ELASTIC ENERGY STORAGE IN PRIMARY FEATHER SHAFTS

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(Received 30 October 1975)

SUMMARY

It is proposed that the kinetic energy of a pigeon's wing, in hovering or slow forward flight, is transferred to the air at the end of the downstroke by a mechanism involving temporary storage of additional energy in bent primary feather shafts. Estimates of the amounts of energy which can be stored and recovered in this way are compared with the requirements of the theory. The hypothesis is not rejected, as far as present evidence goes. If it is correct, high-velocity pulses of calculable magnitude should be detectable in the wake.

INTRODUCTION

In any flying animal or machine that depends on flapping wings, the kinetic energy of rotation of the wings fluctuates between zero at the top and bottom of each stroke, and some positive value as the wing rotates up or down. A certain amount of kinetic energy has to be supplied to the wing and removed from it, at each half cycle. In the most inefficient system possible, this energy would be supplied by the muscles at each acceleration of the wings and dissipated as heat during each deceleration.

Various more economical arrangements are possible, of which the best known is the 'tuned' wing-thorax system found in certain insects. In Diptera, Hymenoptera and Coleoptera the rotating wing distorts the cuticle of the thorax, which acts as a spring absorbing the kinetic energy from the wing. The moment exerted by the distorted cuticle accelerates the wing into the next half cycle, and the stored elastic energy is reconverted into kinetic energy (Pringle, 1965).

Weis-Fogh (1972) considered whether an analogous system could exist in birds and concluded that birds lack any structure with the necessary elastic properties. He estimated the power requirements of hovering hummingbirds, assuming that no elastic energy storage occurs, and obtained good agreement with physiological measurements on this basis.

In forward flight the downward motion of the wing can be stopped aerodynamically, and the kinetic energy extracted from it can in this case be transferred to the air, to contribute to lift and propulsion. In very slow flight or hovering this is not possible, because the relative air speed at the wing tip is not sufficient to produce the necessary force. It is proposed here that under these conditions the downward motion of the wing is stopped by a more roundabout method, as follows:

(1) During the initial part of the downstroke, some of the work done by the
pectoralis muscle is absorbed in bending the shafts of the primary feathers. This work is additional to that done in accelerating the wing.

2. At the extreme end of the downstroke, the feathers straighten rapidly, so that the velocity of their tips relative to the air remains high enough to produce a substantial aerodynamic force, even though the more proximal parts of the wing are now decelerating. The energy released, as the feathers straighten, imparts downward and/or backward momentum to the air, sufficient to cancel the angular momentum of the wing. Thus the work originally done by the pectoralis in bending the feather shafts, and also that done in accelerating the wing, is ultimately converted into useful aerodynamic work.

To establish this hypothesis as a practical possibility it is necessary to show that:

1. The feathers bend and unbend in the appropriate circumstances.
2. Adequate amounts of energy can be stored in the bent feathers.
3. A high percentage of the stored energy can be recovered as work when the feathers straighten.

This paper goes some way towards showing that these requirements are fulfilled, although it is not claimed that the evidence in favour of the hypothesis is conclusive.

SEQUENCE OF EVENTS IN THE DOWNSTROKE

Conspicuous bending and separation of the primary feathers of birds (other than hummingbirds) is typically seen in photographs and films taken during landing, take-off and hovering, in other words when the forward speed is low or zero. Such bending is much less evident at medium and high speeds (Fig. 1).

The bending develops very early in the downstroke and persists until after elevation of the humeri has begun. This may be seen in Fig. 2, which is a tracing from a high-speed film, taken with a Milliken 16 mm camera at 400 frames/s. The pigeon had just taken off, and was climbing directly towards the camera at a very low forward speed.

It is not, of course, practicable to use Fig. 2, or similar semi-quantitative data, to estimate angles of rotation of the wing, or angular velocities. These data are presented merely as justification for using a simplified description of the downstroke in slow flapping flight. In the following discussion the downstroke is considered for the purpose of the analysis to be divided into three non-overlapping phases, as follows:

1. Acceleration phase, in which the wing rapidly accelerates to its maximum angular velocity. The primaries also become bent during this phase. This phase is considered to be complete after the wing has rotated through a small proportion of its total angular travel.

