

# A mechanical model of wing and theoretical estimate of taper factor for three gliding birds

MOOSARREZA SHAMSYEH ZAHEDI<sup>a,b,\*</sup> and MIR YASEEN ALI KHAN<sup>c</sup>

<sup>a</sup>Department of Mathematics, Payame Noor University of Neyshabur, Neyshabur, Iran

<sup>b</sup>Department of Mathematics, University of Pune, Pune 411007, India

<sup>c</sup>Department of Mathematics, Poona College of Arts Science and Commerce, Camp, Pune 411001, India

\*Corresponding author (Email, zahedi@math.unipune.ernet.in)

We tested a mechanical model of wing, which was constructed using the measurements of wingspan and wing area taken from three species of gliding birds. In this model, we estimated the taper factors of the wings for jackdaw (*Corvus monedula*), Harris' hawk (*Parabuteo unicinctas*) and Lagger falcon (*Falco jugger*) as 1.8, 1.5 and 1.8, respectively. Likewise, by using the data linear regression and curve estimation method, as well as estimating the taper factors and the angle between the humerus and the body, we calculated the relationship between wingspan, wing area and the speed necessary to meet the aerodynamic requirements of sustained flight. In addition, we calculated the relationship between the speed, wing area and wingspan for a specific angle between the humerus and the body over the range of stall speed to maximum speed of gliding flight. We then compared the results for these three species of gliding birds. These comparisons suggest that the aerodynamic characteristics of Harris' hawk wings are similar to those of the falcon but different from those of the jackdaw. This paper also presents two simple equations to estimate the minimum angle between the humerus and the body as well as the minimum span ratio of a bird in gliding flight.

[Zahedi M S and Khan M Y A 2007 A mechanical model of wing and theoretical estimate of taper factor for three gliding birds; *J. Biosci.* **32** 351–361]

## List of symbols

$\beta$	angle between humerus and body	m	body mass
$\beta_{\min}$	minimum angle between humerus and body	Re	Reynolds number
$\beta_e$	empirical span ratio ( $b_{\text{obs}}/b_{\text{max}}$ )	S	wing area
$\beta_{\min, sr}$	minimum span ratio	S'	wing area lost owing to flexing
b	wing span	$r_1, r_2, r_3$	length of wing elements
$b_B$	body width	$S_{\text{max}}$	maximum wing area
$b_{\text{max}}$	maximum wing span	$V_{\min}$	stall speed
$b_{\text{obs}}$	observed wingspan	$U_{\infty}$	velocity of the fluid relative to the moving object
c	wing chord	v	kinematic viscosity
$C_{l, \text{max}}$	maximum lift coefficient	$\theta$	angle
e	taper factor	$\rho$	air density
g	acceleration due to gravity		
k	proportionality constant, $b_B = Kb_{\text{max}}$		
l	length		

**Keywords.** Mechanical model; wingspan; wing area; angle between humerus and body; gliding birds; speed; taper factor; span ratio

## 1. Introduction

Gliding is a comparatively inexpensive mode of flight by which a bird covers the aerodynamic cost by losing potential energy. However, the bird needs fuel energy to maintain the force on its wings, by pushing them downwards and forwards, to counteract the force generated by air flow on the wings and by gravity on its mass. This cost is estimated to be approximately 3–4 times the basal metabolic rate (Hedenstrom 1993). Gliding flight has previously been studied in wind tunnels (Pennycuick 1968; Withers 1981; Spedding 1987), by tracking radar (Spaar and Bruderer 1996; Spaar and Bruderer 1997), and by range finder (Tucker 1988; Tucker *et al* 1998). Gliding birds typically change their wingspans while flying, both in nature and in wind tunnels (Pennycuick 1968; Tucker and Parrott 1970; Parrott 1970; Tucker and Heine 1990). The wings appear to swing forward as the wingspan increases (Hankin 1913). It is easy to observe these birds gliding slowly on fully spread wings, and then progressively flexing their wings as they glide faster and faster. A typical feature of gliding flight is that the bird will flex its wings by increasing the forward and sinking speed. Tucker (1987) calculated that, by reducing their wing span, birds are able to minimize the total drag.

There are a few studies available on birds in gliding flight that predict wingspan,  $b$ , and wing area,  $S$ , by using theoretical or empirical models. Gliding birds, however, change their wingspan during flight. Maximum wingspan,  $b_{\max}$ , and wing area,  $S_{\max}$  (figure 1A), can be measured on dead birds by stretching out the birds. Tucker (1987) estimated the relationship between wingspan and wing area of gliding birds by measuring  $b_{\max}$  and  $S_{\max}$ . In addition to  $S_{\max}$  and  $b_{\max}$ , the equations of his mechanical model of wings depend also on two constants and one variable; the taper factor  $e$  (the actual wing chord at the base [figure 1A] divided by the mean wing chord), and the ratio of the body width (figure 1A) to the maximum wingspan,  $k$ ; the variable is the angle between the humerus and the body,  $\beta$  (figure 1B). He studied the relationship between the wingspan and wing area of the falcon and vulture with taper factors of 1.6 and 1.5, respectively. He also used  $k = 0.093$  to describe the relationship between the wingspan and wing area of the albatross. Rosen and Hedenstrom (2001) presented empirical equations to predict the span ratio (the actual wingspan,  $b_{\text{obs}}$ , divided by the maximum wingspan), wingspan and wing area for a bird in gliding flight over a range of speeds.

In this paper we estimate theoretically the values of  $e$  and  $k$  for jackdaw (*Corvus monedula*), Harris' hawk (*Parabuteo unicinctas*), and Lagger falcon (*Falco jugger*), and propose a simple equation to estimate the minimum value of the angle between the humerus and the body for a bird in gliding flight. We compose the empirical and theoretical equations

to derive a relation between flight speed of gliding birds with the angle between the humerus and the body. We then determine the wingspan, wing area, and the angle between humerus and body necessary to maintain sustained gliding for a given flight speed. Finally, we propose another simple equation to estimate the minimum span ratio of a bird in gliding flight. We then compare the relationship between speed, wingspan and wing area for a given angle between the humerus and the body of the three birds.

