Femoral Strength and Posture in Terrestrial Birds and Non-Avian Theropods

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ABSTRACT
Osteological and experimental evidence suggest a change in femoral posture between non-avian dinosaurs (in which the femur presumably was carried in a subvertical position) and birds (in which the femur is held nearly horizontal during most phases of terrestrial locomotion). In this study, we used a broad comparative sample to test the hypothesis that cross-sectional properties of the femur records evidence of this presumed change in posture. I_{max} and I_{min} (second moment of area, related to resistance to bending) and cross-sectional area (indicating resistance to compression) were measured from computed tomography scans of the femora of 30 species of flightless or primarily terrestrial birds, one probable non-dinosaur dinosauromorph, and at least four species of non-avian theropods. It was predicted that birds should have more eccentrically shaped femoral midshafts as measured by I_{max}/I_{min} (reflecting greater bending) and comparatively smaller cross-sectional areas than non-avians. Results show that no significant differences occur between non-avian dinosaurs and birds for any parameter, and the samples overlapped broadly in many cases. Thus, cross-sectional properties cannot be used to infer differences in femoral posture between the two groups. This surprising finding might be explained by the fact that femoral postures were not drastically different or that a gradation of postures occurred in each sample. It is also possible that bone loading during life was not closely correlated with cross-sectional morphology. We conclude that cross-sectional properties should be used with caution in determining the posture and behaviors of extinct animals, and only in conjunction with other morphological information. Anat Rec, 292:1406–1411, 2009.

Key words: Theropoda; second moment of area; locomotion; dinosaur evolution; cross-sectional properties

INTRODUCTION

The evolutionary transition from non-avian theropods to crown-group birds (Neornithes) was filled with numerous, well-documented changes in the body plan and (presumed) changes in function. Although the avian wing has rightfully received a considerable amount of attention, a number of experimental and descriptive studies have also focused on the unique hind limb anatomy, posture, and mechanics of extant birds in relation to their non-avian precursors (e.g., Gatesy, 1990; Carrano and Biewener, 1999; Hutchinson and Gatesy, 2000; Hutchinson, 2001, 2006). During terrestrial locomotion, birds hold their femora relatively horizontally, with most hind limb excursion concentrated at the knee joint. Thus, there is relatively little retraction of the femur during the stance phase of terrestrial locomotion, especially at

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lower speeds, and the femur never passes a vertical position (Gatesy, 1990, 1999). This contrasts with the condition seen in crocodilians (and presumably most non-avian theropods), in which the femur has a wide angle of excursion during the stance phase, and passes the vertical position (e.g., Gatesy, 1995; Hutchinson and Gatesy, 2000). Muscular reconstructions (especially the presumed size and action of m. caudofemoralis longus, an important femoral retractor in non-avian archosaurs which can be reconstructed on the basis of osteological correlates on the femur and caudal vertebrae) have played a key role in understanding femoral posture in non-avian theropods (Gatesy, 1995; Hutchinson, 2001). The best evidence to date suggests that the femur was typically held much more vertically in most non-avian theropods than in extant birds. A strict dichotomy in posture is probably not correct (Hutchinson and Allen, 2009), but overall femoral posture undoubtedly did change throughout theropod evolution. So, what other lines of evidence might provide independent confirmation of femoral posture and modes of hind limb locomotion?

An increasing body of work has focused on using the cross-sectional geometry of long bones as a tool for reconstructing behavior and ontogenetic patterns in both extinct and extant animals (e.g., Heinrich et al., 1993; Ruff et al., 1999; Loewen and Sampson, 2000; Blob, 2006; Habib and Ruff, 2008). Among many other influences (such as hormones or evolutionary constraints), bone adapts to its loading environments. Thus, a bone is at least partly shaped to withstand the forces experienced on a regular basis. If a long bone is modeled as a beam, both the shape of the bone in cross-section, as well as the direction and magnitude of the applied loads, are critical factors in determining the mechanical integrity of the bone. Theoretically, then information on the cross-sectional properties of a bone can be used to interpret the loads associated with a particular cross-sectional morphology, or vice versa. For instance, Habib and Ruff (2008) found that comparisons of humeral strength versus femoral strength (as measured from cross-sectional properties of both bones) were useful in distinguishing locomotor categories in extant birds. In another study, Heinrich et al. (1993) inferred ontogenetic changes in locomotion based on cross-sectional properties of the femur for the ornithopod dinosaur *Dryosaurus*. Thus, cross-sectional properties of long bones have great potential as proxies for locomotor parameters.

