DRAG REDUCTION BY WING TIP SLOTS IN A GLIDING HARRIS' HAWK, *PARABUTEO UNICINCTUS*

VANCE A. TUCKER

Department of Zoology, Duke University, Durham, NC 27708, USA

Summary

The anterior-most primary feathers of many birds that soar over land bend upwards and separate vertically to form slotted wing tips during flight. The slots are thought to reduce aerodynamic drag, although drag reduction has never been demonstrated in living birds. Wing theory explains how the feathers that form the tip slots can reduce induced drag by spreading vorticity horizontally along the wing and by acting as winglets, which are used on aircraft to make wings non-planar and to spread vorticity vertically. This study uses the induced drag factor to measure the induced drag of a wing relative to that of a standard planar wing with the same span, lift and speed. An induced drag factor of less than 1 indicates that the wing is non-planar.

The minimum drag of a Harris' hawk gliding freely in a wind tunnel was measured before and after removing the slots by clipping the tip feathers. The unclipped hawk had 70–90 % of the drag of the clipped hawk at speeds between 7.3 and 15.0 m s^{-1}.

At a wing span of 0.8 m, the unclipped hawk had a mean induced drag factor of 0.56, compared with the value of 1.10 assumed for the clipped hawk. A Monte Carlo simulation of error propagation and a sensitivity analysis to possible errors in measured and assumed values showed that the true mean value of the induced drag factor for the unclipped hawk was unlikely to be more than 0.93. These results for a living bird support the conclusions from a previous study of a feathered tip on a model wing in a wind tunnel: the feathers that form the slotted tips reduce induced drag by acting as winglets that make the wings non-planar and spread vorticity both horizontally and vertically.

Key words: bird flight, emarginated feathers, induced drag, non-planar wing, primary feathers, soaring, span efficiency factor, tip feathers, vortex diffusion, vortex spreading, winglets, Harris' hawk, *Parabuteo unicinctus*.

Introduction

Most birds that soar over land have prominent, separated primary feathers at the tips of their wings. These feathers spread out both horizontally and vertically (see Fig. 1) to form tip slots that are thought to reduce aerodynamic drag (see Hummel, 1980; and reviews by Graham, 1932; Withers, 1981; Kerlinger, 1989; Norberg, 1990; Spedding, 1992; Tucker, 1993). However, drag reduction by the tip slots of a living, free-flying bird has never been measured.

Do tip slots reduce drag? This question is not specific enough to have a single answer. For example, one could remove the slots by clipping the feathers that form them. This operation also reduces the wing span, which increases the drag of even an unslotted wing. Alternatively, one could fasten the tip feathers together, thereby removing the slots without changing the wing span. Each operation would probably affect drag differently.

The question can be phrased specifically by using the concepts of wing theory from the aerodynamic literature (for example, Reid, 1932: von Mises, 1959; Kuethe and Chow, 1986; Katz and Plotkin, 1991). Wing theory explains how the vertically separated feathers that form the tip slots can reduce the drag of a wing with a given span by vertical vortex spreading (see Tucker, 1993, for references); in practice, tip structures that spread vorticity vertically can reduce drag. Some modern aircraft have winglets attached to the wing tips for this purpose (Lambert, 1990). Separated primary feathers at the tip of a model wing can also reduce drag by vertical vortex spreading (Tucker, 1993).

This paper shows, for the first time, that the presence or absence of tip slots has a large effect on the drag of a living bird. The drag of a Harris' hawk (*Parabuteo unicinctus*) gliding freely at equilibrium in a wind tunnel increased markedly when the tip slots were removed by clipping the primary feathers. The slots also appear to reduce drag by vertical vortex spreading, because the greater wing span and other differences in the bird with intact tip slots did not entirely account for its lower drag.

Experimental approach

The drag of a bird gliding at equilibrium in a tilted wind tunnel can be calculated from from the bird's weight and the angle of tunnel tilt (Pennycuick, 1968). This technique was used to measure the effect of removing the tip slots on the hawk's drag. However, to show that that the slots reduce drag by vertical vortex spreading requires wing theory and additional measurements, some of which cannot be made on living birds. I made the feasible measurements, estimated the remaining quantities and used wing theory to show that the hawk's tip slots did reduce drag by spreading vorticity vertically. A sensitivity analysis showed that this finding does not change when the estimated quantities range over plausible values.

Theory

Planar and non-planar wings

Vertical vortex spreading occurs in non-planar, rather than planar, wings. To distinguish between these wing types, consider a wing moving horizontally through the air. If the wing is non-planar, it bends vertically from root to tip; i.e. the trailing edge, when projected on to a vertical plane, forms a curve and this curve sweeps out a non-planar surface as the wing moves. In contrast, a planar wing is straight from tip to tip, and its trailing edge sweeps out a plane. Both types of wing have two kinds of drag – induced and profile drag – but a non-planar wing may have less induced drag than a planar wing with the same lift, span and speed because of vertical vortex spreading.

