# INTERMITTENT GLIDING IN THE HUNTING FLIGHT OF THE KESTREL, *FALCO TINNUNCULUS* L.

By J. J. VIDELER, D. WEIHS* AND S. DAAN

*Department of Zoology, State University, Groningen and Department of Aeronautical Engineering, Technion Haifa**

## SUMMARY

The hunting flight of the kestrel (*Falco tinnunculus*) consists of short bouts of flight at wind speed against the wind with the eyes in a fixed position relative to the ground, and of short flights from one such position to the next.

High speed films taken with a camera in a fixed position of a hunting kestrel of known weight and dimensions, allow estimates to be made of the amount of energy required for this behaviour.

A theoretical model shows how a bird could economise by alternating flapping flight with short gliding bouts, without changing the position of the eyes above the ground, by mere displacement of the centre of gravity relative to the head. High speed film data confirm predictions from this model.

## INTRODUCTION

Avian flapping flight is energetically an expensive means of animal locomotion. Yet many birds use it as an effective way to find and exploit their food sources. Some raptors and terns have adapted flapping flight to a particular purpose. By flying upwind with the speed of the wind they are able to stay in a fixed position relative to the ground, which enables them to scan the surface below and to detect moving prey to swoop down on. The kestrel is well-known for this behaviour which is its primary method of detecting small mammals and insects. In a current study of behavioural strategies in the kestrel we found that flight-hunting yielded on average 2·82 prey per hour compared to 0·31 for soaring, 0·21 for perching and 0·07 for sitting (Rijnsdorp, Daan & Dijkstra, 1981). Behavioural categories are shown in Fig. 1. Yet there appear to be some important constraints on the extent to which flight-hunting can be used for energy gain.

Although flight-hunting is such an effective method of obtaining food, kestrels devote very little time to it. No more than two hours per day are usually spent in flight-hunt, although in the breeding season this is slightly expanded while the males are providing food for their mates (Fig. 2 and see Village, 1982). This is remarkably short if we compare it, for instance, with songbirds which typically forage nearly continuously during daylight, at least when they have nestlings (e.g. the great tit and starling in Fig. 2). Wilson's question arises: 'Why haven't these species evolved so as to keep the members constantly foraging, consuming, growing and reproducing.
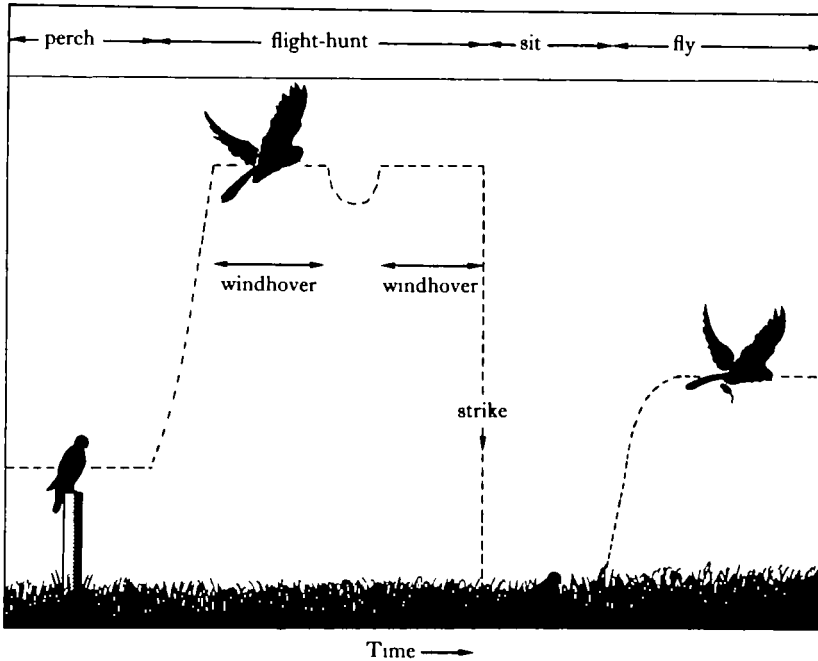
Fig. 1. Hunting behaviour of kestrel.

Shouldn't the most active genotypes have the greatest fitness?' (Wilson, 1975, p. 143). The answer may eventually be found in physiological limitations to the expenditure of energy. The existence of such limits has been suggested by the effects of experimental brood size manipulation on parent performance (Drent & Daan, 1980). In the case of kestrel flight-hunting behaviour constraints are suggested by an analysis of its temporal structure in relation to wind speed.