If a change in femoral posture occurred during the course of bird evolution, it is then expected that this change should be reflected in bone structure. For instance, the femur of a non-avian theropod such as *Coelurus* would primarily (but not exclusively) be subjected to compressional forces during the midstance phase of hind limb locomotion, if it is assumed that the femur was held mostly vertical relative to the ground (Fig. 1A). For a beam, cross-sectional area (equivalent to cortical area in a bone) is most important for resisting these compressive loads. By way of contrast, if the femur was held comparatively horizontally at midstance (Fig. 1B), as in modern birds, the bone was then subjected primarily to bending (and possibly torsion) rather than compression. In this case, a property called second moment of area, I, is most important for measuring a beam's resistance to bending. I can be calculated in various directions, and the direction in which I is greatest represents the plane in which the beam is most resistant to bending. For example, an ellipse elongated in the x direction and comparatively compressed in the y direction would be most resistant to bending forces applied along x, because I is greatest in this direction.

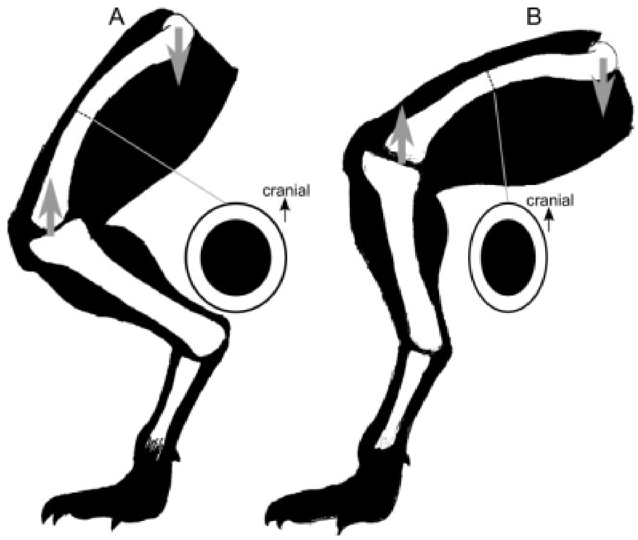

Fig. 1. Schematic of dinosaur hind limbs, showing (A) "erect" posture presumably characteristic of non-avians and (B) "horizontal" femoral posture characteristic of birds. The arrows in each demonstrate the locations and directions of forces acting on the femur at midstance (excluding muscle forces), and the inset cross-sections illustrate predicted femoral geometry at midshaft in response to each loading condition.

Hypothesizing that changes in limb orientation should be reflected in cross-sectional geometry, we measured cross-sectional properties of femora from a variety of avian and non-avian dinosaurs and dinosauromorphs. On the basis of presumed loading conditions and differences in femoral posture, as described earlier, we predicted that the femora of birds should be more resistant to bending forces, rather than compressive forces, and thus should be more asymmetrically shaped in cross-section than those of non-avian dinosaurs (Fig. 1). Furthermore, the femora of non-avians should show relatively greater cross-sectional area for resistance to relatively larger compressive forces during locomotion. Although previous studies have presented estimates of femoral strength or cross-sectional properties (Heinrich et al., 1993; Cubo and Casinos, 1996, 1998, 2000; Casinos and Cubo, 2001; Habib and Ruff, 2008), the present contribution contains the largest sample of computed tomography (CT)-scan derived cross-sectional properties ever assembled for birds and non-avian dinosaurs.