## 2. Definitions and theory of gliding flight

### 2.1 Reynolds number

The Reynolds number,  $Re$ , is a dimensionless number that generally describes the ratio of inertial to viscous forces acting in fluid. It is given by the equation  $Re = \frac{\rho U_{\infty} l}{\mu}$  where  $\rho$  is the density of the fluid medium,  $U_{\infty}$  is the velocity of the fluid relative to the moving object,  $l$  is characteristic length measure and  $\mu$  is the dynamic viscosity of the fluid medium. Flows of the same are dynamically similar. It has effects on the flow pattern, wings and hence on the calculations of lift and drag (Von Mises 1945).

### 2.2 Stall speed

The stall speed (minimum speed) is the speed below which the wings would stall and therefore cannot support the weight of the birds. The stall speed is given by:

$$V_{\min} = \sqrt{\frac{2mg}{\rho S C_{l,\max}}} \quad (2.2.1)$$

where  $m$ ,  $g$ ,  $\rho$ ,  $S$  and  $C_{l,\max}$  are body mass, gravitational acceleration, air density, wing area, and the maximum value of lift coefficient, respectively. We take the minimum speed of jackdaw to be 4.9 m/s (data from Rosen and Hedenstrom 2001) and for Harris' hawk and Lagger falcon to be 6.1 m/s and 6.6 m/s respectively (data from Tucker and Heine 1990; Tucker and Parrot 1970; Tucker 1987). To achieve the above data, their calculations have been done for the range of Reynolds numbers between 3,800 and 7,600 for jackdaw, and 7,800 to 208,000 for Harris' hawk and Lagger falcon.

### 2.3 Theory of gliding flight

Gliding flight occurs when the bird does not flap its wings but rather uses gravity to provide the means for flight. In still air, the path of the bird with spread wings is inclined downwards where the combination of aerodynamic forces generated by the motion through the air and the force of gravity creates a

balance of forces allowing steady gliding flight. We consider that the bird's gliding is in balance at the speed of  $V$  along a flight path inclined at angle  $\theta$  (the glide angle with respect to the horizon), by assuming that  $c$  is constant.

### 3. A simple mechanical model to estimate the wingspan and wing area

Tucker (1987) estimated the relationship between the wingspan and wing area of a simplified, hypothetical wing of any aspect ratio. He adjusted the equations to estimate the relationship between wingspan and wing area of an actual gliding bird. The hypothetical wing has three rigid rectangular elements of lengths  $r_1$ ,  $r_2$  and  $r_3$  (figure 1C), connected at the shoulder, elbow and wrist. Two sets of these elements along with the body's width,  $b_B$ , construct the wingspan. The maximum wingspan is then given by

$$b_{\max} = 2(r_1 + r_2 + r_3) + b_B. \quad (3.1)$$

By expressing  $b_B$  as a proportion of  $b_{\max}$ ,

$$b_B = kb_{\max}, \quad (3.2)$$

the equation (3.1) becomes,

$$r_1 + r_2 + r_3 = \frac{b_{\max}(1-k)}{2}. \quad (3.3)$$

If the angles at the wing conjunctions remain equal as the wing flexes at angle  $\beta$ , then

$$b = 2(r_1 + r_2 + r_3) \sin \beta + b_B \quad (3.4)$$

or,

$$b = b_{\max} [k + (1-k) \sin \beta]. \quad (3.5)$$

Now consider the area of the wing when it flexes. According to figure 1C, the wing loses the area of the quadrilateral  $HIJK$  at the wrist conjunction as the feathers overlap, but it gains the area of  $DEFG$  at the elbow conjunction when the overlaps over feather are exposed. The lost area at the wrist and the gained area at the elbow are equal and cancel each other. Therefore, the net loss in the area with the flexed wing is due to the overlap of the body and the base of the wing (area  $ABM$ ). The lost area ( $S'$ ) at the base of both the wings is

$$S' = c^2 \tan(90 - \beta), \quad (3.6)$$

where  $c$  is the wing chord at the wing base, given by

$$c = \frac{S_{\max}}{b_{\max}}. \quad (3.7)$$

In the tapered wing, the chord at the base of the wing is larger than the value given by the above equation, and the changes in area at the elbow and wrist are no longer equal when the wing flexes. In addition,  $\beta$  may be constrained anatomically

from reaching  $90^\circ$  in an actual wing. For simplicity, we will attribute the entire reduction in area of a flexed, tapered wing to overlap of the body by a wing of chord  $e^{\frac{1}{2}}c$  at its base.

The taper factor,  $e$ , is 1 for a rectangular wing with equal flex angles at each joint. Actual wings would have taper factors greater than 1, to be determined empirically. For an actual wing, the equation (3.6) gets the form

$$S' = ec^2 \tan(90 - \beta). \quad (3.8)$$

The area of both wings when flexed at angle  $\beta$  is

$$S = S_{\max} - e \left(\frac{S_{\max}}{b_{\max}}\right)^2 \tan(90 - \beta). \quad (3.9)$$

### 4. Empirical equations to predict the wingspan and wing area in gliding birds

Rosen and Hedenstrom (2001) examined the gliding flight performance of a jackdaw (*Corvus monedula*) in a wind tunnel. They derived an alternative equation using the observed span ratios to calculate the wingspan and wing area with respect to the forward speed in gliding birds by having information on the body mass, maximum wingspan, maximum wing area and maximum coefficient of lift. These alternative equations can be used in combination with any model of gliding flight where wing area and wingspan are used to calculate the sinking rate with respect to the forward speed. By using the observation and assuming that there is a linear relationship between  $\beta_e$  (empirical span ratio) and speed, they derived the following equation for span ratio as a function of speed:

$$\beta_e = \frac{5}{4} - \frac{V}{4V_{\min}}. \quad (4.1)$$

The wingspan ratio is maximal ( $\beta_e = 1$ ) at  $V_{\min}$ , and decreases linearly when the speed increases. They observed that the minimum value of span ratio is approximately  $\frac{1}{3}$ , therefore  $\frac{1}{3} \leq \beta_e \leq 1$ .