Kestrel flight-hunting consists of short (about 25 s) bouts during which the bird stays in a fixed position relative to the ground and looks downward to detect prey, and short flights from one such position to the next. The stationary movement has previously been called 'hovering' (Rijnsdorp *et al.* 1981) but this term is technically incorrect. 'Hovering' in the aerodynamic sense refers to flight at zero ground speed in still air, and in this sense the statement that 'kestrels cannot hover' (Rayner, 1979) is presumably correct. Also the movement made by the kestrels during this behaviour is quite distinct from the hovering flight as observed for instance in insects and hummingbirds (Weis-Fogh, 1973). To avoid any further confusion we use the term 'wind-hovering' for flight against the wind resulting in zero ground speed. In the example shown in Fig. 3, the durations of 794 windhovering bouts and 'inter-windhovering flights' observed in one female kestrel are plotted as a function of windspeed recorded at a nearby weather station. Windhovering bouts were short (about 10 s), both at low and very high wind speeds, and averaged 25 s in an intermediate range (4–13 m s$^{-1}$).

Fig. 2. Differences in foraging time per day between kestrel, great tit and starling. The points on the great tit curve are calculated from data by Gibb (1954). The starling data are kindly provided by J. Tinbergen.

Fig. 3. Duration of 794 windhovering and flying bouts of one female kestrel in relation to windspeed.
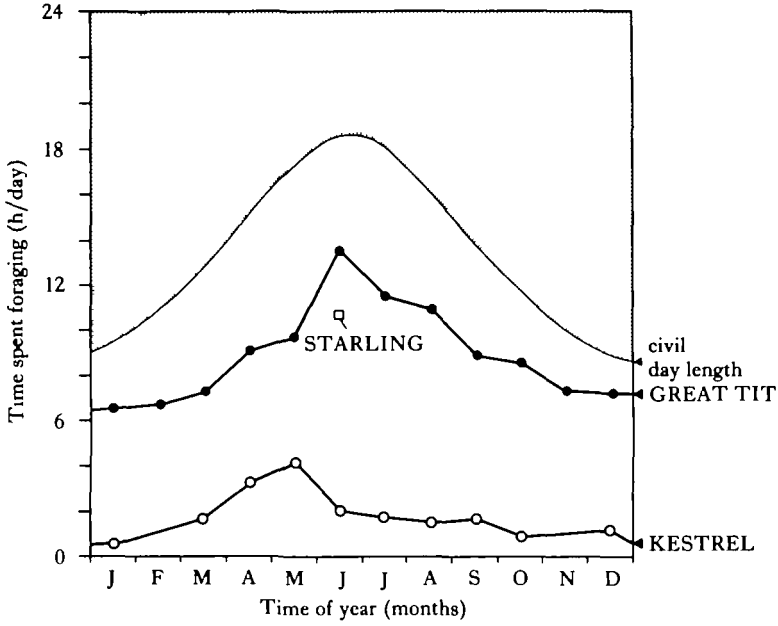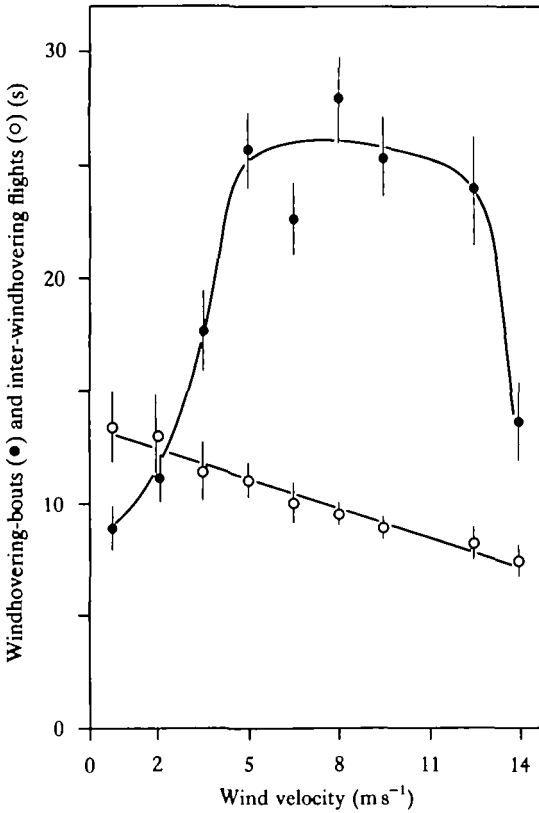
Fig. 2



Fig. 3

This range represents a range of flight speeds nearly symmetrically around the average speed ($8·3 \text{ m s}^{-1}$) of directional flights between perches observed in the same kestrel. We hypothesize that 25 s may be the time span required (or selected) by the bird for detection of prey in the area searched during windhovering. On days without any wind, no windhovering has been observed, as predicted by Rayner (1979), and we surmise that at low and high wind speeds the demands of low and high flight speeds become too high to allow windhovering.

