J. Exp. Biol. (1967), 46, 219–233
With 11 *text-figures*
Printed in Great Britain

THE STRENGTH OF THE PIGEON'S WING BONES IN RELATION TO THEIR FUNCTION

BY C. J. PENNYCUICK
Department of Zoology, University of Bristol

(*Received* 13 *October* 1966)

INTRODUCTION

In the pigeon, as in other members of the three groups of vertebrates which have developed advanced powers of flight—the birds, bats and pterosaurs—the bending and torsional strength of the proximal part of the wing lies in the humerus and radio-ulna. The humerus runs obliquely back from the shoulder joint to the elbow, and from there the radio-ulna runs obliquely forward to the wrist. In flight the radio-ulna is generally set at a large angle to the humerus, often about a right angle (Fig. 8).

The elbow joint is free to bend in the plane of the wing, but transmits bending moments at right angles to this plane, and twisting moments. Because of the large angle between the radio-ulna and the humerus, bending moments applied by the lift force to the radio-ulna are transmitted to the humerus largely as twisting moments, and vice versa. At the shoulder joint, the head of the humerus is free to rotate through large angles in all of the six possible ways—up, down, forward, back, and rotation in the nose-up and nose-down senses: bending and twisting moments cannot, therefore, be transmitted to the body without the help of muscles inserting on the humerus.

In this paper the ultimate strengths of the humerus and radio-ulna under bending and twisting loads are examined. The question is then asked—How much lift would be needed to break the bones in various ways? This can be answered subject to making some assumptions about the distribution of lift over the wing, and, this done, the limitations imposed by the structural strengths of the wing bones on the pigeon's performance can be considered.

MATERIAL

Feral pigeons *Columba livia* were caught in nocturnal raids on Bristol University's clock tower, and were kept in cages until wanted. Strength tests on bones were carried out as soon as possible after killing and dissection.

METHODS

Mounting of bones

In strength tests on bones, the ends of the bones were embedded in Wood's Metal (m.p. 70° C.) in brass cups, and the test forces were then applied to the brass cups. By this means the ends of the bone were firmly gripped, but as the Wood's Metal mould fitted the bone closely, concentrated forces were avoided.

Bending strength

Bending moments were applied to the bones with the apparatus shown in Fig. 1. The lower brass cup was rigidly fixed, and the test force was applied horizontally to the lever arm projecting upwards from the upper one, by means of a string passing

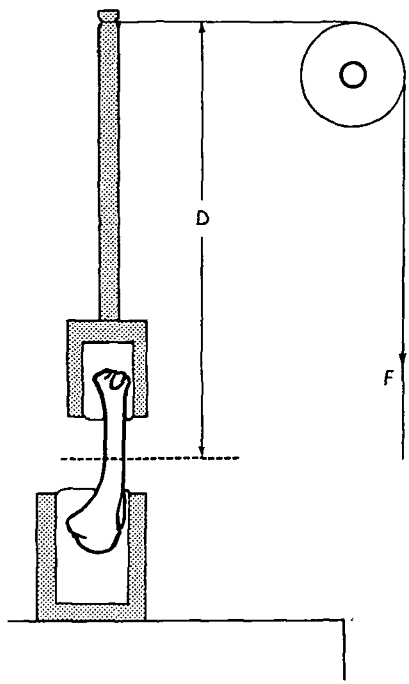

Fig. 1. Apparatus for applying bending moments to bones (see text).

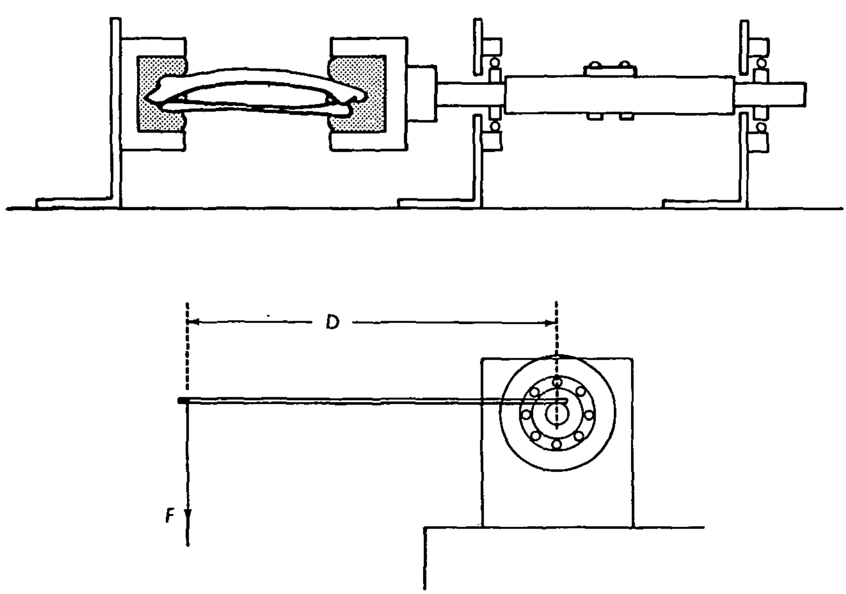

Fig. 2. Apparatus for applying twisting moments to bones (see text).

over a pully. A stream of water was directed into a bucket tied to the end of the string, and diverted as soon as the bone broke. The force F in the string causing failure was then determined by weighing the bucket of water on a spring balance graduated in steps of 100 g. wt. The moment arm D was measured from the point of attachment of the string to the lever, to the point at which the bone broke (dotted line in Fig. 1). FD was then taken as the bending moment causing failure.

