Interspecific scaling of the morphology and posture of the limbs during the locomotion of cats (Felidae)

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Summary

For phylogenetically diverse mammals, ranging from small rodents to large ungulates, the generalization that limb erectness increases with increased size is supported by some size-dependent scaling relationships of appendicular skeletal anatomy as well as a limited number of direct observations of limb posture during locomotion. If size alone is the causal basis for different limb posture, then the erectness of limbs should increase significantly with increased size within a phylogenetically narrow lineage, but such data are sparse. Thus, to better establish the correlation between size and posture of mammalian limbs, we quantified the scaling relationships between mass and limb dimensions and kinematics during walking of nine species within the felid (cat) clade, which has qualitatively similar limb design. We studied the domestic cat, serval, ocelot, lynx, leopard, cheetah, cougar, lion and tiger, which had masses ranging from <4 kg to nearly 200 kg. Apart from variation associated with overall size, the lengths of the appendicular skeletal structures of most of the felid species were morphologically very similar in multivariate space. The kinematics of the limbs were also relatively uniform, and size had little predictive value for limb posture among felid species. Only three out of a total of 24 angular variables at footfall and midstance changed significantly $(0.02 < P < 0.05)$ with increased mass. Thus, in contrast to previous broadly comparative studies of mammals, larger species of felids did not have more upright limbs than smaller species.

Key words: locomotion, scaling, limb posture, kinematics, limb, skeleton, morphology, allometry, Felidae, cat, evolution, phylogeny.

Introduction

Limb posture is an important attribute of animal body plans because it influences the patterns of movements and muscle activity that can contribute to propulsion, and it affects the loading of the appendicular bones (reviewed in Blob, 2001; Biewener, 2005). Whether animals are standing or moving, limb postures in which the joints are more closely aligned vertically with the point of limb attachment are likely to reduce both the muscular effort required to prevent limb collapse and the bending forces as a result of increasing the portion of the load born by simple compression of the long bones of the limb. This theoretical advantage of a straighter upright limb has long been used in part to explain some gross trends in limb postures including the evolutionary transition from a 'sprawling' to an 'erect' posture, differences between cursorial and non-cursorial mammals and differences associated with increased animal size (Osborn, 1900; Gregory, 1912; Howell, 1944; Gray, 1968; Bakker, 1971; Jenkins, 1971; Charig, 1972; Gambaryan, 1974; McMahon, 1975; Alexander, 1977; Biewener, 1983a).

The major movements of most endothermic vertebrates with erect limb posture are flexion and extension within a nearly vertical plane (Goslow et al., 1973; Gatesy and Biewener, 1991), and hence such limbs with 'fully erect' posture appear vertical in anterior view (Bakker, 1971; Charig, 1972). However, the limbs of many birds and mammals are not straight (Gatesy and Biewener, 1991). As evident in a lateral view, rather than having a column-like limb, variable amounts of flexion in joints give rise to limbs in some taxa that have a more crouched appearance (joints more flexed and more bones nearly horizontal). Thus, the proximal element of some avian and mammalian limbs may be nearly as horizontal as that of some reptiles with sprawling posture (Gatesy, 1991), and such a crouched orientation can contribute considerably to bending loads (reviewed in Blob and Biewener, 1999).

In addition to being influenced by the orientation of bones, loads on the limb bones increase with increased animal weight. Consequently, many studies, using comparisons of phylogenetically diverse species of mammals (belonging to different orders), have sought to determine how limb posture and size are interrelated. This work has produced a long-standing generalization that larger species have less crouched limbs than those of smaller animals (Osborn, 1900; Gregory,

1912; Howell, 1944; Gray, 1968; Gambaryan, 1974; McMahon, 1975; Alexander, 1977; Biewener, 1983a; Biewener, 2005). Supporting evidence comes from qualitative observations that large mammals such as elephants and ungulates stand and move with relatively straight limbs (Osborn, 1900; Howell, 1944; Gray, 1968; Gambaryan, 1974; McMahon, 1975; Alexander, 2003), empirical studies of the scaling of skeletal dimensions from hundreds of species (McMahon, 1975; Bertram and Biewener, 1990; Christiansen, 1999; Iriarte-Diaz, 2002) and a limited number of direct observations of limb posture of phylogenetically diverse species of mammals (reviewed in Biewener, 2005).

One drawback of broadly comparative studies of the effects of size, such as the traditional mouse to elephant curve (Alexander et al., 1979; Biewener, 1983a; Biewener, 1983b; Schmidt-Nielsen, 1984), is that size differences among phylogenetically diverse lineages may confound detecting the effects of size alone (Fig. 1) (Gould, 1966). For example, most species in ungulate orders of mammals are large and their limbs are quite straight, but their limbs also have a host of qualitative differences compared with many other clades of mammals with smaller species such as rodents. If size alone is the causal factor underlying erect limb posture, then the limbs should become increasingly erect with increased size within a phylogenetically narrow lineage as well as with increased size among phylogenetically diverse lineages. A neglected area of previous studies is whether size affects limb posture within a phylogenetically narrow lineage.

In this study, we used species within the Felidae to examine the correlation between limb posture and size. Cats are an excellent model system to use for studying limb posture and scaling relationships because they are a well-defined and phylogenetically narrow clade with substantial differences in body sizes (Mattern and McLennan, 2000; Sunquist and Sunquist, 2002). The two main questions we addressed are: does limb posture vary among felids and, if so, does the erectness of limb increase with increased size? We predicted that if, indeed, limb posture is correlated with size then erectness of the limbs will increase with increased size within the Felidae.

Materials and methods
Experimental subjects

We videotaped nine species of cats for this study including the domestic cat (*Felis catus* L.), ocelot (*Leopardus pardalis* Linné 1758), Canadian lynx (*Lynx canadensis* Kerr 1792), serval (*Leptailurus serval* Ischer de Waldheim 1817), cheetah (*Acinonyx jubatus* L.), cougar (*Puma concolor* Linnaeus 1771), leopard (*Panthera pardus* L.), lion (*Panthera leo* L.) and tiger (*Panthera tigris* L.) (Table 1). We observed cats in the Cat Ambassador Program of the Cincinnati Zoo and Botanical Gardens (Cincinnati, OH, USA), the Columbus Zoo (Columbus, OH, USA), The Exotic Feline Rescue Center (Center Point, IN, USA), The Siberian Tiger Conservation Association (Gambier, OH, USA) and A Zoo For You (Newark, OH, USA). All cats were leash trained with the exception of those at The Exotic Feline Rescue Center. The 25 individuals used for final analysis were chosen according to the following criteria: similar gait and duty factors (DF) (the duration of foot contact with the ground divided by stride duration), continuous movement throughout the stride, and straightness of the path taken. The cats ranged in mass from <4 kg to nearly 200 kg (Table 1), and all individuals were within the normal body mass range for their species in the wild (Sunquist and Sunquist, 2002).