Using equation (4.1) to calculate  $\beta_e$ , the wingspan can then be written as

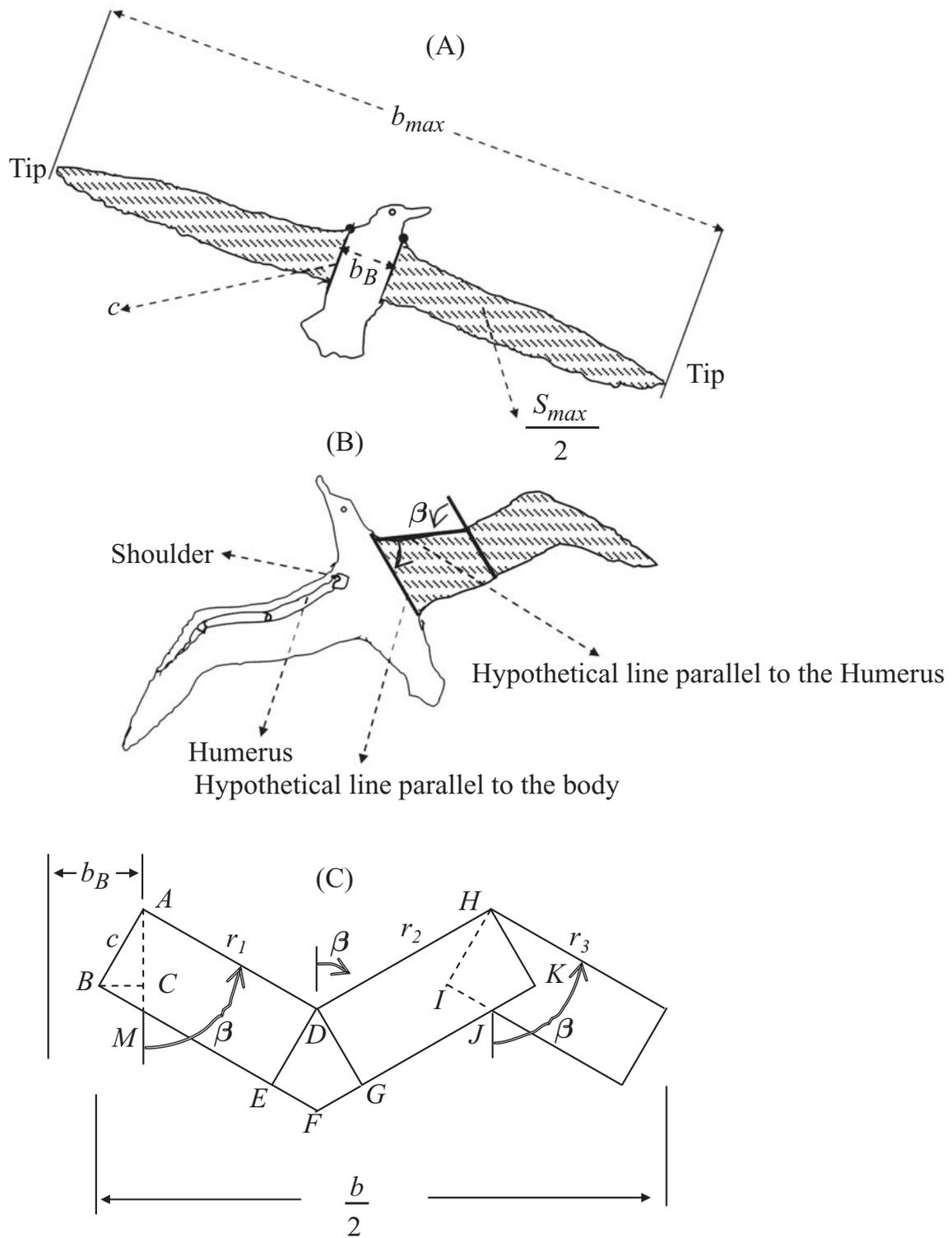
$$b = \beta_e b_{\max}. \quad (4.2)$$

By combining equation (3.7) and (4.2) and assuming that there is a linear relationship between wing area and wingspan, it is possible to calculate the wing area at any speed as:

$$S = c\beta_e b_{\max}. \quad (4.3)$$

### 5. Theoretical estimate of taper factor

In this section, we estimate  $k$  of equation (3.5); using that value of  $k$ , we calculate the value of  $e$  in equation (3.9). One essential parameter needed to estimate the taper factors is



**Figure 1.** (A), (B) Sketch of a bird in gliding flight. (A) At low gliding speeds, the bird’s wings and tail are fully extended to maximum planform area ( $S_{max}$ ) and maximum wing span ( $b_{max}$ ). The sketch also shows the wing chord at the base,  $c$ , and the body’s width  $b_B$ . (B) As speed increases, the bird needs less wing area,  $S < S_{max}$ ,  $b < b_{max}$  therefore  $\beta < 90^\circ$  (angle between a hypothetical line parallel to the body and a hypothetical line parallel to the humerus). (C) Hypothetical bird wing showing changes in wing area with flexing. It models the changes of  $S$ ,  $b$  and  $\beta$  in (A) and (B). See text for explanation.

the stall speed of the birds. As mentioned in the previous section, we will set the values of stall speed of jackdaw, Harris' hawk and Lager falcon to be 4.9 m/s, 6.1 m/s, and 6.6 m/s, respectively.

5.1 Ratio of body width and maximum wingspan

Since the area of  $S'$  is a function of  $\beta$  (the angle between the humerus and body), we suppose that  $L = \{x \mid x = 2c \cos(\beta), m_1 \leq \beta \leq n_1\}$ , where  $m_1$  is the value of  $\beta$  when the bird glides at a speed of  $V = \frac{11}{3}V_{\min}$  (see section 4), and  $n_1$  is its value when  $V = V_{\min}$ . Now consider  $b_B = 2BC$  (figure 1) such that  $BC = \bar{L}$  (the mean value of  $L$ ). Therefore,  $\bar{k} = k = \frac{2\bar{L}}{b_{\max}}$  and equation (3.5) becomes

$$b = [b_{\max}(\bar{k} + (1 - \bar{k})\sin(\beta))] \tag{5.1.1}$$

By using equation (5.1.1), we have calculated the  $b$  for all possible values of  $m_1 \leq \beta \leq n_1$ . These results were compared with the output of equation (4.2). This comparison shows that the  $\bar{k}$  can be a suitable estimation for any of these species. The values of  $\bar{k}$  are 0.144, 0.203 and 0.190 for jackdaw, Harris' hawk and Lager falcon, respectively. If  $V_{\min} \leq V \leq \frac{11}{3}V_{\min}$ , then equations (3.5) and (4.2) tell us that,

$$\frac{1}{3}b_{\max} \leq b \leq b_{\max} \text{ therefore,}$$

$$\beta_{\min} = \text{Arc sin} \left( \frac{1 - 3\bar{k}}{3 - 3\bar{k}} \right) = \text{Arc sin} \left( \frac{1 - 3\bar{k}}{3 - 3\bar{k}} \right) \tag{5.1.2}$$

where  $\beta_{\min}$  is the angle between the humerus and the body at the maximum speed of gliding flight. The values of  $\beta_{\min}$  are 13°, 10° and 11° for steady gliding flight of jackdaw, Harris' hawk and Lager falcon, respectively.

