables (heights of shoulder and hip relative to the ground), six joint angles (elbow, wrist, MCP, knee, ankle, MTP), and eight angles of the limb segments relative to vertical reference (humerus, radius/ulna, metacarpals, femur, tibia/fibula, metatarsals, and fore and hind phalanges) (Fig. 2).

Key indicators of erectness are angles and ratios of heights to total anatomical limb lengths. If the joint angles between bones are large and approach 180^{o} and the angles relative to vertical are small, then the cat has a straight and erect limb. Decreased joint angles and increased angles between the limb segments and the vertical indicate crouched limb posture and one that departs more from a simple vertical column that point in time. If the ratio of shoulder or hip height to the fore- and hindlimb length, respectively, is 100%, then all joints are fully extended and the cat has an erect posture.

Statistical analysis

I used SYSTAT version 9 to perform statistical analyses. I used the mean values of each species to calculate least-squares regressions predicting relationships between $\log_{10}$ transformed values of anatomical lengths and masses. Correlation analyses determined if joint angles, orientation angles, and relative heights were correlated with mass using mean values per species, hence the number of observations is equal to the number of species. Correlational analyses were the main statistical test used rather than regressions because the focus of this study is to determine if joint angles are dependent upon size. I used $\alpha = 0.05$ as the criterion for statistical significance. All mean values of descriptive statistics are presented ± S.E.M based on the number of strides.

Results

Anatomy

The mean linear measurements of the largest species (lions and tigers) were approximately 3 times the size of the smallest species (domestic cat) and mean mass of the largest species was 45 times the size of the smallest (Table 1). The lynx and leopard had only one individual for all anatomical data measured from videotapes and therefore have no standard error or ranges. Within most of the species, the radius/ulna was usually slightly longer than the humerus and the tibia/fibula was slightly longer than the femur (Table 2). Within each species the combined lengths of the metapodials and phalanges were consistently less than that of the humerus or femur (Table2).

The slopes of the regressions relating total lengths of the fore- and hindlimbs and intergirdle distance to mass were all slightly less than the expectation from geometric similarity (0.33), but this was not statistically significant as indicated by 95% confidence limits of all but two of these quantities encompassing 0.33 (Table 3). The slopes of the scaling relationships of total limb length and intergirdle distance were almost exactly 1.0 (Table 3). The values of r^2 for the scaling of total limb length with intergirdle distance were higher ($P<0.001$) than those of any of the scaling equations of limb lengths versus mass (Table 3). The cheetah and lynx consistently had high residuals of fore- and hindlimb length and intergirdle distance when adjusted for mass (Fig. 3A-C). However, the magnitudes of the residual values of limb length of the cheetah determined from intergirdle distance were low (Fig. 3D,E). Thus, the cheetahs had relatively long limbs for their mass but not for their body length.

Kinematics and limb posture

The changes in joint angles and orientation of the limb segments that occurred within the stride cycle were extremely similar for all of the species in this study (Fig. 4). Throughout much of stance, the elbow, wrist, knee and ankle joints were nearly constant (Fig. 4A-D). From footfall to midstance, the knee and ankle often flexed two approximately 150° and 10° respectively (Table 5). The elbow and knee were maximally flexed near midswing (Fig. 4A,B). Maximal plantar flexion of the wrist (Fig. 4C) and maximal dorsiflexion of the ankle (Fig. 4D) also occur near midswing. The wrist was nearly straight throughout stance (Fig. 4C) whereas the angles of the elbow, knee, and ankle are approximately 135° throughout stance (Fig. 4A,B,D). Furthermore, the elbow, knee, and ankle were never straightened completely during stance or at any point in time during the stride cycle.

The angles of the limb segments relative to vertical decreased steadily throughout stance (Fig. 4 E-J). The humerus (Fig. 4E) and tibia (Fig. 4H) were nearest vertical at footfall, whereas the femur was most near vertical at endstance (Fig. 4F). The metacarpals (Fig. 4I), metatarsals (Fig.4J) and radius/ulna (Fig. 4G) limb segments were nearly vertical at midstance. The negative angles of limb segments orientation indicate that the distal portion of the humerus was posterior to the shoulder (Fig. 4E) and the distal portion of the tibia was posterior to the knee (Fig. 4H) throughout the stride cycle. The distal portion of the femur (Fig. 4F) was only briefly posterior to the hip near the stance-swing transition. The radius (Fig. 4G) and distal portion of the forelimb (Fig. 4I) and hindlimb (Fig. 4J) alternated between having distal portions anterior and posterior to the proximal portion during an entire stride cycle.

At midstance, the point of limb attachment is at its highest (Fig. 5) and the foot is nearly beneath the point of limb attachment (Fig. 6). Thus, the overall limb posture is most erect at midstance.

My additional analyses emphasized limb posture at footfall and midstance for several reasons. During walking, peak ground forces occur at footfall and several kinematic quantities have a local maximum at footfall (Fig. 4). Even though we did not analyze running, during running peak ground forces occur near midstance. Thus, footfall and midstance encompass several key biomechanical events and quantifying limb posture at these standardized times should facilitate future comparisons.

Overall, the posture of fore- and hindlimbs at footfall and midstance appear similar among all species studied (Fig. 6). With the exception of the elbow angle at midstance, no joint angles of either fore- or hindlimb at footfall or midstance were highly correlated with mass (Table 5). At footfall, none of the angles of the limb segments relative to vertical were highly correlated with mass and only 2 variables at midstance had moderate correlation with size (Table 6) but even a modest correction for multiple comparisons would render this relationship insignificant.

Good composite indications of whether the limbs were completely straight and vertical are relative heights of the point of limb attachment and none of these was highly correlated with size (Table 6). The mean heights of the shoulder and hip were usually < 80% of total limb length at footfall and at midstance (Table 6). At footfall, the humerus of the leopard and ocelot appeared to be oriented somewhat more horizontally than that of the other species.