The arrangement also subjected the bone to a shearing stress, but as this was generally less than 20 kg. wt./cm.^{2} at failure, it is unlikely to have influenced the result. This feature of the tests is therefore neglected, and results are regarded as a measure of the limiting bending moments which the bones could bear.

Torsional strength

For these tests the bone was mounted horizontally as shown in Fig. 2, the cup at one end being fixed, while that at the other was mounted on a shaft supported on two ball races, so that only torsional stresses could be applied to the bone. A lever projected horizontally from this shaft, at right angles to it, and test moments were applied by hanging weights from the end of this lever.

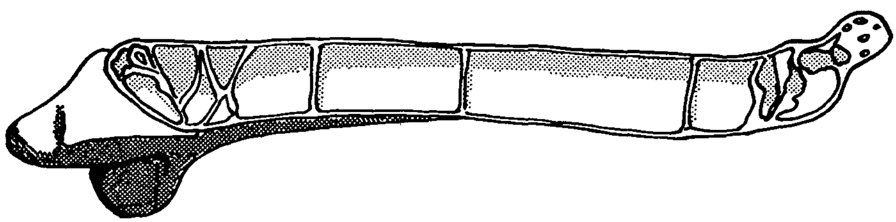

Fig. 3. Oblique longitudinal section through right humerus of pigeon, looking postero-ventrally. Slender bony trabeculae cross the hollow interior of the bone at the ends, and form annular thickenings inside the cylindrical shaft, thus maintaining the thin outer wall under load, and preventing buckling.

RESULTS

Structure of the humerus

Although the anatomy of the pigeon's skeleton is well known, some features of the bones under test will be pointed out here in order to enable the results of the tests to be more readily followed.

The humerus is basically a hollow tube of bone, more or less circular in section, which carries the bending and twisting moments set up by the aerodynamic forces acting on the wing (Fig. 3). It would not appear to be significantly loaded in direct tension or compression as a rule. The ends are widened and reinforced with bony trabeculae, the proximal end to form the ball of the shoulder joint and to carry the insertions of the muscles acting at this joint, and the distal end to form a joint with the radio-ulna which is strong and stiff in torsion and vertical bending, but free to bend fore-and-aft.

Fig. 4 is a view along the axis of the humerus from the proximal end, to show its orientation in life. The deltoid crest forms a shelf jutting forward on the dorsal side of the humerus, with the *pectoralis* muscle inserting on its ventral side. The dorsal surface of the deltoid crest is approximately flat, and parallel with the plane of the wing. This was used as a guide in setting up humeri in the bending apparatus, the bending force being applied at right angles to the flat dorsal face of the deltoid crest, and in such a direction as to bend the distal end of the bone dorsally.

Bending strength

The eight humeri of four pigeons, of average weight 393 g. wt. were broken in the bending apparatus. Failure occurred at points varying between 0·38 and 0·70 (averaging 0·53) of the overall length of the humerus from the proximal end, the average overall length being 4·83 cm. The bending moment at failure varied between 13·4 and 21·1 kg. wt. cm., averaging 17·0 kg. wt. cm.

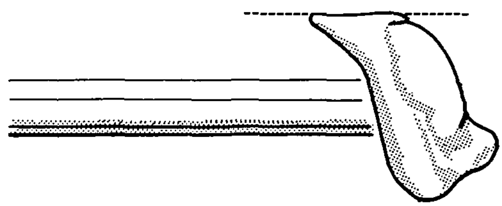

Fig. 4. Head of humerus, looking distad, showing orientation in relation to radio-ulna. Anterior to left of diagram. Dotted line marks flat dorsal surface of deltoid crest—used as a guide in orienting humeri in the bending apparatus.

Torsional strength

Six humeri were subjected to twisting moments in the apparatus of Fig. 2, and broke at moments between 11·2 and 14·1 kg. wt. cm., averaging 12·4 kg. wt.cm.

Structure of the radio-ulna

The radio-ulna of the pigeon shows the typical bird arrangement. The two bones articulate with one another at both ends, but are not fused. The ulna is the thicker bone, and is curved, bulging posteriorly, while the radius is thinner and straight. In the middle part of their length the two bones are quite separate, the radius being anterior to the ulna, and in section the line joining their centres is approximately perpendicular to the direction of the lift. Neither bone is pneumatic.

Bending strength

When subjected to a bending moment simulating the normal action of lift on the wing the two bones are side by side and their strengths are additive. The radio-ulnae of the same four pigeons, whose humeri were tested as described above, were broken in the same manner in the bending apparatus. The average overall length of the ulna was 6·06 cm. and the average point of failure was 0·33 of the overall length from the proximal end, though the variation in this measurement was rather wide, ranging from 0·17 to 0·76. The bending moment at failure varied between 7·7 and 12·4 kg. wt. cm., averaging 10·6 kg. wt. cm.