5.2 The taper factor

By combining equations (3.9) with (4.3) and (5.1.1) with (4.2), the following relationships can be expressed for the angle between the humerus and the body, and the speed of a bird in gliding flight

$$V = (5 - 4\bar{k})V_{\min} - 4(1 - \bar{k})V_{\min} \sin(\beta), \tag{5.2.1}$$

$$V = V_{\min} + 4eV_{\min} \frac{S_{\max}}{b_{\max}^2} \tan(90 - \beta). \tag{5.2.2}$$

We suppose that the birds can glide at speeds between  $V_{\max}$  and  $\frac{11}{3}V_{\min}$ . Then, it is easy to calculate  $\beta$  for a given flight

speed by using equation (5.2.1). By considering this fact that  $e > 1$ , we have computed  $S$  by putting an arbitrary value of  $e$  into equation (3.9). At the same time, by having some estimation of  $\beta$ , we can calculate  $V$  using the equation (5.2.1). Then, by using equations (4.1) and (4.3), we can calculate  $S$  in a different way. We then can compare these two values of  $S$ . By using these comparisons, we estimated the values of taper factor for jackdaw, Harris' hawk and Lager falcon as 1.8, 1.5, and 1.8, respectively.

6. Comparison between theoretical and experimental data

In this section, we compare the output data of equations (3.9) and (5.1.1) with the available experimental data on the birds in gliding flight. By using equations (3.9), (5.1.1) and (5.2.1), we can determine the relation between wingspan and wing area at a given speed. The comparisons show that the measurements of the wing area and the wingspan, using the mechanical model of the birds' wing in gliding flight by Tucker (1987), are very close to those of the experimental data. The small discrepancy between the graphs should be related to the estimation of the taper factors in the theoretical model (figures 2 and 3). All calculations and data output were performed in Matlab V5.3 and SPSS V11.5.

6.1 Wing area and wingspan at different speeds of jackdaw

Rosen and Hedenstrom (2001) found the following relationships between wingspan, speed and wing area over the entire speed range of 6–11 m/s:

$$b = -0.028V + 0.705$$

$$S = 0.0665b^2 + 0.316b + 0.0156, r^2 = 0.99, N = 15,$$

$$P < 0.001.$$

With the same assumptions, by using the theoretical data, we have come to the following relationships between the wingspan, speed and wing area

$$b = -0.0278V + 0.760$$

$$S = 0.0179b^2 + 0.893b - 0.0037, \text{ with } r^2 = 0.999,$$

$$N = 26, P < 0.001.$$

The two results are compared in figure 2. The relationship between wingspan and wing area is approximately linear for  $b > \frac{2}{3}b_{\max}$  (figures 2 and 3).

6.2 Wing area and wingspan of Harris' hawk

Tucker and Heine (1990) found the following relationship between wingspan and wing area of Harris' hawk over the

speed range of 6.1–16.2 m/s. In this case, the wing area increases with wingspan along a parabolic curve fitting by least squares  $S = 0.0736b^2 + 0.0841b + 0.0841b + 0.0278$ . By the same assumptions and using theoretical data, we have come to the following relationship between wingspan and wing area:

$$S = -0.0448b^2 + 0.2992b - 0.0742, r^2 = 0.994, N = 52, P < 0.001.$$

The two results are also compared in figure 3.

## 7. Results and discussion

When a bird glides, its wingspan varies with its speed and also with the angle between the humerus and the body. For a given angle between the humerus and the body, the wingspan decreases as the speed increases. And for a given speed, the wingspan increases as the angle between the humerus and the body increases. We analysed the relationships between these parameters (figure 3) when  $V_{\min} \leq V \leq \frac{11}{3}V_{\min}$ . In the previous sections, we concluded that the data taken from the theoretical equations by Tucker (1987) are very close to the experimental data. These also show that the taper factors are suitable for the birds. Now, to illustrate how the mechanical model can be applied, this section focuses on the theoretical data of jackdaw, Harris' hawk and Lagger falcon. As mentioned earlier, if  $\frac{1}{3} \leq \beta_e \leq 1$  then  $V_{\min} \leq V \leq \frac{11}{3}V_{\min}$  is inequality in the empirical model can be equivalent to  $\beta_{\min} \leq \beta \leq 90^\circ$  in the theoretical model. Therefore, we focus on variations of  $\beta$  for a given speed, wingspan or wing area. Tucker and Heine (1989) reported the aerodynamic characteristics of Harris' hawk at equilibrium in a wind tunnel. They also reported that the aerodynamic characteristics of the Harris' hawk's wings are similar to those of the Lagger falcon. The similarity between Harris' hawk and Lagger falcon's graphs can be related to the similarity between their aerodynamic characteristics (figures 4 and 5). Rosen and Hedenstrom (2001) observed that the minimum value of span ratio of jackdaw is somewhat higher than  $\frac{1}{3}$ , but Pennycuick (1968) reported a minimum span ratio for a pigeon to be very close to  $\frac{1}{3}$ . By using equations (3.5) and (4.2), we derived the following simple equation to estimate the minimum span ratio

$$\beta_{\min, sr} = \lambda + \gamma \sin(\beta) \text{ where } \lambda = \frac{\frac{1}{3} \sin \beta_{\min}}{1 - \sin \beta_{\min}} \text{ and } \gamma = \frac{2}{3(1 - \sin(\beta_{\min}))}. \quad (7.1)$$

$\beta_{\min, sr}$  is also the minimum span ratio of a bird at a steady glide.

By using equation (7.1) and taking  $\beta_{\min} = 13^\circ$  (see section [5.1]), the minimum value of span ratio for jackdaw would be equal to 0.315. It can be concluded that the minimum span ratio of a bird in steady gliding flight is proportional to the minimum value of the angle between the humerus and the body.

