

Short communication

Wall thickness of gas- and marrow-filled avian long bones:
Measurements on humeri, femora and tibiotarsi in crows
(*Corvus corone cornix*) and magpies (*Pica pica*)

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Abstract

We studied how the ratio K of the internal to external diameter of gas- and marrow-filled avian long bones follows the biomechanical optima derived for tubular bones with minimum mass designed to fulfil various mechanical requirements. We evaluated radiographs of numerous humeri, femora and tibiotarsi in *Corvus corone cornix* and *Pica pica*. The K -values of the gas-filled humerus ($K = 0.78 \pm 0.03$) and the marrow-filled femur ($K = 0.79 \pm 0.02$) in *Corvus* are practically the same, while K of the marrow-filled tibiotarsus ($K = 0.71 \pm 0.04$) is significantly smaller. The same is true for the gas-filled humerus ($K = 0.78 \pm 0.02$) and the marrow-filled femur ($K = 0.77 \pm 0.02$) and tibiotarsus ($K = 0.67 \pm 0.05$) in *Pica*. K in *Corvus* is slightly larger than K in *Pica*, but the differences are statistically not significant. The standard deviation ΔK of the tibiotarsi ($\Delta K = 0.04–0.05$) is approximately two times as large as that of the humeri ($\Delta K = 0.02–0.03$) and femora ($\Delta K = 0.02$) in both species. Accepting the assumption of earlier authors that the ratio Q of the marrow to bone density is 0.5, our data show that the marrow-filled tibiotarsi of *Corvus* and *Pica* are optimized for stiffness, while the marrow-filled femora are far from any optimum. The relative wall thickness $W = 1 - K$ of the gas-filled avian humeri studied is much larger than the theoretical optimum $W^* = 1 - K^* = 0.07$, and thus these bones are thicker-walled than the optimal gas-filled tubular bone with minimum mass.

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1. Introduction

The diaphysis of many avian long bones is a hollow tube with an approximately circular cross section filled with marrow or gas. Pauwels (1980), Currey (1982), Alexander (1968, 1982, 1983, 1996), Currey and Alexander (1985) derived different biomechanical optima for the ratio K of the internal to external diameter of marrow- and gas-filled tubular bones with a circular cross section. The optimum value for K , which allows the minimiza-

tion of the mass of a marrow-filled bone, depends on the mechanical requirement that has to be fulfilled. According to the biomechanical optimization theory of Alexander (1982), Currey (1982), Currey and Alexander (1985), the optima for K depend on the ratio Q of the marrow to bone density. The optimum for K of gas-filled tubular bones with minimum mass is $K^* = 0.93$ (Alexander, 1982).

Currey and Alexander (1985) measured the K of long bones from single individuals of certain flying/flightless birds, a flying extinct reptile (*Pteranodon*) and bats. They found that the interspecific variation of K was high, and K ranged from 0.55 to 0.87 in flying birds.

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However, in general, they examined only one bone from any species, and therefore had no estimate of intraspecific variation. To reveal the force of selection, it is necessary to determine both the average and the standard deviation of K of avian long bones within a species. Until now such carefully carried out measurements have not been performed in birds. In order to fill this gap, we repeated the exercise of Currey and Alexander (1985) for large numbers of individuals of two avian species.

According to Alexander (1982, 1983, 1996), the long bones of many vertebrates are optimum structures. Until now this hypothesis have been thoroughly tested only in the case of fox (Bernáth et al., 2004) and human (Évinger et al., 2005) femora. The aim of this work is to present the first experimental study in which K was measured on statistically sufficient numbers of gas-filled (humeri) and marrow-filled (femora and tibiotarsi) avian long bones, and thus both the average and the standard deviation of K could be determined. The most important aspect of our present work is that studying gas- and marrow-filled tubular bones of the same species is a more severe test of the hypothesis of Currey and Alexander (1985). The two corvid species, namely the hooded crow *Corvus corone cornix* and the black-billed magpie *Pica pica* were chosen, because they are common, (in Hungary still) non-protected birds and their wing and limb bones were

easily available in large numbers from a Hungarian hunter.