Neutral axis of torsion

Twisting the radio-ulna produces a somewhat more complicated situation than is seen in the approximately cylindrical humerus. Owing to the asymmetry of the radio-ulna, with two different-sized bones separated by a gap, at least one of the bones must be off the axis about which twisting is applied, and hence is subjected to a combination of bending and twisting moments. The choice of twisting axis therefore affects the results of torsional strength measurements, and in order to minimize bending the neutral axis of torsion was used. By definition, a force applied to this axis, and at right angles to it, produces bending without twisting.

The neutral axis of torsion was located by the method illustrated in Fig. 5. The procedure was carried out at both ends of a radio-ulna, and the position of the neutral axis of torsion, thus located, is marked in Fig. 6.

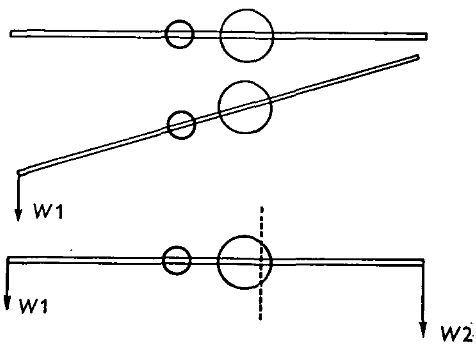

Fig. 5. Method of locating neutral axis of torsion of radio-ulna. Top: A light horizontal bar is attached transversely to one end of the radio-ulna, the other end being fixed. Middle: addition of a weight *W*1 to one end of the bar causes the radio-ulna to bend and twist. Bottom: the weight *W*2 which, when applied to the other end of the bar, balances the twist produced by *W*1, is found. *W*1 and *W*2 then produce equal and opposite moments about the neutral axis (dotted line).

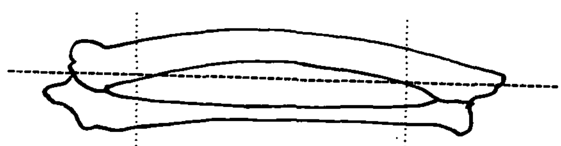

Fig. 6. Radio-ulna of pigeon showing points (thin dotted lines) at which neutral axis of torsion (thick dotted line) was located.

For setting up radio-ulnae in the twisting apparatus a jig was constructed by which a radio-ulna could be supported so that its neutral axis of torsion coincided with the axis of the twisting apparatus. With the specimen so held, Wood's Metal was poured into the cups, and the jig was then removed.

Torsional strength

Five radio-ulnae, from three pigeons, were broken in the twisting apparatus. The twisting moment at failure varied between 7·12 and 8·84 kg. wt. cm., and averaged 7·66 kg. wt. cm.

DISCUSSION

In order to consider the significance of the mechanical properties of the skeleton an estimate of the lift distribution must be made. This is attempted below for two extreme conditions of flight – gliding and the downstroke in hovering.

The difference between these two conditions lies in the distribution of relative air speed over the span. In a straight, unaccelerated glide (Fig. 7*a*) the wings are held motionless relative to the body, and the relative air speed is the same over the whole span—it is just the speed at which the bird is gliding along. In hovering (Fig. 7*b*) the bird's body is not moving at all, and the relative air speed at the body, including the shoulder joint, is zero. If the wing tip is distant r cm. from the shoulder joint, and the wing is flapped at ω radians/sec., then the speed of the tip (and hence the relative air speed at that point) is $r\omega$ cm./sec. The relative air speed increases linearly along the span from the shoulder joint to the tip.

a

b

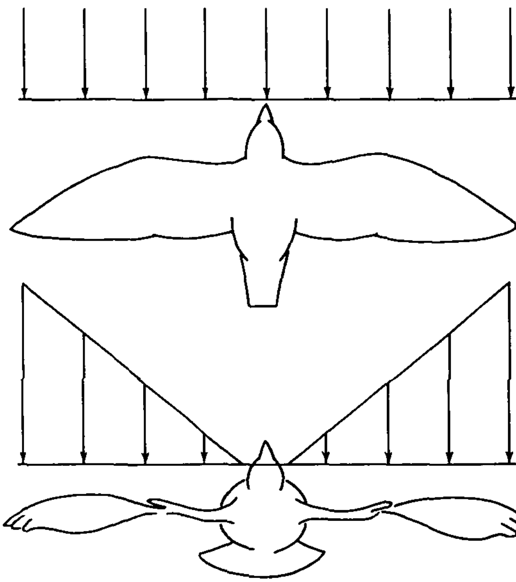

Fig. 7. (*a*) Pigeon gliding. The length of the arrows represents the relative air speed, which is the same at all points across the span. (*b*) Middle of downstroke in hovering. The relative air speed is zero at the body, and increases linearly from the shoulder joints to the wing tips.

In the downstroke of flapping flight other than hovering the relative airspeed at any point on the wing is the resultant of two components, one due to the forward motion of the whole bird, and the other due to the angular motion of the wing relative to the body. The velocity distribution will thus be intermediate between that for the hovering case, in which the former component is zero, and that for the gliding case, in which the latter is zero.

Estimation of lift distribution

To obtain a lift distribution the wing is divided up into 10 chordwise strips, and it is assumed that the lift on each strip is proportional to the product of its area and the square of the local relative air speed, which amounts to assuming that the local section lift coefficient is constant along the span. Readers with aeronautical knowledge may think this assumption somewhat rudimentary, but it provides a simple basis for making an approximation, in the absence of any evidence favouring some more elaborate assumption. The analysis refers, of course, only to positive (i.e. right-way-up) loading of the outstretched wing—more complicated situations, such as the inverted loading seen in the upward 'flick' in the upstroke of slow flapping flight (Brown, 1948) are not considered here.