2. Constant-angular-velocity phase, in which the wing rotates steadily through most of its angular travel. The curvature of the primaries is considered to remain unchanged during this phase.

3. Deceleration phase, in which the angular motion stops and the primaries
Fig. 2. Superimposed tracings at intervals of 5 frames (as numbered) from a film taken at 400 frames/s. The pigeon had just taken off, and was climbing steeply and slowly towards the camera.

Fig. 3. See text for explanation.

straighten. This phase, like the acceleration phase, is considered to occupy a small angle only.

This simplified picture may be used to calculate the energy needed to stop the wing, assuming that this is done by a force \( F \) acting through a point near the wing tip, at a distance \( r \) from the shoulder joint (Fig. 3). If the wing’s moment of inertia is
\( I \) and \( \omega \) is its angular velocity before deceleration starts, then evidently the time \( (T_f) \) needed to stop the rotation is

\[
T = \frac{I\omega}{Fr}.
\]

If the force is a reaction produced by accelerating air, then the momentum which has to be imparted to the air is

\[
FT = \frac{I\omega}{r}.
\]

Now suppose that this momentum is supplied by imparting a velocity \( v \) to a mass \( m \) of air. Then

\[
v = \frac{I\omega}{mr},
\]

and the energy \( (E) \) needed is

\[
E = \frac{1}{2}mv^2 = \frac{I\omega^2}{2mr^2}.
\]

A part of this energy can come from the kinetic energy removed from the wing. The maximum amount which can be supplied from this source is \( E_k \), where

\[
E_k = \frac{1}{2}I\omega^2.
\]

The remainder of the energy, \( E_r \), must come from other sources, such as elastic energy released from bent feathers, or work done directly by the muscles. This fraction is

\[
E_r = E - E_k = \frac{1}{2}I\omega^2\left(\frac{1}{mr^2} - 1\right).
\]

The multiplier \( I/mr^2 \) (which is dimensionless) may be thought of as an inverse efficiency. As \( m \) and \( r \) are increased, so the work needed to stop the wing is reduced. If \( I/mr^2 < 1 \), then \( E_r \) is negative, which means that more energy is available than is needed to stop the wing, so that some of it will have to be dissipated as heat.

The mass of air to be accelerated, \( m \), cannot be ascertained directly. However, it may be surmised that if the relative air speed of the wing as a whole is near zero, then the volume of air which can be accelerated by the straightening primaries will have the same order of linear dimensions as the wing tip itself. \( m \) will be small in this case, and \( I/mr^2 \) large. At a higher forward speed, a larger volume of air can be accelerated, namely that which blows over the primaries during the time \( T \) (as defined above), and in this case \( I/mr^2 \) will be smaller.

Rather than try to estimate \( m \) for different circumstances, we shall first estimate the amount of energy which can be stored, and then recovered, by bending and unbending the primaries. We shall then equate this to \( E_r \) of equation (6), and thus consider how great \( m \) would need to be for our hypothesis to be practicable. It will be noticed that this can be done without explicitly discussing the velocity \( v \) to which the air has to be accelerated.
ENERGY STORED IN BENT FEATHERS

Method

The capacity of the primary feathers to store energy was investigated by rolling the feather shaft around a series of metal cylinders of different radii (Fig. 4). The cylinder (c in Fig. 4) rested on two horizontal steel rails (r), separated by a steel bar (sb) 2.54 cm thick. The top surface of this spacing bar was positioned below the rails and sloped in such a way that the feather (f), when laid upon it, could be positioned with the top edge of the shaft in line with the rails. The proximal end of the feather shaft was taped down to the spacing bar. A strip of paper (p) was also taped to the bar, under the feather. The paper extended just beyond the feather tip, and its end was taped to the cylinder. Thus, when the cylinder was caused to roll along the
distance from tip (cm)

**Fig. 5.** Work diagram from an experiment with the apparatus of Fig. 4. Primary 2 of the right wing was being rolled round a cylinder of 3.8 cm radius. The roll was continued to 13 cm from the tip, after which the diagram was completed by the 'constant-force' approximation (see text). The approximation was not extended to that part of the calamus which was attached in life to the bones of the manus.

rails towards the proximal end of the feather, the paper held the feather in contact with the cylinder, along that part of its length distal to the point of contact between the cylinder and the rails.