The feathers that form the tip slots of a bird's wing bend vertically in flight (Fig. 1) and make the wing non-planar. Clipping these feathers will make the wing more planar, and I shall refer to the clipped wing simply as planar. Clipping also changes the wing span, the wing area and the pitching equilibrium of the bird (Tucker, 1992). The change in wing span influences the induced drag, and the other changes influence other drag components. The following sections discuss the drag components and introduce the induced drag factor as a measure of vortex spreading.

Wing theory and the induced drag factor

Wing theory (for example, see Reid, 1932; von Mises, 1959; Kuethe and Chow, 1986; Katz and Plotkin, 1991) describes the induced drag, but not the profile drag, of planar and non-planar wings. Induced drag arises whenever wings produce lift, thereby generating vorticity that leaves kinetic energy in the wake. Wing theory shows that the induced drag depends on the lift distribution, i.e. the lift per unit span at each point along the wing span. At a given speed (V), the lift distribution of a planar wing with a given lift and span determines the horizontal spread of vorticity in the wake and the amount of kinetic energy left in a unit length of the wake. When the lift distribution is elliptical, with the lift per unit span changing from a maximum at midwing to zero at the tips, the wing has minimum induced drag, D_i, given by:

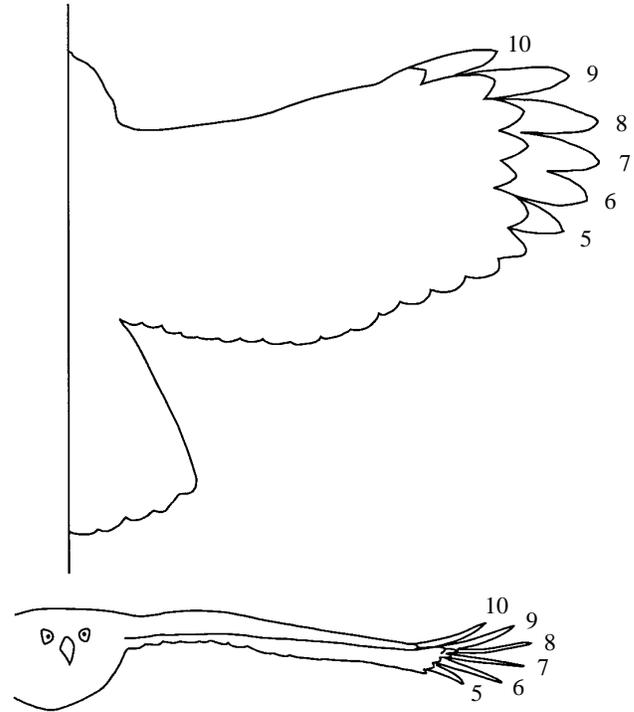$$D_{i,min} = L^2/(0.5\rho V^2 \pi b^2),\qquad(1)$$

Fig. 1. The Harris' hawk in flight, seen from above (unclipped wing span 1.06 m) and head-on (unclipped wing span 0.92 m). Harris' hawks have 10 primary feathers on each wing, numbered from 10 on the leading edge as shown. The lines at the bases of primary feathers 5–10 show the tips of the feathers after clipping. Both views were traced from photographs and are drawn to the same scale.

where L is lift, b is wing span and ρ is the density of air (1.23 kg m^{-3} for the standard atmosphere, von Mises, 1959).

The induced drag factor (k) accounts for the higher induced drag (D_i) of planar wings with other lift distributions:

$$k = D_i/D_{i,min},\qquad(2)$$

where k has a value greater than 1.

Non-planar wings may have k values less than 1 because they curve in the vertical plane and can spread vorticity vertically as well as horizontally. Tucker (1993) discusses the effect of vortex spreading on induced drag in more detail and reviews the aerodynamic literature on the subject.

The question of whether slotted tips reduce induced drag can now be rephrased. Do slotted tips reduce k? The answer depends on lift distribution and hence vortex spreading, rather than on lift, wing span, speed or profile drag. If the slotted tips do reduce k, a second question arises. Is the value of k for wings with slotted tips less than 1? If so, the slotted tips evidently make the wing non-planar and reduce k by spreading vorticity vertically. If not, the slotted tips may reduce k by making the lift distribution approach an elliptical one without necessarily spreading vorticity vertically. This paper uses measurements on a Harris' hawk to answer these two questions.