The lift force acting on each strip of wing is assumed to act through a point whose spanwise position is in the middle of the strip, and whose chordwise position is a quarter of the chord behind the leading edge. The use of this 'quarter-chord point' for the centre of lift of a wing section follows from the theory of thin aerofoils, and is a good approximation for most real wing sections (Abbott & Doenhoff, 1959).

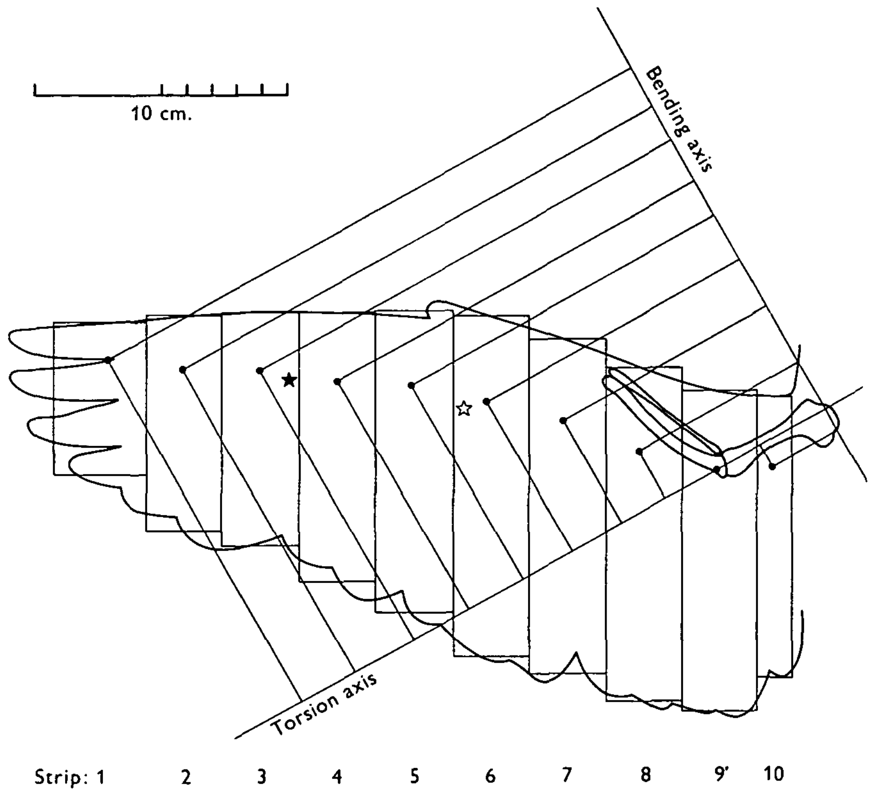

Fig. 8. The pigeon's outstretched wing replaced by ten rectangular strips of equivalent area (numbered at bottom). Solid circles mark the assumed centres of lift of the strips, and bending and twisting arms with respect to the humerus for each strip are drawn perpendicular to their respective axes. The method of finding the centre of lift of the whole wing in gliding (hollow star) and in hovering (solid star) is explained in the text, and the calculation is set out in Table 1.

A *torsion arm* and a *bending arm* are now measured for each strip with respect to the humerus (Fig. 8) and the radio-ulna (Fig. 9). The torsion arm is the distance between the centre of lift of the strip and the neutral axis of torsion of the bone (assumed to coincide with the axis of the cylindrical part of the bone in the case of the humerus). The bending arm is the distance between the centre of lift of the strip and an axis at right angles to the torsion axis. This axis passes through the centre of rotation of the head of the humerus in Fig. 8 and through the average point of failure in bending of the radio-ulna in Fig. 9.

Gliding—location of centre of lift

If speed and local lift coefficient are constant across the span, the lift for each strip is proportional to its area, and the lift distribution is the same as the area distribution (Fig. 10*a*). These conditions represent gliding flight.

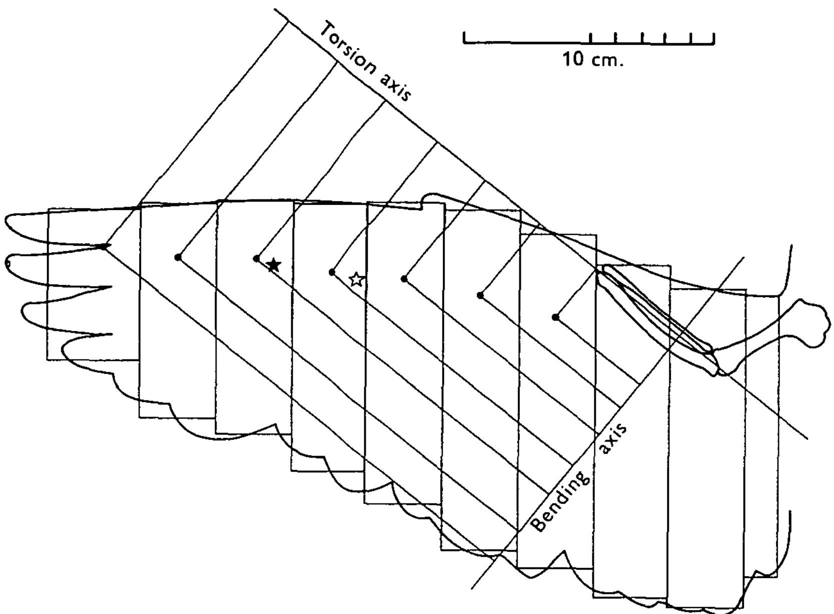

Fig. 9. Moment diagram as Fig. 8, but for the radio-ulna. Only those strips (1–7) distal to the distal end of the radio-ulna are considered in the moment calculation (Table 2).