2. Materials and methods

The avian long bones investigated originated from a Hungarian hunter, Mr. Sen. Mihály Gasparik, who provided us with wild-living adult *Corvus corone cornix* and adult *Pica pica* hunted during the spring and autumn shooting season in 2003 and 2004. The preparation of animals happened as described in detail by Bernáth et al. (2004). The scientific and vernacular names of birds mentioned in the text are according to Sibley and Monroe (1990). The filling material (gas or marrow) of the bone types (humerus, femur, tibiotarsus) was determined by cutting some bones in two.

Latero-medial and cranio-caudal radiographs were taken from every examined humerus, femur and tibiotarsus (Fig. 1) at the Department and Clinic of Surgery and Ophthalmology of the Faculty of Veterinary Science, Szent István University Budapest (EUR-EKA Diamond 150, CEA OGA green sensitive). After standard chemical development of the radiographs, they were digitized using an AGFA Arcus 1200 scanner with a resolution of 400 dpi. The evaluation of the radiographs for the investigated avian bones was as described in detail by Horváth (2001) and Bernáth et al. (2004).

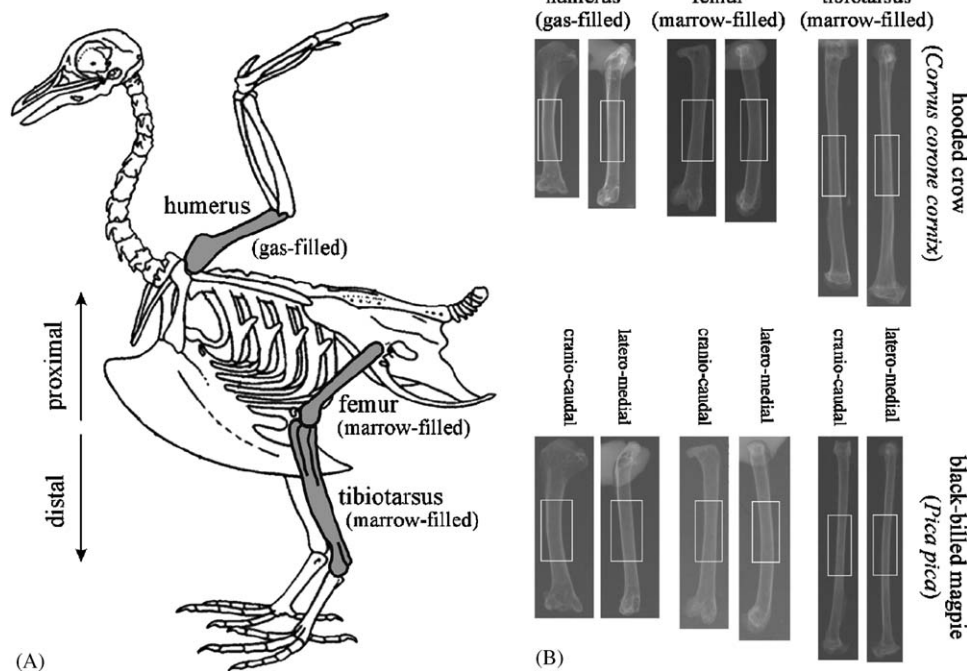


Fig. 1. (A) Schematic drawing of the generalized avian skeleton, in which the humerus, femur and tibiotarsus (the wall thickness of which was measured) are shaded by grey. (B) Examples of radiographs taken from a humerus, femur and tibiotarsus of the hooded crow (*Corvus corone cornix*) and the black-billed magpie (*Pica pica*) from cranio-caudal and latero-medial views, where the rectangular parts demarcated by white line are selected for evaluation.