Aerodynamic measurements on birds

This section summarizes the relationships between drag components on birds gliding at equilibrium. Additional information may be found in Pennycuick (1968, 1989), Pennycuick *et al.* (1992), Tucker (1987, 1990) and Tucker and Heine (1990).

Induced drag

Induced drag can be determined by two methods: (1) by calculation (using equations 1 and 2) from lift, speed, span and an induced drag factor; and (2) by calculation as a difference after other types of drag have been accounted for. The total drag (*D*) of the bird is the sum:

$$D = D_i + D_{pr} + D_{par}, \tag{3}$$

where D_i is induced drag, D_{pr} is profile drag and D_{par} is the parasite drag (the drag on the bird's body exclusive of the wings). Method 2 calculates induced drag from the difference between total drag and the sum of profile and parasite drag.

Total, profile and parasite drag

Total drag depends on the glide angle (*θ*) and the weight of the bird (*m***g**, where *m* is body mass and **g** is the acceleration due to gravity):

$$D = m\boldsymbol{g}\sin\theta. \tag{4}$$

Profile drag can be found by two methods: (1) by calculation from the profile drag coefficient ($C_{D,pr}$), speed and projected wing area (*S*):

$$D_{pr} = 0.5\rho C_{D,pr}SV^2; \tag{5}$$

and (2) by calculation as the difference between total drag and the sum of induced drag and parasite drag. The wake sampling method for measuring profile drag (Pennycuick *et al.* 1992) was not practical in this study.

The profile drag coefficient varies with the lift coefficient (C_L):

$$C_L = L/(0.5\rho SV^2), \tag{6}$$

but is nearly constant for conventional, bird-like and bird wings at lift coefficients between 0.4 and 0.7 (for example, see Tucker, 1987).

Parasite drag depends on the equivalent flat plate area (S_{fp} of the wingless body):

$$D_{par} = 0.5\rho V^2 S_{fp}, \tag{7}$$

where S_{fp} is the product of a parasite drag coefficient and an area, such as the cross-sectional area of the body or the projected area of the tail. Additional information on S_{fp} can be found in aerodynamics texts or in Tucker (1990).

Materials and methods
Experimental design

The induced drag of the hawk with clipped feathers was calculated using method 1 from measurements and an assumed *k* value of 1.1. This value (k_c for clipped wings) describes planar wings without slotted tips and is commonly used for gliding birds. The profile drag was estimated from method 2 and the value of $C_{D,pr}$ was calculated. This value of $C_{D,pr}$ and measurements on the hawk with unclipped feathers were used to calculate the induced drag of the unclipped hawk by method 2. The value of *k* (k_u for unclipped wings) was calculated from the induced drag of the unclipped hawk and describes wings with slotted tips. To evaluate the effects of errors in measurements and assumptions, I used a Monte Carlo analysis and a sensitivity analysis, respectively.

Harris' hawk aerodynamic forces and wing morphology

A male hawk (mass 0.67 kg) was photographed from above as it glided freely at equilibrium at speeds between 6.5 and 15.0 m s^{-1} in a wind tunnel. The tunnel was tilted to the minimum angle (*θ*) at which the bird could just remain motionless. Air speed, lift, total drag, wing span and wing area were measured using the methods described by Tucker and Heine (1990).

The hawk had three wing configurations: (1) with unclipped feathers (Fig. 1), (2) with 38 mm clipped from the tips of each of primary feathers 6–10, and (3) with 38 mm clipped from each primary 5 and an additional 38 mm clipped from each of primary feathers 6–10 (Fig. 1). Only the results of configurations 1 (51 photographs) and 3 (47 photographs) are reported here. The results from configuration 2 were intermediate and support the findings of this study.

The relationships between parasite drag and the angle of attack of the tail and body were calculated by using a wingless model body. The angle of attack is the angle between horizontal and a line drawn from a point on the beak to a point at the tip of the tail. Tucker (1990) describes the model and the method for measuring drag.

Profile drag coefficients

The profile drag of the clipped hawk was calculated using the difference method (method 2 described in Theory) after calculating induced drag (method 1 described in Theory, with k_c=1.1). Parasite drag was calculated using equation 7 and a value for S_{fp} of 0.0012 m^2 from measurements on model and frozen hawk bodies (Tucker, 1990). The mean value of $C_{D,pr}$ for the clipped hawk was used as an estimate of $C_{D,pr}$ for the unclipped hawk.