MATERIALS AND METHODS

The sample comprised 30 species of neornithine birds, one non-dinosaur dinosauromorph (*Dromomeron*), and perhaps four or five species of non-avian theropods (Table 1). The non-avian theropod taxa spanned a wide phylogenetic range, including an abelisauroid (*Masiakasaurus*), a basal coelurosaur (*Coelurus*) and maniraptorans (*Troodon* and unidentified ?dromaeosaurs). The neornithine

TABLE 1. Measurements used in this study

Taxon	Specimens	TA (mm^2)	CA (mm^2)	PCA	I_{max} (mm^4)	I_{min} (mm^4)	I_{max}/I_{min}	P (mm)	Mass (kg)	FL (mm)	Flightless?
Afropavo congensis	YPM 7778	45.2	17.7	39.1	109.2	95.7	1.14	25	1.03	89	No
Alectura lathami	YPM 379	75.9	19.3	25.4	220.9	186.3	1.19	32	2.13	92	No
Argusianus argus	YPM 2100	67.1	18.7	27.8	179.3	164.3	1.09	31	1.83	106	No
Bubulcus ibis	YPM 5702	13.0	7.3	56.0	11.5	10.0	1.15	13	0.18	53	No
Centrocercus urophasianus	YPM 14735	35.9	13.4	37.4	65.2	59.5	1.10	22	0.77	70	No
Chrysolophus pictus	YPM 2094	27.4	11.1	40.7	45.2	33.0	1.37	20	0.54	66	No
Crypturellus undulatus	YPM 11564	17.6	10.0	56.8	22.0	18.4	1.20	16	0.29	56	No
Dendragapus obscurus	YPM 11600	31.6	12.2	38.6	54.3	45.3	1.20	21	0.64	71	No
Eudromia elegans	YPM 6706	17.5	9.5	54.6	20.3	18.3	1.11	15	0.28	54	No
Guttera pucherani	YPM 9472	36.6	14.7	40.3	72.7	64.8	1.12	22	0.78	77	No
Lagopus lagopus	YPM 12705	17.1	8.4	49.3	19.0	15.9	1.20	15	0.27	54	No
Megapodius cumingii	YPM 2090	33.5	12.7	38.1	60.9	49.9	1.22	22	0.70	60	No
Meleagris gallopavo	YPM 2113	117.1	48.6	41.5	816.0	629.6	1.30	40	3.86	153	No
Nothoprocta perdicardia	YPM 2040	18.9	10.0	53.0	22.5	21.5	1.05	16	0.32	55	No
Numida meleagris	YPM 7780	38.1	17.8	46.8	92.0	74.6	1.23	23	0.82	81	No
Ortalis poliocephala	YPM 4417	22.5	10.2	45.4	31.8	25.1	1.26	18	0.41	67	No
Ortalis vetula	YPM 382	26.4	18.7	70.8	56.5	43.9	1.29	19	0.52	80	No
Pauxi pauxi	YPM 2103	57.8	20.4	35.3	181.7	131.9	1.38	29	1.50	102	No
Penelope purpurascens	YPM 376	53.8	15.7	29.2	124.8	105.8	1.18	27	1.33	83	No
Phasianus colchicus	YPM 6658	53.6	16.9	31.4	128.2	114.6	1.12	27	1.30	93	No
Sagittarius serpentarius	YPM 1797, 14510 (average)	129.6	37.8	29.2	788.8	560.2	1.41	43	4.53	108	No
Apteryx australis	YPM 13486	91.9	36.9	40.2	460.5	409.9	1.12	36	2.89	106	Yes
Apteryx owenii	YPM 2118	36.2	14.9	41.2	72.4	64.7	1.12	22	0.76	71	Yes
Casuarius sp.	YPM 2123	361.1	157.0	43.5	7556.5	6542.8	1.15	71	18.44	198	Yes
Dinornis sp.	YPM 421	811.5	467.2	57.6	47379.2	37045.3	1.28	164	177.77	285	Yes
Dromaius novaehollandiae	YPM 2128	596.0	244.7	41.1	21528.5	15061.3	1.43	92	36.77	230	Yes
Pezohaps solitaria	YPM 1154	239.8	142.3	59.3	4808.1	3017.4	1.59	59	10.79	156	Yes
Raphus caculattus	YPM 2064	246.6	103.8	42.1	3739.2	2683.2	1.39	59	10.83	137	Yes
Rhea americana	YPM 6503	285.1	169.2	59.4	6784.5	4265.8	1.59	64	13.68	112	Yes
Struthio camelus	YPM 2124	1147.9	353.4	30.8	79922.0	37036.6	2.16	133	99.48	303	Yes
Troodon formosus[a]	MOR 748	586.8	177.7	30.3	2996.7	2139.7	1.40	95	40.41	320	Yes
Dromomeron romeri[a]	GR 218	68.1	25.7	37.7	257.8	189.3	1.36	31	1.90	116	Yes
Masiakasaurus knopfleri[a]	FMNH PR 2115, 2117, 2208; UA 8684, 8681, 9170 (average)	257.8	140.5	54.8	4733.2	3932.8	1.20	62	12.50	174	Yes
Coelurus fragilis[a]	YPM 2010	307.1	133.5	43.5	6603.7	3878.4	1.70	67	15.20	190	Yes
Dromaeosauridae sp.[a]	CM 30748	193.5	126.6	65.4	2877.4	2395.5	1.20	53	8.14	203	Yes
Dromaeosauridae sp.[a]	CM 30748	198.9	131.5	66.1	3085.0	2520.6	1.22	53	8.23	215	Yes

