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THE RELATIONSHIP OF HINDLIMB BONE DIMENSIONS TO BODY WEIGHT IN BIRDS

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ABSTRACT. An analysis of femur and tibiotarsus least shaft circumference plotted against live body weight in a data set of 795 individuals in 25 orders, 89 families, and 387 species of birds reveals a high correlation between the leg bone dimensions and body weight. No scaling model fits the whole data set very well, but there is a significant fit by different scaling models for some functional and taxonomic groups.

The high correlation observed between leg bone circumference and body weight is related to the support role of the femur and tibiotarsus in birds. A working model to explain this relationship is based on the correct placement of a bird's center of gravity. A cantilever style of support by the femur, as opposed to a pillar style of support, and various aspects of hindlimb locomotory and feeding functions are discussed in an evaluation of the importance of scaling relationships in birds.

The weights of several large, extinct birds are estimated by using the observed relationship of bird bone circumference and body weight in living birds. Estimation of bipedal dinosaur weights requires more careful evaluation of postulated models of dinosaur stance.

Key words: birds, scaling, allometry, geometric similarity, elastic similarity, general structural relation, reduced major axis, body weight, hind-limb function, functional morphology.

INTRODUCTION

In recent years, there have been several attempts to evaluate the relationship between limb bone dimensions and body mass in vertebrates. Prominent among works pertaining to birds are those of Alexander et al. (1979), Maloij et al. (1979), and Alexander (1983a, 1983b). Important works that pertain to mammals include those of McMahon (1973, 1975a, 1975b), Scott (1985), and Bou et al. (1987). Extrapolating from Recent data, others have attempted to predict body mass of dinosaurs (Anderson et al., 1985), fossil birds (Campbell and Tonni, 1983), and artiodactyls (Scott, 1983).

A principal function of the vertebrate skeleton is to provide support to the body mass. Therefore, it would appear logical that within a series of similarly shaped animals of many different sizes one might expect to find a clear functional relationship between body mass and the size of the supporting skeletal structure. Such a relationship is best termed scaling, "... the study of the influence of body size on form and function" (LaBarbera, 1989:97). Several scaling models have been proposed, each based on differing mechanical considerations of support mechanisms. The books by Schmidt-Nielsen (1984) and McMahon and Bonner (1983) give excellent, readable discussions of scaling.

In addition to support, the relationship between body mass and the size of supporting skeletal structure in vertebrates is related to the fact that the skeleton fulfills a crucial role in locomotion and a separate, sometimes correlated, role in feeding. Because adaptive specialization in birds has led to a considerable diversity of skeletal structures, sometimes within closely related taxa, one problem in developing scaling models is the separation of the skeleton's support role from its locomotory and feeding roles.

One important study of the influence of locomotory or feeding functions on leg bone allometry is that of Scott (1985). Scott discusses the role of adaptive factors in determining limb dimensions and deviations from expected scaling relationships. Variability beyond that predicted by scaling models for distal long bone lengths was cited as one prime example of the role of adaptive factors. Maloij et al. (1979) recognized that the lengths of hindlimb bones in birds did not scale as expected. Alexander (1983a) showed that in moas and other birds there is a higher correlation between body mass and femur length and diameter than between body mass and tibiotarsus or tarsometatarsus length and diameter, a result comparable to that observed by Scott (1985) for the Bovidae. Alexander (1983a) associated this disagreement with taxonomic differences and not with functional adaptations.

This paper is an outgrowth of a paper by Campbell and Tonni (1983). These authors attempted to estimate the weight of the world's largest known flying bird, the late Miocene *Argentavis magnificens* Campbell and Tonni 1980 from Argentina, by using the relationship between tibiotarsus least shaft circumference and live body weight in 324 individual birds from 19 orders and 45 families. We expanded their data base to test their results using a larger data set and to determine if there were different trends within subgroups of birds. The augmented data set contained 795 individual birds from 25 orders, 89 families, and 387 species.

We review avian hindlimb functional morphology in an attempt to identify the origin of the observed relationship between body weight and hindlimb dimensions. We use the expanded data set to revise Campbell and Tonni's (1983) weight prediction for *Argentavis magnificens* and to estimate the weights of several other extinct birds. We then discuss the applicability of the bird data for estimating the weight of bipedal dinosaurs.

MATERIALS AND METHODS

MEASUREMENTS

The plane of greatest shaft weakness in any long bone is the transverse plane of least shaft circumference, especially when bending moments are the largest stresses bearing upon the bone. The tests of Clark and Alexander (1975) on the breaking strength of quail leg bones, while not quantifiable, provide qualified support for this hypothesis. Biewener (1982) states that stresses resulting from bending moments are likely to be greatest at the midshaft of a bone. Although this may be true, it does not necessarily follow that the midshaft is the weakest part of the shaft. This is particularly true for the tibiotarsus, where fusion of the fibula to the tibiotarsus in the midshaft region often greatly affects shaft geometry.

We used least shaft circumference of the femur and tibiotarsus instead of least shaft diameter as our key measure for analysis because in cross-section the shafts of both femora and tibiotarsi are not perfectly round tubes. However, we did not determine to what extent deviation from a round tube contributed to the error value.

We measured the circumference by wrapping a narrow strip of cellophane tape around the shaft of the bone in the plane of its least circumference. This plane was determined, if possible, by first finding the least width and least depth of the shaft, although in some cases a qualitative determination was required if the least width and least depth did not coincide. The tape was marked in the area where the two ends overlapped, laid out flat, and the distance between the lines measured with calipers. Several researchers assisted us in taking these measurements, so it is not possible to state the quality of the calipers or the exact degree of accuracy present in the data. We calculated the circumference from width and depth for the smallest specimens because their circumferences were extremely difficult to measure directly.

This procedure differs from the work of Alexander (1983b), Alexander et al. (1979), and Maloiy et al. (1979), in which the measure used was the sagittal diameter measured midway between the proximal and distal ends. Our data also differ from those of Prange et al. (1979) because they measured width at the midpoint of the shaft across a diameter parallel with the anteroposterior axis of the animal, and from those of Anderson et al. (1985) because they used midshaft circumference, which does not always coincide with the least shaft circumference.

The least shaft circumference of a bird femur usually lies near or distal to the midpoint of the shaft length. Exceptions to this are noted in larger birds, especially the ratites, in which the least shaft circumference lies proximal to the midpoint of the shaft. The position of the least shaft circumference of bird tibiotarsi varied among the many species of birds we measured, but it was almost always at or distal to the midpoint of the shaft length. In the great majority of specimens measured, it occurred in the distal one-third of the shaft length.

In addition to measurement error associated with each individual researcher, there were other sources of potential error in the data. There is no control over the time of day, season, or year when any given specimen was collected, and each time factor has a potentially large impact on the registered weight of the bird. Any sick, and thus probably underweight, specimens, could not be identified. Effects of migratory habits on weight were ignored. The data came from many collections and the specimens were taken in the field by numerous different collectors and weighed on different types of scales at differing periods of time after being taken. Only adult birds, as determined by

the degree of ossification of the leg bones, were used in this study.

BIVARIATE RELATIONSHIPS

Bivariate plots and regressions of logarithm to the base 10 of weight, i.e., $\log_{10}(\text{weight})$, on $\log_{10}(\text{femur circumference})$ and $\log_{10}(\text{tibiotarsus circumference})$, and the latter two on each other, provide the most important display of our results for comparing groups of birds. One can visually assess the strength of the correlation and the linearity of the data.

We predicted the weights of fossil birds using the standard regression fit of $\log(\text{weight})$ on $\log(\text{circumference})$ (Model I of Sokal and Rohlf, 1981). LaBarbera (1989) reviewed scaling models in general and Rayner (1985) presented a clear, comprehensive discussion of fitting such models in birds when the data include measurement error and taxonomic diversity. We were unable to control or determine measurement error, but the hierarchical nature of our data corresponds to the interspecific situation described in Rayner (1985: fig. 1b). In that case, one is interested in finding the functional relation between two measures in a higher level (e.g., family or order, or other grouping) and has data for many species within the higher taxa and samples of varying numbers of individuals for the species.

A general structural relation (*gsr*) is the least restrictive regression model, and Rayner (1985) gave the procedure for fitting the *gsr*. He clearly stated how the assumptions implied in other fitting schemes are all special cases of the *gsr*.

If at all possible, one should fit the *gsr* to the species means, adjusting for the within species variation and covariation. If assumptions about the nature of the variability and covariability within species cannot be made with confidence, then the reduced major axis (*rma*) is the most appropriate model. Details are given in Rayner (1985). Because sample sizes were small within each species and morphofunctional group, we pooled the within species variability and covariability over all species and used these statistics to estimate the general structural relation (*gsr*). Ordinary least squares regression (OLS), or prediction regression, used here for estimating body weights, and the major axis (*ma*) are also special cases of the *gsr*.

If the within and among species standard deviations are equal, the *gsr* simplifies to the *rma*. This is estimated as the ratio of the standard deviations of the two variables among species. It is given the sign of the correlation coefficient. The *rma* ratio for the pooled data within species tended to be similar to that among species, but the standard error was so high for the ratio within species as to be uncertain. Where possible, both the *gsr* and *rma* were calculated. Rayner (1985:425) points out that "If the error distribution [variability within species in our case] is unknown, the r.m.a. models exhibit both within- and between-population variation with the least bias." He goes on to suggest that the *gsr* is best, but if the subpopulation variability is not available then the *rma* should be used. An empirical study of McArdle (1988) gives additional support to the use of the *rma*.

We report the *gsr*, *rma*, and *ma* slopes together with their 95 percent confidence intervals for each group. A nested analysis of variance (ANOVA) of the log data was used to generate sums of squares and cross-products for groups, families, genera, species, and individuals within species using PROC NESTED in PC SAS (6.03). Correlations, least-squares regressions, *rma*, *ma*, the covariance ratio estimate (Kuhry and Marcus, 1977), and both the correlated and uncorrelated form of the *gsr* were estimated from the results of the ANOVA using a program written in Quick Basic. For the results reported here, we used species means

weighted by the number of specimens available for each species. This was thought to reflect the variability in the data best, and it is a natural consequence of using the nested ANOVA.

Confidence intervals for the slope of the *rma* and *ma* were computed following the exact method of Jolicoeur (1990), as he has shown that some of Rayner's (1985) earlier formulae for the *rma* give unreasonably large confidence intervals. Jolicoeur favors the *ma* (which makes the assumption that the ratio of error variances is 1) to the *rma* because of better behavior of the slope confidence intervals. However, our correlations are high and samples large enough for these effects to be minimal. Furthermore, the *ma* is sensitive to weight and linear dimension relationships in log form. A suitable transformation, such as the cube root of weight, removes some of this difficulty (Jolicoeur, 1990). This was not attempted here because we wished to keep the data in a form most comparable to scaling model parameters and to be consistent with the earlier work of Campbell and Tonni (1983).