$C_{D,pr}$ and profile drag were computed for the clipped and unclipped hawk only when the bird kept its tail folded. This restriction helped to keep S_{fp} constant, because S_{fp} probably increases when the hawk spreads its tail at slow speeds and large wing spans (Tucker, 1992). The clipped hawk kept its tail folded at mean wing spans of 0.78 m or less (which occurred at speeds of 12.2 m s^{-1} or above with lift coefficients between 0.37 and 0.52). The unclipped hawk kept its tail folded at mean wing spans of 0.93 m or less (which occurred at speeds of 9.6 m s^{-1} or above with lift coefficients between 0.36 and 0.65).

The profile drag coefficient varies with Reynolds number (*Re*) for the range of *Re* in this study, and I used a correction

factor (F) to correct all reported $C_{D,pr}$ values to a Reynolds number of 10^5:

$$F = 1.21 - 0.226Re \times 10^{-5} + 0.0151(Re \times 10^{-5})^2. \quad (8)$$

F is the ratio $C_{D,pr}/(C_{D,pr}$ at $Re=10^5)$. At sea level in the standard atmosphere (von Mises, 1959):

$$Re = 68436c'V, \quad (9)$$

where c' is the mean wing chord (0.205 m) of the hawk with unclipped wings at maximum wing span. In calculations, $C_{D,pr}$ values were corrected to the Re value for the speed under consideration. Tucker (1987) discusses c' and the correction for Re in more detail.

Induced drag factor of the unclipped hawk

The induced drag factor of the unclipped hawk (k_u) was computed from the induced drag calculated by difference (method 2, see Theory) after calculating the profile drag from the mean profile drag coefficient of the clipped hawk and parasite drag from equation 7 and $S_{fp}=0.0012\,m^2$.

Monte Carlo simulation for error propagation analysis

Some of the equations used in this study are empirical functions fitted to scattered data points. These functions yield a mean value of the dependent variable for each independent variable value, but the actual value of the dependent variable varies around this mean by some departure, or error. I used a Monte Carlo technique (Hammersley and Handscomb, 1964) to show the effect of these errors on the k values calculated for the unclipped hawk (k_u).

A computer program calculated k 55 times, each time with a new set of values for all of the dependent variables from empirical functions. The program formed each new set by adding normally distributed random errors to the mean values calculated from the empirical functions. The errors had means
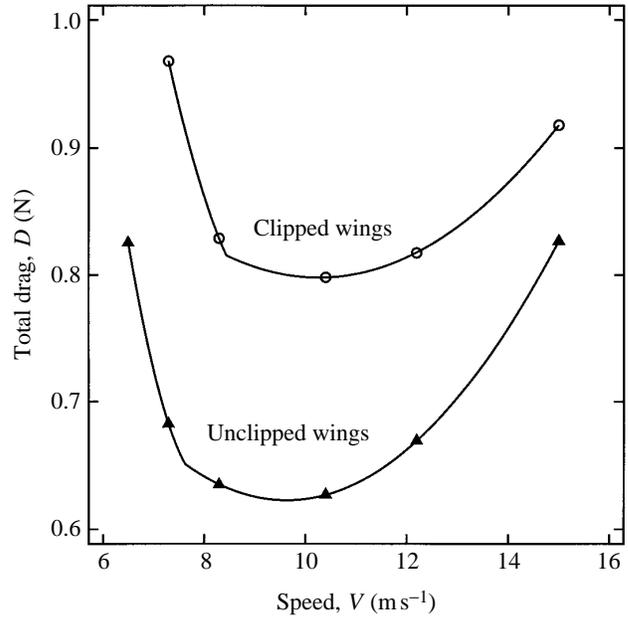

Fig. 2. Minimum total drag of the Harris' hawk at different speeds with clipped (circles) and unclipped (triangles) wings. Each point represents 3–17 observations (mean 9). There was no discernible variation in the minimum drag at each speed.

of zero and standard deviations equal to the standard deviations of the scattered data points around the empirical functions.

Results

Total drag depended on both speed and clipping (Fig. 2; Table 1). There was no variation in the minimum glide angle at each speed. Wing span increased as speed decreased for both the clipped and unclipped bird (Fig. 3; Table 1) and wing area increased as wing span increased (Fig. 4; Table 1).