Experimental protocol

We used a JVC digital camera (GR-DVL 9800) to videotape (30 Hz) 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. We 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 and manipulating the joint to find its exact location. The camera was perpendicular to the vertical plane containing the path traveled by a cat. The *x*-axis of the two-dimensional coordinate system was parallel to the overall

Table 1. *Anatomical measurements*

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	3	167±2 (165–170)	90±1 (87–93)	69±1 (63–76)	82±1 (71–86)	1.19
Tiger	5	169± 6 (155–192)	85±1 (75–92)	68±1 (62–74)	81±1 (72–92)	1.19

Values are means ± s.e.m. Ranges are indicated parenthetically. IGD, intergirdle distance; FLL, forelimb length; HLL, hindlimb length; *N*, number of individuals observed per species.
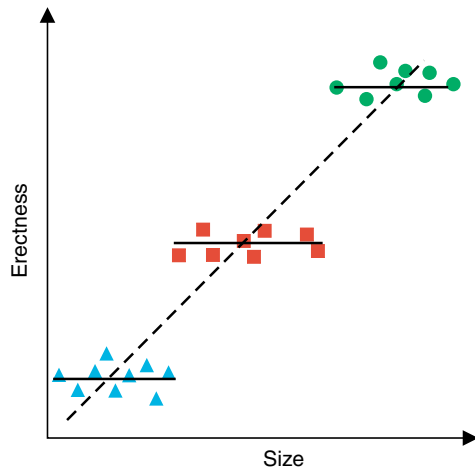
Fig. 1. Hypothetical example of how different limb postures among phylogenetically diverse clades (different symbols) could cause a correlation with increased size even when such a correlation is absent within each of the phylogenetically narrow clades. The broken line indicates an overall trend of increased erectness with increased size, and each short solid line indicates the trend within each phylogenetically narrow clade.

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 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

We obtained masses of each cat from keeper records. We calculated the following anatomical lengths from averages of the two-dimensional analysis of the video footage for a single stride of each individual: lengths of the humerus, radius/ulna, metacarpal, femur, tibia/fibula, metatarsal and phalanges and the intergirdle distance (the two-dimensional distance between the shoulder and hip joints). 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

For detailed motion analysis, we only selected strides that had a similar walking gait as indicated by a small range of DFs with a grand mean of 64% (Table 2). We used DgeeMe v.1.0 (GeeWare.com) for frame-by-frame motion analysis of at least 20 images per stride (from footfall for one limb until the subsequent footfall of that same limb). 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 the times near when some of the largest forces are experienced by a limb during locomotion. In addition, the overall orientation of the limbs is often closest to vertical at midstance since the foot is usually beneath the joint between the limb and the body at this time. Duty factors, speed, relative stride length, relative speed and Froude numbers were not highly correlated with size, but stride frequency was negatively correlated with mass (Table 2). Stride length was the difference between 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, we measured 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 a 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°, 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 at that point in time. If the ratio of shoulder or hip height to the fore-

Table 2. *Whole-stride variables*

Variable	Domestic 4 (16)	Serval 2 (7)	Ocelot 2 (7)	Lynx 1 (4)	Leopard 1 (3)	Cheetah 3 (12)	Cougar 3 (10)	Lion 3 (9)	Tiger 5 (18)	r	P
Fore DF (%)	62±1	60±2	59±2	68±2	62±2	65±1	67±1	66±1	67±1	0.55	0.119
Hind DF (%)	59±1	60±1	60±2	67±2	60±1	64±1	66±1	66±1	66±1	0.60	0.089
v (cm s^{-1})	80±3	85±6	87±9	79±5	173±11	103±4	75±4	81±5	75±3	–0.18	0.648
f (Hz)	1.5±0.07	1.1±0.07	1.3±0.09	1.0±0.06	1.4±0.07	0.84±0.01	0.90±0.03	0.76±0.03	0.69±0.01	–0.72	0.028
SL (%HLL)	165±3	183±8	163±12	122±3	159±7	142±3	130±4	129±3	129±3	–0.59	0.095
v (%HLL s^{-1})	244±10	199±19	213±15	125±7	227±14	126±5	118±6	99±7	91±4	–0.65	0.072
Fr	0.25±0.02	0.20±0.03	0.27±0.05	0.16±0.02	0.48±0.07	0.16±0.01	0.11±0.01	0.10±0.01	0.09±0.01	–0.50	0.170

Values are means ± s.e.m. Number of individuals (and strides measured) are indicated beneath each species. DF, duty factor; v, forward speed; f, frequency; SL, stride length; HLL, hindlimb length; Fr, Froude number (v^2 divided by gravitational acceleration × the midstance hip height).
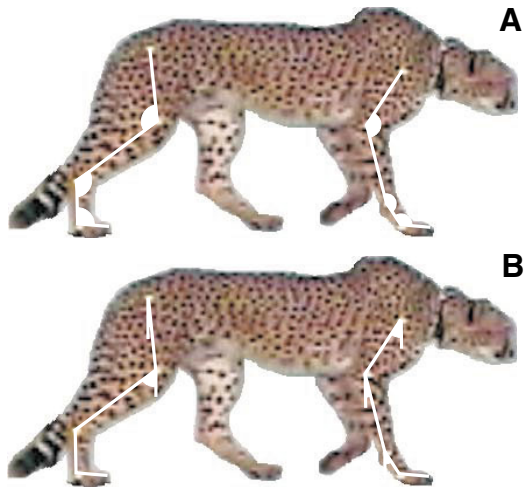
Fig. 2. A right lateral view of a cheetah showing joint locations and conventions for measuring angles of the joints (A) and the long bones relative to vertical (B). The image is near midstance of the right forelimb and late stance of the right hindlimb. From proximal to distal, joint angles were labeled as follows: elbow, wrist, metacarpal–phalange (MCP) for the forelimb and knee, ankle, and metatarsal–phalange (MTP) for the hindlimb. From proximal to distal, the names of the angles relative to vertical (B) are humerus, radius and metacarpals for the forelimb, and femur, tibia and metatarsals for the hindlimb. The angles relative to vertical (B) were positive when the distal portion of a limb segment was anterior to its proximal portion and negative when the distal portion of a limb segment was posterior to its proximal portion.

and hindlimb length, respectively, is 100%, then all joints are fully extended and the cat has a fully erect posture.