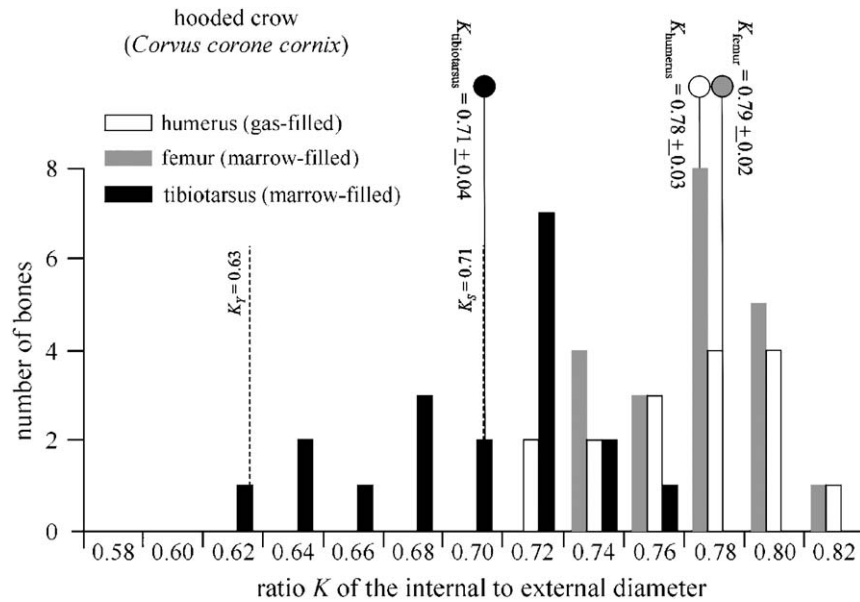


Fig. 2. Frequency of the ratio K of the internal to external diameter of the gas-filled humerus (white columns), marrow-filled femur (grey columns) and marrow-filled tibiotarsus (black columns) in the hooded crow, *Corvus corone cornix* measured at the mid-point of the shafts with evaluation of the radiographs of the bones. Dashed vertical lines show the theoretical optima $K_Y(Q = 0.5) = 0.63$ and $K_S(Q = 0.5) = 0.71$. Vertical lines with dots on their top represent the average K_{average} for the humerus, femur and tibiotarsus.

After the evaluation we obtained the ratio K of the internal to external diameter of the bone at the selected mid-section for both the latero-medial and cranio-caudal radiographic views. The reliability of this method was tested by comparison of computationally obtained K -values with data measured directly by a caliper on bone cross sections. Our method based on the evaluation of radiographs of tubular bones can measure the K -value with an accuracy of $\pm 1\%$ (Bernáth et al., 2004).

The lack of difference between the average K -values obtained for the cranio-caudal and latero-medial views of the bones was confirmed using associated two-tailed paired t -test. Statistical tests were performed with the statistical software StatSoft STATISTICA 6.1.

3. Results

Cutting the bones in two, we found that in the adults of *Corvus* and *Pica* the humeri are filled with gas, while the femora and tibiotarsi are marrow-filled. We investigated only adult birds, consequently, our results are valid for mature long bones rather than for juvenile forms that have not completed the transformation to being filled with gas. The K -values of humeri, femora and tibiotarsi in *Corvus* and *Pica* measured with the evaluation of radiographs taken from cranio-caudal and latero-medial views were practically the same due to the nearly circular cross section. Thus, $K = (K_{\text{cranio-caudal}} + K_{\text{latero-medial}})/2$ was calculated for every bone. The K -values of the gas-filled humerus ($K = 0.78 \pm 0.03$) and

the marrow-filled femur ($K = 0.79 \pm 0.02$) in *Corvus* are practically the same, while the K of the marrow-filled tibiotarsus ($K = 0.71 \pm 0.04$) is significantly smaller (Fig. 2, Table 1). The same is true for the gas-filled humerus ($K = 0.78 \pm 0.02$), marrow-filled femur ($K = 0.77 \pm 0.02$) and marrow-filled tibiotarsus ($K = 0.67 \pm 0.05$) in *Pica* (Fig. 3, Table 1). K in *Corvus* is slightly larger than K in *Pica*, but the difference is statistically not significant (Figs. 2 and 3, Table 1). The standard deviation ΔK of the tibiotarsi ($\Delta K = 0.04$ – 0.05) is approximately two times as large as that of the humeri ($\Delta K = 0.02$ – 0.03) and femora ($\Delta K = 0.02$) in both bird species.