### 7.1 Wingspan at different speeds and the angle between the humerus and the body

The following relationships between speed, wingspan and the angle between the humerus and body of jackdaw, Harris' hawk and Lagger falcon, when  $V_{\min} \leq V \leq \frac{11}{3}V_{\min}$ , can be expressed respectively as

$$b = -0.068\beta - 0.043V + 0.918, N = 20, r^2 = 0.999, P < 0.001$$

$$b = -0.117\beta - 0.059V + 1.552, N = 20, r^2 = 0.999, P < 0.001$$

$$b = -0.077\beta - 0.048V + 1.444, N = 20, r^2 = 1, P < 0.001.$$

To compare these relationships, see figure 4.

### 7.2 Speed at different angles between the humerus and the body

The following relationships between speed and the angle between the humerus and the body of jackdaw, Harris' hawk and Lagger falcon, when  $\beta_{\min} \leq \beta \leq 90^\circ$ , are expressed respectively as

$$V = 41.053 - 75.87\beta + 60.184\beta^2 - 17.04\beta^3, N = 27, r^2 = 0.997, P < 0.001$$

$$V = 49.033 - 91.95\beta + 73.92\beta^2 - 21.005\beta^3, N = 28, r^2 = 0.999, P < 0.001$$

$$V = 49.282 - 96.55\beta + 80.93\beta^2 - 23.57\beta^3, N = 30, r^2 = 0.995, P < 0.001$$

To compare these relationships see figure 5 (A).

### 7.3 Wing area at different angles between the humerus and the body

The following relationships between wing area and the angle between the humerus and the body of jackdaw, Harris' hawk and Lagger falcon, when  $\beta_{\min} \leq \beta \leq 90^\circ$ , are expressed respectively as

$$S = -0.0494 + 0.2260\beta - 0.1778\beta^2 + 0.0498\beta^3, r^2 = 0.998, N = 27, P < 0.001$$

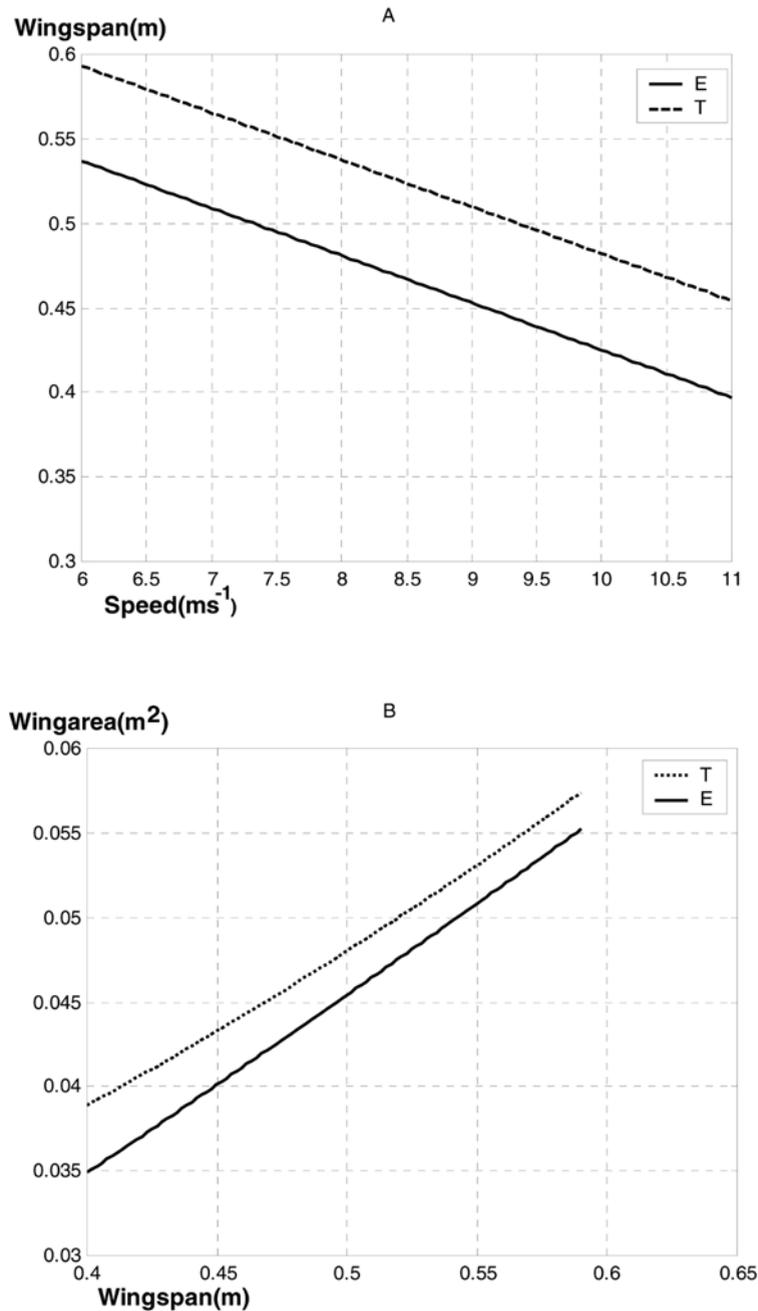
$$S = -0.1454 + 0.7167\beta - 0.5751\beta^2 + 0.1631\beta^3, r^2 = 0.997, N = 28, P < 0.001$$

$$S = -0.0833 + 0.4906\beta - 0.4158\beta^2 + 0.1223\beta^3, r^2 = 0.995, N = 30, P < 0.001$$

To compare these relations see figure 5 (B).

### 7.4 Wingspan at different angles between the humerus and the body

The following relationships between wingspan and the angle between the humerus and the body of jackdaw, Harris' hawk and Lagger falcon, when  $\beta_{\min} \leq \beta \leq 90^\circ$ , are



**Figure 2.** (A) Comparison of the relationship between wingspan and speed of jackdaw using theoretical and experimental data. (B) Comparison of the relationship between wing area and wingspan of jackdaw, using theoretical and experimental data.

expressed as

$$b = 0.1106 + 0.5921\beta - 0.1776\beta^2, r^2 = 1, N = 27, P < 0.001$$

$$b = 0.1998 + 1.0062\beta - 0.3071\beta^2, r^2 = 0.996, N = 28, P < 0.001$$

$$b = 0.1391 + 1.049\beta - 0.3129\beta^2, r^2 = 1, N = 30, P < 0.001$$

To compare the above relationships see figure 5 (C).