Three scaling models were tested by seeing if the 95 percent confidence intervals contained the parameter for the model. The models were elastic similarity, compressive similarity, and geometric similarity, or isometry. Isometry predicts that the coefficient of $\log(\text{circumference})$ or slope will be 3 in the log form of the allometric formula because identically shaped birds will increase weight to the third power of their linear dimensions according to this model. Compressive similarity predicts a coefficient of 2 because failure under compression leads to a prediction that cross-sectional area, which is approximately proportional to the square of the diameter (or circumference), will keep pace with weight. McMahon (1973) has shown that bending force failure scales as the $8/3$ power of diameter (or circumference = $\pi \cdot \text{diameter}$ for an assumed circular bone) and bones that follow this model are said to scale according to elastic similarity. Therefore, we may see which of these scaling models fits our data best. Because our data are heterogeneous and we have no information about bone thickness and have not considered cross-sectional shape, if a model provides a good fit it only indicates that the law may be appropriate and that the problem should be studied in greater detail.

We analyzed the overall data set (AL) and the following taxonomically and morphologically determined groups of the data. The families included in each group are listed in Table 1 and in their respective plots.

- AN: order Anseriformes; a taxonomic group with low diversity in morphology but a high size diversity.
- CH: order Charadriiformes; a taxonomic group with high diversity in morphology and size.
- HB: heavy-bodied terrestrial birds; unrelated birds that are similar in morphology (relatively short-legged and heavy-bodied) and have a diverse size range.
- LL: long-legged birds; unrelated birds of diverse size that share the trait of having relatively long legs.
- MF: marine flyers; unrelated marine birds of diverse morphology and habits.
- NP: non-passerine birds; all non-passerine families in the data set.
- PB: predatory birds; a morphological grouping of predatory flying birds (hawks, falcons, ospreys, and owls).
- PS: order Passeriformes; a taxonomic group of all passerine families, with a wide diversity in habits but general similarity in form.
- SF: order Apodiformes; a taxonomic group of very small flying birds that do not use their legs for much more than perching.

Table 1. Names of the 89 families that comprise each subgroup of the data set are given here. For explanation of grouping, see text.

AL: All 89 families listed below.
AN: Anatidae and Anhimidae.
CH: Scolopacidae, Recurvirostridae, Rostratulidae, Jacanidae, Haematocephalidae, Phalaropodidae, Burhinidae, Charadriidae, Thinocoridae, Laridae, Stercorariidae, Rhynchopidae, and Alcidae.
HB: Tinamidae, Apterygidae, Anhimidae, Cracidae, Numididae, Phasianidae, Tetraonidae, Meleagridae, Turnicidae, Pteroclidae, and Columbidae.
LL: Struthionidae, Rheidae, Phoenicopteridae, Plataleidae, Ardeidae, Cochleariidae, Scopidae, Ciconiidae, Rallidae, Gruidae, Aramidae, Otididae, and Burhinidae.
MF: Diomedeidae, Procellariidae, Hydrobatidae, Phaethontidae, Pelecanidae, and Fregaridae.
NP: Sixty-nine families of non-passerines, in alphabetical order. Accipitridae, Alcedinidae, Alcidae, Anatidae, Anhimidae, Anhingidae, Apodidae, Apterygidae, Aramidae, Ardeidae, Burhinidae, Charadriidae, Ciconiidae, Cochleariidae, Coliidae, Columbidae, Cracidae, Cuculidae, Diomedeidae, Eurypygidae, Falconidae, Fregatidae, Gaviidae, Gruidae, Haematopodidae, Heliornithidae, Hydrobatidae, Jacanidae, Laridae, Meleagridae, Meropidae, Momotidae, Numidiidae, Nyctibiidae, Opisthomocomidae, Otididae, Pandionidae, Pelecanidae, Phaethontidae, Phalacrocoracidae, Phalaropodidae, Phasianidae, Phoenicopteridae, Picidae, Plataleidae, Podicipedidae, Procellariidae, Psittacidae, Pteroclidae, Rallidae, Ramphastidae, Recurvirostridae, Rheidae, Rhynchopidae, Rostratulidae, Scolopaciidae, Scopidae, Spheniscidae, Stercorariidae, Strigidae, Struthionidae, Tetraonidae, Thinocoridae, Tinamidae, Trochilidae, Trogonidae, Turnicidae, Tytonidae, Vulturidae.
PB: Accipitridae, Falconidae, Pandionidae, Strigidae, and Tytonidae.
PS: Dendrocolaptidae, Furnariidae, Formicariidae, Pipridae, Tyrannidae, Hirundinidae, Corvidae, Paridae, Troglydytidae, Mimidae, Turdidae, Sylviidae, Laniidae, Vireonidae, Coerebidae, Icteridae, Thraupidae, Fringillidae, Emberizidae, and Ptilonotidae.
SF: Trochilidae and Apodidae.
SW: Gaviidae, Podicipedidae, Spheniscidae, Phalacrocoracidae, Anhingidae, and Phalaropodidae.

SW: swimmers; a morphological group of unrelated swimming birds.

RESULTS

The plots for all of our data and some of our subgroups are given in Figs. 1–7 for the logarithm (base 10) of weight against the logarithm of least circumference of the femur and tibiotarsus. The individual *rma* lines for all subgroups are plotted in Fig. 8. The two groups AN (order Anseriformes) and PB (orders Accipitriformes and Strigiformes), which overlap considerably in weight but have different-sized limb bones, are contrasted in Fig. 9. Figures 1–8 have the same scaled axes so they can be compared over groups. Slopes and intercepts, with 95 percent confidence intervals, are given in Table 2. The confidence intervals are asymmetrical except those for OLS regressions.

The *rma*'s and *ma*'s, as well as the general structural equation fit and their confidence intervals, are presented in Table 2. There is diversity in the slopes of the lines among groups. There is little difference among the *gsr*, *ma*, and *rma* results; therefore, the *rma* results will be discussed in what follows. The estimation equations based on OLS are also given in Table 3 and that for AL is used for weight prediction later in the paper.

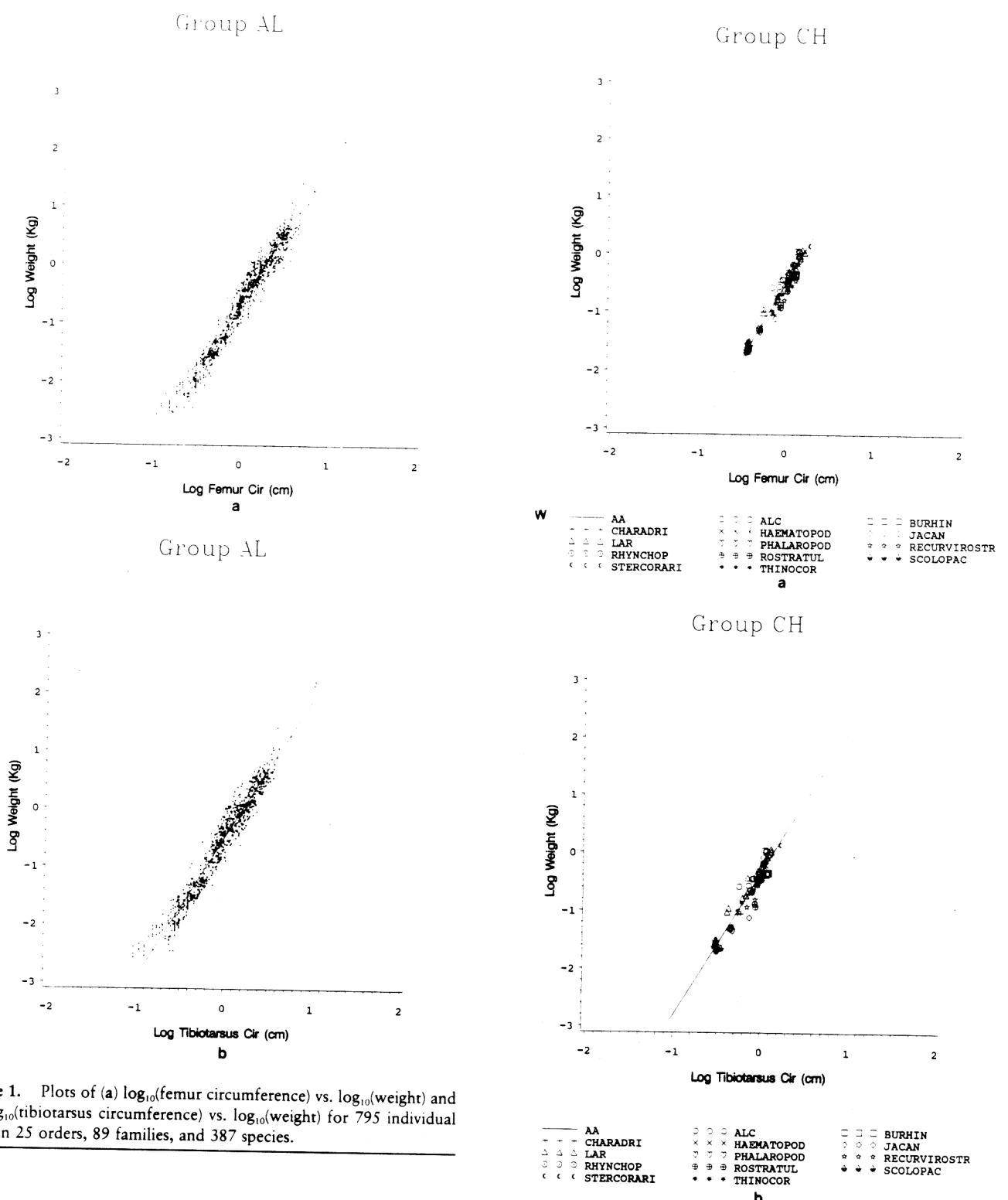
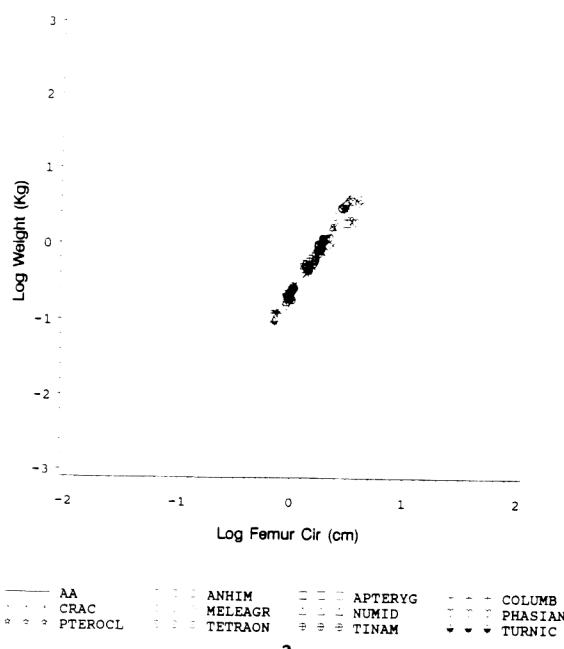


Figure 1. Plots of (a) \log_{10} (femur circumference) vs. \log_{10} (weight) and (b) \log_{10} (tibiotarsus circumference) vs. \log_{10} (weight) for 795 individual birds in 25 orders, 89 families, and 387 species.

