

Contribution of internal bony trabeculae to the mechanical properties of the humerus of the pigeon (*Columba livia*)

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(With 1 plate and 1 figure in the text)

Mechanical properties of the pigeon humerus are significantly influenced by internal bony trabeculae. Experimental testing of braced (intact trabeculae) and unbraced (trabeculae experimentally removed) humerus pairs extracted from the same individuals demonstrates that the flexural rigidity, strength and toughness (work of fracture) of the pigeon humerus are all augmented by an intact framework of trabeculae. Measured differences in mechanical properties in braced/unbraced comparisons generally exceed discrepancies attributable to random variation in construction and thus cannot be ascribed to inherent skeletal asymmetry. The structural contribution of bony trabeculae is apparently greater in subadult birds, possibly due to thickening of cortical bone and/or increasing mineralization of bone tissue with age.

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Introduction

Forces developed during avian flight are transmitted from the feathers of the wing through the more distal bones of the forelimb, and are ultimately concentrated at the head of the humerus (Pennycuick, 1972). Thus, for a bird to maintain control and efficiency during flight, the humerus must resist both bending and twisting moments (Pennycuick, 1967; Bou, Olmos & Casinos, 1989). The avian humerus must also maintain a low mass to conform with a flight-adapted body plan.

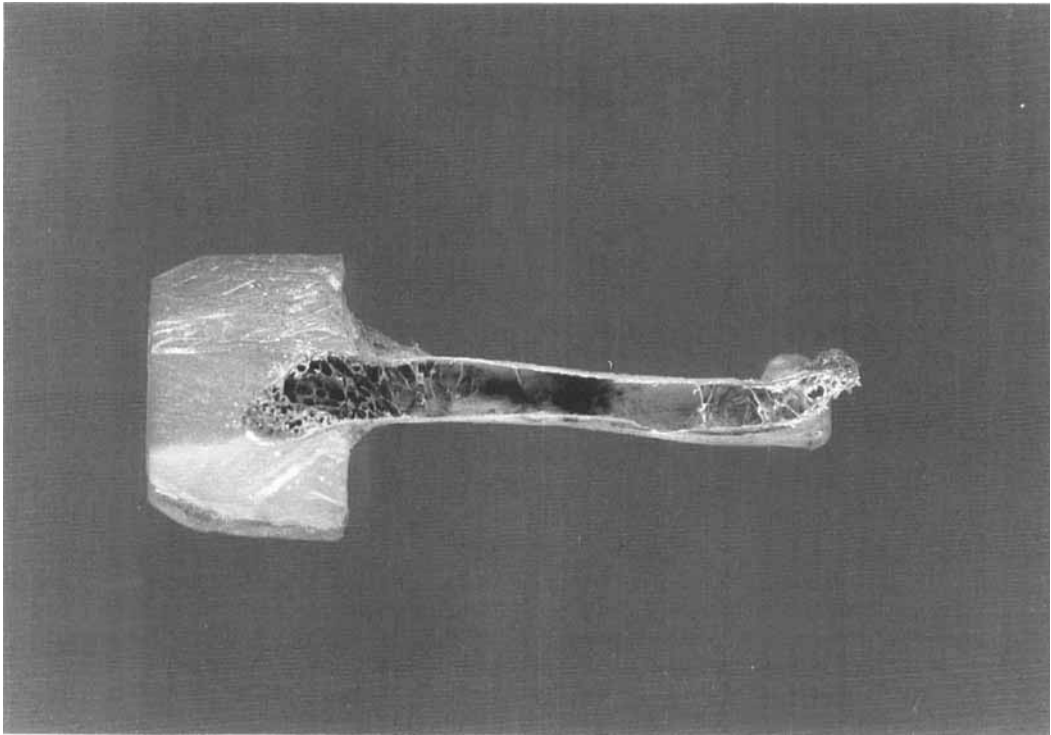


PLATE I. Longitudinal section through a left pigeon humerus (postero-ventral view, image $2\times$ actual size); proximal end of humerus is mounted in epoxy base. Bony trabeculae are restricted to proximal and distal ends of the bone.

Birds fulfil these basic requirements with a humerus approximating a thin-walled, hollow cylinder. Such a structure provides high stiffness with a minimum investment of osseous material (Wainwright *et al.*, 1982; Currey & Alexander, 1985), and furnishes ample surface area for the attachment of flight muscles.