Statistical analysis

We used SYSTAT version 9 to perform statistical analyses. Our primary interest was in determining whether or not kinematics indicating limb posture covaried significantly with increased size rather than determining a functional relationship. Thus, we calculated product moment correlation coefficients using the mean values of kinematic variables and mass for each species. For some morphometric data, we were most interested in predicting values of anatomical measurements from some indices of overall size such as mass and length. The residual values between the observed and predicted values thus allowed us to address such issues as which species had limbs that were unusually long for their length, and some of these size-corrected values were used for additional correlational analyses with kinematics. When the primary goal of a regression analysis is prediction, then least squares regressions are often viewed as most appropriate (Sokal and Rohlf, 1995). Before performing regression analyses of morphometric data, we $\log_{10}$ transformed values of anatomical lengths and masses of each species. Hence, the number of observations for the correlation and regression analyses was equal to the number of species. We used $\alpha=0.05$ as the criterion for statistical significance. Unless indicated otherwise, all mean values are presented ± s.e.m. based on the number of strides.

To provide an overview of differences in anatomy and kinematics among the species, we performed principal component analyses (PCA) on the correlation matrices of the data. The numbers of observations for the PCA of anatomical and kinematic data were the number of individuals and the number of strides, respectively. The PCA of anatomical data used nine distances including that between the girdles and those of the four segments within both the fore- and hindlimbs. The PCA of kinematics used 10 variables including the orientation angles of the three most proximal limb segments and the angles of the two most proximal joints within both the fore- and hindlimbs. We performed separate PCAs for the kinematics at the times of footfall and midstance.

Results

Anatomy

The mean linear measurements of the largest species (lions and tigers) were approximately three times the size of the smallest species (domestic cat) (Table 1). The mean mass of the largest species was 45.7 times that of the smallest, and the mass of the largest individual was 58.2 times that of the smallest individual (Table 1). For all species, the hindlimbs

Table 3. *Proportions of individual limb segment length relative to total limb length*

Relative length	Domestic (4)	Serval (2)	Ocelot (2)	Lynx (1)	Leopard (1)	Cheetah (3)	Cougar (3)	Lion (3)	Tiger (5)
Forelimb segment (% forelimb 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
Phalanges	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 (% hindlimb 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
Phalange	10.5±0.3	11.2±1.0	9.9±0.4	12.6	11.4	11.1±0.5	10.7±0.5	9.7±0.3	9.9±0.7

Values are means ± s.e.m. Number of individuals measured is indicated parenthetically beneath each species.

Table 4. *Least-squares regression parameters of the scaling equations for log_10-transformed values of species means of lengths (cm) and masses (kg)*

Dependent variable	Independent variable	Slope ± 95% CL	Intercept ± 95% CL	N	r^2	P
log IGD	log Mass	0.238±0.081	1.445±0.126	9	0.87	<0.001
log FLL	log Mass	0.249±0.096	1.310±0.149	9	0.84	<0.001
log HLL	log Mass	0.231±0.107	1.440±0.166	9	0.79	0.001
log Mass	log IGD	3.663±1.250	−5.110±2.244	9	0.87	<0.001
log FLL	log IGD	1.059±0.093	−0.107±0.024	9	0.99	<0.001
log HLL	log IGD	1.001±0.182	−0.015±0.046	9	0.96	<0.001

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

were longer than the forelimbs (Table 1). 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 3). Within each species, the combined lengths of the metapodials and phalanges were consistently less than that of the humerus or femur (Table 3).

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 difference was usually not statistically significant (Table 4). The slopes of the scaling relationships of total limb length and intergirdle distance were almost exactly 1.0, and compared to mass, intergirdle distance had better

predictive value for scaling of the total limb lengths (value of r^2 in Table 4). 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. Although servals are commonly described as a long-legged species of felid (Sunquist and Sunquist, 2002), the servals in our sample did not have unusually long limb lengths when adjusted either for mass or for intergirdle distance (Fig. 3). The servals did have relatively long metacarpal and metatarsal bones (Table 2).
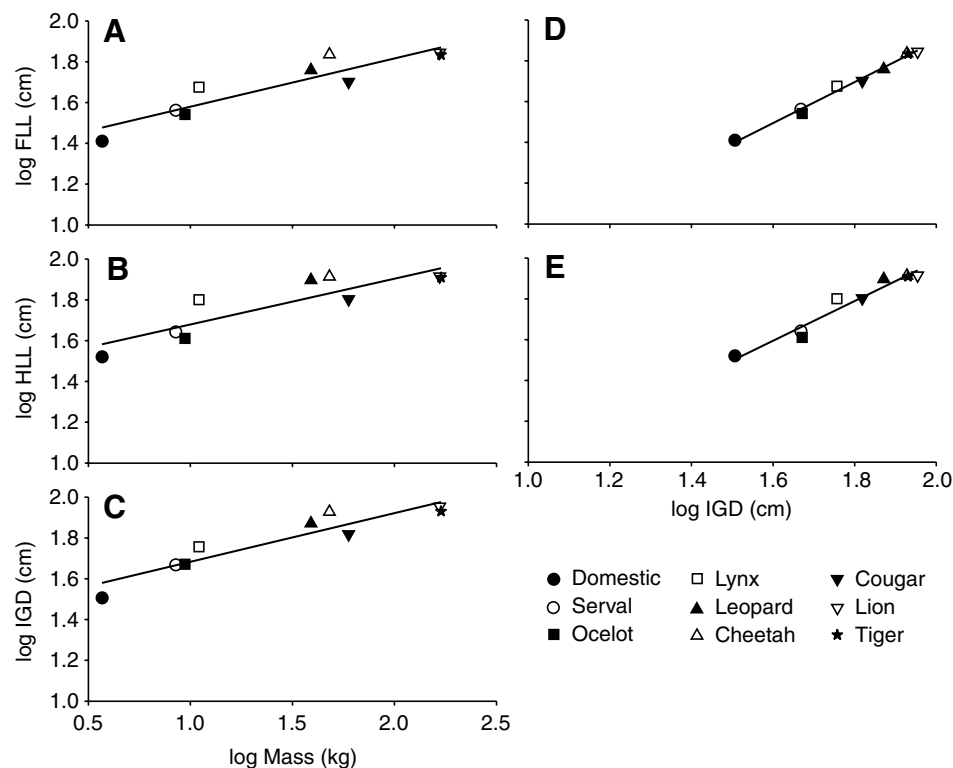

Fig. 3. Scaling relationships of log_10-transformed mean values of each species for anatomical lengths of the forelimb (A), hindlimb (B) and intergirdle distance (C) *versus* mass, and forelimb length (D) and hindlimb (E) length *versus* intergirdle distance. See Table 4 for the scaling equations.