TA, total cross-sectional area; CA, cortical area; PCA, percent cortical area; I_{max}, maximum second moment of area; I_{min}, minimum second moment of area; P, perimeter; m, mass; FL, femoral length.
[a]Indicates non-avian dinosaur or dinosauromorph.

TABLE 2. Institutional abbreviations

Abbreviation	Institution	Location
CM	Carnegie Museum of Natural History	Pittsburgh, Pennsylvania
GM	Ghost Ranch Ruth Hall Museum of Paleontology	Abiquiu, New Mexico
MOR	Museum of the Rockies	Bozeman, Montana
UA	University of Antananarivo	Madagascar
YPM	Yale Peabody Museum of Natural History	New Haven, Connecticut

sample was restricted to taxa that spend (or were believed to have spent, in the case of recently extinct species) a significant portion of their time moving on dry ground (rather than perching, flying, or swimming). Both paleognath and neognath birds were included in the sample. The non-avian sample was restricted to taxa that were believed to overlap in body mass with the avian sample (based on estimations of body mass from femoral circumference). This restriction was imposed to avoid extreme allometric effects. Only intact, uncrushed femora were included. This greatly reduced sample size, but also ensured the accuracy of measurements. All specimens, to the best of our knowledge, were adult individuals (wild-shot in the case of extant taxa), and only a single femur (typically the right femur, when available) was scanned for each specimen. Two different individuals (based on differences in femoral size and morphology) are included in the non-diagnostic dromaeosaur CM 30748 (see Table 2 for list of institutional abbreviations).

Specimens were scanned on a medical CT scanner with an in-plane resolution of 0.188 mm/pixel. Bones were aligned so that the scan axis was parallel to the bone, and so that the midshaft of the bone would be scanned in as close to a transverse section as possible. Midshaft was identified on the CT scans as the point on the femur exactly half-way between the proximal and distal extremities of the element. In the case of *Troodon*, a photograph of a histological slide was used instead of a CT scan. All CT data are on file at the relevant institutions.

Images of the femoral midshaft for each specimen were imported into the program ImageJ 1.37 (Rasband, 2008), and thresholded using the half-maximum height protocol of Spoor et al. (1993). Cross-sectional properties for each section were then measured using MomentMacroJ 1.3 (Warfel et al., 2006).