Bony trabeculae span the hollow medullary cavity of the humerus in several avian species; trabeculae are typically localized in the proximal and distal ends of the bone (Plate I). Crisp (1857: 218) was early in recognizing the likelihood that strength is added to the avian humerus by these 'cross and transverse beams'. A 'stiffening effect' of internal trabeculae within vertebrate limb bones was proposed by D'Arcy Thompson (1943: 981) in his text *On form and growth*. Pennycuik (1967) also proposed that bony trabeculae within the avian humerus, specifically the humerus of *Columba livia*, should serve to maintain the integrity of the thin cortical bone under load and help prevent buckling. In this paper, we experimentally test and quantify the contribution of internal bony trabeculae to the flexural rigidity, strength and work of fracture (toughness) of the pigeon humerus.

Materials and methods

Eight feral pigeons (*Columba livia*), 5 adults and 3 fledglings, were used in this experiment. Frozen carcasses were obtained from a standing sample of birds culled for evolutionary research (Clayton, 1989). Humerus

pairs were excised from each bird, and one bone from each pair was randomly selected for alteration. A small hole (0.25 cm) was hand-drilled into the centre of the head of the chosen humerus, and the trabeculae within this bone were destroyed by inserting a probe and breaking all trabeculae encountered. Bony trabeculae within the humerus of the pigeon are exceedingly thin, and thus minimal effort was needed to remove them. Care was taken, however, to minimize damage to cortical bone tissues. After the internal trabecular framework was destroyed, the drill-hole in the head of the humerus was filled with modelling clay.

Braced-unbraced humerus pairs were mounted vertically within DEVCON 5-minute epoxy, with the head of the humerus embedded to an average depth of 0.8 cm. Each matched pair of humeri was mounted simultaneously within the same mixture of epoxy to avoid significant 'within-pair' variations in epoxy composition, setting time and compliance. Mounted bones were stored in a refrigerator (*c.* 4 °C), and tested within 5 days of excision to avoid excessive dehydration. All bones retained a greasy feel at the time of testing.

Mounted humerus pairs were loaded in bending as fixed cantilevers on a Monsanto tensometer. Force (± 1 N) was measured via a strain gauge attached to the tensometer's force transducer (a steel beam loaded in 3-point bending); deformation was measured indirectly with an LVDT. Force vs. displacement curves were generated on a chart recorder. Bones were loaded manually (using a handcrank), at an approximate rate of 42 $\mu\text{m/s}$, until fracture occurred. Force was applied to the ventral epiphysis of the humerus, perpendicular to the plane of the deltoid crest, in order to mimic forces during the downward 'power stroke' of a bird in flight (Pennycuik, 1967) (Fig. 1). Table I lists humeri lengths, measured from the top of the epoxy base to the position on the ventral epiphysis where the point load was focused, for each humerus pair. The average moment arm (exposed humerus length) was 0.0325 m. Experimentally altered specimens within each pair—(R) right or (L) left—are also indicated. All experiments were performed at room temperature (*c.* 21 °C).

The compliance of the mounting apparatus was determined by loading steel rods of known length, diameter and elastic modulus as cantilevers (mounted identically to the bones) and comparing measured deflections with calculated deflections. Significant compliance of the apparatus was not detected in the range of forces used in this experiment.

Bending moments were calculated by multiplying the length of each humerus (as given in Table I) by the force (newtons) applied to the specimen. The work of fracture for each humerus was normalized by dividing the area under each force vs. displacement curve by the cantilever length of the associated humerus.

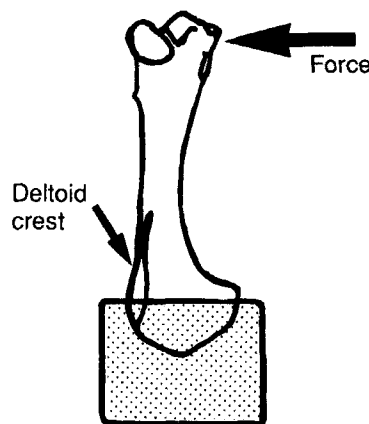


FIG. 1. Schematic illustration of mounted humerus (anterior view, epoxy base is stippled). Force was applied to the ventral epiphysis, perpendicular to the plane of the deltoid crest, in order to mimic forces during the avian power stroke. Bones were loaded as fixed cantilevers in a Monsanto tensometer.