If the area of the *i*th strip is s_i, and its torsion arm about the humerus t_i, then the lift on the strip applies a twisting moment proportional to $s_i t_i$ to the humerus. The total twisting moment M_t of the lift about the axis of the humerus is the sum of the contributions made by each strip, that is

$$M_t = \sum_{i=1}^{i=10} s_i t_i. \tag{1}$$

M_t, referred to as a 'moment' actually has the dimensions of volume, since wing area has been substituted for lift force. To obtain the mean torsion arm $\bar{t}$ for the whole wing, M_t is divided by the total wing area, S

$$\bar{t} = \frac{M_t}{S}. \tag{2}$$

Similarly, if the bending arm of the *i*th strip is b_i, the total bending 'moment' is

$$M_b = \sum_{i=1}^{i=10} s_i b_i. \tag{3}$$

and the mean bending arm $\bar{b}$ is

$$\bar{b} = \frac{M_b}{S}. \tag{4}$$

In Table 1 this calculation is carried out for the humerus, and the mean bending arm is found to be 12·4 cm., while the mean torsion arm is 7·0 cm. These distances are marked relative to their respective axes in Fig. 8, giving the point marked with a hollow star. This is the centre of lift in gliding, and may be regarded as the point through which the lift appears to act.

Table 1. *Moment analysis for humerus, from Fig.* 8

					Gliding		Hovering		
Strip	Area (cm.²)	Flapping radius (cm.)	Bending arm (cm.)	Torsion arm (cm.)	Bending 'moment' (cm.³)	Twisting 'moment' (cm.³)	'Lift' (cm.⁴)	Bending 'moment' (cm.⁵)	Twisting 'moment' (cm.⁵)
1	21·6	28·5	23·7	15·6	512	337	17,500	415,500	273,000
2	25·5	25·5	21·3	13·8	543	352	16,600	354,000	229,000
3	27·9	22·5	18·6	12·3	519	343	14,100	262,000	173,000
4	32·1	19·5	16·1	10·4	516	334	12,200	196,000	127,000
5	36·2	16·5	13·7	8·8	496	319	9,900	136,000	87,000
6	40·8	13·5	11·4	6·8	465	277	7,400	84,000	50,000
7	40·0	10·5	9·2	4·6	368	184	4,400	40,000	20,000
8	39·9	7·5	7·2	2·2	287	88	2,200	16,000	5,000
9	38·3	4·5	4·8	0·1	184	4	800	4,000	0
10	15·0	2·3	3·0	−0·9	45	−14	100	0	0
Totals	317·3	—	—	—	3,935	2,224	85,200	1,507,000	964,000

	Gliding	Hovering
Mean bending arm (cm.)	12·4	17·7
Max. bending moment (kg. wt. cm.)	17·0	17·0
Max. lift (kg. wt.)	1·72	1·12
Ultimate load factor (*g*)	8·8	5·7
Mean torsion arm (cm.)	7·0	11·3
Max. twisting moment (kg. wt. cm.)	12·4	12·4
Max. lift (kg. wt.)	1·77	1·10
Ultimate load factor (*g*)	9·0	5·6

Loading of the humerus

The bending moment $M_{b(\text{ult.})}$ and the twisting moment $M_{t(\text{ult.})}$ at which the humerus breaks having been found, two estimates are available for the maximum lift $L_{\text{max.}}$ which the wing can develop without breaking the humerus. $L_{\text{max.}}$ is obtained by dividing each maximum moment by the appropriate moment arm. The mean bending arm $\bar{b}$ is the distance between the centre of lift and the centre of rotation of the head of the humerus, but the humerus failed, on average, at a point 2·5 cm. distal to this. Therefore $L_{\text{max.}}$ is given by

$$L_{\text{max.}} = \frac{M_{b(\text{ult.})}}{\bar{b}-2\cdot 5} = \frac{17\cdot 0}{9\cdot 9} = 1\cdot 72 \text{ kg. wt.}$$

Similarly, from the twisting measurements

$$L_{\text{max.}} = \frac{M_{t(\text{ult.})}}{\bar{t}} = \frac{12\cdot 4}{7\cdot 0} = 1\cdot 77 \text{ kg. wt.}$$

The average weight of the pigeons used was 393 g. wt., so if the body is assumed to contribute no lift, each wing must carry half the weight, or 196 g. wt., in a straight, unaccelerated glide. The bending and torsional strengths of the humerus are thus sufficient to carry 8·8 and 9·0 times the weight respectively. The humerus may be said to have 'ultimate load factors' of 8·8 and 9·0 in bending and torsion respectively. The similarity of the two figures indicates that the humerus is about as likely (or unlikely) to break in bending as in torsion.