In an attempt to understand the restrictions on flight speed we have started to collect high-speed films of windhovering kestrels in both field and wind tunnel conditions. In a cursory analysis of such films we noticed that the flight during windhovering actually consisted of bouts of flapping alternating with short episodes of gliding. This is a third mode of intermittent gliding in bird flapping flight. It differs markedly from undulating flights and bounding flight in that the glide episodes still allow the head and searching eyes of the bird to stay in a stationary position. It is the purpose of the present paper to derive theoretically the parameters restricting glides during windhovering behaviour, and to consider how they may affect the output of energy during flight-hunt.

## MATERIALS AND METHODS

### Cinematography

High speed cine films of windhovering kestrels were made in the field. A Locam (Red Lake) camera fitted with a 600 mm lens was mounted on the roof-rack of a motor-bus. The wind speed at 4 m above the bus was continuously recorded using a V.D.O. wind velocity transducer mounted on top of the vehicle on a pole. The birds were filmed in the 'Lauwersmeer', which is the most recent Dutch polder, reclaimed from the sea in 1969. This area provides a flat open countryside without woodland or high obstacles that could cause serious distortion of the wind flow.

Windhovering birds could be spotted from a large distance and a car may sometimes approach a bird to within 30 m without any obvious disturbance to its behaviour.

The camera was directed at the bird and as soon as the head was in focus in the centre of the field of view, the camera was secured in fixed position and started at a frame rate of 100 or 200 frames per s. The Locam has a built in reference grid and movements seen on the films are movements relative to the grid and to the ground.

Filming was stopped when the bird had made a strike or flew away. Sometimes a bird was caught by bal-chatri (Cavé, 1968) immediately after a shot had been taken and measurements of mass, wing area and wingspan were recorded. On one occasion a male kestrel was caught within 2 min of three film sequences of successive windhovering bouts. Data from this bird have been used as an example throughout this paper: body mass, 0·207 kg; wingspan, 0·76 m; wing area, 0·065 m².

### Theory of intermittent gliding

Films, analysed frame by frame on a Vanguard motion analyser, show that kestrels manage to keep the head in a very precisely fixed position in three dimensional space during windhovering. In Fig. 4 lateral and vertical displacements of the beak relative

o the average beak position are plotted against time. Displacements are smaller than ʊ mm either side of the average position and show no relation to the wing beat cycle. This precision seems to be a requirement for acquisition of a target, and analysis of its motion (and thus planning of the attack).

Simple gliding into the wind, which would require no energy for propulsion, is probably not compatible with efficient prey detection, although some bird prey are detected by soaring kestrels (Rijnsdorp *et al.* 1981).

Gliding at constant speed, U, in still air is only possible at an angle $\alpha$ (known as the gliding angle) downwards from the horizontal plane defined by

$$\tan \alpha = \frac{D}{L} \simeq \frac{D}{W} \tag{1}$$

where D and L are the aerodynamic drag and lift of the bird, W its weight, and $\alpha$ is assumed to be small. This glide must take place at a speed which is higher than the bird's stalling speed. The stalling speed is the lowest speed relative to the surrounding air, where the lift produced still equals the weight. Thus, when gliding into a
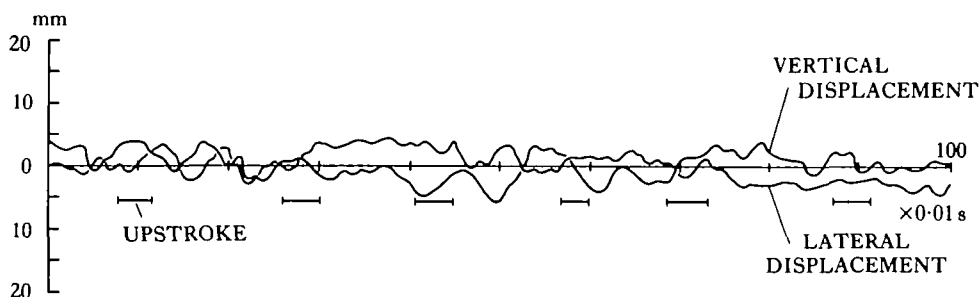


Fig. 4. Vertical and lateral displacements of the head relative to nominal position as a function of time, taken from shot 3 of Table 1.

horizontal, oncoming wind faster than the bird's stalling speed, the bird can stay in the same horizontal position relative to the ground, i.e., it appears to stand still. However, it would have a downward speed of $U \sin \alpha$ and could not stay at constant height.