TABLE I

Lengths (moment arms) of humeri loaded in bending as fixed cantilevers, altered specimens (unbraced) are indicated by (R)-right or (L)-left

Humerus pair	Length (10 ⁻² m)	
	Braced	Unbraced
SA-1 (L)	3.293	3.234
SA-2 (R)	3.253	3.380
SA-3 (R)	3.282	3.252
A-1 (L)	3.351	3.451
A-2 (R)	3.060	3.182
A-3 (L)	3.313	3.167
A-4 (R)	3.181	3.149
A-5 (R)	3.243	3.235

Percentage discrepancies (δ) in measured properties between paired humeri were calculated using the equation:

$$\delta = 200(x_b - x_u)/(x_b + x_u)$$

where δ is the discrepancy of interest (e.g. deflection, strength, work of fracture, etc.) expressed as a percentage, x_b is the quantity of interest for the braced humerus, and x_u is the quantity of interest for the unbraced humerus. This 'discrepancy equation', the difference between 2 values divided by their mean expressed as a percentage, was used by Alexander *et al.* (1984) to compare differences in mechanical properties between paired right and left avian limb bones in a study of limb bone symmetry.

Our results were evaluated for statistical significance using parametric (Paired *t*-test) and non-parametric (Wilcoxon's signed ranks, Wilcoxon's 2-sample) statistical tests. *P* values of 0.05 or less (e.g. $\geq 95\%$ confidence level) are herein accepted as an indication of statistical significance.

Results

Empirical breakage patterns

Unaltered (intact trabeculae) pigeon humeri tested as end-loaded cantilevers within the tensometer exhibited catastrophic, brittle fracture at bending moments ranging from 1.15 N m to 2.96 N m. Altered humeri failed catastrophically at bending moments ranging from 0.78 N m to 2.19 N m. The initial stages of deformation in all cases were elastic; however, 13 of the 16 bones tested experienced a phase of plastic deformation, with the bone exhibiting continuous yield with no addition of force, immediately prior to failure. Spiral fracture was the most common mode of breakage, with a single fracture climbing invariably toward the dorsal surface of the humerus. Longitudinal fractures (e.g. fractures running parallel to the shaft of the humerus) occurred in two specimens.

All humeri broke within 1.0 cm of the basal attachment, and most specimens fractured within 0.5 cm of the basal attachment. Four of the eight humerus pairs tested (SA-1, A-2, A-4, A-5) showed no obvious variation in the location of fracture. Specimen pair A-3 exhibited differential breakage, with the braced humerus fracturing closer to the base than its unbraced counterpart. The three remaining humerus pairs (SA-2, SA-3, A-1) exhibited the opposite condition, with the unbraced humeri fracturing closer to the base. This last mode of differential breakage may offer insight into the function of the internal bony trabeculae of the pigeon humerus, and will be addressed below.

Deflection at 0.65 N m bending moment

Deflections of the eight braced-unbraced humerus pairs exposed to a 0.65 N m bending moment are presented in Table II. A 0.65 N m bending moment was chosen for comparison because all humerus pairs withstood a 0.65 N m bending moment without fracturing or yielding plastically. Moreover, a bending moment of 0.65 N m is within the range of forces the humerus could conceivably experience during flight; 1.0 N m is the greatest bending moment the pectoralis muscle can apply to the humerus before the pectoralis insertion on the deltoid crest detaches (Pennycuik & Parker, 1966).

Humerus pairs SA-1, SA-2, SA-3, A-2, A-3, A-4 and A-5 all showed greater deflections when exposed to a 0.65 N m bending moment in the unbraced condition, with an average deflection of 5.8×10^{-4} m braced and 7.4×10^{-4} m unbraced. Humerus pair A-1 exhibited a greater relative deflection for the braced humerus— 5.1×10^{-4} m braced, 4.2×10^{-4} m unbraced. The percentage discrepancy in deflection for these eight humerus pairs ranged from -19.3% (A-1) to 52.6% (A-3) and averaged 23.1%. Overall, deflection values in our braced-unbraced tests were significantly different ($n=8$; $P<0.04$; Paired t -test; $P<0.05$: Wilcoxon's signed ranks).