The torque causing the cylinder to roll was supplied by two strings (s) passing round the cylinder and taped to it. A scale pan (sp), to which weights were progressively added, hung from the strings below the rails. When the cylinder rolled horizontally, the scale pan descended vertically through the same distance, which was read on the scale (sc).

Suppose that the force in the string is $F$, and the addition of a small increment of force causes the scale pan to descend through a distance $\Delta h$. The work done against the elastic resistance of the feather is $\Delta W$, where

$$\Delta W = F\Delta h.$$  

The total work done as the pan descends from a position $h_0$ to $h_1$ is evidently

$$W = \int_{h_0}^{h_1} Fdh.$$  

To evaluate the work, $F$ was plotted against $h$ as weights were added to the pan, and the area beneath the curve was then measured (Fig. 5).

In no case was it found to be possible to get the thickest part of the feather shaft
to conform to the cylinder, and so the roll had to be abandoned before the cylinder reached the proximal end of the feather. Some assumption therefore had to be made to enable the work diagram to be completed. This was done by assuming that $F$ would remain constant from the point where the roll was abandoned until the cylinder reached the proximal end of the feather. This most probably led to the work being somewhat underestimated, since $F$ was invariably still increasing quite steeply at the point where the roll was abandoned, as in Fig. 5.

**Results**

The above measurements were made at each of three radii of curvature (5.7, 3.8 and 3.2 cm), on nine primary feathers, all from the same pigeon (*Columba livia*). They were the first five primaries on each side, except for primary 2 on the left side, which had been recently moulted. The results plotted in Fig. 6 represent the mean of the two strain energies determined for corresponding feathers on the two sides, except for primary 2, which was present on the right side only.

It is shown in texts on engineering mechanics (e.g. Langhaar, 1962) that the strain energy, stored in simple bending of a beam composed of a linear elastic material, is inversely proportional to the square of the radius of curvature ($c$) to which the beam is bent. The energy is therefore plotted against $1/c^2$, in the expectation that the results for each feather should yield a straight line of the form

$$W = k/c^2,$$

where $k$ is a constant. Table 1 shows estimates for $k$ from the first five primaries, obtained by calculating a linear regression of $W$ on $1/c^2$, passing through the origin.
Table 1. Regression coefficients \((k)\) for strain energy on \(1/c^2\), where \(c\) is the radius of curvature to which the feather is bent (see Fig. 6). \(k'\) is the slope to the first point on each curve in Fig. 6.

<table>
<thead>
<tr>
<th>Primary no.</th>
<th>(k) ((\text{J cm}^3))</th>
<th>(k') ((\text{J cm}^3))</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.23</td>
<td>1.74</td>
</tr>
<tr>
<td>2</td>
<td>1.25</td>
<td>1.72</td>
</tr>
<tr>
<td>3</td>
<td>1.03</td>
<td>1.66</td>
</tr>
<tr>
<td>4</td>
<td>1.08</td>
<td>1.51</td>
</tr>
<tr>
<td>5</td>
<td>0.70</td>
<td>1.35</td>
</tr>
</tbody>
</table>

It can be seen at once from Fig. 6 that the results do not closely fit the straight line represented by equation (7). In each case the first of the three experimental points is well above the regression line, and the last is well below it. In other words, as the radius of curvature was reduced, the strain energy did not increase as much as the initial trend would lead one to expect. Two explanations for this can be suggested:

1. The smaller the radius, the more difficult it was to get the feather to conform to the cylinder. Consequently the roll had to be abandoned at an earlier stage with the smaller radii, so leaving a larger portion of the work diagram to be completed by means of the approximation described above. It has been noted that this approximation is likely to lead to an underestimate of the strain energy, and in this case the underestimate will be expected to be greatest at the smaller radii.

2. The feather shafts offered less resistance to bending in the antero-posterior direction than in the intended dorsal direction. When bent to a small radius, the shafts tended to twist and be bent in the easier direction. This too would lead to an underestimate of the strain energy.