To keep its eyes fixed in space, wing motions imparting an upward speed $U \sin \alpha$ must be made. These entail a rate of work of

$$P = W \, U \sin \alpha \tag{2}$$

or, in terms of windspeed V

$$P = W \, V \tan \alpha = DV. \tag{3}$$

The drag D has several components, most of which (known as parasite drag) are quadratically dependent on speed (equal to windspeed in this case). The induced drag (caused by the production of lift by means of deflecting parts of the airstream downwards), however, is proportional to $V^{-2}$, so that the total power required for level flight into the wind at the wind speed is

$$P = A_1 V^{-1} + A_2 V^3 \tag{4}$$

where $A_1$ and $A_2$ are constants, specific to the bird in question. (The dimension of $A_1$

is $N\,m^2\,s^{-2}$ and of $A_2$ is $N\,m^{-2}\,s^2$, if V is expressed in $m\,s^{-1}$ and P in W.) At very low
speeds the equation (4) is increasingly incorrect as the total power for hovering in still
air is finite, but this is a correction important at speeds much lower than the stall speed
and so is irrelevant for our purposes. For the sample kestrel, $A_1 \simeq 10$ and $A_2 \simeq 0.01$
(Greenewalt, 1975).

The analysis of sinking speed, in equations 1–4, describes the motion of the centre
of gravity (c.g.) of this bird. By utilizing body flexibility the bird could let its c.g.
move while its head (and eyes) stayed at a constant position. The behaviour can then
be described as starting off with the bird's body (centre of gravity) close to the head.
At this stage, provided that a wind of higher than stalling speed exists, the bird would
start a powerless glide with its body, keeping the head at the initial height and
position. This persists until the neck is fully stretched and the body configuration is
such that any further motion of the centre of mass will force motion of the head. Then
the bird, by normal flapping flight, returns to the initial state, and starts the cycle
again. Periodic flapping-gliding behaviour has been shown by Rayner (1977) to save
energy (in his case, undulating flight in still air) compared to continuous flapping.

The prediction of cyclic behaviour can serve as a test of the theory, since it precisely
defines the length of gliding periods. In wind of constant speed body flexibility sets
an upper limit to the duration of motionless gliding. As such constant wind intensity
(on the scale of the bird wing chord) is a rather rare occurrence, many attempted
gliding bouts will be aborted or cut short as a result of wind speed changes.

To predict the duration of possible gliding we have to know the maximum distance
the centre of gravity can move relative to the head. The distance was measured in a
sample of five freshly-dead adult kestrels and found to be 4 cm on average. There are
two different basic modes in which this stretch can be utilized, in a vertical (A) and
a horizontal (B) relative motion between the head and centre of gravity (Fig. 5). Other
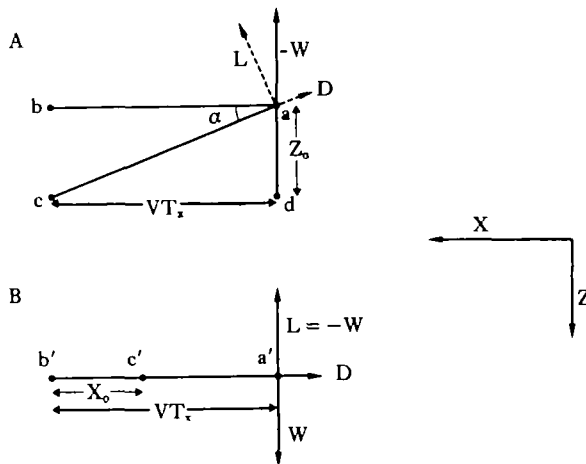motions can be seen as linear combinations of these two. In the vertical mode the



Fig. 5. Trajectory of centre of gravity for A, vertical mode and B, horizontal mode, of gliding with
the head fixed in space.
ab = a'b' = path of the head relative to the wind
ac = a'c' = path of the c.g. relative to the wind
ad = b'c' = path of the c.g. relative to the head

maximum stretching distance is $z_0$. The time needed to move the c.g. vertically over a distance $z_0$ is called $t_z$. In the same time the wind has moved an air element by $Vt_z$ (section ab in Fig. 5A). From this figure

$$\frac{z_0}{Vt_z} = \tan \alpha = \frac{D}{L}$$

$$\text{or} \qquad t_z = \frac{z_0}{V \tan \alpha} = \frac{z_0}{V} \frac{L}{D}$$

i.e., in this mode, the gliding time is inversely proportional to the windspeed and proportional to the lift over drag ratio.