For the PCA of anatomical measurements, the first and second components explained 93.4% and 2.9% of the total variance, respectively. All of the absolute lengths had high positive loadings for PC1 (>0.94), and the scores of PC1 increased conspicuously with the mass of individual cats (Fig. 4A). Thus, much of the segregation of species from low to high values of PC1 is consistent with the effects of overall size (Fig. 4A). In contrast to PC1, scores of PC2 had few consistent differences either among species or with increased mass (Fig. 4B).

Kinematics and limb posture

The changes in joint angles and orientation of the limb segments that occurred within the stride cycle were consistent across all of the species in this study (Fig. 5). Throughout much of stance, the angles of the elbow, knee and ankle joints were nearly constant and approximately 135°, whereas the wrist
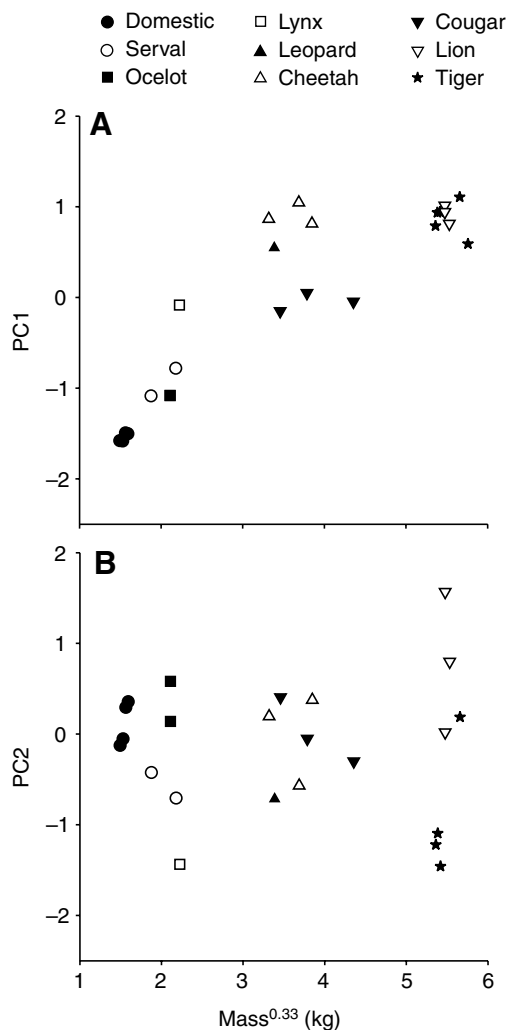

Fig. 4. Principal component (PC) scores from analyses of anatomy *versus* the cube root of mass. Each point represents an individual. Many of the felid species are anatomically distinct, mainly as a result of overall size.

remained nearly straight (Fig. 5A–D; Table 5). Near midswing, the elbow and knee were maximally flexed (Fig. 5A,B), and maximal plantar flexion of the wrist (Fig. 5C) and maximal dorsiflexion of the ankle (Fig. 5D) also occurred. The elbow, knee and ankle were never straightened completely during stance or at any other time during the stride cycle.

The angles of the limb segments relative to vertical decreased steadily throughout stance (Fig. 5E–J). The humerus (Fig. 5E) and tibia (Fig. 5H) were nearest vertical at footfall, whereas the femur was most near vertical at endstance (Fig. 5F). The metacarpal (Fig. 5I), metatarsal (Fig. 5J) and radius/ulna (Fig. 5G) limb segments were nearly vertical at midstance. The negative angles of limb segment orientation indicate that the distal portion of the humerus was posterior to the shoulder (Fig. 5E), and the distal portion of the tibia was posterior to the knee (Fig. 5H) throughout the stride cycle. The distal portion of the femur (Fig. 5F) was only briefly posterior to the hip near the stance–swing transition. The radius (Fig. 5G) and more distal portions of the forelimb (Fig. 5I) and hindlimb (Fig. 5J) alternated between having their distal portions anterior and posterior to their proximal portion during an entire stride cycle.

At midstance, the point of limb attachment was at its highest (Fig. 6) and the foot was nearly beneath the point of limb attachment (Fig. 7). Thus, the overall limb posture was most erect at midstance.

Overall, the postures of fore- and hindlimbs at footfall and midstance were similar among all species studied (Fig. 7). With the exception of the elbow angle at midstance, no joint angles of either the 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 was highly correlated with mass and only two variables at midstance had moderate correlation with size (Table 6). However, even a modest correction for multiple comparisons would render these relationships 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 orientations of the humerus of the leopard and ocelot were somewhat more horizontal than those of the other species.

To evaluate the potential effects of limb length relative to the overall size of felids in our study, we performed additional correlation analyses between residual values of limb length predicted from mass and all of the kinematic variables in Tables 5 and 6. None of the kinematic variables of the forelimb was significantly correlated with the residual values predicted either from our sample of nine species (Table 4). The two highest correlations between hindlimb length residual and kinematics were for femur orientation at midstance (r=0.70, two-tailed P=0.036) and orientation of the phalanges at midstance (r=0.66, P=0.051). These two 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.