Table 2. *Moment analysis for radio-ulna, from Fig.* 9

					Gliding		Hovering		
Strip	Area ($cm.^2$)	Flapping radius (cm.)	Bending arm (cm.)	Torsion arm (cm.)	Bending 'moment' ($cm.^3$)	Twisting 'moment' ($cm.^3$)	'Lift' ($cm.^4$)	Bending 'moment' ($cm.^5$)	Twisting 'moment' ($cm.^5$)
1	21·6	28·5	20·0	11·6	432	251	17,500	350,000	203,000
2	25·5	25·5	17·4	10·0	444	255	16,600	289,000	166,000
3	27·9	22·5	15·0	8·1	418	226	14,100	211,000	114,000
4	32·1	19·5	12·3	6·6	395	212	12,200	150,000	80,000
5	36·2	16·5	9·9	5·0	358	181	9,900	98,000	50,000
6	40·8	13·5	7·1	3·7	289	151	7,400	53,000	27,000
7	40·0	10·5	4·3	2·5	172	100	4,400	19,000	11,000
Totals	224·1				2,508	1,376	82,100	1,170,000	651,000

	Gliding	Hovering
Mean bending arm (cm.)	11·2	14·2
Max. bending moment (kg. wt. cm.)	10·6	10·6
Max. lift (kg. wt.)	0·95	0·75
Ultimate load factor (*g*)	6·9	4·0
Mean torsion arm (cm.)	6·1	7·9
Max. twisting moment (kg. wt. cm.)	7·66	7·66
Max. lift (kg. wt.)	1·26	0·97
Ultimate load factor (*g*)	9·1	5·1

Pennycuick & Parker (1966) found that the *pectoralis* insertion is strong enough to apply a maximum bending moment of 10·2 kg. wt. cm. about the centre of rotation of the head of the humerus. Dividing this by $\bar{b}$, the corresponding lift would be 0·82 kg. wt., or 4·2 times the half-weight. If the lift exceeded this amount, the pectoralis would presumably be forcibly extended (assuming that the muscle is not capable of breaking its own insertion), and the wings would rise, so preventing the lift from becoming great enough to break the humerus. One may conclude from this that it would be practicable, and safe, for a pigeon to develop lift equal to about four times its own weight in gliding flight, and that the ultimate strength of the humerus would stand about 2¼ times this. It may be said that the 'proof load factor' is about four, with the ultimate load factor being about 2¼ times as great.

In glider design a proof load factor of 4 would be considered low, 6 being more usual. An ultimate load factor of 1·5 times the proof load factor would, however, normally be regarded as giving an adequate margin of strength, so that ultimate load factors are commonly around 9 in gliders, as in the pigeon.

An important difference is that, whereas virtually any aircraft can be broken up in flight by violent application of the controls at high speed, it appears that the pigeon would not be able to break its wings in this way. The wings would be forced up, so relieving the load, before the lift could become dangerously large.

Lift equal to 4 times the weight ($4g$) is as much as a prudent glider pilot would intentionally apply in flight, and the pigeon, for the reason just given, can go up to about the same limit without danger. This limits the maximum acceleration which can be applied normal to the flight path, and hence the minimum turning radius. For instance, if the pigeon is assumed to be able to develop a maximum lift coefficient of 3, which is reasonable, if not conservative, in view of the calculations set out below (pp. 231–232), it would be able to circle at a speed of 11·5 m./sec. with 75° of bank, and its minimum turning radius would be 3·4 m.

Loading of the radio-ulna

Since none of the flight feathers insert on the humerus in the pigeon, one may be reasonably confident in assuming that the moments set up by the lift are applied *in toto* to its distal end. In the case of the radio-ulna the lift contributed by strips 8–10 approximately (Fig. 8) acts along the length of the radio-ulna, and is not applied to its distal end. These strips represent 29·4 % of the area, and hence of the lift on current assumptions, but as can be seen from Fig. 8 their moment arms in both bending and torsion would be small with respect to the radio-ulna. Their moment contributions would therefore be small as well as doubtful, and to simplify matters they are neglected.

The moments acting on the distal end of the radio-ulna are assumed to be due to the lift on strips 1–7, as shown in Fig. 9, in which bending and torsion arms for these seven strips are drawn in. The mean bending and torsion arms for this distal part of the wing with respect to the radio-ulna are calculated as before (Table 2), and the resulting centre of lift in gliding is marked with a hollow star in Fig. 9. By the same reasoning as before, the lift acting through this point, sufficient to break the radio-ulna in bending, would be 0·95 kg. wt., while 1·26 kg. wt. would be required to break it in torsion. The lift carried by strips 1–7 would be 70·6 % of the half-weight, i.e. 138 g. wt., so that the ultimate load factors of the radio-ulna in bending and torsion are 6·9 and 9·1 respectively. Once again there is no danger of these values being approached before the *pectoralis* muscle is forcibly extended.

Hovering—centre of lift

The calculation of the position of the centre of lift in hovering proceeds as for the gliding case, except that the lift on each chordwise strip is no longer proportional to the area of the strip, because each strip is moving at a different speed. The speed of the ith strip is proportional to its flapping radius, r_i, which is the spanwise distance between the centre of lift of the strip and the centre of rotation of the head of the humerus. The lift is therefore proportional to the product of the area of the strip and the square of the flapping radius—assuming as before that local section lift coefficient is constant over the whole span.