In this study, we examined Tucker's mechanical model of wing (Tucker 1987). We calculated the taper factor  $e$  for three species of gliding birds using his theoretical model. By using the taper factors, we compared the output data of equations (3.9) and (5.1.1) with the available experimental data on the birds in gliding flight (figure 3). This comparison

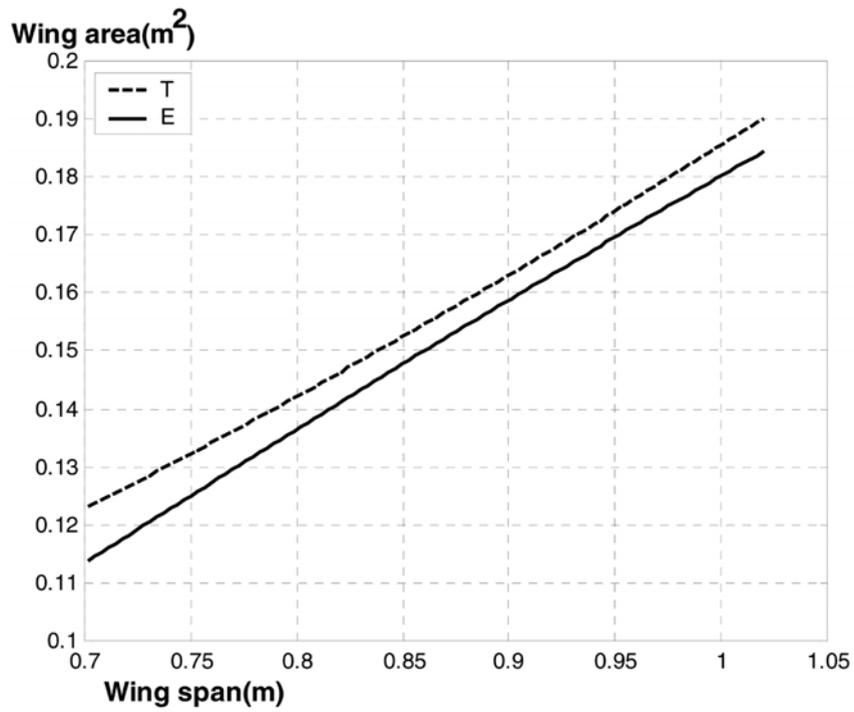


Figure 3. Comparison of the relationship between wingspan and wing area of Harris' hawk using theoretical and experimental data.

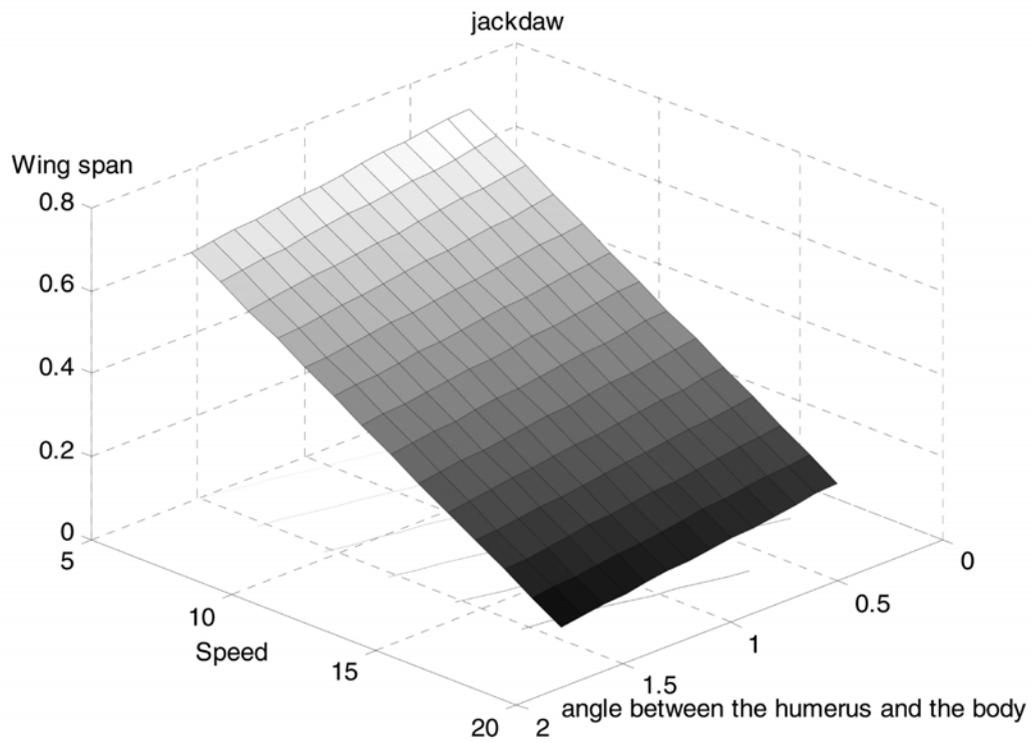
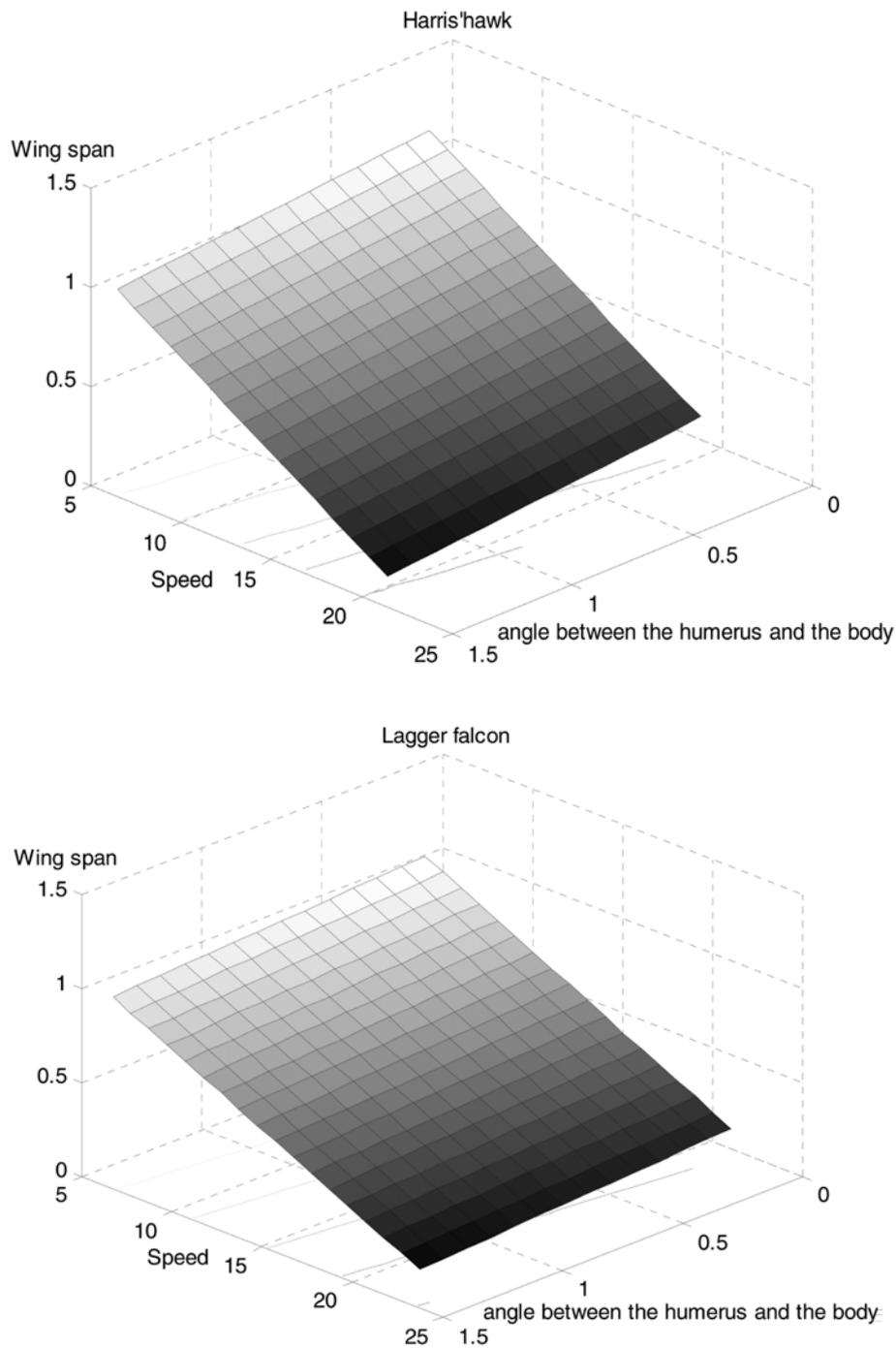