The PCAs of kinematic data emphasized the similarity among the felid species and the lack of a clear pattern that was associated with the size of the species (Fig. 8). For the data at
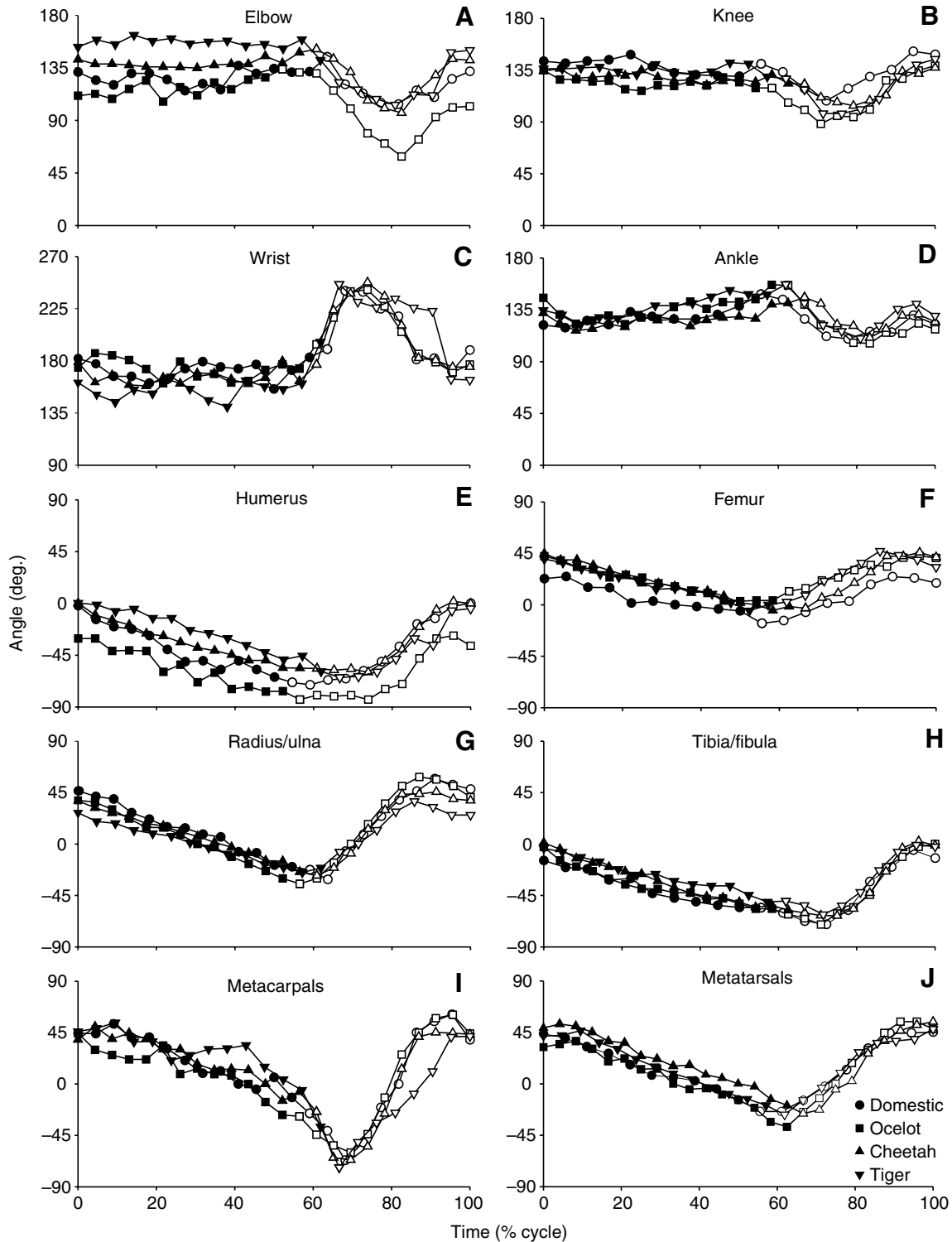

Fig. 5. Joint angles (A–D) and angles relative to a vertical (E–J) *versus* time for one stride of a single individual for the domestic cat, ocelot, cheetah and tiger. Filled symbols indicate stance phase, while open symbols indicate swing phase during the stride cycle, where 0% indicates footfall. The ranges of all *y*-axes are 180°.

Table 5. *Joint angles at footfall and midstance of the fore- and hindlimbs*

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

Values are means ± s.e.m. *r*, correlation coefficient between the mean values of kinematics and mass for *N*=9 species. MCP, metacarpal–phalange joint; MTP, metatarsal–phalange joint. The numbers of individuals (and strides measured) are indicated beneath each species.

footfall, PC1 and PC2 accounted for 31% and 20% of the total variance observed, and these quantities for PC1 and PC2 for midstance data were 35% and 22%, respectively.

Discussion

In contrast to previous generalizations that increased size correlates with more erect limb posture, the limb postures of

Fig. 6. Relative (% total limb length) height of the shoulder (A) and relative hip height (B) *versus* time for one stride of a single individual for the domestic cat, ocelot, cheetah and tiger. Filled symbols indicate stance, and open symbols indicate swing phase of the stride cycle where *t*=0% and 100% indicates footfall. The data are for the same strides as shown in Fig. 5.

felids in our study were uniform overall and unrelated to size despite the masses of individual felids in this study ranging from 3.3 kg (domestic cat) to 192 kg (tiger). Support for size affecting limb posture has come from comparisons of phylogenetically diverse species (belonging to different orders) including some rather qualitative observations (Osborn, 1900; Gregory, 1912; Howell, 1944; Gray, 1968; Gambaryan, 1974; McMahon, 1975; Alexander, 1977), implications from the scaling of limb morphology (Bertram and Biewener, 1990; Christiansen, 1999) and quantitative measurements of effective mechanical advantage (EMA), mainly at the trot–gallop transition (reviewed in Biewener, 2005). In light of this variety of approaches used to study limb posture, interpreting our results is facilitated by first evaluating the likely effects of methodological differences such as: (1) the conditions during which limb posture was observed, (2) the methods of measuring limb posture, (3) the range in size of the study taxa and (4) the phylogenetic and ecological diversity of the study taxa.

Speed and limb posture

As is the case for most vertebrates, many aspects of the kinematics of felid limbs change significantly with locomotor speed and gait (Goslow et al., 1973). Thus, evaluating the potential effects of variation in speed can clarify whether variation in speed could confound either our conclusions regarding the effects of size among the felid species within our study or comparisons between our conclusions on the effects of size and those of other studies. The criteria for determining physiologically 'equivalent' speeds of animals of different size include similarities in gaits, gait transitions, relative speed, DFs, Froude numbers, phase relationships between potential and kinetic energy, and preferred speeds of animals within a single gait, but among different sizes or species of animals gait
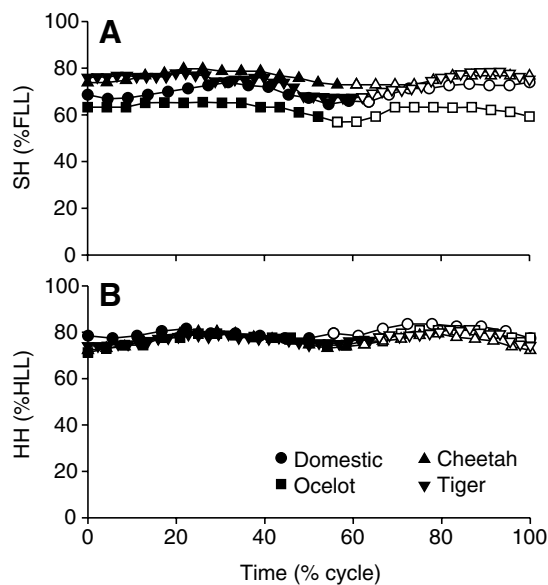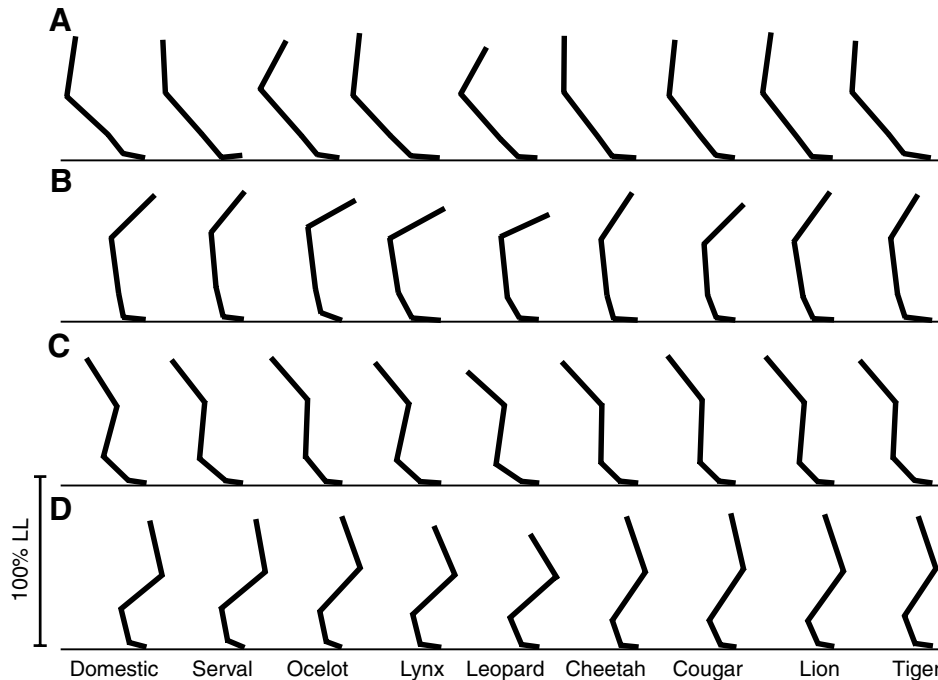
Fig. 7. Mean values of joint angles and limb segment orientation. The relative length (% total limb length) of each segment within a limb is also a mean value for each of the study species of the fore and hindlimbs at footfall (A,C) and midstance (B,D) for all species. From proximal to distal, the end points of the line segments represent shoulder, elbow, wrist, distal end of the metacarpals and tips of the toes of the forelimb at footfall (A) and midstance (B). From proximal to distal, the end points of the line segments represent hip, knee, ankle, distal end of the metatarsals and tips of the toes of the hindlimb at footfall (C) and midstance (D). The reference scale on the left indicates the potential height of a limb if all limb segments were vertical and all joint angles were 180°.