4. Discussion

If $Q = 0.5$ (assumed by Alexander, 1982), the biomechanical optima for K of a marrow-filled tubular bone with minimum mass for yield/fatigue strength (Y), stiffness (S), impact loading (I) and bending fracture (F) are (Currey and Alexander, 1985; Bernáth et al., 2004): $K_S(Q = 0.5) = 0.71$, $K_Y(Q = 0.5) = 0.63$, $K_I(Q = 0.5) = 0.52$, $K_F(Q = 0.5) = 0.50$. $K_{\text{average}} = 0.71$ of the marrow-filled tibiotarsus in *Corvus* is equal to $K_S(Q = 0.5) = 0.71$, and $K_{\text{average}} = 0.67$ of the marrow-filled tibiotarsus in *Pica* is very near to $K_S(Q = 0.5) = 0.71$ (Table 1). Thus, the tibiotarsi in *Corvus* and *Pica* seem to be optimized for stiffness. $K_{\text{average}} = 0.79$ and 0.77 of the marrow-filled femora in *Corvus* and *Pica*, respectively, are significantly greater than any of the theoretical optima K_S , K_Y , K_I , K_F if $Q = 0.5$. Thus the femora in

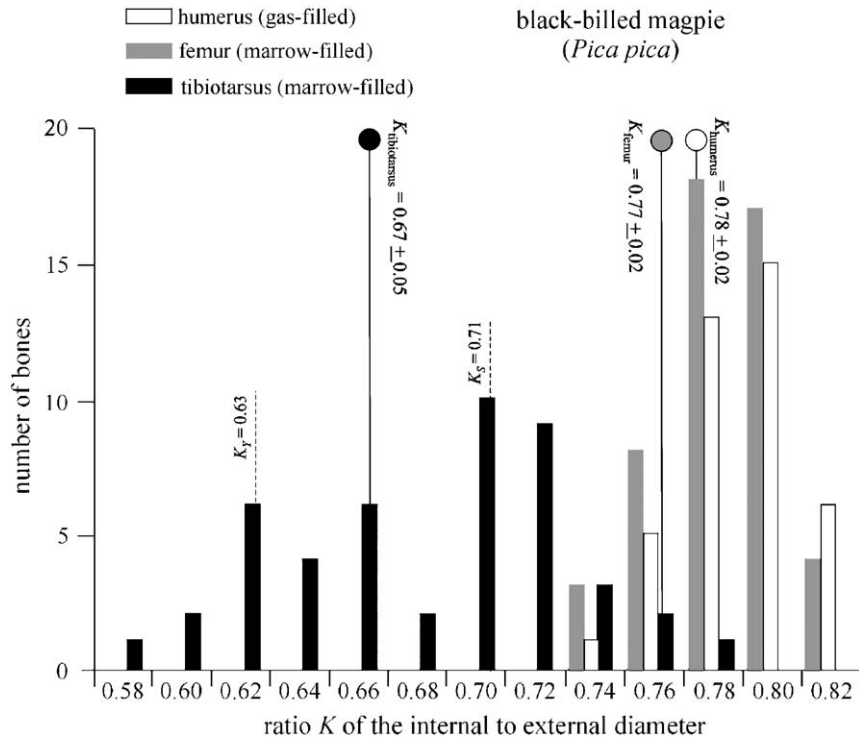


Fig. 3. As Fig. 2 for the black-billed magpie, *Pica pica*.

Table 1

Average K_{average} , standard deviation ΔK , minimum K_{min} , maximum K_{max} (of the ratio K of the internal to external diameter) and number N of the gas-filled humerus, marrow-filled femur, and marrow-filled tibiotarsus in the hooded crow, *Corvus corone cornix* and the black-billed magpie, *Pica pica* measured at the mid-point of the shafts with evaluation of the radiographs of the bones

Species	Bone type	Filled by	K_{average}	ΔK	K_{min}	K_{max}	N
<i>Corvus corone cornix</i>	Humerus	Gas	0.78	0.03	0.72	0.83	16
	Femur	Marrow	0.79	0.02	0.75	0.82	21
	Tibiotarsus	Marrow	0.71	0.04	0.62	0.76	19
<i>Pica pica</i>	Humerus	Gas	0.78	0.02	0.74	0.81	40
	Femur	Marrow	0.77	0.02	0.73	0.81	50
	Tibiotarsus	Marrow	0.67	0.05	0.57	0.77	46

Corvus and *Pica* are far from the minimum mass condition. K of the marrow-filled femora in *Corvus* ($K = 0.79 \pm 0.02$, $K_{\text{max}} = 0.82$) and *Pica* ($K = 0.77 \pm 0.02$, $K_{\text{max}} = 0.81$) is high in comparison with K of the marrow-filled femora in the red fox *Vulpes vulpes* with $K = 0.68 \pm 0.036$ (Bernáth et al., 2004) and the marrow-filled human femora with $K_{\text{posterior}} = 0.498 \pm 0.085$ for the posterior view, and $K_{\text{medial}} = 0.589 \pm 0.070$ for the medial view (Évinger et al., 2005).