Discussion

I was not able to detect any significant correlations between limb posture and size despite the fact that the masses of individual felids in this study ranged from 3.3 kg (domestic cat) to 192 kg (tiger). In contrast to my findings, an increasing amount of information from phylogenetically diverse terrestrial mammals generally supports a trend of increasingly erect limb posture with increased size (Biewener, 1983b; 1989; Bertram and Biewener, 1990; Christiansen, 1999; Biewener, 2000). Two lines of evidence used to explore the relationships between limb posture and size include direct observations of limb posture (Biewener, 1983b; 1989; Biewener, 2000) and implications from the scaling relationships of skeletal dimensions (Bertram and Biewener, 1990; Christiansen, 1999). These large scale comparative data sets regarding size often involve phylogenetically diverse taxa with qualitative differences in limb morphology and different ranges of size. Hence, whether trends with size that occur among clades also occur within clades is not clear (Fig. 1). Thus, interpreting the results of my study of a clade having qualitative similar limb morphology requires methodically accounting for the size of my study species compared to those of previous studies as well as the any peculiarities resulting from sampling different evolutionary lineages.

Size and Phylogeny

Biewener (2005) recently reviewed the results of several studies with direct observations of limb posture (EMA = Effective Mechanical Advantage) for fourteen phylogenetically diverse species mammals, including eight rodents, three ungulates, and one carnivore (dog). Thus, the preponderance of large and small species for which EMA has been determined are ungulates and rodents, respectively. The subset of rodent species within the data of Biewener (2005) may provide the most informative comparison with my phylogenetically restricted sample of felid carnivores. Unlike the lack of scaling of limb posture over the 60 fold range in mass of the felids that I studied, eight rodent species ranging from deer mice (5 g) to capybaras (4 kg) had significant scaling of EMA with mass that was indistinguishable from that of the combined sample of Biewener (2005). In addition to being very large, capybaras may be an unusual rodent because of their semi-aquatic lifestyle (Biewener, 2005), and they and agoutis belong to a different suborder than the other rodents studied by Biewener. The small sample size of mammalian lineages other than rodents precluded Biewener (2005) from making additional comparisons while attempting to correct for phylogeny.

In contrast to the limited direct observations of limb posture, scaling studies of the appendicular anatomy and locomotion of terrestrial mammals commonly have several dozen species (McMahon, 1975; Bertram and Biewener, 1990; Christiansen, 1999; Iriarte-Diaz, 2002) and a recurrent finding of the following studies is that scaling relationships differ for large and small species. For example, Bertram and Biewener (1990) found differential scaling for a sample of 118 species including seven families of terrestrial Carnivora (0.1-500 kg). They suggested that the positive allometry for limb bone diameter versus length of large (>100 kg) species compensated for minimal differences in limb posture, whereas the nearly isometric scaling of skeletal dimensions small mammals was possible as a result of larger species having more upright limb posture. Thus, some expectations for an effect of size on limb posture are size dependent. However, seven of the nine felid species in my study had a wide range of masses within the range of size for which Bertram and Biewener (1990) predicted differences in limb posture, and yet no differences in limb posture were apparent.

Rather than having much conspicuous variation in shape, much of the morphological diversity in Felidae is a result of variation in size, which has been analyzed phylogenetically by Mattern and McLennan (2000). The ancestral felid was probably large (>40 kg), thus the large size throughout the species in the *Panthera* clade (lions, tigers, leopards and jaguars) is probably symplesiomorphic. Within the *Panthera* clade body size increased in the common ancestor of the genus *Panthera* with an additional increase in body size in the lineage containing lions, tigers and jaguars (Fig. 7). Two additional increases in size occurred independently in the lineage containing the serval and another containing lynx, puma and cheetah. The evolutionary changes in body size within felids without attendant changes in extant felid limb posture are striking. The most parsimonious explanation for the lack of variation in limb posture that I observed within the felid clade is that limb posture of extant felids has been retained from a common ancestor. Even though size of extant felid species doesn’t have predictive value for limb posture of extant species, perhaps, the limb posture retained throughout extant Felidae does conform to that predicted for the mass of the ancestral felid based on the scaling equations of Biewener (2005) for the limb posture and mass of diverse extant mammals.

Ecological and Behavioral Diversity

Many specializations common to felids are associated with their strategy for capturing prey by stalking, ambushing prey with a short rush and leap, and then using a quick killing bite (Eisenberg, 1981; Macdonald, 2001). Many felids can attain impressive sprinting speeds such as >16 M h^{-1} for domestic cats (Goslow et al., 1973) and 64 M h^{-1} for cheetahs (Sharp, 1997). However, felids lack the capacity of canids to sustain high speeds for prolonged periods of time, which may result in partly from a greater mobility of the vertebral column (Hildebrand, 1985) and greater mobility of the limbs that is associated with climbing and prey manipulation (Andersson, 2004). The claws of felids are able to retract more than those of other carnivores (Russell and Bryant, 2001). Nearly all felids are adept at climbing and jumping, but the amounts of these activities vary considerably among felid species and among different habitats occupied by individual species (Sunquist and Sunquist, 2002). Many felid species occupy different habitats (tundra, rocky montane areas, grasslands, desert, savanna and a variety of forests) but have few conspicuous morphological differences that are associated with ecological differences. In addition, ecological separation of the felid species may have been a major factor in the rapid diversification of this relatively young (5-8 million years) diversification (Mattern and McLennan, 2000).