The horizontal mode of stretching can be used when the bird is gliding in a wind with a velocity higher than the gliding stalling speed. The angle of attack between wings and head-on wind and the aerodynamic properties of wings and body assure that the lift L exactly balances the weight W. There is no force produced to counter the drag D so that the bird slows down without losing height (Fig. 5B). As a result, the centre of gravity is accelerated backwards as

$$D = m\frac{d^2x}{dt^2}$$

where x is the distance between head and c.g. The initial conditions for this differential equation are:

$$x = 0; \quad \frac{dx}{dt} = 0 \quad \text{at} \quad t = 0, \tag{6}$$

where $dx/dt$ is the relative horizontal speed between the head and c.g. of the kestrel, and $t = 0$ is the time at which gliding starts for a specific cycle. Integrating twice results in:

$$x = \frac{Dt^2}{2m}, \tag{7}$$

if we assume the drag to be constant. This assumption is valid only when the relative velocity between bird and wind does not change too much during a gliding bout, as we shall show below.

For $x = x_0$, the maximum stretching distance, a gliding time $t_x$ is obtained:

$$t_x = \left\{\frac{2x_0 m}{D}\right\}^{\frac{1}{2}} \tag{8}$$

Rewriting the mass as $W/g$ (where g is the gravitational acceleration) and recalling that the lift equals weight. The horizontal stretching time can then be rewritten as:

$$t_x = \left\{\frac{2x_0}{g} \frac{L}{D}\right\}^{\frac{1}{2}} \tag{9}$$

Since equation (7) holds only for constant speed relative to the wind, the relative speed $dx/dt$ must be much smaller than V if equation (9) is to be valid. This will be proved *a posteriori*.

Tucker & Parrott (1970) investigating gliding flight of a laggar falcon (weight 5·6 N). We used their equations (22) and (23) to calculate maximum L/D values at different wind speeds for our male kestrel (weight 2 N). Tucker & Parrott (1970) used a factor 'K', comparing the parasite drag coefficient of the bird with that of a flat plate with an equivalent surface area, orientated parallel to the direction of the flow. The 'K' value at maximum L/D found for the laggar falcon was 2·4 and is used in our
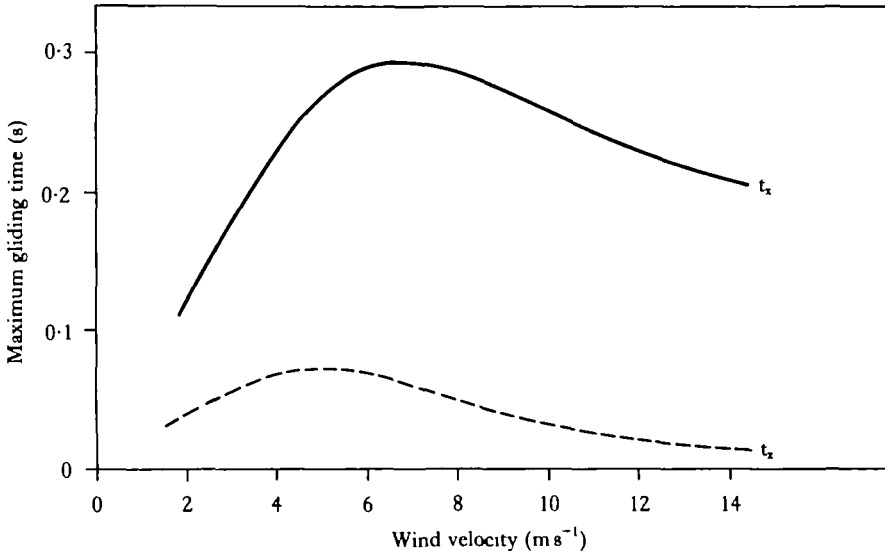
Fig. 6. Duration of gliding intervals during windhovering at different wind speeds: $t_z$ is the maximum gliding time when the c.g. glides downwards with respect to the head, $t_x$ is the maximum gliding time when c.g. slows down with respect to head and wind. (The model is explained in the text.)

calculations of the parasite drag coefficients and L/D values for different wind speeds. These are used to estimate gliding times $t_z$ and $t_x$ as functions of wind speed. Fig. 6 shows that the maximum gliding time in the vertical mode is slightly more than 0·07 s at a windspeed of 5 m s$^{-1}$. The maximum gliding times in the horizontal mode are more than four times as long and reach over 0·29 s at wind velocities around 7 m s$^{-1}$. The horizontal mode is therefore likely to be preferable.