Thin-walled and gas-filled tubes are liable to fail by local buckling. The K -values of the gas-filled humeri in *Corvus* ($K_{\text{average}} = 0.78$, $K_{\text{max}} = 0.83$) and *Pica* ($K_{\text{average}} = 0.78$, $K_{\text{max}} = 0.81$) (Table 1) are far below the theoretical optimum $K^* = 0.93$ for thin-walled, gas-filled bones. Thus the humeri in *Corvus* and *Pica* are far

from the minimum mass condition. The average K -values of the humeri and femora in both bird species are practically the same although the former are gas-filled and the latter are marrow-filled. Since the optimum for K of gas-filled tubular bones is much larger than the optima for K of marrow-filled tubular bones, significantly larger K -values of the humeri could be expected than those of the femora.

In flying birds the distal long bones (e.g. tibiotarsus) tend to have smaller K than proximal bones (e.g. femur) in the same limb (Currey and Alexander, 1985). This is corroborated also by our measurements: In *Corvus* $K_{\text{tibiotarsus}} = 0.71 < K_{\text{femur}} = 0.79$, and in *Pica* $K_{\text{tibiotarsus}} = 0.67 < K_{\text{femur}} = 0.77$ (Fig. 1A, Table 1). Note, however, that the standard deviation ΔK of the

tibiotarsi ($\Delta K = 0.04\text{--}0.05$) is two times as large as that of the femora ($\Delta K = 0.02$) both in *Corvus* and *Pica*.

Currey and Alexander (1985) measured K of a single humerus ($K_{\text{humerus}} = 0.76$) and tibiotarsus ($K_{\text{tibiotarsus}} = 0.55$) in the common raven *Corvus corax*, being a very close relative of *Corvus corone cornix* (Table 1). $K_{\text{humerus}} = 0.76$ in *Corvus corax* is very close to $K_{\text{average}} = 0.78$ in *Corvus corone cornix* (with $K_{\text{min}} = 0.72$, $K_{\text{max}} = 0.83$). On the other hand, $K_{\text{tibiotarsus}} = 0.55$ in *Corvus corax* is much smaller than $K_{\text{average}} = 0.71$ in *Corvus corone cornix* (with $K_{\text{min}} = 0.62$, $K_{\text{max}} = 0.76$). According to Currey and Alexander (1985), gas-filled avian bones are usually thinner-walled, i.e. possess higher K than marrow-filled bones. However, this is not the case for *Corvus corone cornix* and *Pica pica*, for which the gas-filled humeri ($K_{\text{average}} = 0.78$) have practically the same K as the marrow-filled femora ($K_{\text{average}} = 0.77\text{--}0.79$).

The K -values measured in *Corvus* and *Pica* are much smaller than the theoretical optimum $K^* = 0.93$. A possible reason for this may be that for resistance to localized impact it is better to have a bone that is more solid rather than more hollow, that is, the K of which is smaller (Currey and Alexander, 1985). The K -values of the gas-filled bones in *Corvus* and *Pica*, which are considerably lower than would be appropriate for minimum mass, may be adaptations to the mode of life of these birds: Beside flight, terrestrial locomotion is also an important ecological function for corvids which spend a great deal of their time on the ground, mainly to feed. Black-billed magpies walk, run and hop (Verstappen et al., 1998; own observations), but they prefer hopping at speeds higher than walking (Verstappen et al., 2000), while hooded crows walk and hop only (Hayes and Alexander, 1983; own observations). K -values lower than K^* allow for some direct violence on the bones in crows and magpies.

The humeri of adult *Corvus* and *Pica* are gas-filled, while the femora and tibiotarsi are marrow-filled. We found that the values for K for the marrow-filled femora are essentially the same as for the gas-filled humeri, while the marrow-filled tibiotarsi have significantly lower K -values. Thus, one of the predictions made by Currey and Alexander (1985) is not corroborated by these results. Although the theory and findings of Currey and Alexander (1985) are probably broadly correct, the fact that their prediction for the humeri, femora and tibiotarsi in crows and magpies is not corroborated is interesting. The biomechanical reasons for this lack of corroboration is, however, unknown.

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