Measured properties included the maximum and minimum second moments of area (I_{max} and I_{min}, respectively). These properties describe the maximum and minimum resistance of an idealized beam to bending, respectively. We did not measure moments of area in the x- and y-planes (I_x and I_y), as is commonly done, because it was not feasible to define an anatomically meaningful and comparable axis for a group of such morphologically disparate taxa. Additionally, cortical area (CA) and total area (TA) were calculated. Where multiple specimens were available for a taxon (in the case of *Masiaksaurus knopfleri* and *Sagittarius serpentarius*), values were averaged.

To measure the eccentricity of the femoral cross-section, we calculated the ratio I_{max}/I_{min}. A ratio approaching 1 reflects a more circular cross-section that is equally resistant to bending in multiple directions. A ratio exceeding 1, in contrast, is more resistant to bending in one direction than in another. The ratios for the groups of avians and non-avians were compared using a Mann–Whitney U-test. To account for possible differences between completely flightless birds and primarily terrestrial birds that retained flight capabilities, we analyzed the data in two sets. One set compared the non-avians with the entire avian sample; the other compared the non-avians with only completely flightless avians.

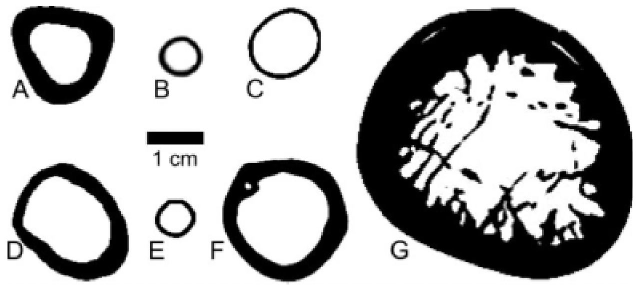

Fig. 2. Cross-sections at midshaft of selected femora, for (A) *Masiakasaurus knopfleri* (UA 8681); (B) *Numida meleagris* (YPM 7780); (C) *Sagittarius serpentarius* (YPM 14510); (D) *Coelurus fragilis* (YPM 2010); (E) *Centrocercus urophasianus* (YPM 14735); (F) *Casuarius* sp. (YPM 2123); and (G) *Dinornis* sp. (YPM 421). The cranial surface is to the top in all cases, and the scale bar equals 1 cm.

We compared cortical area (reflecting resistance to compression) for the samples in two different fashions. First, CA was compared to body mass as estimated from femoral circumference using the formula of Anderson et al. (1985). To avoid circularity and basing all comparisons on estimates, percent cortical area (calculated as CA/TA) was also compared between groups. All statistical analysis was completed in the program PAST 1.85 (Hammer et al., 2008).

RESULTS

Examples of femoral cross-sections at midshaft are presented in Figure 2, and full numerical data are contained in Table 1. When examining I_{max}/I_{min}, no significant differences in the ratio distinguish avians and non-avians ($P = 0.143$ in comparison with the entire sample and $P = 0.953$ with the flightless subsample). On average, although the difference was not significant, non-avians had a larger ratio (1.35) than the whole avian sample (1.27), but a smaller ratio than the exclusively flightless subsample (1.43). In the latter case, much of this difference was driven by *Struthio camelus*, which had a ratio of 2.16 (versus the next highest ratio for flightless birds, 1.593 for *Pezohaps solitaria*). Excluding *S. camelus*, the average ratio for exclusively flightless birds drops to 1.34, but it is still not significantly different from the non-avian sample.

No significant differences between avians and non-avians were identified when cortical area was normalized by estimated body mass ($P = 0.132$ and $P = 0.517$ for the entire avian and flightless avian samples, respectively). Differences between samples were also nonsignificant for comparisons of percent cortical area, $P = 0.361$ for the entire avian versus non-avian sample and $P = 0.768$ for exclusively flightless avians versus non-avians.