Cheetahs were the study species that was morphologically most distinct. The cheetah's limbs are long for their body mass (Fig. 3) allowing them to cover the same distance in one stride as a galloping horse and achieve high speeds (Sunquist and Sunquist, 2002). Although the claws of cheetahs are retractable (relative to the foot bones) they are not covered by a sheath in the retracted position (Russell and Bryant, 2001). Cheetahs also have a thin waist (Fig. 2) and appear narrow in an anterior view compared to other felids. Although cheetahs can climb trees if necessary, they spend most of their time on the ground in relatively open habitats (Sunquist and Sunquist, 2002).

The length of the limbs relative to mass of the Canadian lynx was second only to that of the cheetah. In addition, the ratio of hindlimb to forelimb length of the lynx was also the second highest value of all the study species, which could contribute to the tipped forward look described by Sunquist and Sunquist (2002). Lynx are adapted to live in colder climates and have snowshoe-like feet that facilitate moving on snow (Sunquist and Sunquist, 2002), but lynx did not have any conspicuous differences in limb posture when compared to other study species.

Servals are commonly considered long legged felids, and they are usually found in habitats with long grasses in which a tall and slim build may facilitate detecting and capturing small mammalian prey (Sunquist and Sunquist, 2002). For my limited sample of nine felid species, servals did not have long limb lengths when adjusted for mass (Table 7) or for intergirdle distance (Fig. 3). Steudel and Beattie (1993) quantified mass and limb dimensions for a much larger sample of 22 species of felids including servals, but they did not calculate scaling relationships for the felids which were part of a much larger data set for diverse mammals. I calculated scaling equations for this larger sample of Felidae plus my measurements of three species (tigers, cheetahs, and leopards) not included in Steudel and Beattie (1993) to determine how the resulting regressions might affect residual limb length values including those of servals (Table 7). These additional analyses support previous suggestions that servals do have relatively long limbs. In addition, servals have relatively long metacarpal and metatarsal bones (Table 2), which may contributes to their remarkable ability to jumping 2 to 3 meters up to catch a bird or insect in mid-flight (Sunquist and Sunquist, 2002).

In light of the variation in length relative to the overall size of felids in my study, I performed additional correlation analyses between residual values of limb length predicted form mass and all of the kinematic variables in Tables 5 and 6. None of the kinematic variables of the forelimb were significantly correlated with the residual values either for my sample of nine species or for the pooled data (Table 7 rows 1 and 3, respectively). The only three significant correlations between hindlimb length residual and kinematics were for femur orientation at midstance (r = 0.70, *P* = 0.036) and orientation of the phalanges at midstance (r = 0.66, *P* = 0.051) using the unpooled scaling relationship, and the angle at the metatarsal-phalange joint (r = -0.71, *P* = 0.031) for the pooled scaling relationship. All of these correlations indicate leg segments that are less vertical as limb length residual increases, but the overwhelming generality is that limb posture had little systematic change with increased relative limb length similar to the lack of correlations between limb posture and overall size.

Of the species I studied, the ocelot and leopard are most arboreal. The leopard is one of the few felids that can climb down a tree head-first, this species sometimes drags prey as massive as 50 kg up into trees (Sunquist and Sunquist, 2002). Although not a strictly arboreal cat, the ocelot often takes refuge in the trees and reportedly has excellent climbing abilities (Sunquist and Sunquist, 2002). The leopard had the most crouched fore- and hindlimb posture of any of the species in my study (Fig. 6), and the relative heights of the hip and shoulder of the ocelot were among the three lowest values observed (Table 6). In arboreal habitats and on inclines, diverse species of vertebrates commonly use a more crouched limb posture (opossum (Lammers and Bikenvicius, 2004), domestic cat (Carlson-Kuhta et al., 1998), lizards (Jayne and Irschick, 1999), primates (Cartmill, 1974)). Presumably crouched limbs lower the center of mass and hence reduce the tendency to tip over sideways on a narrow perch or fall back and away from a steeply inclined surface (Cartmill, 1985; Vilensky et al., 1994; Carlson-Kuhta et al., 1998; Jayne and Irschick, 1999). Thus, the slightly more crouched positions of the leopards and ocelots observed in this study might be associated with their arboreal tendencies.

The tiger is the largest of all the cat species (record size of wild individual 258 kg) (Hewitt, 1938), and tigers are adept swimmers but they do not frequently climb. The masses of adult lions have considerable overlap with those of tigers, and these large species frequently attack prey with a mass that exceeds their own. Gonyea (1976) suggested that a slightly higher ratio of radius to humerus length in lions makes them more specialized for running. However, the analogous ratios of lions measured in my study did not exceed those of the tiger for both fore and hindlimbs, and both of these species had much smaller values compared to those of the cheetahs.

The felids I studied had more than a 50-fold range in mass, but lacked any substantial correlations between mass and limb posture. The absence of a correlation between two quantities can occur if one quantity is invariant or if both quantities vary but variation in one quantity has no predictive value for variation in the other quantity. The lack of correlations between limb posture and mass that we observed corresponds best with the former case. Thus, neither the phylogeny nor the ecology of the felids appears to have much predictive value for limb posture because it is nearly invariant. Consequently, my results agree with some previous suggestions regarding the evolutionary conservatism in locomotor style and appendicular morphology of the carnivoran mammals (Flynn et al., 1988; Bertram and Biewener, 1990).

Bears are the only group of terrestrial carnivores larger than the largest extant felids. Rather than having limbs that are conspicuously more upright than felids, bears have plantigrade foot posture which seems likely to decrease the values of effective mechanical advantage (EMA) that Biewener and colleagues have used to quantify the extent to which limbs are crouched (low values of EMA) erectness. All other terrestrial mammals larger than the largest felid have unguilgrade limb posture and some of these species also exceed the size of the largest species of bears. Christiansen (2002) suggested that the allometry of appendicular anatomy has constrained maximal size of terrestrial animals the largest of which (sauropod dinosaurs) are less than ½ the mass of the largest extant aquatic animal (blue whale 187 metric tons). Yet, whether the limb design has constrained the evolution of size within well-defined clades, such as the felids, remains an open question. Thus, for very large terrestrial carnivores, experimental data similar to those of Biewener (1983a) could provide interesting insights into this issue.