It therefore seems likely that the anomalous shape of the curves in Fig. 6 is due to a progressively increasing underestimate of the strain energy as the radius of curvature is reduced. It may well be that the slope of the line from the origin to the first point is a better indicator of \(k\) than the regression line through all the points. These slopes are also listed (as \(k'\)) in Table 1.

**ELASTIC EFFICIENCY**

The strain energy considered above is the work needed to bend the feather. Not all of this is recovered in the form of mechanical work when the feather unbends. The elastic efficiency \((\eta)\) is defined as that proportion of the strain energy which can be recovered as mechanical work (the rest is presumed to be converted into heat).

**Method**

The efficiency was estimated by a method devised by Jensen & Weis-Fogh (1962), who applied it to locust cuticle. Tests were made on short lengths of feather shaft, 1–2 cm long, from which the barbs had been removed. One end of the specimen was fixed with dental wax into a length of glass tubing, which was supported on a rigid stand. The other end was loaded with a variable amount of Plasticine, in which was embedded a small piece of soft iron. The specimen was first held in a bent position
by a small electromagnet, and then released. The resulting damped oscillation was recorded by shining a beam of light through a lens on to a small mirror fixed to the specimen. The beam focused as a spot on a ground-glass screen, which was photographed from the other side on continuously moving film by an oscilloscope camera.

The trace, represented diagrammatically in Fig. 7, is regarded as a record of amplitude of deflexion. Fig. 7 has been drawn with an arbitrary zero for the ordinate, since there was no easy way to locate the mean line (y). Instead, the peak-to-peak amplitude (y$ _{i} - y_{i+1}$) was used as the primary measurement. Suppose $A$ is the ratio of the peak amplitudes in successive half-cycles, that is

\[ A = \left| \frac{y_{i+1} - y_0}{y_{i} - y_0} \right|. \]  

It can be seen that the ratio of peak-to-peak amplitudes in successive cycles is then

\[ (y_{i+2} - y_{i+3})/(y_{i} - y_{i+1}) = A^2. \]  

The problem is to find $\eta$, the ratio of the energy stored at the peak of half-cycle $i + 1$ to that stored at the peak of half-cycle $i$. Some assumption about the elastic behaviour of the specimen has to be made before the energy can be calculated from the amplitude of deflexion. We shall make the simplest assumption, that the elasticity is linear. In that case the strain energy is proportional to the square of the amplitude of deflexion, and

\[ \eta = A^2. \]
Table 2. Elastic efficiency in various species

<table>
<thead>
<tr>
<th>Species</th>
<th>No. observations</th>
<th>Mean η</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domestic pigeon, Columba livia</td>
<td>20</td>
<td>0.926</td>
<td>1.13 x 10^-1</td>
</tr>
<tr>
<td>Marabou stork, Leptoptilos crumeniferus</td>
<td>17</td>
<td>0.947</td>
<td>3.34 x 10^-1</td>
</tr>
<tr>
<td>Herring gull, Larus argentatus</td>
<td>34</td>
<td>0.926</td>
<td>8.86 x 10^-1</td>
</tr>
<tr>
<td>Mistle thrush, Turdus viscivorus</td>
<td>17</td>
<td>0.944</td>
<td>4.64 x 10^-1</td>
</tr>
<tr>
<td>Guillemot, Uria aalge</td>
<td>7</td>
<td>0.932</td>
<td>2.79 x 10^-1</td>
</tr>
<tr>
<td>Barn owl, Tyto alba</td>
<td>11</td>
<td>0.908</td>
<td>8.80 x 10^-1</td>
</tr>
<tr>
<td>Hodgson’s murre, Lonchura striata</td>
<td>3</td>
<td>0.900</td>
<td>8.74 x 10^-1</td>
</tr>
<tr>
<td>African porcupine, Hystrix galeata</td>
<td>5</td>
<td>0.797</td>
<td>4.76 x 10^-2</td>
</tr>
</tbody>
</table>

If we write \( p_0 \) for the peak-to-peak amplitude of the zeroth cycle measured, and \( p_n \) for the \( n \)th, then it follows from equation (9) that

\[
p_n = p_0 A^{2n},
\]

which can be represented logarithmically as

\[
\ln p_n = \ln p_0 + 2n \ln A.
\]