Figure 4. For caption, see page No. 359



**Figure 4.** Wingspan at different speeds and the angle between the humerus and the body of jackdaw, Harris’ hawk and Lagger falcon.

showed that the data taken from the theoretical equations by Tucker (1987) are very close to the experimental data. It also shows that taper factors are suitable for the wings of birds.

We have tried to give two simple equations to calculate the minimum angle between the humerus and the body, and

the minimum span ratio. Equation (7.1) gives predictions reasonably close to the values observed by Pennycuik (1968); and Rosen and Hedenstrom (2001). The few discrepancies that remain can be attributed to the small error in the assumed value of the minimum angle between the humerus and the body.

By using theoretical data, we analysed the gliding flight of the birds (figures 4 and 5). We focused on variations of the angle between the humerus and the body for a given speed, wingspan or wing area. This was the main motivation for this paper, as only a few researchers in the area of gliding flight have considered this parameter. However, these analyses showed that the aerodynamic characteristics of Harris' hawk's wings are similar to

those of Lager falcon. The similarity between the Harris' hawk and Lager falcon's graphs can be related to the similarity of their aerodynamic characteristics (figures 4 and 5).

There remains a need for more studies in which the kinematics is carefully monitored to be able to test the predications of existing gliding flight theory. The use of experimental data (a wind-tunnel study) and further