Table 1. *Equations for curves in Figs 2, 3 and 4*

| Variable x and range | Variable y and condition | Coefficients | | | | |
		C_0	C_1	C_2	$s_{y \cdot x}$	N
Speed (m s^{-1})	Drag (N) (Fig. 2)					
6.5–7.6	Unclipped	5.441	−1.1830	0.07276	0	13
7.6–15.0	Unclipped	1.281	−0.1367	0.00710	0	38
7.3–8.4	Clipped	4.415	−0.7652	0.04013	0	10
8.4–15.0	Clipped	1.361	−0.1098	0.00535	0	37
Speed (m s^{-1})	Wing span (m) (Fig. 3)					
6.5–15.0	Unclipped	1.354	−0.0438	0	0.0250	51
7.3–8.3	Clipped	0.834	0	0	0.0119	10
8.3–15.0	Clipped	0.851	0.0126	−0.0017	0.0184	44
Wing span (m)	Wing area (m^2) (Fig. 4)					
0.67–1.07	Unclipped	0.1530	−0.2087	0.2530	0.00234	75
0.62–0.85	Clipped	0.0760	−0.0800	0.2325	0.00197	75

Equations are least-squares fits, of the form $y=C_0+C_1x+C_2x^2$.
$s_{y \cdot x}$ is the standard deviation of y around the fitted curve, and N is the number of x,y pairs.
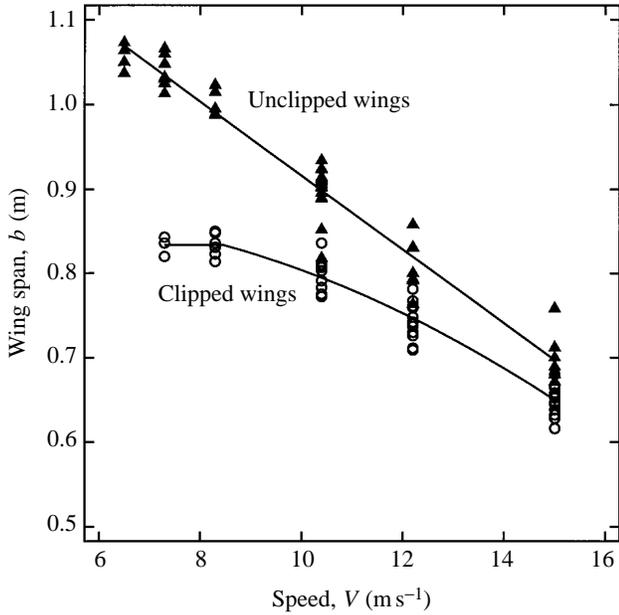
Fig. 3. Wing span of the Harris' hawk at minimum glide angles at different speeds with clipped (circles) and unclipped (triangles) wings. Each point represents a single observation.
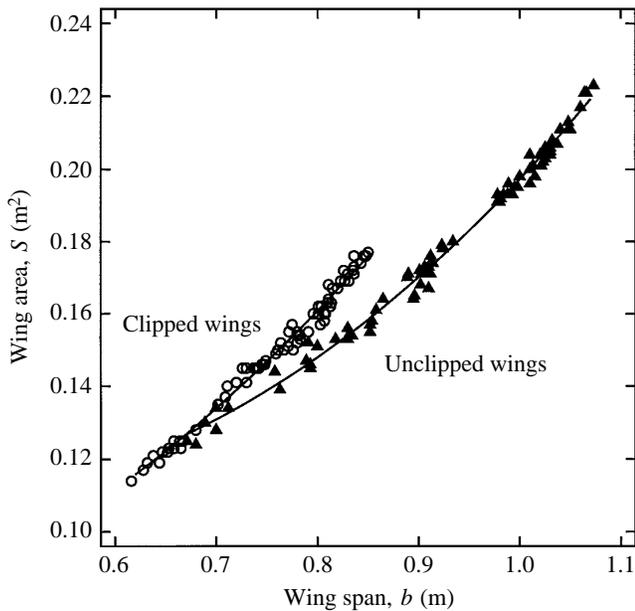

Fig. 4. Wing area of the Harris' hawk at different wing spans with clipped (circles) and unclipped (triangles) wings. Each point represents a single observation.

The profile drag coefficient ($C_{D,pr}$) of the clipped hawk was essentially constant at speeds of $12.2\,\mathrm{m\,s^{-1}}$ and above, with a mean value of 0.0359 ± 0.00075 (S.D., $N=27$).

Discussion

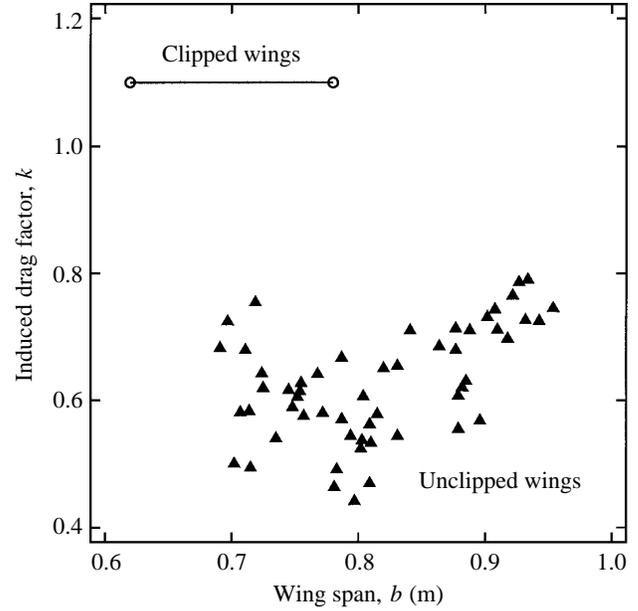The slotted tips of the unclipped hawk wing reduced the