Bending moment at failure

Bending moments of braced and unbraced humeri at fracture, here considered a proxy of the ultimate strength of the humeri, are presented in Table III. The eight humerus pairs tested showed significantly different bending moments at fracture in braced-unbraced comparisons ($n=8$; $P<0.01$: Paired t -test; $P<0.02$: Wilcoxon's signed ranks).

Braced humeri withstood a greater bending moment before fracture in seven out of eight tests. Bending moments at fracture ranged from 1.15 N m to 2.96 N m for intact humeri and 0.78 N m to 2.19 N m for unbraced humeri. Discrepancy values (Table III) varied from -3.4% (A-3) to 38.3% (SA-1), and averaged 20.8%. The single humerus pair (A-3) in which the unbraced humerus fractured at a greater bending moment than its braced counterpart showed a discrepancy value of only -3.4%.

TABLE II
*Deflection of braced-unbraced humerus pairs
subjected to a 0.65 N m bending moment with
associated discrepancy (δ) values*

Humerus pair	Deflection (10^{-4} m)		δ (%)
	Braced	Unbraced	
SA-1	8.9	9.7	8.6
SA-2	5.4	8.5	44.6
SA-3	4.4	7.4	50.8
A-1	5.1	4.2	-19.3
A-2	3.9	5.2	28.6
A-3	2.1	3.6	52.6
A-4	7.8	8.6	9.8
A-5	8.1	8.9	9.4

TABLE III

Bending moments of braced-unbraced humerus pairs at fracture with associated discrepancy (δ) values

Humerus pair	Bending moment (N m)		δ (%)
	Braced	Unbraced	
SA-1	1.15	0.78	38.3
SA-2	1.61	1.18	30.8
SA-3	1.36	1.07	23.8
A-1	2.68	2.14	22.4
A-2	2.96	2.19	29.9
A-3	2.02	2.09	-3.4
A-4	2.38	2.01	16.8
A-5	2.11	1.94	8.4

Work of fracture

Work of fracture values listed in Table IV are normalized for cantilever length, as cantilever length was the only significant variation in this 'within-bird' comparative study of homologous structures. Values are thus reported as joules per metre (J/m).

In accord with the other parameters investigated, the work of fracture showed significant variation between braced and unbraced humeri ($n = 8$; $P < 0.05$: Paired t -test; $P < 0.03$: Wilcoxon's signed ranks). Indeed, seven of the eight humerus pairs tested required more work to fracture the braced humerus; only one humerus pair (A-3) required greater work to fracture the unbraced specimen. The average discrepancy in work of fracture was 46.9%.

Ontogenetic variation

On average, humerus pairs derived from fledgling birds—SA-1, SA-2, SA-3—were characterized by lower rigidity, strength and toughness than adult humerus pairs—A-1, A-2, A-3, A-4, A-5—in both braced and unbraced comparisons (Table IV). Moreover, this apparent ontogenetic

TABLE IV

Work of fracture for braced-unbraced humerus pairs normalized for cantilever length; associated discrepancy (δ) values are also given

Humerus pair	Work of fracture (J/m)		δ (%)
	Braced	Unbraced	
SA-1	0.073	0.028	89.1
SA-2	0.070	0.035	66.6
SA-3	0.048	0.028	52.6
A-1	0.155	0.078	66.0
A-2	0.281	0.116	83.0
A-3	0.094	0.114	-19.0
A-4	0.207	0.146	34.6
A-5	0.209	0.204	2.4

TABLE V

Means and standard error of the means of deflection at 0.65 Nm, breaking strength, and work of fracture for adult ($n=5$) and fledgling ($n=3$) humeri

Humeri	Deflection ($\times 10^{-4}$ m)		Strength (N m)		Work of fracture (J/m)	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Fledgling Braced	6.2	1.38	1.37	0.13	0.064	0.008
Adult Braced	5.4	1.16	2.43	0.17	0.189	0.031
Discrepancy	13.8%		55.8%		98.8%	
Fledgling Unbraced	8.5	0.69	1.01	0.12	0.030	0.002
Adult Unbraced	6.1	1.12	2.07	0.04	0.131	0.021
Discrepancy	32.8%		68.8%		125.5%	

variation was amplified in unbraced test results (see δ , Table IV). Despite small sample sizes ($n_1 = 5$ (adult), $n_2 = 3$ (juvenile)), ontogenetic variability in mechanical properties was statistically significant ($P \leq 0.025$; Wilcoxon's two-sample) for all attributes tested except deflection at 0.65 N m. These data corroborate the ontogenetic variability in stiffness and strength of avian humeri demonstrated by Carrier & Leon (1990) for the California gull (*Larus californicus*), and further suggest interesting functional aspects of the internal trabeculae of the pigeon humerus through ontogeny (see below).