The resulting lift distribution is compared with the gliding lift distribution in Table 3 and Fig. 10, the total lift represented being the same for both curves. The lift is now concentrated on the distal part of the wing—the proximal parts, although large in area, develop little lift because they are only moving slowly. Eighty-two per cent of the lift is developed on the distal five strips, in the hovering case, as opposed to 45 % in the gliding case.

Loading of the humerus

The calculation of mean bending and torsion arms for the humerus in hovering is set out in Table 1 (the 'moments' now have dimensions L^5), and the centre of lift in hovering thus located is marked with a solid star in Fig. 8.

It can be seen that the centre of lift is considerably further out in hovering than in flapping, and this, of course, reduces the maximum lift which can be developed without breaking the humerus. The bending strength of the humerus would limit the lift to 1·12 kg. wt. (5·7g), and the torsional strength would limit it to 1·10 kg. wt. (5·6g). The maximum lift which could be carried by the *pectoralis* tendon would be 580 g. wt. (2·9g). Once again it would not be possible to develop enough lift to break the humerus, though the ratio of the ultimate to the proof load factor is reduced to about 2 in hovering, instead of $2\frac{1}{4}$ as in the gliding case. Aerodynamical considerations (see below, pp. 231–232)) suggest that the wing would be able to develop only marginally over 1g in hovering, so in fact there is a substantial reserve of strength.

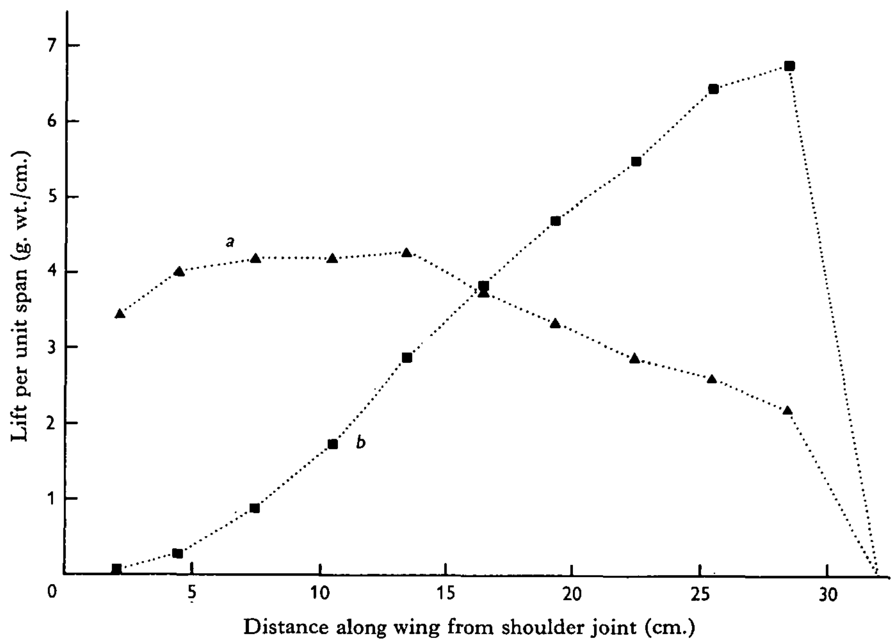

Fig. 10. Spanwise lift distribution calculated in (*a*) gliding and (*b*) hovering. From Table 3.

Table 3. *Lift distribution in gliding and hovering*

Strip	Gliding lift (g. wt.)	Hovering lift (g. wt.)
1	13·3	40·2
2	15·8	38·2
3	17·2	32·5
4	19·8	28·1
5	22·4	22·8
6	25·2	17·0
7	24·7	10·1
8	24·6	5·1
9	23·7	1·8
10	9·3	0·2
Total (1 wing)	196·0	196·0

Loading of the radio-ulna

The hovering lift distribution (Fig. 10*b*) shows that only 3·6 % of the lift would be developed on strips 8–10, as opposed to 29·4 % in the gliding case, so one may assume with greater confidence than in the gliding case that the moments applied to the distal end of the radio-ulna are entirely due to the lift on strips 1–7.

The calculation set out in Table 2 shows that the radio-ulna would fail in bending if the total lift on strips 1–7 exceeded 0·75 kg. wt. (4·0g) and in torsion if it exceeded 0·97 kg. wt. (5·1g).

Lift coefficient in hovering

The lift coefficient C_L is a dimensionless number which enables direct comparisons to be made between wings of different sizes flying at different speeds. It is the ratio of the lift to a standard force, the latter being the product of the wing area and the pressure which would be obtained in a blind tube pointed upstream. It is given by

$$C_L = \frac{L}{\frac{1}{2}\rho v^2 S} \tag{5}$$

where L is the lift in dynes, ρ the density of the fluid in g./c.c., v the speed in cm./sec., and S the wing area in cm.^{2} If all the relevant quantities are expressed in some other compatible system of units (like the F.P.S. system, for instance) the same lift coefficient results.

If a pigeon is assumed to be hovering in such a way that the lift during the downstroke just equals the weight, the lift on each chordwise strip can be obtained from Table 3, while its area is given in Table 1. The density of air is taken as $1 \cdot 22 \times 10^{-3}$ g./c.c., the sea level value in the I.C.A.O. standard atmosphere.