Fig. 5. The induced drag factors (triangles) calculated by a Monte Carlo simulation for the clipped and unclipped Harris' hawk at different wing spans. The horizontal line between the circles shows the induced drag factor of 1.1 assumed for the clipped hawk wing.

calculated induced drag factor (k_u) to a mean value of 0.62 ± 0.088 (S.D., $N=55$), well below the induced drag factor (k_c) of 1.10 assumed for the clipped bird (Fig. 5). In fact, the reduction was even less than that predicted by wing theory. Cone (1962) calculated that a wing with slotted tips similar to those in Fig. 1 would have a k value that was 75 % of the value for an unslotted wing, whereas the mean value of k_u/k_c in this study is 0.56.

Sensitivity analysis

Could the reduction in k_u be due to errors in the theory rather than the effect of slotted tips? This section discusses the changes in four quantities in the theory that could make k_u and k_c equal at a wing span of 0.8 m. The mean value of k_u at this wing span is 0.56, and I shall use the ratio k_u/k_c to measure nearness to equality. First, I discuss the effects of changes in a single quantity while the others remain constant, and then I estimate a minimum or maximum plausible multiplier for the quantity. The multiplier increases k_u/k_c when applied to the quantity. Then I multiply all four quantities by their minimum or maximum plausible multipliers and calculate the combined effect on k_u/k_c. The combined effect corrects for the rather unlikely event that all four original quantities in the theory had extreme errors, all in directions that happened to reduce k_u/k_c.

Making the equivalent flat plate area of the clipped bird higher than that of the unclipped bird

In this situation, k_u increases because an increase in S_{fp} for the clipped bird causes a decrease in the calculated value for $C_{D,pr}$. The induced drag calculated for the unclipped bird increases as a result.

S_{fp} for the clipped bird could be higher than that for the unclipped bird because clipping alters the pitching moment (Tucker, 1992), and the bird makes three changes to compensate: (1) changes in the wing span, (2) changes in the tail span and angle of attack, and (3) perhaps changes in the angle of attack of the folded tail. The first of these could change $C_{D,pr}$, and I discuss this further in a later section. The second possibility is not relevant, since this study uses data only from speeds at which the hawk kept its tail folded. Therefore, the remainder of this section discusses increases in S_{fp} due to changes in the angle of attack of the folded tail.

In normal gliding flight, aerodynamic forces on the tail and on the body exclusive of the wings produce pitching moments. The moment from the tail can be larger than that from the body because the tail can produce a larger lift component that is centered farther from the bird's center of mass. However, slender wing theory (Katz and Plotkin, 1991) predicts that a flat tail produces lift only when it spreads into a delta shape (Thomas, 1993). The folded tail had parallel sides, and it would not produce lift at angles of attack less than 15 °.

When the hawk kept its tail folded, it was presumably not controlling pitch by changing the angle of attack of its tail or body. If it were, it could do so with a lower cost in drag merely by spreading its tail. In fact, the hawk with a folded tail did not obviously change the angle of attack of its tail and body before and after the wing tip feathers had been clipped, and any change greater than 6 ° would have been obvious.

If, as a worst case, the hawk did increase the angle of attack of its tail and body by 6 ° after clipping, the maximum plausible multiplier for S_{fp} would be 1.14. This value comes from the drag measurements on the model body, which increased by 14 % with a 6 ° change in angle of attack. Even this worst case has only a small effect on k_u/k_c (Fig. 6).

Increasing the equivalent flat plate areas of both the clipped and unclipped birds

There is some doubt about the value of S_{fp} that should be used for flying birds (Pennycuick, 1989; Tucker, 1990). The value used in this study is a compromise between measured values on a model body and a frozen body (Tucker, 1990) and is lower than Pennycuick's estimate. Accordingly, the maximum plausible multiplier for S_{fp} is 1.3. The ratio k_u/k_c has a low sensitivity to this multiplier (Fig. 6).

Increasing the k value of the clipped bird

Increasing the assumed value of k_c increases the computed value of k_u and the ratio k_u/k_c. Increasing k_c decreases $C_{D,pr}$ which, in the unclipped bird, leads to higher k_u values.