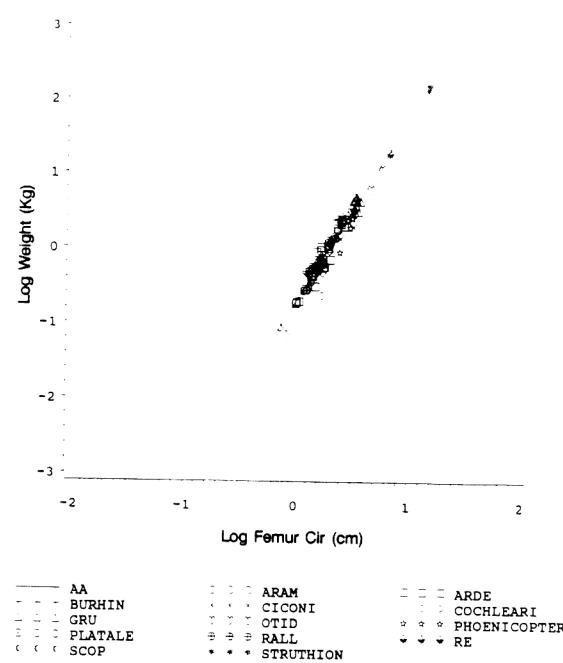
For log weight and log femur circumference regressions, the *rma* slopes vary from 2.071 for the Apodiformes (SF), near the 2.0 predicted by compressive similarity, to 2.673 for the swimming birds (SW), near the value of $8/3$ (2.67) predicted by elastic similarity scaling. For the femur, the groups PB, LL, CH, PS, and SW show values consistent with elastic similarity scaling of

Figure 2. Plots of (a) \log_{10} (femur circumference) vs. \log_{10} (weight) and (b) \log_{10} (tibiotarsus circumference) vs. \log_{10} (weight) for subgroup CH (=order Charadriiformes). Separate symbols for each family. In this figure and Figs. 3–7, family names are given minus ending *-idae*. In this and all other figures where it appears, AA = reduced major axis (*rma* in text).

Group HB



Group LL



Group HB

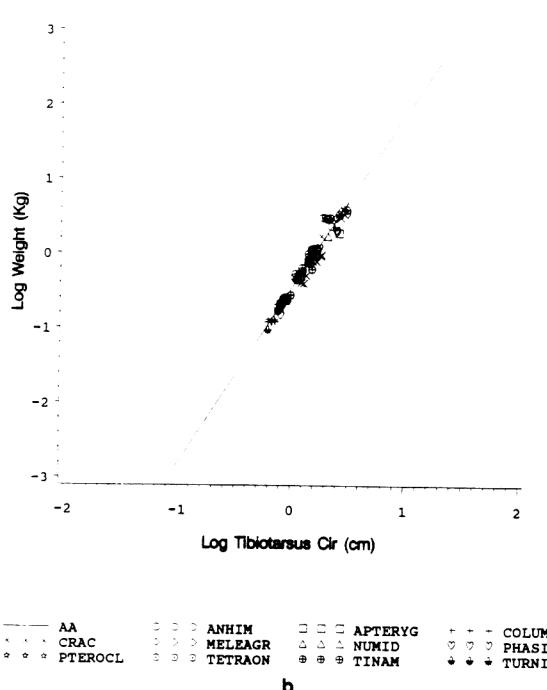


Figure 3. Plots of (a) \log_{10} (femur circumference) vs. \log_{10} (weight) and (b) \log_{10} (tibiotarsus circumference) vs. \log_{10} (weight) for subgroup HB (=heavy-bodied terrestrial birds).

Group LL

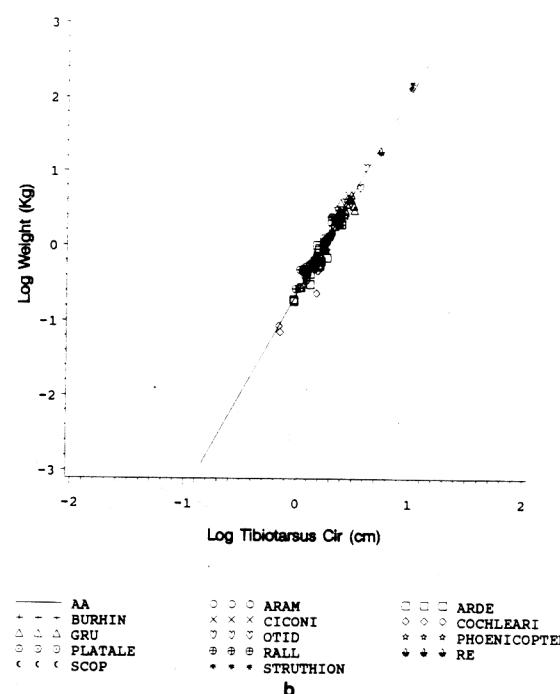


Figure 4. Plots of (a) \log_{10} (femur circumference) vs. \log_{10} (weight) and (b) \log_{10} (tibiotarsus circumference) vs. \log_{10} (weight) for subgroup LL (=long-legged birds).

Group PS

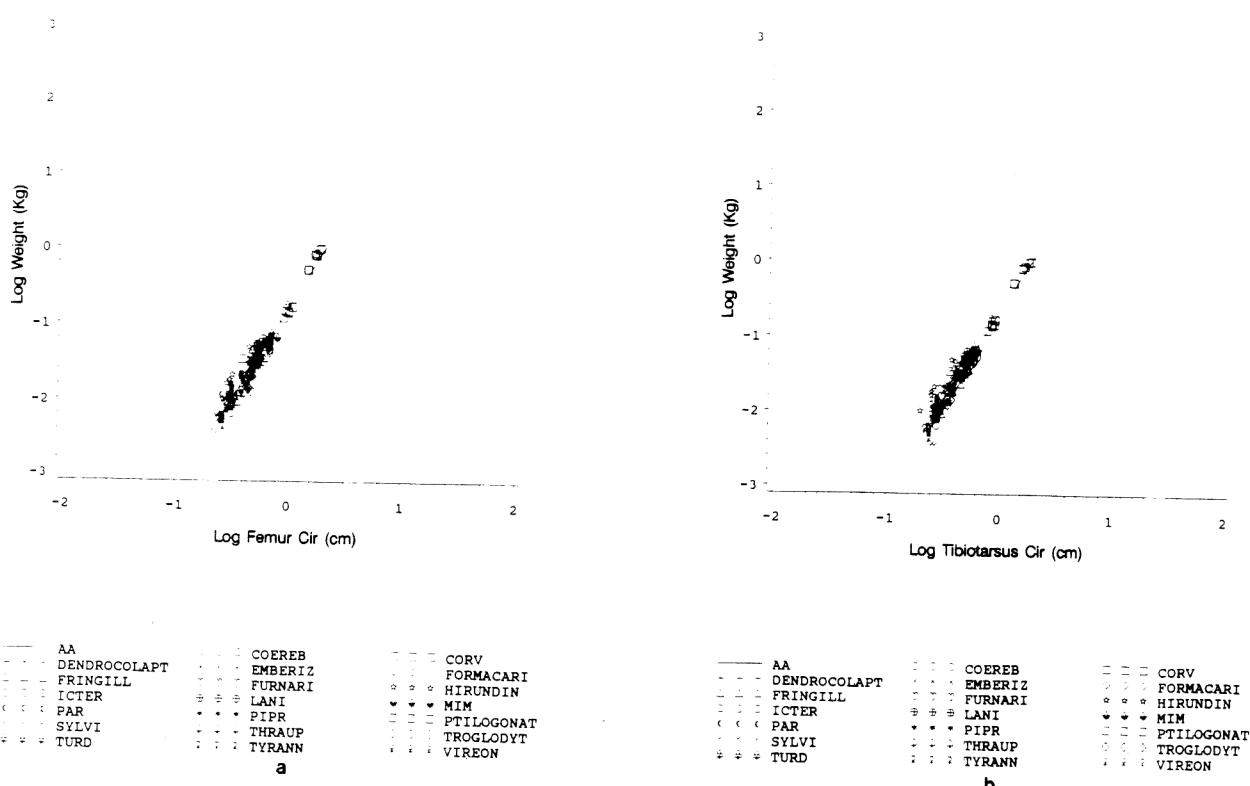


Figure 5. Plots of (a) \log_{10} (femur circumference) vs. \log_{10} (weight) and (b) \log_{10} (tibiotarsus circumference) vs. \log_{10} (weight) for subgroup PS (=order Passeriformes).

8/3. The groups MF, AN, and SF are consistent with the model of compressive similarity. CH is the only group whose confidence interval comes very close to 3.0, the value for isometry. The heavy-bodied (HB), non-passernines (NP), and all birds together (AL) fit none of the scaling models. Because NP and AL are heterogeneous combinations of the groups that show agreement with one or another of the scaling models, it is possible that the heterogeneous HB group could also be subdivided if more data were available.

The tibiotarsi follow similar trends, but there is greater diversity among slopes. The lowest value for the tibiotarsus is for the Anseriformes (AN), 1.951, and the largest, 2.758, is for the long-legged group (LL). The same groups as for the femur contain the parameter for elastic similarity; however, among these, PB, LL, and CH also come close to including geometric similarity. SF and AN are still consistent with a coefficient of 2.0, whereas the MF confidence interval also contains 2.0. The slope is greater for the tibiotarsi for AL, PB, HB, LL, and MF, whereas it is less for AN, PS, SF, CH, SW and NP. The slopes are almost equal for PS and NP, differing by less than 0.01.

The pattern for the Anseriformes (AN) fits a compressive model best, as indicated by a less steep trend of data points, whereas the steeper trend of the data points for the predators (PB) is very close to the bending model. However, when we examine in even more detail those groups for which we have

enough data, there are more subtle differences and trends. For example, among the Anseriformes (AN) we found that several small subgroups came close to the bending model, whereas the group as a whole more closely follows a compressive model. There is insufficient data, however, to test trends in the subgroups of Anseriformes.

A plot of AN and PB together (Fig. 9) shows how different the weights are for two groups of birds with overlapping hindlimb bone circumference ranges. The two patterns intersect for larger weights and circumferences. The differences in intercepts indicates that, for the same weight, smaller members of the group AN have smaller limb bones than the group PB. This suggests that the stresses borne by hindlimb bones in smaller members of the group AN are less than for group PB, which is not surprising because species in group PB are predators that capture prey with their feet. The additional stresses of prey capture with the feet, which can be expected to be significant, are not limited to the feet but are transmitted throughout the hindlimb structure.