The peak-to-peak amplitudes \( p \) were measured for 10–20 consecutive cycles on each record, and a linear regression was then calculated for \( \ln p \) on \( n \). From equation (12) the regression coefficient (\( \beta \)) was

\[
\beta = 2 \ln A,
\]

whence, from equation (10)

\[
\eta = e^{\beta}.
\]

Results

Observations of \( \eta \) for various bird species are listed in Table 2. The measurements covered a frequency range of 4.4–27 Hz, but in no case was the correlation between \( \eta \) and frequency significant at the 5% probability level. Some observations on quills from a young African porcupine have been included for comparison, as an example of a keratin structure whose elastic properties are presumably not of great significance to the animal.

The results from the feathers show a high degree of consistency, although it may be noted that no special precautions were taken regarding preservation of the specimens prior to testing. The feathers were either moulted by captive birds, or taken from dead birds collected in the field, or brought in by local people.

RECOVERABLE ENERGY

The radius of curvature taken up by a bent feather in flight no doubt varies along the feather shaft. In any case we had no means at our disposal for actually measuring the shapes of feathers in known circumstances. However we were able to get a very rough estimate of the curvatures which actually occur, by searching through our collection of slides of flying pigeons until we found one in which the primaries were strongly bent, in a plane roughly perpendicular to the viewing direction (Fig. 1a). The radii of curvature seen in the primaries of the right wing in this photograph, estimated on the assumption that the feathers were the same length as the
Table 3. Energy recoverable as work from bent feathers

<table>
<thead>
<tr>
<th>Primary no.</th>
<th>Radius (cm)</th>
<th>Recoverable energy (J)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7.7</td>
<td>0.00273</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
<td>0.0071</td>
</tr>
<tr>
<td>3</td>
<td>23</td>
<td>0.0029</td>
</tr>
<tr>
<td>4</td>
<td>23</td>
<td>0.0027</td>
</tr>
<tr>
<td>5</td>
<td>23</td>
<td>0.0024</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>0.0424</td>
</tr>
</tbody>
</table>

corresponding ones used for our measurements, are listed in Table 3. The recoverable strain energies ($W_r$) are calculated from the formula

$$W_r = \eta k'/c^2,$$

where the values of $k'$ are taken from Table 1, and $\eta$ is taken as 0.93 throughout.

It has been pointed out that our method of determining the strain energy in bent feathers probably leads to an underestimate. It is also perhaps unlikely that we would happen to have a slide showing the feathers bent to the maximum extent possible. Furthermore, we have considered only the first five primaries, and it is possible that more proximal feathers may store some recoverable energy. We therefore consider that the figure given in Table 3 for the total recoverable energy is a minimal estimate. Almost certainly more energy can be stored and recovered than this, and possibly much more. In the discussion we shall consider the effects of having available three different amounts of energy, 0.04, 0.08 and 0.20 J. These values represent roughly the estimate of Table 3, and two and five times that estimate respectively.

**DISCUSSION**

We are now in a position to return to equation (6), which relates the amount of energy available for imparting momentum to the air, to the mass of air ($m$) which has to be accelerated. If the air is to be accelerated entirely by the energy which can be recovered from the bent feathers ($W_r$), then rearranging equation (6) yields

$$m = \frac{I^2\omega^2}{r^2(2W_r + I\omega^2)},$$

where $I$ is the moment of inertia of the wing about the shoulder joint, $\omega$ is the angular velocity during the middle phase of the downstroke, and $r$ is the moment arm about the shoulder joint of the force which decelerates the wing. We shall assume that this force acts near the middle of the third primary, through a point 21.5 cm from the shoulder joint (see Fig. 8). Values for $I$ (1.83 x 10^-4 kg m^2) and $\omega$ (47 rad/s) are taken from an earlier paper (Pennycuick & Parker, 1966). We shall also take a value of $\rho = 1.22$ kg/m^3 to represent the sea-level air density, and then convert equation (14) to yield the volume ($V$) of air to be accelerated, rather than the mass:

$$V = m/\rho = \frac{I^2\omega^2}{\rho r^2(2W_r + I\omega^2)}.$$  

Table 4 shows the volumes of air calculated from equation (15) for the three hypothetical values of $W_r$ mentioned above, and also the radii of spheres of the same
Fig. 8. Scale drawing of an extended pigeon’s wing, with the shafts of the primaries and secondaries marked. The circles represent spheres of air, indicating the approximate amounts that would have to be accelerated, under various assumptions, as explained in the text.