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Table 1. *Mean values of anatomical measurements (±SEM)*

Species	N	Mass (kg)	IGD (cm)	FLL (cm)	HLL (cm)	HLL/FLL (%)
Domestic	4	3.7±0.2 (3.3-4)	32±1 (26-44)	24±1 (22-26)	33±1 (30-35)	1.38
Serval	2	8.5±1.9 (6.6-10)	47±1 (41-52)	34±1 (30-37)	43±1 (38-46)	1.26
Ocelot	2	9.4 (9.4-9.4)	47±1 (45-49)	33±1 (32-36)	41±1 (40-41)	1.24
Lynx	1	11	57	46	63	1.37
Leopard	1	39	74	57	76	1.33
Cheetah	3	48±6 (37-57)	85±1 (76-89)	67±1 (63-70)	82±1 (79-83)	1.22
Cougar	3	60±12 (42-83)	66±1 (61-70)	49±1 (45-52)	63±1 (59-68)	1.29
Lion	5	167±2 (165-170)	90±1 (87-93)	69±1 (63-76)	82±1 (71-86)	1.19
Tiger	3	169± 6 (155-192)	85±1 (75-92)	68±1 (62-74)	81±1 (72-92)	1.19

IGD, intergirdle distance; FLL, forelimb length; HLL, hindlimb length

N, number of individuals observed per species

Ranges are indicated parenthetically

Table 2. *Mean relative length of individual limb segment lengths compared to mean total limb length of fore- and hindlimb*

Relative length	Domestic (4)	Serval (2)	Ocelot (2)	Lynx (1)	Leopard (1)	Cheetah (3)	Cougar (3)	Lion (3)	Tiger (5)
Forelimb segment (% fore limb length)									
Humerus	36.8±1.0	33.3±4.1	33.3±2.0	35.4	34.4	34.0±1.3	35.5±0.3	37.4±0.5	36.4±0.5
Radius	34.2±0.3	34.5±2.5	38.2±0.5	33.3	37.6	38.8±1.2	34.9±0.7	34.9±1.1	33.6±1.6
Metacarpal	14.6±0.3	18.9±2.5	14.6±0.7	17.3	16.0	15.0±0.7	14.6±1.2	15.0±0.4	16.0±1.3
Fphalange	14.1.±0.7	13.3±0.7	14.0±0.7	14.0	12.0	12.2±0.3	15.1±0.2	12.8±0.6	13.8±0.8
Hindlimb segment (% hind limb length)									
Femur	34.7±1.0	32.8±0.8	33.8±0.4	33.1	31.5	31.7±0.7	35.8±0.4	36.4± 0.9	34.2±0.8
Tibia	32.4±1.3	34.9±1.0	33.8±0.4	35.9	37.7	38.0±0.9	36.7± 0.8	37.3±0.6	38.2±0.5
Metatarsal	22.1±0.3	21.1±0.8	19.3±0.4	18.4	19.4	19.2±0.5	16.9±0.3	16.7±0.4	17.3±0.4
Hphalange	10.5±0.3	11.2±1.0	9.94±0.4	12.6	11.4	11.1±0.5	10.7±0.5	9.7±0.3	9.93±0.7

Fphalange, phalanges of forelimb; Hphalange, phalanges of hindlimb

Number of individuals measured is indicated parenthetically beneath each species, values are ± SEM

Table 3. *Least-squares regression parameters of the scaling equations of log_{10} slope and intercept transformed values of species means of lengths and masses*

Dependent Variable	Independent Variable	slope±95%CL	intercept±95%CL	r^2	*P*
Log IGD	Log Mass	0.235±0.082	1.450±0.128	0.87	<0.001
Log FLL	Log Mass	0.240±0.097	1.346±0.151	0.84	0.001
Log HLL	Log Mass	0.230±0.106	1.443±0.163	0.79	0.001
Log FLL	Log IGD	1.072±0.099	-0.248±0.180	0.99	<0.001
Log HLL	Log IGD	1.002±0.180	-0.020±0.322	0.96	<0.001
Log FLL*[1]	Log Mass*	0.295±0.047	1.066±0.054	0.88	<0.001
Log HLL*[1]	Log Mass*	0.293±0.051	1.253±0.059	0.86	<0.001

FLL, forelimb length; HLL, hindlimb length; IGD, intergirdle distance

*For 22 species listed in Table 1 from Steudel and Beattie (1993) plus my measurements of leopard, tigers and cheetahs, [1]indicates limb length excluding phalanges

Table 4. *Descriptive stride mean values (±SEM)*

Species	N	Fore DF	Hind DF	*v* (m s^{-1})	F (Hz)	SL (% HLL)	*v* (% HLL)
Domestic	4	0.62±0.01	0.59±0.01	0.8±0.03	1.53±0.07	165±2.7	244±10
Serval	2	0.60±0.02	0.60±0.01	0.85±0.06	1.08±0.07	183±7.7	199±19
Ocelot	2	0.59±0.02	0.60±0.02	0.87±0.09	1.31±0.09	163±11.5	213±15
Lynx	1	0.68±0.02	0.67±0.02	0.79±0.05	0.99±0.06	122±3.2	125±7.2
Leopard	1	0.62±0.02	0.60±0.01	1.73±0.11	1.43±0.07	159±6.7	227±14
Cheetah	3	0.65±0.01	0.64±0.01	1.03±0.04	0.84±0.01	142±3.0	126±4.8
Cougar	3	0.67±0.01	0.66±0.01	0.75±0.04	0.90±0.03	130±4.2	118±6.3
Lion	3	0.66±0.01	0.66±0.01	0.81±0.05	0.76±0.03	129±2.9	99±6.6
Tiger	5	0.67±0.01	0.66±0.01	0.75±0.028	0.69±0.01	129±3.2	91±3.5
	r	0.55	0.60	-0.18	-0.72	-0.59	-0.65
	p	0.119	0.089	0.648	0.028	0.095	0.072