This example points to some of the types of information that may be extracted from data sets such as ours. The summary plot (Fig. 8) of rma's of all of our groups demonstrates their differing slopes and intercepts, and we suggest that a larger data base could prove a fruitful source for interpretive morphological studies. Unfortunately, although we have several hundred birds

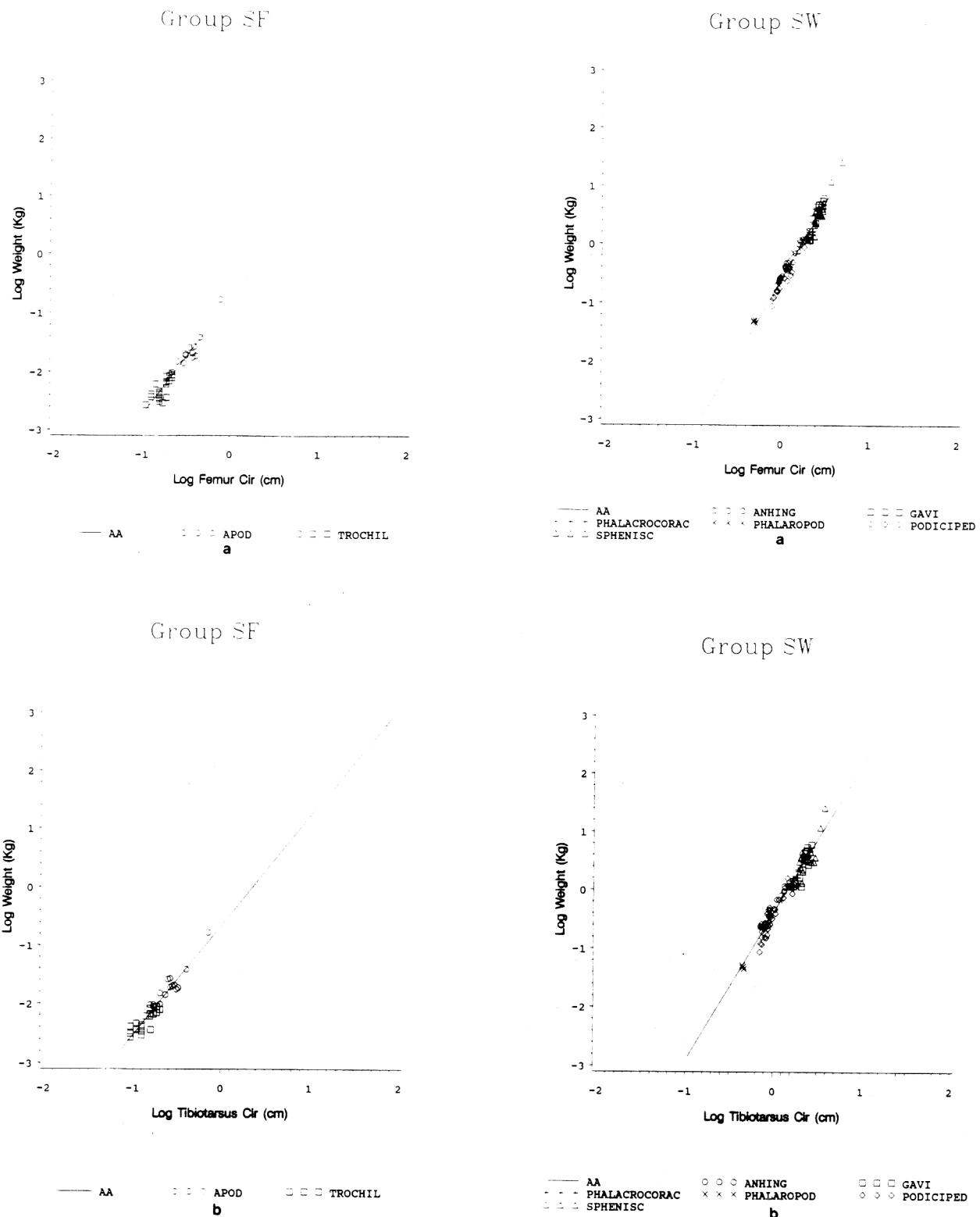


Figure 6. Plots of (a) \log_{10} (femur circumference) vs. \log_{10} (weight) and (b) \log_{10} (tibiotarsus circumference) vs. \log_{10} (weight) for subgroup SF (=small flyers of order Apodiformes).

Figure 7. Plots of (a) \log_{10} (femur circumference) vs. \log_{10} (weight) and (b) \log_{10} (tibiotarsus circumference) vs. \log_{10} (weight) for subgroup SW (=swimmers).

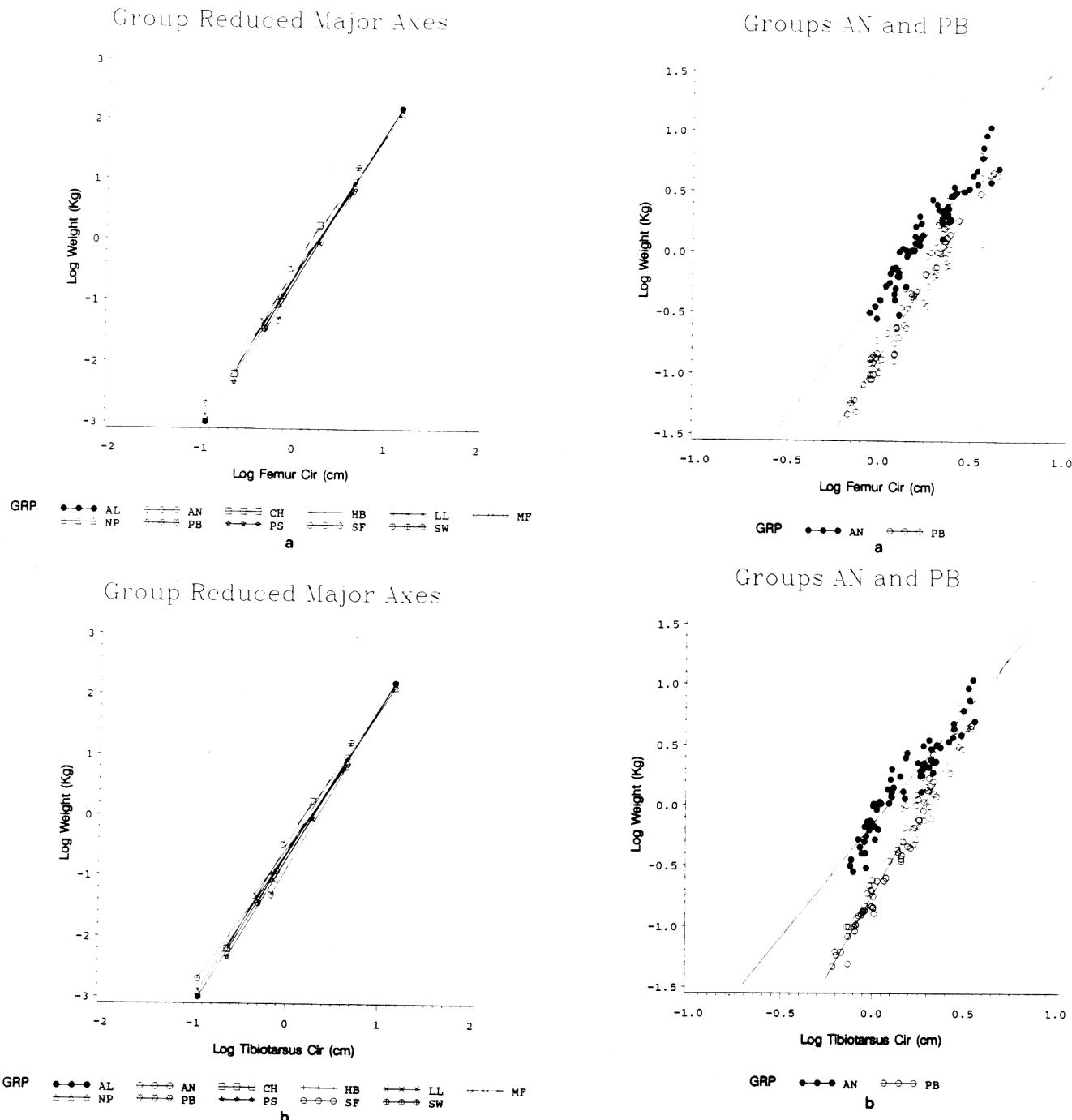


Figure 8. Plots of all subgroup reduced major axes (*rma*) of **a** $\log_{10}(\text{femur circumference})$ vs. $\log_{10}(\text{weight})$ and **(b)** $\log_{10}(\text{tibiotarsus circumference})$ vs. $\log_{10}(\text{weight})$.

in our overall data set, the numbers in subsets of the data are insufficient to extract conclusions with confidence.

Finally, the comparison of log femur to log tibiotarsus circumferences is largely consistent with an isometric slope of 1.0 (Table 2; Fig. 10). However, the long-legged (LL) group departs

Figure 9. Plots of the regression lines for subgroups AN and PB of **a** $\log_{10}(\text{femur circumference})$ vs. $\log_{10}(\text{weight})$ and **(b)** $\log_{10}(\text{tibiotarsus circumference})$ vs. $\log_{10}(\text{weight})$. Small birds of the group AN have smaller hindlimb bones than birds of the group PB of the same weight, whereas the two groups become more similar as the individuals become larger.

from 1.0 by more than 0.01 in its lower confidence bound, which means that in this group femur circumference increases faster for larger birds relative to the tibiotarsus than strict geometric scaling would predict.

Our data demonstrate diversity, but the broad band of points comprising our entire data set encompasses all of this diversity. Overall (AL), the bird data, with a slope of 2.5 for both femur and tibiotarsus, are closer to what we would expect if the bones were resisting bending more than compression (see Discussion). Our data tend to corroborate our interpretation of the bird femur as fulfilling its support function as a cantilever, rather than as a pillar.

DISCUSSION

If one accepts the premise that a primary role of the skeleton is to provide support for the rest of the body, and that it is this role that identifies a scaling model, then the skeletal elements that reflect body weight in birds are logically the three primary hindlimb bones: the femur, tibiotarsus, and tarsometatarsus. The bone in a bird's hindlimb that has the least variation in general form and structure from one kind of bird to another, particularly as regards its shaft structure, is the femur. The second least variable is the tibiotarsus. Of these two, the femur would appear to be the better indicator of body weight because its principal function is to provide static support for the bird's body weight. The tibiotarsus provides support for the body as well, but it also plays a more dynamic role in locomotion, and consequently its shape is often modified for its function.

The tarsometatarsus not only provides support and serves a locomotory function; it also often serves an important role in feeding. In this case, it may be much modified for a series of different functions. Cross-sections through the shaft of several tarsometatarsi of birds adapted to different locomotory and feeding strategies (Fig. 11) show that their structure is not readily comparable throughout the class, although it may be that within any given morphotype a constant relationship between some tarsometatarsal dimensions and body weight exists. Given the observed variety in form, it is difficult to identify a weak part of the shaft of tarsometatarsi in common to all members of the class.

ANALYSIS OF HINDLIMB FUNCTION

Support

To serve their support roles, the hindlimb bones must be sufficiently large to support the body without breaking, and include a safety factor (Alexander, 1981; Biewener, 1982, 1990), but yet not be so large as to be energetically too expensive to maintain. To understand why the femur and tibiotarsus have a close relationship to weight, it is necessary to examine how they perform their support function.