The value of k_c cannot plausibly increase much, because its value of 1.1 is already at the upper limit for conventional wings. In planar wings, k does not increase much for lift distributions that are not elliptical (Prandtl and Tietjens, 1957). For example, k is less than 1.1 for a wing with a nearly rectangular lift distribution (Reid, 1932; von Mises, 1959). The maximum plausible multiplier for k_c is 1.05, and it has only a small effect on k_u/k_c (Fig. 6).
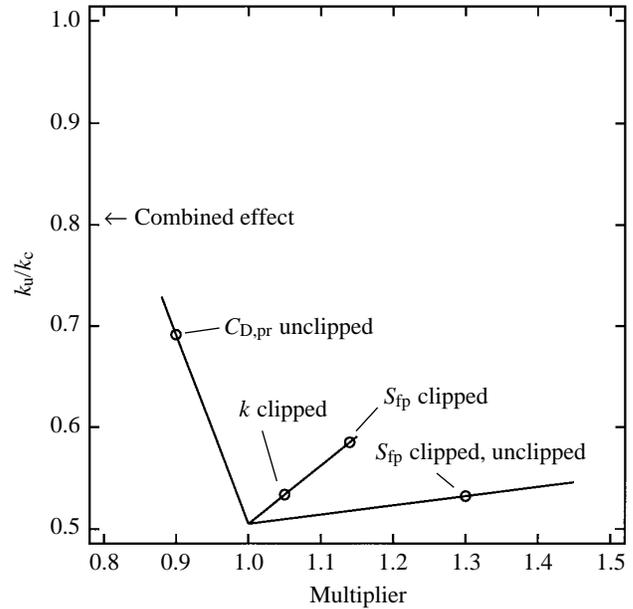

Fig. 6. The sensitivity of the induced drag factor ratio to changes in four quantities at a wing span of 0.8 m. (The curves for k_c and S_{fp} are identical.) The circles indicate points obtained by multiplying one quantity by its maximum or minimum plausible multiplier. The arrow shows the combined effect on the ratio when all four quantities are multiplied by their maximum or minimum plausible multipliers. See text for further explanation.

Making the profile drag coefficient of the unclipped bird less than that of the clipped bird

This change would increase k_u/k_c, which is quite sensitive to $C_{D,pr}$ (Fig. 6). However, there is no reason to think that this change should be made. Both when clipped and when unclipped, the hawk had lift coefficients between 0.36 and 0.65, and $C_{D,pr}$ is typically constant over this range. In fact, it seems more likely that the $C_{D,pr}$ of the unclipped hawk would be higher than that of the clipped hawk rather than lower, because the small, separated tip feathers have lower Reynolds numbers than the base wing. Drag coefficients tend to increase at low Reynolds number. (This effect is probably small for the hawk, since the tip feathers make up only about 10 % of the area of the fully spread wing; Tucker, 1992.)

The minimum plausible multiplier for $C_{D,pr}$ of the unclipped hawk is 0.9.

Combined effects

When the minimum and maximum plausible multipliers are used with all four quantities in Fig. 6, k_u and k_c are still far from equal – the combined effect increases k_u/k_c to 0.80. The significance of this ratio relative to the scattered data in Fig. 5 can be seen by computing k_u with the combined effect. k_c with the combined effect is 1.1×1.05, or 1.16; and k_u is $0.80 \times k_c$, or 0.93. This value is significantly below 1.16 relative to the scatter in Fig. 5.

The effect of slotted tips on lift distribution and vortex spreading

The two questions posed in the Theory section can now be answered. Do slotted tips reduce k? The measurements and the Monte Carlo and sensitivity analyses suggest that they do. Evidently the slotted tips reduce k by influencing the lift distribution or by making the wing non-planar, or both. Is the value of k for wings with slotted tips less than 1? If so, the slotted tips make the wing non-planar and reduce k by vertical vortex spreading. Otherwise, no conclusion can be drawn about whether the slots make the wing non-planar, for two reasons: (1) the sensitivity analysis examines only changes that would increase k and ignores changes that would reduce it, and (2) even if k_u were 1 or more, the slotted tips could make the wing non-planar, but with a non-optimum lift distribution.

k_u has a mean value of 0.56, calculated from measured and assumed values at a wing span of 0.8 m. The sensitivity analysis shows that even if four of these values were extremely biased in directions that make k_u too low, the true value of k_u would not exceed 0.93. It seems likely that the induced drag factor for unclipped wings is indeed less than 1, leading to the conclusion that the tip slots make the wing non-planar and spread vorticity both horizontally and vertically. This conclusion from measurements on a free-flying bird is the same as that reached from earlier measurements on a model wing with a slotted tip formed by primary feathers (Tucker, 1993).