DF, duty factor; *v*, speed; F, frequency; SL, stride length; HLL, hind limb length

N, number of individuals observed per species

Table 5. *Mean joint angles (±SEM) at footfall and midstance of the fore- and hindlimbs*

	Domestic	Serval	Ocelot	Lynx	Leopard	Cheetah	Cougar	Lion	Tiger		
Joint Angle	4 (16)	2 (7)	2 (7)	1 (4)	1 (3)	3 (12)	3 (10)	3 (9)	5 (18)	r	*P*
Elbow FF	129±2	132±5	109±3	129±4	108±4	142±2	129±2	134±2	134±3	0.50	0.166
Elbow MSt	127±2	137±6	111±3	110±2	108±4	139±1	130±3	135±3	140±2	0.75	0.021
Wrist FF	184±2	183±2	181±3	177±2	175±4	180±2	179±3	181±2	184±3	0.14	0.713
Wrist MSt	176±3	169±3	173±2	161±4	156±4	170±1	163±3	165±2	169±2	-0.21	0.581
MCP FF	133±3	135±3	138±3	139±1	138±9	130±1	137±2	131±2	137±2	-0.51	0.158
MCP MSt	107±2	111±3	122±3	123±3	125±10	109±2	118±3	118±2	115±2	-0.06	0.877
Knee FF	130±3	134±2	132±1	127±1	121±6	133±2	137±1	134±2	135±2	0.46	0.214
Knee MSt	115±3	118±6	116±2	107±4	99±10	124±1	132±1	124±2	125±2	0.48	0.191
Ankle FF	118±3	124±2	134±5	119±3	113±7	134±2	132±2	131±3	133±2	0.42	0.258
Ankle MSt	114±3	117±2	123±2	119±1	106±4	125±1	121±3	119±4	125±2	0.32	0.406
MTP FF	140±2	143±2	134±4	141±3	152±7	140±1	141±3	137±3	143±2	-0.16	0.675
MTP MSt	112±2	120±7	118±2	109±2	119±5	113±2	122±3	121±4	116±2	0.56	0.116

r, correlation coefficient between the mean values of a kinematics and mass N=9 species

FF, footfall; MSt, midstance; MCP, metacarpal-phalange joint; MTP, metatarsal-phalange joint

Below each species at the top of each column are the numbers of individuals and (strides) measured

Table 6. *Mean values of angles relative to vertical (±SEM) at footfall and midstance of fore- and hindlimbs*

	Domestic	Serval	Ocelot	Lynx	Leopard	Cheetah	Cougar	Lion	Tiger		
Variable	4 (16)	2 (7)	2 (7)	1 (4)	1 (3)	3 (12)	3 (10)	3 (9)	5 (18)	r	*P*
Orientation Angles (degrees)											
Humerus FF	-7±2	-3±4	-28±3	-6±3	-29±2	-1±1	-12±2	-7.6±1	-4±1	0.48	0.195
Humerus MSt	-45±2	-38±5	-60±2	-60±2	-65±2	-34±1	-45±2	-36±2	-32±2	0.75	0.020
Radius/Ulna FF	42±2	43±2	41±3	43±1	41±4	37±1	38±1	38±2	41±2	-0.29	0.457
Radius/Ulna MSt	8±1	4±2	7±2	9±2	6±3	6±1	4±2	9±2	7±1	-0.09	0.827
Metacarpal FF	38±2	40±2	40±3	45±2	45±8	36±1	39±1	37±1	38±1	-0.38	0.312
Metacarpal MSt	11±2	14±3	13±3	28±2	30±7	16±2	21±2	25±2	18±1	0.16	0.673
Femur FF	33±1	39±2	42±2	40±2	49±1	44±1	38±1	41±2	41±2	-0.08	0.839
Femur MSt	13±2	10±3	20±2	24±2	31±6	20±1	13±1	19±2	21±1	-0.06	0.881
Tibia/Fibula FF	-15±2	-5±1	-2±2	-12±1	-8±2	1±1	-2±2	-4.9±1	-1±1	0.50	0.170
Tibia/Fibula MSt	-51±2	-50±3	-43±3	-47±3	-49±5	-35±1	-34±1	-37±1	-34±2	0.62	0.075
Metatarsal FF	46±2	50±1	43±3	47±3	57±5	46±1	46±2	44±2	46±2	-0.20	0.598
Metatarsal MSt	13±2	11±2	13±1	13±2	23±3	19±2	25±3	24±3	21±2	0.67	0.049
Relative heights (% total limb length)											
Shoulder FF	72±0.9	71±2.7	67±2.0	68±0.6	59±3.4	77±1.3	75±2.0	77±1.9	75±1.7	0.28	0.465
Shoulder MSt	74±1.5	76±4.2	72±1.4	69±2.1	61±1.8	80±1.1	78±1.1	79±2.2	77±1.3	0.51	0.160
Hip FF	75±1.7	73±3.7	72±1.8	72±1.6	65±0.6	78±3.8	77±1.4	78±2.6	76±1.5	0.50	0.169
Hip MSt	77±1.7	78±1.4	76±1.9	74±1.6	63±1.8	80±0.3	82±1.6	79±1.5	80±1.4	0.29	0.450

r, correlation coefficient between the mean values of kinematics and mass for N=9 species