The hindlimbs must provide for total support on land, regardless of whether the bird is standing or perching or is in motion. Also, each leg must be strong enough to support the entire weight of the body because in many instances one leg may be involved in another activity and not provide any support. The forelimbs may be used to assist in support, but their modifications for flight or reduction to rudimentary status in flightless birds preclude them from a significant terrestrial support role.

In bipedal humans, the body is elongated vertically, hence its mass has its center of gravity concentrated over the hips. Bird bodies, however, tend to be elongated horizontally, and the center of gravity lies craniad to the articulation of the femur with the pelvis (Fig. 12; Gatesy, 1990: fig. 4). If a bird's legs attached to the body in a manner similar to that in humans, i.e., if the femora were in a vertical position, a bird would topple forward every time it tried to stand.

When a bird is standing at rest, the long axis of its femur is held at between 0° and 45° below the horizontal and generally much nearer the former than the latter (Fig. 12). This position was noted by Alexander (1975:358) when he stated that birds "... actually stand with their femur nearly horizontal . . ." It is no accident that this position is also that seen in mounted museum specimens, fossil or Recent, and published illustrations of complete bird skeletons in works of all kinds.

When a bird is standing at rest, the sagittal (craniocaudal) axis of a bird's synsacrum is, as far as we can determine, never in a horizontal position. Rather, it varies from about 20° to 80° from the horizontal, depending upon the species. In general, the angle between the sagittal axis of the synsacrum and the long axis of the femur is much less than 90° and often less than 45°.

Unfortunately, in almost all illustrations of avian hindlimb anatomy in which the limb is illustrated apart from the rest of the bird, the longitudinal axis of the synsacrum is placed in a horizontal position. This places the femur into a nearly vertical position, which is quite unnatural. Becoming accustomed to viewing the femur in this position can lead to misinterpretations of how it actually provides support for the body. For example, Clark and Alexander (1975:90) illustrated and analyzed hindlimb musculature as if the femur approached the vertical, whereas in film tracings of running quail (Clark and Alexander, 1975:93) they depicted the femur remaining fairly steady between 20° and 25° from the horizontal at different intervals in the stride. However, in the latter illustrations the sagittal axis of the synsacrum is at approximately the same angle to the horizontal, or about 20°–25°.

When the bird is standing at rest, then, the femur must function as a nearly horizontal beam, or cantilever, supported by the tibiotarsus at one end and in turn supporting the rest of the body via the pelvis at the other end (Fig. 13). A bird's leg is kept from collapsing by muscles and tendons, not because the hindlimb bones are stacked one on top of the other, pillar-fashion, as in humans. The femur experiences its greatest stress when it approaches the horizontal plane; therefore, its shaft must be large enough in minimal cross-sectional circumference so as not to break under the bending forces being exerted on its ends when in that position.

For similar reasons, the least circumference of the tibiotarsus should also reflect a bird's body weight. The tibiotarsus is usually held in a more vertical position than the femur, but it often approaches the horizontal when a bird is walking, running, jumping, taking off, or landing. One might suspect that because of its greater locomotory functions the tibiotarsus would not be quite as good an indicator of a bird's weight because it experiences a greater variety of forces than the femur. However, the plane of least shaft circumference still cuts a tubular shaft that would be subjected to considerable bending forces. Our results show that the correlation for tibiotarsus least shaft circumference vs. body weight is not quite as high as that for femur least shaft circumference vs. body weight for the combined data set (AL) (Table 2). The two correlations are, however, very close and that for the tibiotarsus is even stronger in some groups. Regression of least shaft circumferences of bird femora on the least shaft circumferences of tibiotarsi shows that they are even more highly correlated (Table 2; Fig. 1D) to each other than either is to weight. If you know the circumference of one of these two bones, you can predict that for the other with fairly high confidence, and the least shaft circumference of either can be a reliable indicator of the weight of a fossil bird.

For both the femur and tibiotarsus, the plane of least shaft circumference almost always passes through a hollow tube.

Table 2. Correlation coefficient squared (RSQ), intercepts (int) and slopes [with confidence intervals given as lower confidence limits (lcl) and upper confidence limits (ucl) for reduced major axes (*rma*'s) for groups], slopes for major axis (*ma*), and general structural relation (*gsr*, uncorrelated errors), based on species means within groups weighted by sample size. Abbreviations: nb, number of specimens; ns, number of species; OLS, ordinary least squares regression.

Results for relation between $\log_{10}(\text{weight})$ and $\log_{10}(\text{femur circumference})$																				
Group	nb	ns	RSQ	int	lcl	<	<i>rma</i>	<	ucl	lcl	<	<i>ma</i>	<	ucl	lcl	<	<i>gsr</i>	<	ucl	Cor <i>gsr</i>
AL	795	387	0.961	-0.118	2.415	<	2.463	<	2.512	2.449	<	2.498	<	2.510	2.411	<	2.460	<	2.510	2.458
AN	65	40	0.908	0.538	1.796	<	2.079	<	2.406	1.850	<	2.144	<	2.523	1.739	<	2.038	<	2.365	1.983
CH	88	37	0.957	-0.157	2.399	<	2.667	<	2.966	2.444	<	2.713	<	3.039	2.394	<	2.668	<	2.973	2.668
HB	82	39	0.969	0.110	2.131	<	2.268	<	2.413	2.155	<	2.293	<	2.445	2.121	<	2.261	<	2.407	2.240
LL	95	49	0.968	-0.216	2.316	<	2.499	<	2.695	2.346	<	2.529	<	2.737	2.310	<	2.496	<	2.695	2.494
MF	39	15	0.947	0.262	1.858	<	2.174	<	2.544	1.896	<	2.213	<	2.629	1.844	<	2.169	<	2.547	2.165
NP	656	319	0.952	0.002	2.315	<	2.371	<	2.429	2.354	<	2.412	<	2.473	2.309	<	2.366	<	2.425	2.358
PB	76	33	0.953	-0.516	2.420	<	2.632	<	2.865	2.425	<	2.681	<	2.933	2.425	<	2.643	<	2.883	2.668
PS	139	67	0.948	-0.233	2.309	<	2.499	<	2.705	2.355	<	2.549	<	2.772	2.305	<	2.500	<	2.712	2.500
SF	34	27	0.909	0.230	1.812	<	2.071	<	2.367	1.865	<	2.135	<	2.474	1.815	<	2.085	<	2.402	2.102
SW	100	35	0.973	-0.294	2.542	<	2.673	<	2.812	2.569	<	2.701	<	2.846	2.535	<	2.668	<	2.808	2.662

Results for relation between $\log_{10}(\text{weight})$ and $\log_{10}(\text{tibiotarsus circumference})$; ns and nb as above																		
Group	RSQ	int	lcl	<	<i>rma</i>	<	ucl	lcl	<	<i>ma</i>	<	ucl	lcl	<	<i>gsr</i>	<	ucl	Cor <i>gsr</i>
AL	0.947	0.007	2.438	<	2.494	<	2.552	2.485	<	2.544	<	2.605	2.439	<	2.492	<	2.551	2.489
AN	0.909	0.871	1.688	<	1.951	<	2.256	1.733	<	2.007	<	2.358	1.629	<	1.908	<	2.210	1.873
CH	0.927	0.103	2.243	<	2.573	<	2.953	2.310	<	2.647	<	3.082	2.234	<	2.576	<	2.973	2.581
HB	0.964	0.140	2.231	<	2.385	<	2.549	2.261	<	2.416	<	2.590	2.222	<	2.379	<	2.545	2.363
LL	0.967	-0.418	2.555	<	2.758	<	2.978	2.590	<	2.794	<	3.028	2.555	<	2.762	<	2.986	2.765
MF	0.912	0.344	1.827	<	2.238	<	2.742	1.888	<	2.309	<	2.917	1.783	<	2.216	<	2.728	2.188
NP	0.939	0.170	2.303	<	2.366	<	2.431	2.353	<	2.419	<	2.488	2.294	<	2.359	<	2.426	2.349
PB	0.964	-0.515	2.558	<	2.755	<	2.967	2.596	<	2.794	<	3.021	2.556	<	2.756	<	2.973	2.760
PS	0.944	-0.124	2.293	<	2.489	<	2.702	2.341	<	2.542	<	2.774	2.288	<	2.489	<	2.709	2.490
SF	0.916	0.440	1.721	<	1.956	<	2.223	1.764	<	2.007	<	2.309	1.722	<	1.966	<	2.249	1.967
SW	0.956	-0.004	2.423	<	2.582	<	2.753	2.463	<	2.626	<	2.808	2.418	<	2.581	<	2.755	2.580

Results for functional relation between $\log_{10}(\text{femur circumference})$ and $\log_{10}(\text{tibiotarsus circumference})$; ns and nb as above																		
Group	RSQ	int	lcl	<	<i>rma</i>	<	ucl	lcl	<	<i>ma</i>	<	ucl	lcl	<	<i>gsr</i>	<	ucl	Cor <i>gsr</i>
AL	0.990	0.051	1.003	<	1.013	<	1.023	1.003	<	1.013	<	1.023	1.003	<	1.013	<	1.023	1.013
AN	0.984	0.159	0.883	<	0.938	<	0.997	0.882	<	0.938	<	0.997	0.882	<	0.938	<	0.997	0.937
CH	0.983	0.097	0.903	<	0.965	<	1.030	0.903	<	0.964	<	1.031	0.903	<	0.965	<	1.031	0.965
HB	0.969	0.000	0.977	<	1.046	<	1.121	0.977	<	1.047	<	1.123	0.973	<	1.044	<	1.120	1.032
LL	0.984	-0.081	1.047	<	1.104	<	1.164	1.047	<	1.105	<	1.166	1.048	<	1.105	<	1.166	1.109
MF	0.965	0.037	0.906	<	1.029	<	1.170	0.904	<	1.030	<	1.174	0.901	<	1.027	<	1.168	1.010
NP	0.988	0.071	0.986	<	0.998	<	1.010	0.986	<	0.998	<	1.010	0.986	<	0.998	<	1.010	0.998
PB	0.981	0.013	1.002	<	1.052	<	1.104	1.002	<	1.052	<	1.105	1.002	<	1.052	<	1.105	1.055
PS	0.982	0.043	0.950	<	0.996	<	1.044	0.949	<	0.996	<	1.044	0.950	<	0.996	<	1.044	0.996
SF	0.950	0.101	0.856	<	0.944	<	1.042	0.852	<	0.943	<	1.044	0.853	<	0.944	<	1.044	0.942
SW	0.978	0.108	0.923	<	0.966	<	1.011	0.922	<	0.966	<	1.011	0.924	<	0.967	<	1.013	0.969

Results for all data to compare to Campbell and Tonni and for estimation purposes													
Model	RSQ	All data (n = 795)				Weighted species means (ns = 391)							
		OLS		<i>rma</i>		OLS		<i>rma</i>		OLS		<i>rma</i>	
Weight—femur	0.958	-0.065	2.411	0.119	2.463	0.961	-0.069	2.414	-0.119	2.463	0.961	-0.069	2.463
Weight—tibiotarsus	0.944	0.076	2.424	0.074	2.495	0.947	0.072	2.428	0.074	2.494	0.947	0.072	2.494
Femur—tibiotarsus	0.987	0.057	1.006	0.051	1.013	0.989	0.056	1.008	0.051	1.013	0.989	0.056	1.013

Table 2. Continued.