The remaining quantity required to calculate C_L is the speed of the strip, which is equal to the product of the flapping radius (listed in Table 1) and the angular velocity of the wing. Pennycuick & Parker (196) found that pigeons at take-off, which approximates to hovering, could flap their wings 8·9 times per second, through an angle of 142°, and that the downstroke lasts for about two thirds of the cycle. This gives an average angular velocity of about 33 radians/sec. during the downstroke.

Since the calculation of lift distribution was based on the assumption that C_L does not vary across the span, Eqn. (5) can be solved using data for any strip, and the answer should be the same whichever one is chosen. For instance, using values from strip 1:

$$\text{lift } L = 40 \cdot 2 \times 981 = 3 \cdot 94 \times 10^4 \text{ dynes;}$$

$$\text{flapping radius } r = 28 \cdot 5 \text{ cm.;}$$

$$\text{angular velocity } \omega = 33 \text{ radians/sec.;}$$

$$\text{speed } v = r\omega = 940 \text{ cm./sec.;}$$

$$\text{area } S = 21 \cdot 6 \text{ cm.}^2,$$

$$C_L = \frac{2 \times 3 \cdot 94 \times 10^4}{1 \cdot 22 \times 10^{-3} \times 940^2 \times 21 \cdot 6} = 3 \cdot 4.$$

Higher lift coefficients than this have been obtained from aircraft wings without using active boundary-layer control devices, but this has been done at Reynolds

Numbers in the region of a few millions. In the hovering pigeon the Reynolds Number varies across the span (Fig. 11), but would be between 40,000 and 50,000 for strips 1–6. It is difficult to obtain lift coefficients above about 1·5 at Reynolds numbers as low as this (Schmitz, 1960), and although the pigeon's wing is elaborately slotted, its performance in this respect is somewhat startling.

Pigeons definitely can hover in still air (inside a pigeon loft, for instance), even if only for a few wingbeats, and can indeed generate lift slightly over their weight, sufficient to accelerate them into normal flight, so there seems no escape from the conclusion that the maximum lift coefficient, averaged over the span, must be in the region of $3\frac{1}{2}$. If the assumption of constant lift coefficient over the span were abandoned, it would follow that the local lift coefficient of some parts of the wing would have to be higher still.

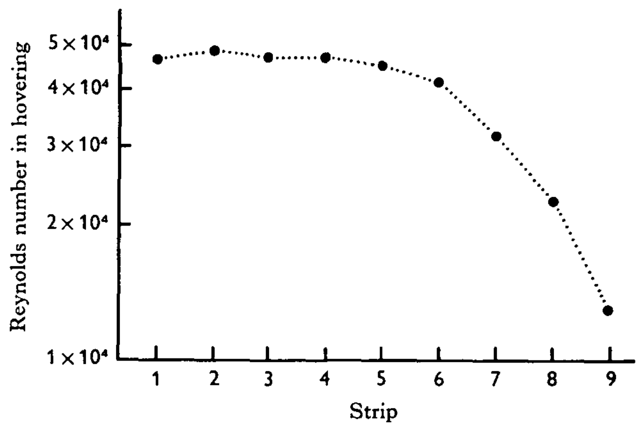

Fig. 11. Spanwise Reynolds number distribution in hovering.

Owing to the difference in velocity distribution it does not necessarily follow that the same maximum lift coefficient can also be achieved in gliding flight, but if it could, the minimum gliding speed would be about 5·4 m./sec. (18 ft./sec., 12 m.p.h.). This should be accessible to measurement.

SUMMARY

1. Simple methods are described for applying known bending and twisting moments to pigeon bones. The ultimate bending and torsional strengths of the humerus and radio-ulna are determined.

2. Lift distributions are calculated from a strip diagram on the assumption that local lift coefficient is constant across the span. The position of the centre of lift is calculated for (*a*) gliding, in which the relative air speed is entirely due to the forward motion of the bird; and (*b*) hovering, in which it is entirely due to rotation of the wing about the shoulder joint.

3. Estimates of the ultimate load factor of the humerus in bending and twisting yielded 8·8 and 9·0 respectively in gliding, and 5·7 and 5·6 in hovering. Corresponding figures for the radio-ulna were 6·9 and 9·1 in gliding, and 4·0 and 5·1 in hovering.

4. The *pectoralis* insertion is strong enough to apply 4·2*g* in gliding and 2·9*g* in

hovering, so the muscles would be forcibly extended before any danger could arise of the bones being broken by excessive lift.

5. A lift coefficient of at least 3·4 is achieved during the downstroke of hovering.

The bending apparatus was built by Mr B. Knights, who also carried out the torsional strength tests on humeri. Mr W. R. H. Andrews made the torsion apparatus, and carried out the torsional strength measurements on radio-ulnae.

REFERENCES

Abbott, I. H. & von Doenhoff, A. E. (1959). *Theory of Wing Sections*. New York: Dover Publications.

Brown, R. H. J. (1948). The flight of birds: the flapping cycle of the pigeon. *J. Exp. Biol.* **25**, 322–33.

Pennycuick, C. J. & Parker, G. A. (1966). Structural limitations on the power output of the pigeon's flight muscles. *J. Exp. Biol.* **45**, 489–98.

Schmitz, F. W. (1960). *Aerodynamik des Flugmodells*. Duisburg: Carl Lange.