transitions may occur at slightly different values to many of these other quantities (Heglund et al., 1974; McMahon, 1975; Alexander, 1977; Hoyt and Taylor, 1981; Biewener, 1983a; Gatesy and Biewener, 1991; Irschick and Jayne, 1999; Hutchinson et al., 2003). Consequently, different authors have emphasized different criteria for equivalent speeds rather than a single criterion being universally accepted.

Goslow et al. (Goslow et al., 1973) quantified the kinematics of domestic cats (2–3 kg) for three gaits over a wide range of speed and DFs including a 'slow walk' (0.68 m s^{-1}, DF=63%), trot (1.62 m s^{-1}, DF=43%) and a high speed gallop (7.34 m s^{-1}, DF=22%). With increased speed, the absolute duration of the stance phase decreases considerably for cats moving at slow to moderate speeds, whereas the duration of the swing phase

Table 6. *Limb segment angles relative to vertical and relative heights of the shoulder and hip*

Variable	Domestic 4 (16)	Serval 2 (7)	Ocelot 2 (7)	Lynx 1 (4)	Leopard 1 (3)	Cheetah 3 (12)	Cougar 3 (10)	Lion 3 (9)	Tiger 5 (18)	r	P
Footfall											
Humerus (deg.)	−7±2	−3±4	−28±3	−6±3	−29±2	−1±1	−12±2	−8±1	−4±1	0.48	0.195
Radius (deg.)	42±2	43±2	41±3	43±1	41±4	37±1	38±1	38±2	41±2	−0.29	0.457
Metacarpal (deg.)	38±2	40±2	40±3	45±2	45±8	36±1	39±1	37±1	38±1	−0.38	0.312
SH (%FLL)	72±1	71±3	67±2	68±1	59±3	77±1	75±2	77±2	75±2	0.28	0.465
Femur (deg.)	33±1	39±2	42±2	40±2	49±1	44±1	38±1	41±2	41±2	−0.08	0.839
Tibia (deg.)	−15±2	−5±1	−2±2	−12±1	−8±2	1±1	−2±2	−5±1	−1±1	0.50	0.170
Metatarsal (deg.)	46±2	50±1	43±3	47±3	57±5	46±1	46±2	44±2	46±2	−0.20	0.598
HH (%HLL)	75±2	73±4	72±2	72±2	65±1	78±4	77±1	78±3	76±2	0.50	0.169
Midstance											
Humerus (deg.)	−45±2	−38±5	−60±2	−60±2	−65±2	−34±1	−45±2	−36±2	−32±2	0.75	0.020
Radius/Ulna (deg.)	8±1	4±2	7±2	9±2	6±3	6±1	4±2	9±2	7±1	−0.09	0.827
Metacarpal (deg.)	11±2	14±3	13±3	28±2	30±7	16±2	21±2	25±2	18±1	0.16	0.673
SH (%FLL)	74±2	76±4	72±1	69±2	61±2	80±1	78±1	79±2	77±1	0.51	0.160
Femur (deg.)	13±2	10±3	20±2	24±2	31±6	20±1	13±1	19±2	21±1	−0.06	0.881
Tibia (deg.)	−51±2	−50±3	−43±3	−47±3	−49±5	−35±1	−34±1	−37±1	−34±2	0.62	0.075
Metatarsal (deg.)	13±2	11±2	13±1	13±2	23±3	19±2	25±3	24±3	21±2	0.67	0.049
HH (%HLL)	77±2	78±1	76±2	74±2	63±2	80±1	82±2	79±2	80±1	0.29	0.450

Values are means ± s.e.m. *r*, correlation coefficient between the mean values of kinematics and mass for *N*=9 species. SH, shoulder height; HH, hip height; FLL, total forelimb length; HLL, total hindlimb length. The numbers of individuals (and strides measured) are indicated beneath each species.

changes little. The amplitudes of joint angles may also vary with speed, but the magnitude of this variation depends on the joint, when a value is measured during the stride cycle and whether or not a gait change occurs. Overall, the angles measured at midstance vary less with speed than those measured at other times during the stride cycle (Goslow et al., 1973). Over a wide range of walking speeds (0.33–1.19 m s^{-1}) several limb angles of domestic cats are effectively constant (Kuhtz-Buschbeck et al., 1994). In addition, the changes with speeds ranging from a walk to a trot are generally subtle compared to between a trot and a gallop (Goslow et al., 1973). Similar findings have been used by some as justification for pooling data from walking and trotting (Fischer et al., 2002) over a much wider range of relative speeds and gait than in our sample of felids walking.