Table of means of \log_{10} measurements based on all individuals								
	Individuals			Unweighted species				
	nb	Femur	Weight	Tibio-tarsus	ns	Femur	Weight	Tibio-tarsus
AL	795	1.032	2.424	0.969	390	1.008	2.384	0.943
AN	65	1.262	3.162	1.262	41	1.247	3.123	1.155
CH	88	0.921	2.300	0.854	41	0.967	2.409	0.900
HB	82	1.183	2.793	1.112	40	1.196	2.806	1.126
LL	95	1.311	3.059	1.261	50	1.303	3.014	1.250
MF	39	1.329	3.151	1.255	16	1.188	2.901	1.120
NP	656	1.262	2.633	1.041	322	1.087	2.597	1.017
PB	76	1.194	2.629	1.142	34	1.242	2.762	1.183
PS	139	0.668	1.436	0.627	68	0.634	1.376	0.592
SF	34	0.346	0.947	0.259	28	0.338	0.927	0.251
SW	100	1.209	2.938	1.139	37	1.228	2.994	1.155

Biewener (1982:298) states that "... a 'hollow cylinder' characteristic of a whole bone has a larger second moment of area (I) than a solid rod, and will therefore resist greater bending loads." Bühler (this volume), citing Bock (1974), disagrees, saying that a solid rod is stronger than a hollow tube. Currey (1984: 103) illustrates that a hollow cylinder is the least mass solution to providing strength to long bones and that as a cylinder gets larger, its walls may become thinner and still provide an equal amount of support. Currey and Alexander (1985) discuss the complexities of the factors that determine the thickness of the walls of tubular bones. With only a few exceptions, our data show that the least shaft circumference of the femur is greater than that of the tibiotarsus. Although we have not measured the bone wall thicknesses, it is our qualitative judgment that femoral shaft walls are thinner than tibiotarsal shaft walls. We postulate that this is because bending moments are the greatest forces stressing the femur, in contrast to compressive forces, and that these occur when the femur is in the horizontal position. For the tibiotarsus, there are two periods when bending moments are high. One is when it is near the vertical and passing into the main propulsive phase of a stride, at a time when compressive forces would also be at their highest level. The other is in the course of landing, when significant compressive force generated by the impact is passed on to the tibiotarsus from the tarsometatarsus. This compressive force is much reduced before being passed on to the femur.

Another reason why all birds have somewhat similar relationships between their body weight and the least shaft circumference of their femur and tibiotarsus, regardless of their size, behavior, or style of locomotion, is because *all* birds lay eggs on land, and, hence, must spend some time, however limited, on land or some other hard substrate. This is true whether they spend almost all of their time in water, on the ground, or in the air. It is not possible to lay eggs successfully while in flight or while swimming. Regardless of how short is the period of time that a bird spends on land to nest, even if it were only minutes, the legs must provide support for the body.

Factors Determining the Location of the Center of Gravity

The maintenance of proper balance when you have only two legs for support and locomotion, instead of four, is an engi-

neering design problem. Not only is it necessary to counteract laterally acting forces, but forward movement will tend to set up a rocking motion about a horizontal transverse axis of rotation determined by the point of articulation of the femora with the pelvis (Clark and Alexander, 1975). In birds, this rocking motion might seem to be accentuated by the fact that a bird's center of gravity is placed well anterior to the transverse axis of rotation.

Two different centers of gravity are germane to this discussion. One is the center of gravity of the entire animal, which is important only in certain specialized activities, such as floating upon or swimming in water. A second center of gravity is far more important: the center of gravity of the entire bird *minus* the legs distal to the articulation of the femur with the pelvis (Fig.

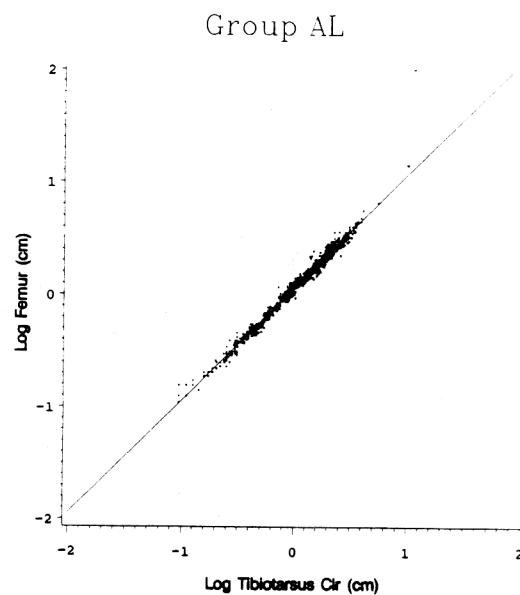


Figure 10. Plot of $\log_{10}(\text{femur circumference})$ vs. $\log_{10}(\text{tibiotarsus circumference})$ for 795 individual birds in 25 orders, 89 families, and 387 species.

Table 3. Ordinary least-squares regression estimates based on all individuals in each group. Abbreviations: int, intercept; RSG, correlation coefficient squared.

	All individuals			Species means (unweighted)		
	RSQ	Int	Slope	RSQ	Int	Slope
Log₁₀(weight) vs. log₁₀(femur circumference)						
AL	0.958	-0.065-0.020	2.411-0.018	0.959	-0.018-0.027	2.382-0.025
AN	0.899	0.663-0.107	1.980-0.084	0.905	0.557-0.139	2.058-0.105
CH	0.950	-0.099-0.060	2.601-0.064	0.894	-0.128-0.143	2.624-0.141
HB	0.962	0.154-0.059	2.230-0.049	0.954	0.135-0.096	2.233-0.080
LL	0.955	-0.144-0.073	2.444-0.054	0.955	-0.173-0.102	2.446-0.081
MF	0.934	0.356-0.124	2.103-0.092	0.962	0.218-0.152	2.258-0.151
NP	0.949	0.070-0.024	2.310-0.021	0.951	0.115-0.033	2.283-0.029
PB	0.942	-0.414-0.089	2.548-0.073	0.971	-0.517-0.156	2.639-0.124
PS	0.936	-0.179-0.038	2.418-0.054	0.910	-0.138-0.061	2.387-0.092
SF	0.906	0.265-0.044	1.970-0.112	0.915	0.229-0.047	2.065-0.121
SW	0.963	-0.238-0.064	2.627-0.052	0.968	-0.280-0.107	2.665-0.092
Log₁₀(weight) vs. log₁₀(tibiotarsus circumference)						
AL	0.958	0.076-0.022	2.424-0.021	0.942	0.140-0.030	2.380-0.030
AN	0.899	0.979-0.094	1.858-0.079	0.898	0.922-0.121	1.905-0.103
CH	0.920	0.187-0.068	2.702-0.077	0.828	0.224-0.162	2.427-0.177
HB	0.957	0.193-0.062	2.337-0.055	0.955	0.214-0.093	2.301-0.081
LL	0.953	-0.332-0.079	2.690-0.062	0.950	-0.384-0.114	2.717-0.090
MF	0.903	0.477-0.147	2.131-0.115	0.924	0.197-0.214	2.415-0.186
NP	0.935	0.250-0.026	2.289-0.024	0.937	0.312-0.035	2.274-0.033
PB	0.955	-0.442-0.079	2.690-0.068	0.937	-0.526-0.152	2.778-0.127
PS	0.935	-0.072-0.036	2.406-0.054	0.900	-0.021-0.060	2.361-0.097
SF	0.910	0.464-0.034	1.865-0.104	0.920	0.436-0.036	1.957-0.113
SW	0.944	0.079-0.072	2.510-0.062	0.930	0.091-0.138	2.514-0.117
Log₁₀(femur circumference) vs. log₁₀(tibiotarsus circumference)						
AN	0.979	0.171-0.020	0.929-0.017	0.975	0.185-0.028	0.919-0.024
CH	0.978	0.106-0.013	0.954-0.015	0.960	0.117-0.028	0.944-0.031
HB	0.976	0.029-0.021	1.038-0.018	0.972	0.052-0.032	1.015-0.028
LL	0.977	-0.063-0.022	1.089-0.017	0.977	-0.070-0.031	1.098-0.024
MF	0.963	0.060-0.042	1.011-0.033	0.969	-0.002-0.058	1.062-0.051
NP	0.986	0.078-0.005	0.991-0.005	0.987	0.085-0.007	0.985-0.006
PB	0.963	0.019-0.027	1.029-0.024	0.971	0.017-0.038	1.035-0.032
PS	0.974	0.052-0.009	0.983-0.014	0.965	0.056-0.014	0.983-0.014
SF	0.948	0.108-0.012	0.919-0.038	0.941	0.108-0.014	0.915-0.045
SW	0.969	0.127-0.020	0.919-0.038	0.963	0.142-0.039	0.941-0.031
TO	0.987	0.058-0.004	1.006-0.004	0.988	0.064-0.006	1.002-0.006

12). It is the portion of the body minus the legs that is balanced about the horizontal transverse axis running through the heads of the femora and supported by the hindlimb skeleton. It is this weight that the femora must support when the bird is standing, whereas the tibiotarsi must support that weight plus the hindlimb weight proximal to it. When the bird is supported by one leg only, the mass of the second leg must be considered in determining this second center of gravity. The close relationship between femoral least shaft circumference and body mass throughout the Class Aves suggests that the percentage of total body mass comprising the legs is relatively consistent throughout the class. On the other hand, some of the differences in the observed slopes among our several groups of birds might in fact be related to differences in this percentage.

The center of gravity of a bird body *minus* the hindlimbs is, of course, located farther craniad than the center of gravity of the whole body. At first glance, this would appear to destabilize

a bird because of the increase in the moment arm about the transverse axis of rotation. A bird maintains its balance and does not topple forward because the distal ends of the femora are at or slightly anterior to its center of gravity. The larger the bird, the farther the center of gravity is from where the femora attach to the pelvis and the longer the femora must be in order to extend under it. This explains the observed relationship between the length of the femora and the weight of the bird (Prange et al., 1979). If the distal ends of the femora were to extend posterior to the center of gravity, the bird would become unstable. From this consideration alone one can predict that the arc that the femur passes through when the bird is walking or running must be very limited.