Table 4. Amounts of air to be accelerated, for different amounts of recoverable work
(see text)

<table>
<thead>
<tr>
<th>$W_s$ (J)</th>
<th>Volume (cm$^3$)</th>
<th>Radius (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.04</td>
<td>$2.71 \times 10^4$</td>
<td>8.65</td>
</tr>
<tr>
<td>0.08</td>
<td>$2.32 \times 10^4$</td>
<td>8.22</td>
</tr>
<tr>
<td>0.20</td>
<td>$1.63 \times 10^4$</td>
<td>7.30</td>
</tr>
</tbody>
</table>

volume. Fig. 8 is a scale drawing of a pigeon’s wing, with the shafts of the flight feathers shown in position. The spheres of air, whose radii are listed in Table 4, are shown superimposed on the wing, centred on the point, 21.5 cm from the shoulder joint, through which the decelerating force is assumed to act. It can be seen that the radius of the sphere of air required is not very sensitive to the amount of stored elastic energy available for accelerating the air. The three radii shown cover a five-fold energy range, of which the middle one, for 0.08 J, is probably nearest the true value.

The above argument does not prove that our postulated mechanism for stopping the wing at the end of the downstroke actually exists, but it does show that the volume of air which would have to be accelerated, for the mechanism to work, would be comparable in size to the feathers which are supposed to be accelerating it. This volume has been represented arbitrarily as a sphere in order to make it easy to visualize, and to compare with the wing in Fig. 8. Of course the air accelerated does not really have to be a sphere. If it were distributed so that the mass were concentrated more distally than has been assumed, then less air would be needed.

The speed $v$ to which the air has to be accelerated can be found from equation (3).
Feather bending

Taking the middle case of Table 4, the mass of air to be accelerated is 2.28 g, whence from equation (3), \( v = 15.7 \text{ m/s} \). The acceleration, assuming this speed to be imparted in 25 ms, is \( 628 \text{ m s}^{-2} \). At first sight this may seem excessive, but the force required to produce it is only 1.43 N, or somewhat over one third of a pigeon's body weight. This is not an excessive force to be distributed over the distal 40% or so of one wing. Whether the relative airflow over the tip feathers is capable of producing this force is a question which cannot be answered on present evidence. It seems conceivable at any rate that sufficient force could be produced by non-steady effects, caused by the sudden unbending of the feathers.

The requirements for annulling the angular momentum of the wing are most difficult to meet at zero forward speed (hovering). It is possible that our mechanism exists but cannot transfer the whole of the wing's kinetic energy to the air in hovering, leaving some energy to be absorbed by the muscles. In that case the mechanism could still reduce the energy wasted in this way, and become fully effective at some low forward speed.

The benefits to be gained from our mechanism would be partly offset by a loss of span efficiency which must result from it. Simple momentum theory indicates that the induced velocity below a hovering pigeon should be about 2.1 m/s, and maximum span efficiency would be obtained if this velocity were uniformly maintained over the whole wing disc. The presence of intermittent velocity components of the order of 16 m/s, as just calculated, must reduce the span efficiency. The presence of these high-velocity components in the wake should be readily detectable, if our hypothesis is correct.

CONCLUSION

It may be noted that the system postulated here differs fundamentally from the tuned mass-spring system seen in insects. In that system the initial work done in accelerating the wing is transferred back and forth between kinetic and elastic forms. Our system is a one-way energy transfer system, in which no energy is retained from one cycle to the next. Instead the work done in accelerating the wing is transferred at the end of each stroke to the air. The system is not tuned, and unlike the insect system, is not restricted to operating at one particular frequency. The equations involve the angular velocity of the wing, but not the frequency as such.

REFERENCES