The directionality of some speed effects is opposite that required to confound our finding of non-significant correlations with felid size. For example, the mean angle of the knee at midstance during a trot is three degrees less than that during a walk, and during a gallop is seven degrees less than during a

trot of domestic cats (Goslow et al., 1973). This decreased knee angle indicates a slightly more crouched posture with increased speed. Such an effect of speed would actually bias the results in favor of finding a positive correlation with size in our study since the domestic cats were both the smallest species and the species moving at the fastest relative speed (Table 2). However, we did not detect a significant correlation between and size and the knee angle or most other kinematic variables.

Finally, many of the mean effects of speed between the walk and trot of a cat (Goslow et al., 1973) are so small that they are a similar magnitude to the stride-to-stride variation we observed within an individual moving at a constant speed. Although the absolute speeds of walking varied considerably among the felid species we studied, we did not study a range of speeds that included any substantial gait changes. All of our cats were performing lateral sequence walking (DF>50%), and 27% and 56% of the strides analyzed were either a fast (50%<DF<60%) or a moderate (60%<DF<70%) speed walk, respectively (Hildebrand, 1976). Our ability to control speed precisely was limited in part because many individuals had a strong preference for walking over a limited range of speed, which suggests that they were near their preferred speed. Thus, the slight variation in the relative speeds within our sample seems unlikely to affect our fundamental conclusion that size of the felid species is not correlated with most measures of limb posture during walking.

Straighter limb posture can have theoretical benefits at all locomotor speeds as well as during standing (Osborn, 1900; Gregory, 1912; Howell, 1944; Gray, 1968; Bakker, 1971; Charig, 1972; Gambaryan, 1974; McMahon, 1975; Alexander, 1977), but our study did not find that larger felids walked with overall differences in limb posture that were consistent with these theoretical benefits of straighter limbs. Much of the recent literature on the effects of size on limb posture has carefully controlled for the speed of different size species by studying EMA at midstance only during running at the trot–gallop transition (reviewed in Biewener, 2005). However, earlier work found that for three species of different size mammals (ground squirrel, dog and horse) EMA did not change significantly over a wide range of speeds including some walking and running gaits (Biewener, 1989). Small species of birds that are more crouched during walking also tend to be more crouched during running (Gatesy and Biewener, 1991). During walking, trotting and galloping the limbs of dogs are consistently less crouched than those of cats using similar gaits, and the differences in the midstance kinematics between these two species within a gait tend to be large compared with those among gaits within each of the species (Goslow et al., 1973; Goslow et al., 1981). Thus, many of the interspecific trends in limb posture that are apparent at one speed and gait also tend to occur at other speeds and gaits.
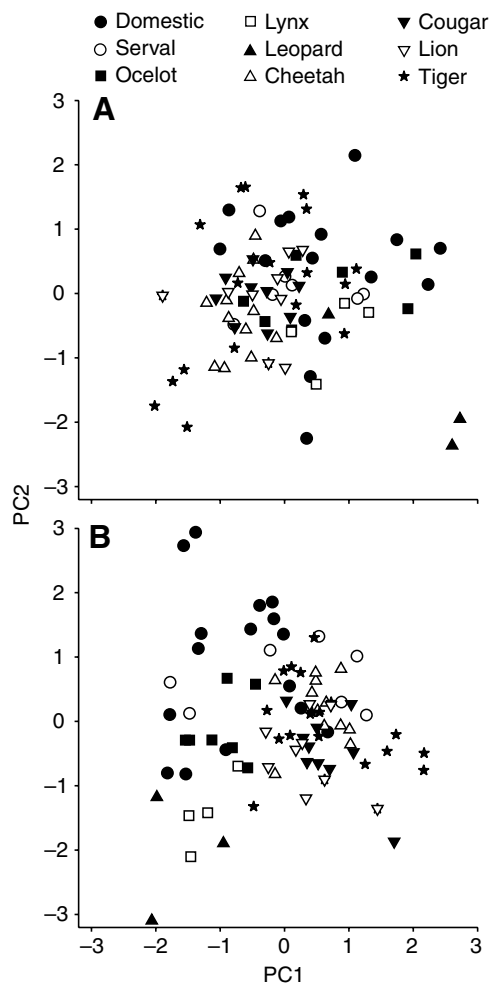

Fig. 8. Principal component (PC) scores from analyses of limb posture at both footfall (A) and midstance (B). Each point represents a single stride. The limb postures of different species have a large overlap in multivariate space.

Limb posture versus EMA

Although 'crouched' is convenient short hand for describing how EMA varies among mammals of different size, for a given EMA the extent to which a limb is crouched may vary and *vice versa*. EMA is a weighted average of the ratios of the moment

arms upon which the limb extensor muscles act (r) and the moment arms (R) between the joints and the ground reaction force (GRF) (Biewener, 2005). Thus, EMA can vary in two major ways even when the orientation of limb segments and joint angles are constant. First, a change in the orientation of the GRF is sufficient to change EMA when all other factors are constant. Second, if two individuals have different lengths of the moment arms upon which the extensor muscles are acting (r), then EMA could vary event when the joint angles and orientation of the GRF were constant.

Two key consequences of the manner in which EMA varies with the size of the diverse mammals at the trot–gallop transition are that stresses and safety factors are nearly constant (Biewener, 2005). We cannot definitively exclude the possibility that EMA increased with increased size of the felids that we studied, but this seems unlikely. The orientations of the GRF generally change little even among phylogenetically diverse taxa (Biewener, 2005), and thus large increases in the lengths of the muscle moment arms (r) of felids would be required for EMA to increase significantly with increased size of walking felids. Perhaps, the nearly constant limb posture that we observed in felids is accommodated by increased stresses in larger species even though similar gaits were being used. Given how small the loads are during walking *versus* running at the trot–run transition, the safety factors during walking seem unlikely to be a very important aspect of limb design, posture and function.

Larger values of EMA for an entire limb need not indicate that all segments of the limb are more crouched. For example, the hindlimb EMA of running horse is approximately eight times that of the ground squirrel, but the orientation of the tibia relative to vertical is nearly identical in these two species (Biewener, 1990). Thus, data on angles of individual joints and limb segments greatly facilitate interpreting composite measures of overall limb posture such as EMA or relative hip height. However, such comparative kinematic data over a large range in size are still quite limited.