Discussion

The pigeon, deemed a highly proficient flier (Aulie, 1983; Simpson, 1983), devotes considerable muscle mass to the forelimb locomotory system. Flight muscles comprise as much as 32% of pigeon body weight (Hartman, 1961), with the pectoralis muscles, which insert upon the deltoid crest of the humerus, contributing most to this percentage (c. 20%). During flapping flight, the humerus of the pigeon must resist cyclic bending and twisting moments (Pennycuick, 1967; Bou *et al.*, 1989) with minimal deformation. As a thin-walled, hollow structure the pigeon humerus is well designed for this task (Wainwright *et al.*, 1982; Currey & Alexander, 1985), especially considering weight constraints imposed by the streamlined avian body plan.

Crisp (1857) and Pennycuick (1967) postulated that bony trabeculae localized in the proximal and distal ends of the avian humerus should serve to reinforce the limb bone under dynamic loads. Bock (1966), using theoretical calculations, showed that bony trabeculae within the bill of the common crow (*Corvus brachyrhynchos*) correspond closely with the arrangement of force trajectories in a stressed bill.

We have shown experimentally that internal trabeculae contribute significantly to the stiffness, strength and toughness of the pigeon humerus. End-loaded pigeon humeri with intact trabeculae consistently showed greater flexural rigidity and strength, and required more work to fracture than experimentally altered counterparts (see Tables II, III and IV). Discrepancy values reported in Tables III and IV generally exceed discrepancies in strength and work of fracture reported by Alexander *et al.* (1984) for humeri of *Columba livia* in a study of avian limb bone symmetry. Thus, our results cannot be explained by inherent skeletal asymmetry. However, random variations in

bone construction probably account for humerus pairs A-1 and A-3, for which the pattern of greater strength, stiffness, and/or toughness of braced humeri is equivocal or reversed.

Differential breakage patterns in three humerus pairs (A-1, SA-2, SA-3) also suggest that trabeculae within the proximal end of the pigeon humerus influence mechanical properties. An intact framework of trabeculae seems capable of directing fracture further up the shaft, away from proximal reaches of end-loaded bones where bending moments are greatest (Wainwright *et al.*, 1982). By reinforcing proximal reaches of the humerus with lightweight internal trabeculae, the pigeon in effect increases the potential for energy absorption, and thus increases the absolute amount of energy required to induce failure in the humerus.

Our results further suggest that humeri of fledgling birds may benefit to a greater extent than those of adults from a framework of internal trabeculae (see Table V). In all mechanical attributes measured, discrepancies in unbraced adult–fledgling comparisons exceed those in braced adult–fledgling comparisons. Data suggest that as the pigeon matures, cortical bone contributes more to overall bone rigidity, strength and toughness. Thickening of cortical bone during maturation (Carrier & Leon, 1990) and/or increasing mineralization of bone tissue with age (Currey, 1984; Brear, Currey & Pond, 1990) may explain this phenomenon.

Summary

(1) Paired humeri excised from eight feral pigeons (*Columba livia*) were loaded in bending as fixed cantilevers in order to test the contribution of internal trabeculae to mechanical properties (flexural rigidity, strength and work of fracture) of the humerus. One bone from each pair was experimentally altered (e.g. trabeculae removed) prior to testing.

(2) Humeri with intact trabeculae consistently showed greater flexural rigidity, strength and toughness. Discrepancy values recorded in braced–unbraced comparisons generally exceeded discrepancies reported for paired comparisons of strength and work of fracture for unaltered pigeon humeri (Alexander *et al.*, 1984). Our results support previous suggestions that trabeculae influence the mechanical properties of the pigeon humerus.

(3) On average, humerus pairs derived from fledgling birds showed less rigidity, strength and toughness than adult humerus pairs in both braced and unbraced comparisons. This apparent ontogenetic variation was amplified in the unbraced test results, suggesting that internal trabeculae may play a greater role in reinforcing the mechanical properties of subadult pigeon humeri. This phenomenon may be due to thickening of cortical bone and/or increased mineralization with maturation.

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