Nonetheless, with the center of gravity located well anterior to the transverse axis of rotation it could prove to be energetically very expensive to control the dorsoventral rocking motion about this axis. This motion may be checked, i.e., damped

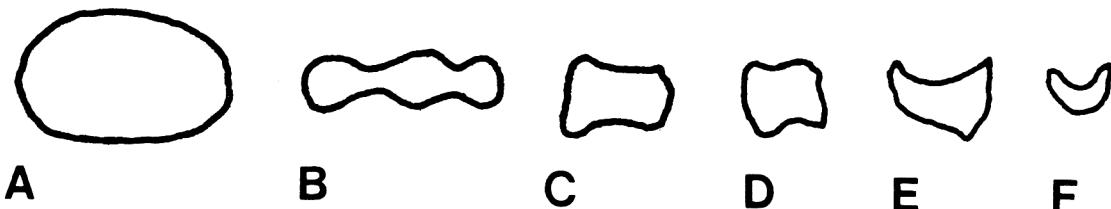


Figure 11. Cross-sections through the tarsometatarsi of several different groups of birds show the wide variety in their structure. Sections are taken in plane of least width, which does not always coincide with plane of least depth. A, Ostrich, *Struthio camelus*; B, King Penguin, *Aptenodytes patagonicus*; C, California Condor, *Gymnogyps californianus*; D, Marabou Stork, *Leptotilos crumeniferus*; E, Golden Eagle, *Aquila chrysaetos*; F, Great-horned Owl, *Bubo virginianus*. 1×.

or absorbed, by the femoral-pelvic musculature or in the small vertical movements of the distal end of the femur.

If bird legs were centered under their body so that the femora could be held vertically, this would eliminate some of the problems associated with the anterior-posterior rocking moment caused by having the center of gravity anterior to the transverse axis of rotation. However, when the first birds started flying, two mechanical adaptations had to evolve. One was getting as big a boost into the air as possible before they began to flap their wings, and the other, which is perhaps more important, was overcoming or absorbing the impact of landing. Birds accomplish both of these functions by maintaining their leg bones in an approximate Z-configuration, when viewed from the right. This configuration serves as a hinge-shaped mechanical spring that provides acceleration for jumping and shock absorption for landing.

Some terrestrial birds, especially those with long legs, may hold their lower leg bones in more of a vertical position when standing or walking, reverting to a Z-configuration only on landing or taking off. It appears that for standing or walking in very long-legged birds a more vertical configuration of the distal leg bones is best, but for landing and taking off the Z-configuration is required. Biewener (1989) claimed that birds show a shift to a more "upright" limb posture as size increases, analogous to that seen in mammalian quadrupeds. There are many small birds, e.g., thickknees and stilts, however, that have their lower legs as "upright" as an ostrich.

Birds cannot bring food to their mouths with their forelimbs, so they must take their mouths to food. Because food is seldom at the same horizontal level as their mouths, this often requires much dorsoventral rocking of the body about the transverse axis of rotation. If control over this motion were the sole factor determining where the center of gravity should be located, it would be on the transverse axis of rotation, thereby balancing the body on the axis of rotation and minimizing the effort required to feed. However, if a Z-configuration of the leg bones is required for landing and taking off, having the center of gravity over the transverse axis of rotation would increase the moment arm about the femur-tibiotarsus joint, thereby increasing the bending movement on the femoral shaft. Upon landing, with the center of gravity over the femur-tibiotarsus (knee) joint, forward rocking about the transverse axis of rotation reduces the bending moment on the femoral shaft by allowing the force of impact of landing to be absorbed over time. Absorption of the energy of impact is thus distributed not only through the braking action of the hinged joints of the leg bones, but also through the musculature associated with the femur over the length of the synsacrum.

Storer (1971) argued that in bipeds the center of gravity must

lie over or between the feet. He suggested that this should lead to tibiotarsi and tarsometatarsi of nearly equal length in long-legged birds with small feet, which would enable the bird to go from a standing position to a sitting position without losing its balance. Alexander (1983a) disagreed, pointing out that few birds have tarsometatarsi equal in length to their tibiotarsi. He went on to suggest that the center of gravity of a standing bird is not in the same place as in a sitting bird. This may be true for the whole body center of gravity, but the center of gravity of the bird minus the hindlimbs, which is what must be balanced, is not displaced. He then went on to suggest that birds with very short tarsometatarsi shift their femora from a near vertical to a near horizontal position when going from a standing to a sitting position. Because birds do not hold their femora vertically while standing, as he himself has noted, and the projected range of movement is outside the physical capabilities of femora, it must be questioned if indeed the center of gravity must be located over the feet.

We think not, although having the center of gravity over the feet would certainly seem to be the most energy-efficient and stable positioning. But because the leg bones provide support in turn to each more proximal bone and in the end to the main body mass as cantilevers, it is not necessary that the center of gravity be positioned directly over the support base on the ground. It is only necessary that the most proximal segment of the cantilever system providing support, in this case the knee joint, be positioned under the center of gravity, which is what we observe

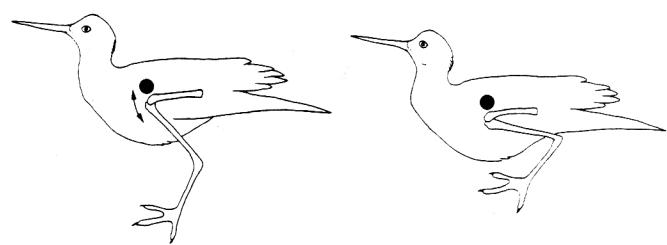


Figure 12. A bird's femora support the bird's weight at the point where their proximal ends articulate with the pelvis, but the bird's center of gravity lies forward of this point. Consequently, the femur is normally held near a horizontal position so that its distal end always remains under the center of gravity, thereby allowing the bipedal animal to maintain its balance. The double-headed arrow indicates the small arc through which the femur can move, an arc that keeps the distal end of the femur under the center of gravity. When a bird squats in preparation for jumping, the Z-configuration of the leg bones compresses, an action that provides the bird with greater "spring" in lift off.

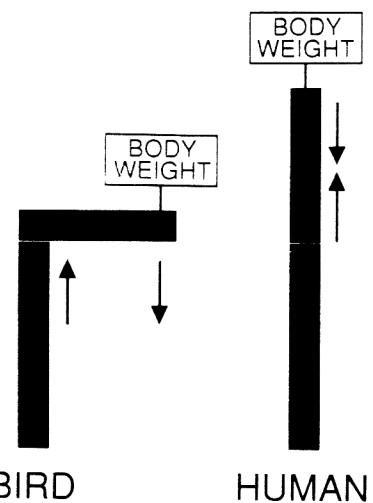


Figure 13. Diagrammatic view of the femur and tibiotarsus of a bird illustrating the origin of the bending moments stressing the femur. The femur acts as a cantilever, supporting the weight of the bird at its proximal end while being supported in turn by the tibiotarsus at its distal end. In contrast, animals that hold their leg bones in a vertical position experience compressive forces on the femur. Bending and compressional forces affect bone in different ways, so femora designed to withstand one type of force may not be able to resist breaking under an equal amount of the other type of force.

to be the case. This positioning does require, of course, a constant energy expenditure through the musculature to maintain the cantilever structure and provide for balance, but the only alternative is to position the center of gravity over legs that have a pillar-like structure, which apparently is inappropriate for birds.

Locomotion

As observed by Cracraft (1971), Clark and Alexander (1975), Alexander et al. (1979), and Gatesy (1990), the movement of the femur about the acetabulum during walking or running is, in the birds they studied, very small; therefore, the leg swings from the knee joint. This means that during periods of rapid locomotion the femur is passing up and down in a small arc (Fig. 12) as the bird moves through its gait. This limited degree of movement holds for large cursorial birds, such as the ostrich, as well as for the small birds these authors studied.

That this is true for ostriches was demonstrated experimentally by Fedak et al. (1982) when they analyzed the kinetic energy of limb segments in running ostriches. They illustrate graphically (Fedak et al., 1982: fig. 1) just how little the femur moves by showing that in a striding ostrich the upper leg segment (femur and associated musculature, which comprises by far the bulk of the mass of the whole leg) possesses only a very minimal percentage of the total internal kinetic energy of the leg. Most internal kinetic energy of the leg in running animals is associated with backward and forward movements of the leg (Alexander, 1984; Fedak et al., 1982), so the conspicuously small amount of observed internal kinetic energy in the upper leg segment can only mean that it moves very little in a striding ostrich. These experimental results can be supplemented through qualitative direct observations as well as in photographs of ostriches (e.g., Chadwick, 1983). It is the middle and lower leg segments, com-

prising the tibiotarsus, tarsometatarsus, and foot, that move back and forth when a bird is walking or running.

Gatesy (1990) documented that the femur has an excursion of about 5° during slow walking in *Numida* Linnaeus 1766 and suggested that this excursion increases to about 50° during running. He does not, however, indicate whether or not the latter figure takes into account the dorsoventral rotation of the sacrum about the transverse axis of rotation at the point of maximum excursion. This rotation may account for a significant portion of the 50° "excursion" of the femur.

Another clue to the fact that a bird's femur does not move through a significant anteroposterior arc is the large mass of associated femoral musculature that must be moved with it. It is a widely recognized aspect of vertebrate anatomy that in swinging limbs the limb musculature is concentrated proximally as much as possible to reduce the moment of inertia about the various hinge joints in the limb (e.g., Hildebrand, 1987). However, a comparison between the location of the major propulsive muscle masses of the avian wing with those of the avian leg shows a considerable contrast. Either the femur does not move much in locomotion or the adaptive advantage of reducing its associated muscle mass for locomotion is outweighed by some other, currently unrecognized functional requirement. Additionally, it should be noted that for a femur to swing through an anteroposterior arc as large as commonly depicted, i.e., from the horizontal to posterior to the vertical, would require that some of its associated musculature elongate far beyond what is physically possible.

PREDICTING WEIGHTS OF FOSSIL BIRDS

Using the mathematical equation based on all birds derived from the expanded data set gives a predicted weight of 71.9 kg for *Argentavis magnificens*, compared to the original estimate of 78.8 kg (Campbell and Tonni, 1983). We consider the difference of 6.9 kg (9 percent) between the two estimates to be an acceptable result.

Using this equation, we also attempted to estimate the weights of some other fossil birds, including the Dodo, Elephant Bird, and two moas. The predicted weights, based on measurements of the femora, ranged from 13.2 to 16.4 kg ($x = 14.26$ kg, $n = 3$) for the Dodo, *Raphus cucullatus* (Linnaeus 1758). Measurements from eight femora of the Elephant Bird, *Aepyornis maximus* Geoffroy Saint-Hilaire 1851, which had a very stocky build, gave results of 333–663 kg ($x = 526$ kg). Two specimens of the largest known moa, *Dinornis maximus* Owen 1867, gave results of 245 and 299 kg. Estimates based on two specimens of *Pachyornis elephantopus* (Owen 1856), perhaps the most heavily built moa but considerably shorter in stature than *Dinornis maximus*, ranged from 180 to 211 kg. If, instead of the regression equation based on all birds, the species means are used, a slightly smaller value for the estimates is obtained.

There is still room for error in our estimates of the weights of these fossil birds. If *Argentavis magnificens* were a much smaller bird, we would have greater faith in the estimate of its weight because there are very few species of very large flying birds living today and they are not well represented in our data. We suggest that if such data were available and added to what we already have, our estimate of the weight of *Argentavis magnificens* would be greater than that currently predicted because the prediction equation now available is based mainly on small birds. The weight estimates for the Elephant Bird and the two moas would be greatly enhanced if data for the largest living

birds that approximate their body build, the ratites, were available. Unfortunately, these data are very rare.