Size and phylogeny

Biewener reviews the results of several studies using EMA to quantify the limb posture of 14 phylogenetically diverse species mammals, including eight rodents, three ungulates and one carnivore (dog) (Biewener, 2005). Thus, the preponderance of large and small species for which EMA is known are ungulates and rodents, respectively. The subset of rodent species within the data of Biewener (Biewener, 2005) may provide the most similar comparison with our phylogenetically restricted sample of felid carnivores. Unlike the lack of scaling of limb posture over the nearly 50-fold range in mass of the felids that we studied, eight rodent species ranging from deer mice (<30 g) to capybaras (>30 kg) have significant scaling of EMA with mass that was indistinguishable from that of the combined sample of Biewener (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 from the other rodents studied by Biewener. The small sample size of mammalian lineages other than rodents precluded

Biewener (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 these studies is that scaling relationships differ for large and small species. For example, a sample of 118 species including seven families of terrestrial Carnivora (0.1–500 kg) had differential scaling (Bertram and Biewener, 1990). This observed positive allometry for limb bone diameter *versus* length of large (>100 kg) species may compensate for minimal differences in limb posture, whereas the nearly isometric scaling of the skeletal dimensions of smaller mammals is possible as a result of larger species having more upright limb posture (Bertram and Biewener, 1990). Thus, some expectations for an effect of size on limb posture are size dependent. However, seven of the nine felid species in our study had a wide range of masses within the range of size for which differences in limb posture are expected (Bertram and Biewener, 1990), 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 (Mattern and McLennan, 2000). The ancestral felid was probably large (>40 kg). Consequently, much of the large size throughout the species in the *Panthera* clade (lions, tigers, leopards and jaguars) is probably symplesiomorphic, but relative to the most recent common ancestor of this clade some additional increases in body size probably occurred in the lineage containing lions, tigers and jaguars (Fig. 9). Two additional increases in size occurred independently in the lineage containing the serval and another containing lynx, puma and cheetah. Although a more recent phylogeny of felids (Johnson et al., 2006) differs in some details from that used by Mattern and McLennan (Mattern and McLennan, 2000), it also supports separate evolutionary origins of both increased and decreased overall size within the felids. 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 we observed within the felid clade is that limb posture of extant felids has been retained from a common ancestor. Even though the size of extant felid species does not 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 (Biewener, 2005) for the limb posture and mass of diverse extant mammals.

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, and available illustrations (Gambaryan, 1974) suggest that their hindlimbs are more crouched than those of felids. All other terrestrial mammals larger than the largest felid
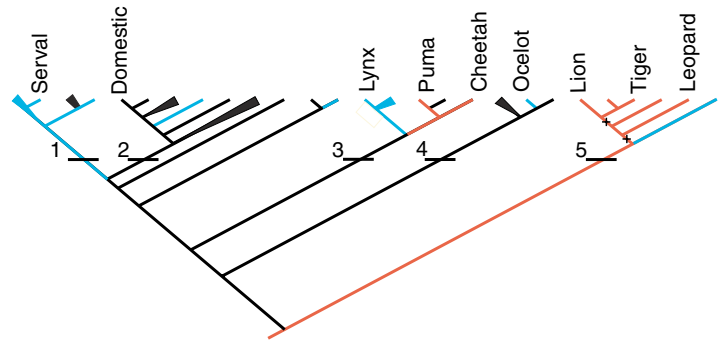
Fig. 9. A simplified phylogeny of Felidae modified from Mattern and McLennan (Mattern and McLennan, 2000) showing trends in the evolution of size. Numbers indicate cat clades: 1, caracal and leopard cat; 2, domestic; 3, lynx and puma; 4, ocelot; 5, *Panthera*. Wedges indicated multiple species at that branch. Red, blue and black indicate large (>40 kg) medium (11–40 kg) and small (1–10 kg) species, respectively. Only the nine species of this study are labeled. + indicates additional increases in body size.

have unguilgrade limb posture and some of these species also exceed the size of the largest species of bears. Christiansen (Christiansen, 2002) suggested that the allometry of appendicular anatomy has constrained maximal size of terrestrial animals, the largest of which (sauropod dinosaurs) is less than half 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 (Biewener, 1983a) could provide interesting insights into this issue.

Several studies of the limb structure and function of mammals have recognized that different conclusions regarding the effects of size can result from gathering data from samples with different phylogenetic diversity (Gambaryan, 1974; McMahon, 1975; Alexander et al., 1979; Bertram and Biewener, 1990; Steudel and Beattie, 1993; Schmidt, 2005). A persistent challenge to the study of limb posture and size in mammals is that many aspects of limb design tend to covary with differences in size among orders and families (Gambaryan, 1974), and hence obtaining comparable kinematic data over a large range of size for species within a phylogenetically narrow clade is difficult. Consequently, whether the similarity of limb kinematics within felids of different size is an anomaly or a generality for a phylogenetically narrow lineage will only become apparent after more quantitative data on limb posture are gathered for other phylogenetically restricted samples of mammals.

Ecological and behavioral diversity

If the morphology and limb posture of felids are correlated with ecological and behavioral specializations, then this could confound detecting correlations with size. Consequently, examining the ecological and behavioral diversity within the felids we studied provides helpful context for interpreting the extent to which limb morphology and limb posture vary.

In our sample of felids, the cheetah appears most unusual as it has the fastest sprinting speed (103 km h^{-1}) known for a terrestrial vertebrate (Sharp, 1997), and this species has the longest limbs for its mass. Most felids have substantial mobility of the limbs that is associated with climbing and prey manipulation, but cheetahs have notable specializations in the

forelimb joints that probably help to stabilize them during high-speed running (Andersson, 2004). Lynx also have relatively long limbs for their mass, and their snowshoe-like feet facilitate moving in snow (Sunquist and Sunquist, 2002). Servals often occur in habitats with long grasses, in which their tall and slim build may facilitate detecting and capturing small mammalian prey, and they have a remarkable ability to jump 2–3 m high to catch a bird or insect in mid-flight (Sunquist and Sunquist, 2002). Despite some of these specialized habits, none of these three species had especially unique limb posture (Fig. 8).

All of the felid species in our study appear to be capable of climbing, but the ocelot and leopard are commonly considered more arboreal that the other species in our study (Sunquist and Sunquist, 2002). The leopard had the most crouched fore- and hindlimb posture of any of the species in our study (Fig. 7), 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, which presumably lowers the center of mass and hence reduces 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; Lammers and Bikenvicius, 2004). Thus, the slightly more crouched positions of the leopards and ocelots observed in this study might be associated with their arboreal tendencies.

Hence, the extent to which felid species inhabit open or forested environments or have increased reliance on high-speed pursuit, jumping or climbing does vary. However, these factors seem to have little overall influence on our observations of felid limb posture.

Conclusions

The felid species we studied had nearly a 50-fold range in mass, but largely lacked 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.

The moderately erect limb posture of all extant felids seems to have been evolutionarily conservative and perhaps similar to that of a relatively large ancestral felid. Consequently, our 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).

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