FF, footfall; MSt, midstance; SH, shoulder height; HH, hip height

Below each species at the top of each column are the number of individuals and (strides) measured

Table 7. *Fore- and hindlimb length residuals using Steudel and Beattie (1993) data*

	Domestic	Serval	Ocelot	Lynx	Leopard	Cheetah	Cougar	Lion	Tiger
LogFLL	-0.069	-0.004	-0.033	0.091	0.042	0.101	-0.063	-0.026	-0.038
LogHLL	-0.063	-0.023	-0.062	0.113	0.090	0.080	-0.052	-0.040	-0.043
LogFLL*	0.023	0.068	-0.049	0.109	0.065	0.099	-0.021	0.001	-0.053
LogHLL*	0.016	0.052	-0.065	0.123	0.110	0.124	-0.026	-0.044	-0.048

r, correlation coefficient between the mean values of relative lengths and mass

LogFLL, $\log_{10}$ of forelimb length; LogHLL, $\log_{10}$ of hindlimb length

* indicates residual values from Steudel and Beattie (1993) data in cm plus 3 species from Day

Figure 1

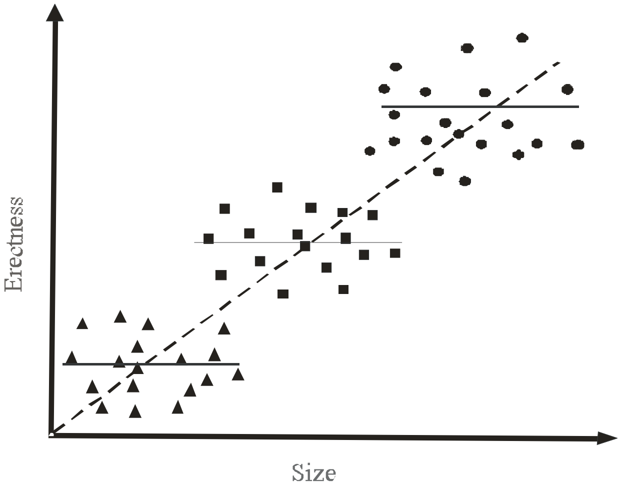


Figure 2

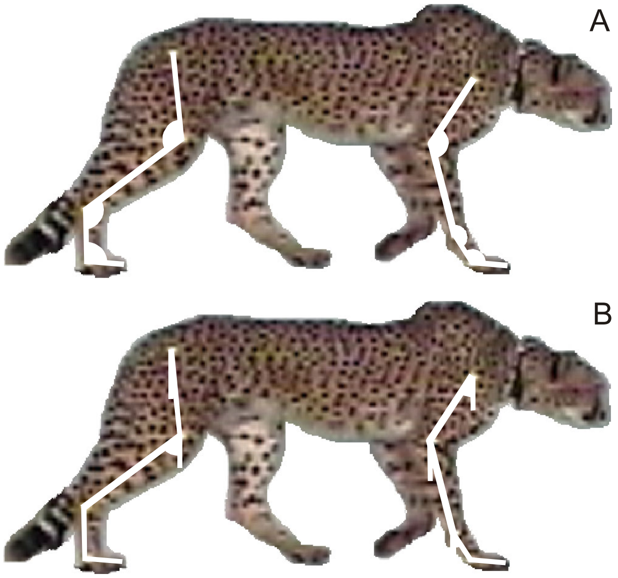


Figure 3

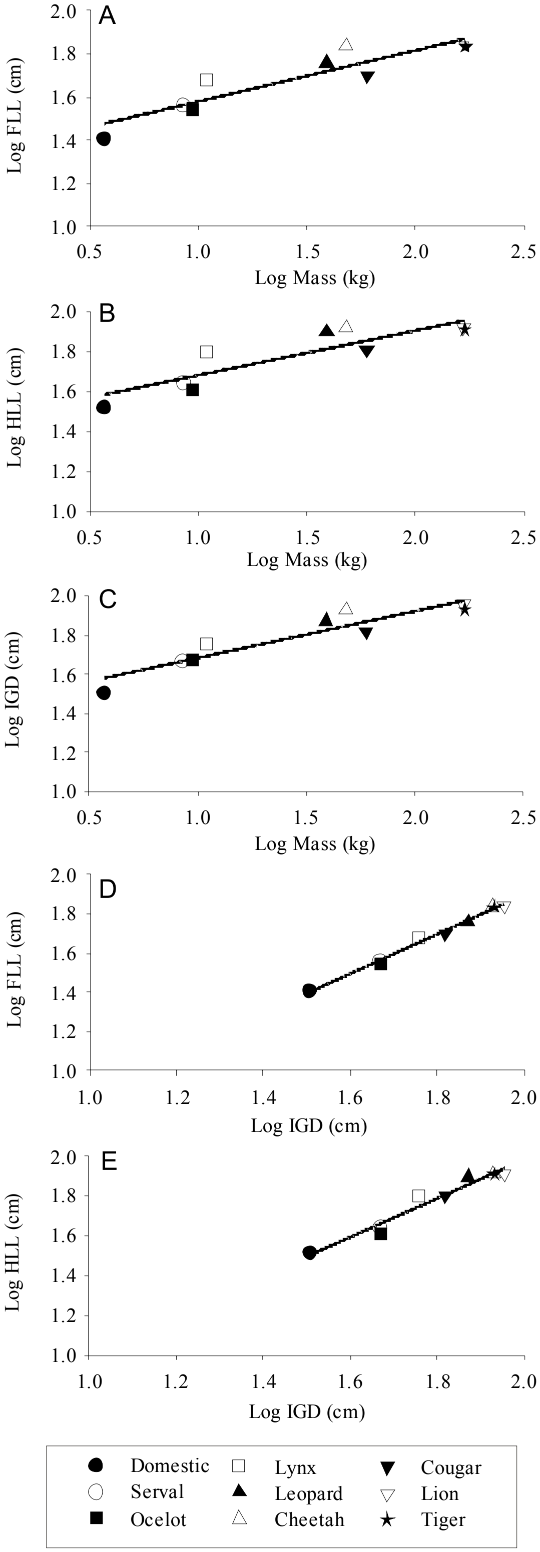

A
Log FLL (cm)
Log Mass (kg)
B
Log HLL (cm)
Log Mass (kg)
C
Log IGD (cm)
Log Mass (kg)
D
Log FLL (cm)
Log IGD (cm)
E
Log HLL (cm)
Log IGD (cm)
2.0
1.8
1.6
1.4
1.2
1.0
0.5
1.0
1.5
2.0
2.5
1.0
1.2
1.4
1.6
1.8
2.0
● Domestic
○ Serval
■ Ocelot
□ Lynx
▲ Leopard
△ Cheetah
▼ Cougar
▽ Lion
★ Tiger

Figure 4

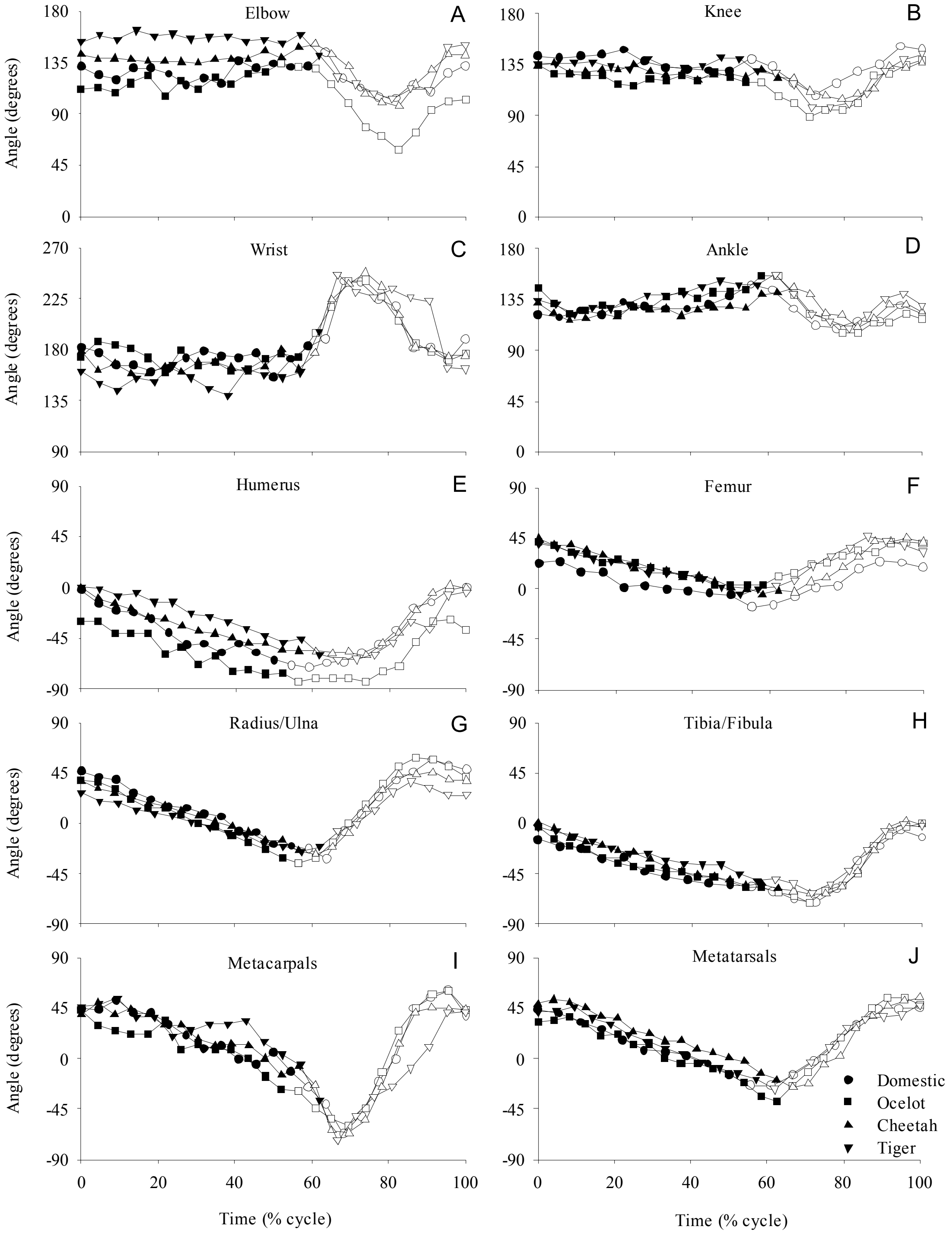

Elbow
A
Knee
B
Wrist
C
Ankle
D
Humerus
E
Femur
F
Radius/Ulna
G
Tibia/Fibula
H
Metacarpals
I
Metatarsals
J
Angle (degrees)
Time (% cycle)
180
135
90
45
0
270
225
-45
-90
20
40
60
80
100
● Domestic
■ Ocelot
▲ Cheetah
▼ Tiger