List of symbols

b	wing span
C_0, C_1, C_2	coefficients for fitted equations
$C_{D,pr}$	profile drag coefficient
C_L	lift coefficient
c'	mean wing chord
D	total drag
D_i	induced drag
$D_{i,min}$	minimum induced drag
D_{par}	parasite drag
D_{pr}	profile drag
F	correction factor for Re
$\boldsymbol{g}$	acceleration due to gravity
k	induced drag factor
k_c	induced drag factor for clipped wings
k_u	induced drag factor for unclipped wings
L	lift
m	body mass
Re	Reynolds number
S	projected area of a wing
S_{fp}	equivalent flat plate area
V	free-stream air velocity
π	circumference/diameter of a circle
ρ	density of air
θ	glide angle

References

CONE, C. D., JR (1962). The theory of induced lift and minimum induced drag of non-planar lifting systems. *Nat. Aeronautics and Space Administration, Tech. Rept.* **R-139**.

GRAHAM, R. R. (1932). Safety devices in wings of birds. *J. R. aeronaut. Soc.* **36**, 24–58.

HAMMERSLEY, J. M. AND HANDSCOMB, D. C. (1964). *Monte Carlo Methods*. London: Methuen and Co. Ltd.

HUMMEL, D. (1980). The aerodynamic characteristics of slotted wing-tips in soaring birds. In *Acta XVII Congressus Internationalis Ornithologici* (ed. R. Nöhring), pp. 391–396. Berlin: Verlag der Deutschen Ornithologen-Gesellschaft.

KATZ, J. AND PLOTKIN, A. (1991). *Low-speed Aerodynamics*. New York: McGraw-Hill Inc.

KERLINGER, P. (1989). *Flight Strategies of Migrating Hawks*. Chicago: University of Chicago Press

KUETHE, A. M. AND CHOW, C. (1986). *Foundations of Aerodynamics*. New York: John Wiley and Sons.

LAMBERT, M. (1990). *Jane's All the World's Aircraft 1990–1991*. Surrey: Jane's Information Group Ltd.

NORBERG, U. (1990). *Vertebrate Flight*. Berlin: Springer Verlag.

PENNYCUICK, C. J. (1968). A wind-tunnel study of gliding flight in the pigeon *Columba livia*. *J. exp. Biol.* **49**, 509–526.

PENNYCUICK, C. J. (1989). *Bird Flight Performance*. Oxford: Oxford University Press.

PENNYCUICK, C. J., HEINE, C. E., KIRKPATRICK, S. J. AND FULLER, M. R. (1992). The profile drag of a hawk's wing measured by wake sampling in a wind tunnel. *J. exp. Biol.* **165**, 1–19.

PRANDTL, L. AND TIETJENS, O. G. (1957). *Applied Hydro- and Aero-Mechanics*. New York: Dover Publications.

REID, G. R. (1932). *Applied Wing Theory*. New York: McGraw Hill.

SPEDDING, G. R. (1992). The aerodynamics of flight. *Adv. comp. env. Physiol.* **11**, 51–111.

THOMAS, A. L. R. (1993). On the aerodynamics of birds' tails. *Phil. Tran. R. Soc. Lond. B* **340**, 361–380.

TUCKER, V. A. (1987). Gliding birds: the effect of variable wing span. *J. exp. Biol.* **133**, 33–58.

TUCKER, V. A. (1990). Body drag, feather drag and interference drag of the mounting strut in a Peregrine falcon, *Falco peregrinus*. *J. exp. Biol.* **149**, 449–468.

TUCKER, V. A. (1992). Pitching equilibrium, wing span and tail span in a gliding Harris' hawk, *Parabuteo unicinctus*. *J. exp. Biol.* **165**, 21–41.

TUCKER, V. A. (1993). Gliding birds: reduction of induced drag by wing tip slots between the primary feathers. *J. exp. Biol.* **180**, 285–310.

TUCKER, V. A. AND HEINE, C. (1990). Aerodynamics of gliding flight in a Harris' hawk, *Parabuteo unicinctus*. *J. exp. Biol.* **149**, 469–489.

VON MISES, R. (1959). *Theory of Flight*. New York: Dover Publications.

WHITCOMB, R. T. (1976). A design approach and selected wind-tunnel results at high subsonic speeds for wing-tip mounted winglets. *Nat. Aeronautics and Space Administration, Tech. Note* **D-8260**.

WITHERS, P. C. (1981). The aerodynamic performance of the wing in red-shouldered hawk *Buteo linearis* and a possible aeroelastic role of wing-tip slots. *Ibis* **123**, 239–247.