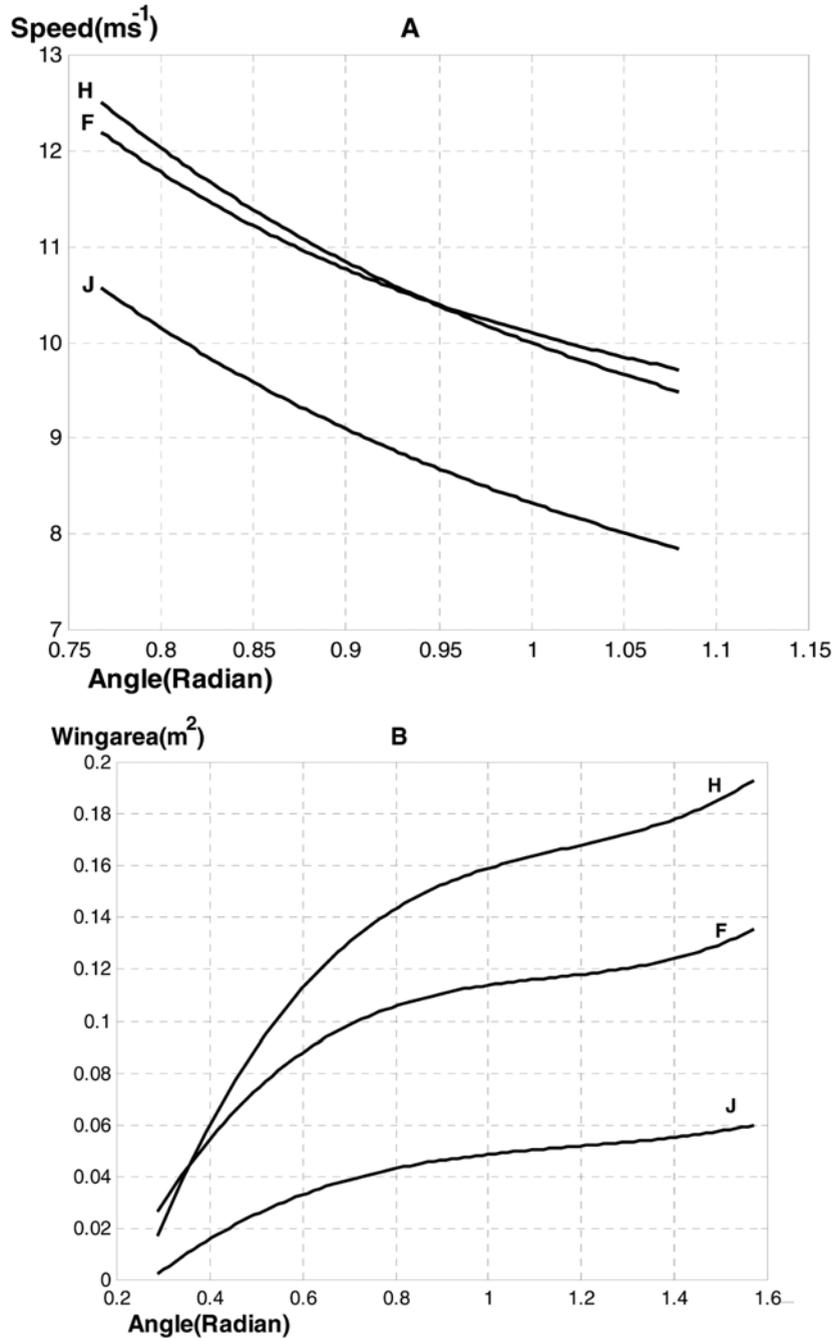
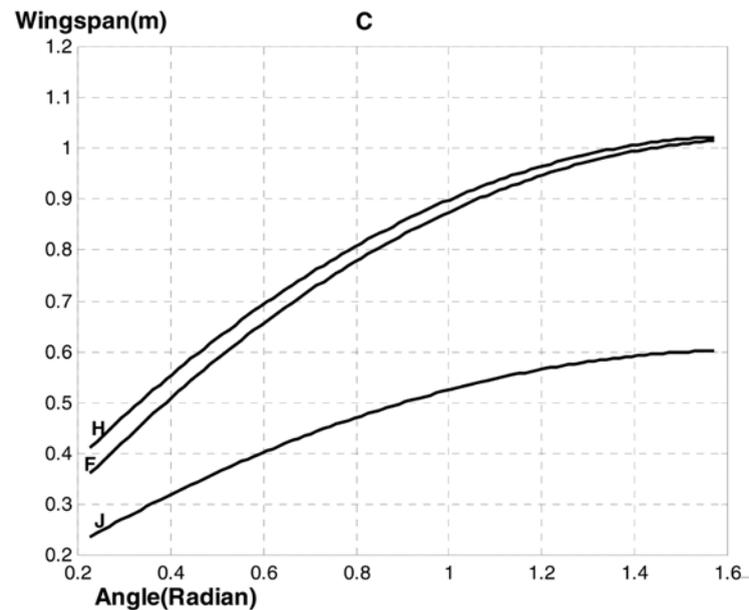


Figure 5. For caption, see Page No. 361.



**Figure 5.** (A) Speed at different angles between the humerus and the body of jackdaw, Harris' hawk and Lagger falcon. (B) Wing area at different angles between the humerus and the body of jackdaw, Harris' hawk and Lagger falcon. (C) Wingspan at different angles between the humerus and the body of jackdaw, Harris' hawk and Lagger falcon.

investigation of  $\beta_{\min}$  and its effects on the taper factor and flight angle  $\theta$  of gliding birds are the best prospects for future studies. Also, by studying more species of gliding birds, it should be possible to achieve a better comparison of the two empirical and theoretical models and obtain more accurate estimates of  $e$  and  $\beta_{\min}$ .

#### Acknowledgments

We are grateful to Professor Vance A. Tucker for his constructive comments. We are also grateful to Professor Sanjay P. Sane, Professor Adeel Ahmed, Dr Iraj Gholami and Dr Mohammad Saadatfar for their help and guidance. An anonymous referee provided careful and constructive criticism that significantly improved the paper.

#### References

- Hedenstrom A 1993 Migration by soaring or flapping flight in birds: the relative importance of flight cost and speed; *Phil. Trans. R. Soc. Lond. B* **342** 353–361
- Hankin E H 1913 *Animal flight: a record of observation* (London: Iliffe)
- Pennycuik C J 1968 A wind-tunnel study of gliding flight in the pigeon *Columbalivia*; *J. Exp. Biol.* **49** 509–526
- Rosen M and Hedenstrom A 2001 Gliding flight in a jackdaw: a wind tunnel study; *Exp. Biol.* **204** 1153–1166
- Spedding G R 1987 The wake of a kestrel *Falco tinnunculus* in gliding flight; *J. Exp. Biol.* **127** 45–57
- Tucker V A 1987 Gliding birds: the effect of variable wingspan; *J. Exp. Biol.* **133** 33–58
- Tucker V A and Heine C 1990 Aerodynamic of gliding flight in a Harris' hawk, *Parabuteo unicinctus*; *J. Exp. Biol.* **149** 469–489
- Tucker V A and Parrott G C 1970 Aerodynamic of gliding flight in a falcon and other birds; *J. Exp. Biol.* **52** 345–367
- Tucker V A 1988 Gliding birds: descending flight of the white-backed vulture, *Gyps africanus*; *J. Exp. Biol.* **140** 325–344
- Tucker V A, Cade T J and Tucker A E 1998 Dividing speeds and angles of a gyrfalcon (*Falco rusticolus*); *J. Exp. Biol.* **201** 2061–2070
- Von Mises R 1945 *Theory of flight* (New York: McGraw-Hill)
- Withers P C 1981 The aerodynamic performance of the wing in red-shouldered hawk *Buteo laneaeis* and a possible aeroelastic role of wing-tip slots; *Ibis* **123** 239–247
- Parrott C G 1970 Aerodynamic of gliding flight of black vulture *Coragyps atratus*; *J. Exp. Biol.* **53** 363–374
- Spaar R and Bruderer B 1996 Soaring migration of steppe eagles *Aquila nipalensis* in southern Israel: flight behaviour under various wind and thermal conditions; *J. Avian Biol.* **27** 289–301

MS received 11 November 2005; accepted 30 October 2006

ePublication: 25 January 2007

Corresponding editor: VIDYANAND NANJUNDIAH