Figure 5

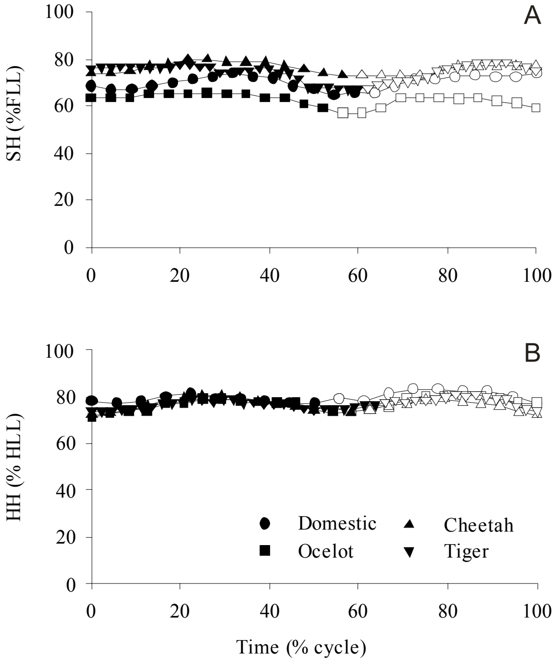
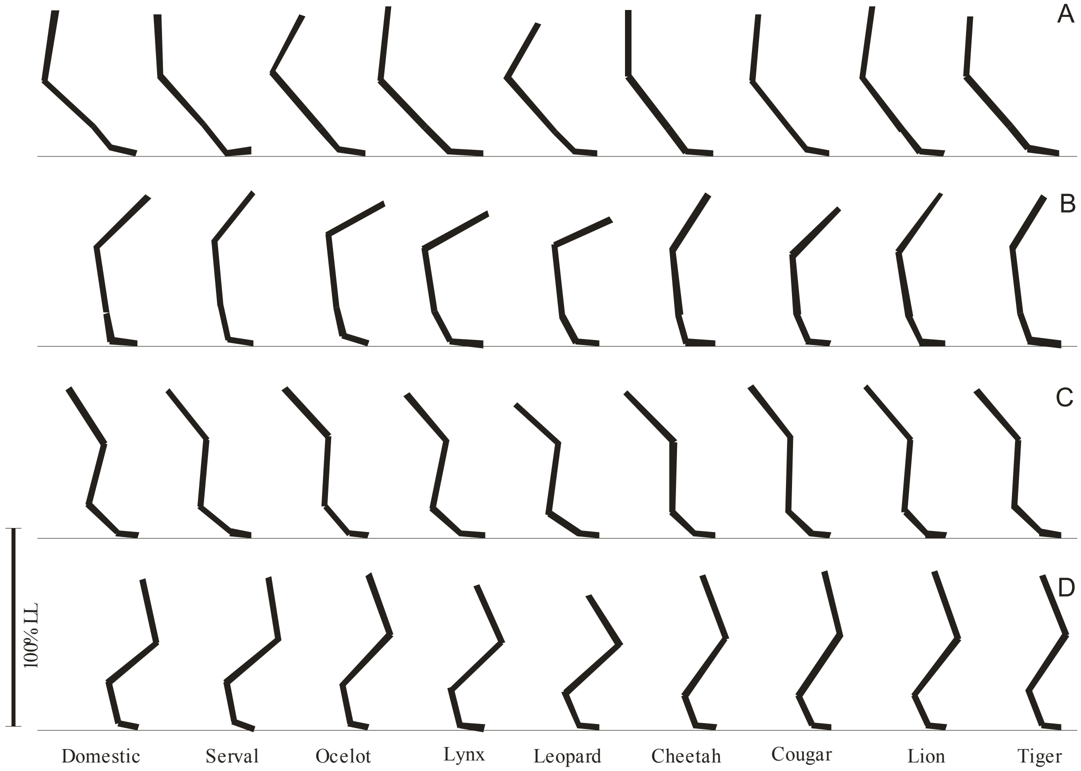
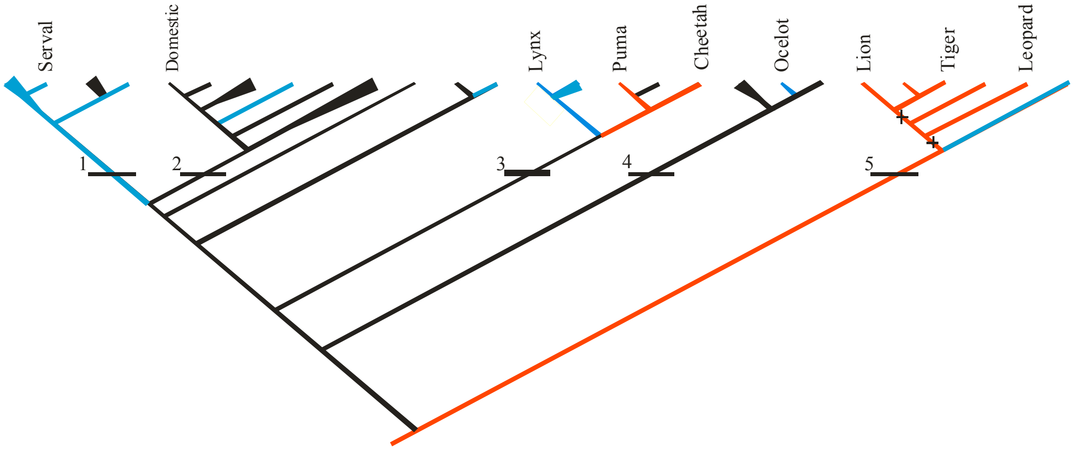

A
SH (%FLL)
0
20
40
60
80
100
0
20
40
60
80
100
B
HH (% HLL)
0
20
40
60
80
100
0
20
40
60
80
100
Time (% cycle)
● Domestic
■ Ocelot
▲ Cheetah
▼ Tiger

Figure 6



A
B
C
D
100% LL
Domestic
Serval
Ocelot
Lynx
Leopard
Cheetah
Cougar
Lion
Tiger

Figure 7


Serval
Domestic
Lynx
Puma
Cheetah
Ocelot
Lion
Tiger
Leopard
1
2
3
4
5
+
+