Comparisons with Previous Weight Estimates for Fossil Birds

Alexander (1983a) estimated the body masses for moas by using four different techniques, none of which correspond to that used here. It can be seen (Table 4) that our estimates fall within the high and low estimates of Alexander (1983a) for *Dinornis*, whereas our estimates for *Pachyornis* were slightly higher. In later papers, Alexander (1985b, 1989a) looked at *Pachyornis* again, posing the question of why its leg bones were so massive compared to those of *Struthio*. Because his plot of moa tibiotarsi diameter falls right on the regression line he presents for flying birds, we find that the logical conclusion is that the log bone diameters scaled appropriately for the weight of the bird. *Pachyornis* had massive leg bones because for its stature it was simply a very heavy bird.

This conclusion is supported by the fact that much of Alexander's work (e.g., 1979, 1985) was based on conclusions drawn from an ostrich that weighed 41.5 kg. In contrast, Anderson et al. (1985) gave weights for two ostriches as 80.9 kg. Amadon (1947) used 100 kg as an average weight for ostriches, although he quotes a source as saying ostriches weigh about 136 kg. The weights of the two ostriches in our sample were 138 and 161 kg, more than the 137 kg average estimate of Alexander (1985) for the body mass of *Pachyornis elephantopus*. This large range in size in the ostrich makes it obvious that much larger data sets are required for this species before we can safely interpret any aspect of its functional morphology or energetics.

Amadon (1947) estimated the weights of *Dinornis* Owen 1843a and *Aepyornis* Geoffroy Saint-Hilaire 1851 by using proportions based on body length vs. weight and the cross-sectional area of the femoral shaft in the plane of least shaft circumference vs. weight of these extinct birds, relative to comparable proportions in living ratites. His results (Table 4) show some similarity to ours, although it should be noted that his weight estimates represent a mean figure for an unspecified number of individuals, whereas our estimates are for individual specimens. When viewed so, his estimate of 438 kg for *Aepyornis* is considerably less than the mean based on our eight specimens (526 kg).

Anderson (1989) reviewed weight estimates for moas and summarizes attempts by several authors to arrive at these estimates. His preferred weight estimate of 105 kg for *Pachyornis elephantopus* is much lower than what we give above, but it was derived in roughly the same manner; i.e., it is based on the cross-sectional area of the femur. We have not seen the original source for this figure (Smith, 1985), so we do not know the method used or the data upon which the estimates were based. He did not provide a new estimate for *Dinornis maximus*, which he synonymized with *D. giganteus* Owen 1843.

PREDICTING WEIGHTS OF BIPEDAL DINOSAURS

Anderson et al. (1985) estimated the weight of bipedal dinosaurs using a scaling equation derived from the relationship between femur mid-shaft circumference and live body weight in birds, based on a data set of 126 birds. The results obtained by using our scaling equation and the circumference measurements provided by Anderson et al. (1985: table IV) are presented in Table 5.

The validity of using scaling relationships from birds to estimate the weight of bipedal dinosaurs is by no means estab-

Table 4. Some weight estimates (kg) of large, extinct birds from different sources.

	Amadon (1947)	Alexander (1983)	From our femur regression equation
<i>Aepyornis maximus</i>	418, 457 $x = 438$	— —	333–725 $x = 542$ $n = 8$
<i>Dinornis giganteus</i>	242	—	255–300
<i>Dinornis maximus</i>	230	—	255–300 $x = 278$ $n = 2$
<i>Dinornis</i> sp.	—	179–304 $x = 231$	143–211
<i>Pachyornis elephantopus</i>	—	— $x = 137$	115–163 $x = 177$ $n = 2$
<i>Raphus cucullatus</i>	—	—	13.2–16.5 $x = 14.3$ $n = 3$

lished. First, the data set drawn from birds is at the small end of the bird-dinosaur size spectrum, with only a few ratites at the upper size limit of birds and lower size limit of dinosaurs at that. The assumption that the observed scaling relationship would hold to the size of an animal as large as *Tyrannosaurus rex* Osborn 1905 simply cannot be supported with the available data. If we must present estimated weights of large extinct ratites with pleas for caution, these caveats must be reinforced for the estimates for weights of dinosaurs.

A fundamental problem is the stance of bipedal dinosaurs. The location of a bird's center of gravity is well anterior to the transverse axis of rotation, and we have presented the hypothesis that this location is an adaptation to avian locomotion. It seems fairly clear from observations of reconstructed bipedal dinosaur skeletons that their centers of gravity are also located well anterior to the transverse axis of rotation, even taking into consideration their long tails. Regardless, bipedal dinosaurs are often illustrated with their hindlimbs stretched out behind them as if their center of gravity were at or posterior to the transverse axis of rotation (e.g., McMahon and Bonner, 1983:126), an impossible pose. Of course, it is possible to conclude that the center of gravity is located at or near the transverse rotational axis if its location is determined by suspending complete models of dinosaurs by strings, as is commonly done (Alexander, 1985a, 1989b). However, as mentioned earlier for birds, the legs must be discounted in determining the center of gravity for purposes of analyzing balance in locomotion. And if a model dinosaur were used to determine the center of gravity that had the hindlimbs stretched out behind them, as most do, then it would be concluded that the center of gravity was even farther posterior from its true position than if the legs were in their correct position.

Paul (1987:12) admits that bipedal dinosaur knees were very bird-like and that the femur never retracted past the vertical, although he then goes on to illustrate the femur of *Albertosaurus* swinging well past the vertical (Paul, 1987: fig. 5). In the same illustration, he depicts femoral movement in an ostrich that is unnatural, despite his express claim to the contrary.

Table 5. Weight estimates for some bipedal dinosaurs in comparison to those of Anderson et al. (1985). Circumferences for femora from Anderson et al. (1985).

	Femur circum- ference (mm)	Estimated weight (kg)	
		From Anderson et al. (1985)	From our femur regression equation
<i>Parkosaurus warreni</i> (Hypsilophodontidae)	103	50	61
<i>Struthiomimus altus</i> (Ornithomimidae)	136	110	120
<i>Thescelosaurus garbani</i> (Thescelosauridae)	201	310	308
<i>Ceratosaurus nasicornis</i> (Ceratosauridae)	267	670	610
<i>Allosaurus fragilis</i> (Allosauridae)	348	1,400	1,155
<i>Hypacrosaurus altispinus</i> (Hadrosauridae)	400	2,000	1,616
<i>Edmontosaurus regalis</i> (Hadrosauridae)	504	3,800	2,822
<i>Anatosaurus copei</i> (Hadrosauridae)	512	4,000	2,931
<i>Tyrannosaurus rex</i> (Tyrannosauridae)	534	4,500	3,244

We think it is probable that the femora of bipedal dinosaurs were held in a more horizontal position than normally depicted, that the anteroposterior movement of the femur was restricted to a small arc, and that the distal end of the femur certainly never moved posterior to the vertical plane. In other words, the functional morphology of the hindlimbs of bipedal dinosaurs was essentially avian. Padian and Olsen (1989) arrived at a similar conclusion by comparing footprints of ratites and theropod dinosaurs. As in birds, the leg probably swung from the knee joint and not at the hip. If bipedal dinosaurs had an avian-like knee joint, it is logical to assume that it functioned in a similar manner. However, because dinosaurs did not fly, the selective pressure exerted by the need to jump for lift-off or to cushion landing did not exist, so the adaptive advantage of a Z-configuration of the hindlimb bones to meet this need did not exist. This being the case, it is possible that the femora of bipedal dinosaurs were held closer to the vertical than in birds.

In this regard, it is noted that the femoral shafts in bipedal dinosaurs are usually arched dorsally as they are in birds (see also Padian, 1986:52). It is also noted that the more elongated the tarsals the more the femur appears to be arched dorsally. This suggests more of a cantilever-type of support system, as in birds, than a pillar-like support system, as in heavy quadrupeds where the femoral shafts are quite straight and the tarsals and metatarsals quite short. A particularly good example of this arching is seen in the femora of the ostrich dinosaurs. Russell (1972) presents a good review of some of these animals and attempts a reconstruction of their myology and life habits. Unfortunately, he based his analysis of cursoriality of the ostrich dinosaurs on comparisons with *Struthio* that assume that the femora of the latter are oriented in a vertical position and swing through a large arc, which we have shown not to be the case.

If the femora of bipedal dinosaurs were not held in a position

similar to that seen in birds and were not similarly restricted in movement, then the use of scaling relationships derived from birds to predict their weight is not justified because the bending moments stressing the femora would not be the same. In this case, a different mathematical equation describing scaling based on femora would prevail. If the femora of bipedal dinosaurs were held and moved in a fashion after birds, then the use of the avian scaling relationship could be used to predict their weight. However, without a far larger data base drawn from living ratites, we cannot claim to really understand the avian scaling relationship and extrapolating to dinosaurs is risky at best.

SUMMARY AND CONCLUSIONS

An analysis of hindlimb bone dimensions and live body weight in 795 birds reveals that not all groups of birds fit the same scaling model. Overall, our data suggest that birds most closely approximate the model for elastic similarity. Nonetheless, some groups show values consistent with compressive similarity scaling, whereas another approached the value for geometric scaling. More data are required to assess scaling trends in different groups of birds with confidence.

We propose that the observed overall scaling relationship is a result of the functional morphology of the hindlimb, where the femur serves its support function as a cantilever and not a pillar, thereby being subjected more to bending moments than to compressive forces. The tibiotarsus is also subject to considerable bending moments, but it must also withstand greater compressive forces than the femur.

The center of gravity of a bird that is most important to balance during locomotion is that of a bird's body minus the hindlimbs. This center of gravity is found on the midline of the bird dorsal to the distal end of the femur, providing an explanation for the observed fact that the length of a bird's femur is related to its body mass; i.e., the larger the body, the farther the center of gravity is from the transverse axis of rotation and the longer the femur must be to support it. The whole body center of gravity is of much less importance in discussions of the functional morphology of the hindlimbs.

When birds walk or run, the distal ends of their femora move up and down in a small arc near the horizontal plane. It is the middle (tibiotarsal) and lower (tarsometatarsal + foot) limb segments that swing through an arc and define the stride of a bird.

Our data set allows a new estimation for the weight of *Argentavis magnificens*, the world's largest known flying bird, which is 71.9 kg [as opposed to 78.8 kg estimated by Campbell and Tonni (1983)]. Weights of other large extinct birds estimated on the basis of our data sometimes agree with earlier estimates, but in general they tend to indicate a larger size than previously estimated. The largest bird for which we have a weight estimate is a specimen of *Aepyornis maximus*, for which the estimate is 663 kg.

The use of estimation equations derived from birds to predict the weights of bipedal dinosaurs is a valid exercise only if bipedal dinosaurs had a hindlimb stance like birds. We conclude that the leg stance of some bipedal dinosaurs was similar to that of birds, i.e., that the femur served its support role as a cantilever and not a pillar, and that the closer the dinosaur hindlimb approaches that of birds in its proportions and femoral arching, the greater is this similarity. Bipedal dinosaur locomotion should be re-evaluated using the interpretations of avian functional morphology presented herein to eliminate misinterpretations

based on erroneous hypotheses of avian hindlimb stance and locomotion.

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