DISCUSSION

Given the well-documented osteological evidence for hind limb locomotor and postural changes during the evolution of birds from non-avian dinosaurs (e.g., Gatesy, 1995), it is surprising that no significant structural patterns distinguish the femoral shafts of the two groups. Based on predictions from beam theory, it was expected that non-avian femora should, on average, show more circular cross-sections than those of birds—yet, the opposite may well be the case (even if the difference is not significant). What, if anything, does this indicate about postural differences between avians and non-avians, and how might sample limitations or faulty assumptions hinder interpretation?

Even though the sample size is small, we do not feel that limited sampling is the only factor behind the nonsignificant differences. The samples are characterized by considerable overlap in all values (Table 1); even if a larger sample showed statistically significant differences, the differences between the two samples would be so subtle as to be relatively useless for reconstructing posture based on cross-sectional properties alone. Similarly, the broad overlap in values between the two groups at least partially negates the potential criticism that a postural dichotomy is falsely expected in the sample. Assuming that the distinctive avian femoral posture evolved in a series of steps rather than a single step (Hutchinson and Allen, 2009), this should still be reflected in significant differences between the samples.

The assumption that midstance and average resting posture of the femur are the prime determinants of femoral cross-section may be too simplistic or incorrect. Muscle insertions also play a role in determining bone form (for instance, in the greatly expanded fourth trochanter seen in some ornithischian dinosaurs), and myological differences between avians and non-avians (e.g., Hutchinson, 2001) may obscure the bony signal due to loading. Perhaps femoral motion was not entirely equivalent in the two groups—a previously unreconstructed and undocumented degree of rotation in the femur (which can be quite prominent in at least some extant birds; Hutchinson and Gatesy, 2000) or lateral splay could also affect the loading environment, and thus bone morphology, in unexpected ways. Furthermore, the greatest load-bearing point may not have been precisely at the midshaft, but slightly proximal or distal; this could be ascertained only by knowing the posture (which is the initial unknown in this study!) or modeling techniques and sensitivity analyses beyond the scope of the present work. In future studies, it might be fruitful to calculate and compare structural parameters along a segment of the femoral shaft instead of a single slice. Differences in relative lengths of the femur between avians and non-avians, as well as shifts in the center of mass, may also be important and should be investigated further. Finally, more investigation is needed on how the bowed femoral shaft of some non-avians might have affected mechanical strength.

Possibly, the taxa considered in this taxa are so small in body mass that this factor is not a primary determinant in cross-sectional geometry of the femur. Or, the relatively small non-avian dinosaurs maintained a "crouched" posture relative to their larger relatives, as seen in many mammals (e.g., Biewener, 1989).

Another complicating factor may be the somewhat nebulous relationship between bone form and function when it comes to cross-sectional geometry. Although it is not disputed that applied loads influence bone structure (e.g., Bouvier and Hylander, 1981; Fajardo and Müller, 2001; Dumont and Nicolay, 2006), it is questionable how precise this match actually is (Lieberman et al., 2004). Long bone cross-sections may indeed be indicative of general activity patterns and loads, but it may not be possible to tease out subtle differences in posture in all cases. Here, trabecular architecture or subchondral density may offer alternative, informative data (e.g., Fajardo and Müller, 2001; Carlson and Patel, 2006).

In the end, this study illustrates potential limitations in using cross-sectional anatomy to infer posture in extinct groups. Although the true source of the discrepancy between inferred posture based on overall femoral morphology versus cross-sectional geometry is not immediately knowable—whether the cause be small sample size or faulty assumptions in the degree to which the cross-section actually correlates with posture, or even in the reconstructed postures themselves, these results should not eliminate cross-sectional properties of long bones as a worthwhile avenue of research. Recent work has shown that intraskeletal comparisons, comparing humeri to femora, may hold useful information on some aspects of locomotion (Habib and Ruff, 2008). These data are not available for the present sample, but would likely fill in another piece of the picture.

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