For equation (9) to be valid, we still need to prove that the change of velocity during the glide is small compared to the wind speed. From (7), differentiating once we obtain, at time $t_x$ :

$$\frac{dx}{dt} = t_x D/m = t_x g D/W = t_x g D/L \qquad (10)$$

Using the maximum values from Fig. 6 we obtain $t_x = 0·29$ s and D/L = 0·09 which gives a maximum dx/dt of 0·26 m s$^{-1}$ at 7 m s$^{-1}$ wind speed. That is, the change in speed is 3·7 % and equations (7) and (9) can be applied.

### Empirical results

Bouts of windhovering of our male kestrel were filmed at 100 frames s$^{-1}$. During filming, the gusty wind varied in speed between 4·8 and 7·5 m s$^{-1}$. Table 1 shows three sequences of sections of windhovering bouts. The gliding periods comprise 7–21 % of the total filming time. Two out of 17 cases are considerably longer than the 0·29 s predicted as the maximum gliding time in the previous section. The variability in the gliding time percentage can be explained by the gustiness of the wind. Actual instantaneous gusts could not be correlated with the bird's movements, as the wind-speed indicator was over 30 m away from the bird, and at a lower height. Thus, approximately 5 s elapsed between the passage of a gust near the bird, and at the indicator. This is longer than the time scale for gusts, and therefore no attempt was made to correlate the two.

The average duration of gliding periods was 0·305 s. This is in good agreement with the maximum gliding time possible for horizontal stretching predicted by Fig. 6. The actual time the bird can glide in the horizontal mode is probably increased by the fact that the wings can be moved relative to the body. Backwards motion of the wings can be performed with small or negligible changes in the total lift, so that the centre of gravity can be moved somewhat more, and the gliding time can be slightly prolonged.

After a gliding bout the bird has to restore the original position of the c.g. with respect to the head by generating lift force greater than the body weight, if the vertical

Table 1. *The duration of flapping flight and gliding on three shots of cinefilm taken at 100 frames s$^{-1}$ of a windhovering kestrel*

| Bout duration | Flapping flight (s) | Gliding (s) |
|---|---|---|
| Shot 1 | 0·59 | 0·32 |
| | 2·14 | 0·55 |
| | 7·28 | 0·18 |
| | 2·65 | |
| Shot 2 | 1·13 | 0·26 |
| | 3·49 | 0·25 |
| | 0·82 | 0·29 |
| | 1·58 | 0·26 |
| | 0·12 | |
| Shot 3 | 3·79 | 0·23 |
| | 0·05 | 0·22 |
| | 0·47 | 0·13 |
| | 0·60 | 0·24 |
| | 1·73 | 0·43 |
| | 2·95 | 0·85 |
| | 1·11 | 0·19 |
| | 0·18 | 0·12 |
| | 0·41 | 0·33 |
| | 0·08 | 0·34 |
| | 0·05 | |

| | Shot duration (s) | Average gliding time (s) | Percentage of time spent gliding (%) |
|---|---|---|---|
| Shot 1 | 13·7 | 0·347 | 7·6 |
| Shot 2 | 8·2 | 0·265 | 12·9 |
| Shot 3 | 14·5 | 0·308 | 21·2 |

Wind speed varying between 4·8 and 7·5 m s$^{-1}$ (average 6·3 m s$^{-1}$).

mode was used, and by flying at a velocity slightly higher than the wind speed in the horizontal mode. Energy saving is only possible if the extra effort required to do this is lower than the energy used for flapping flight at wind speed during the same period as was used for gliding.

Energy gains by alternating flapping and gliding are possible, as the drag while flapping is approximately three times the gliding drag (Goldspink, 1981; Videler & Weihs, 1982; Weihs, 1974).

The relation between power and speed, predicted by equation (4), can be calculated

with the use of models described by Pennycuick (1975), Tucker (1974) and
Greenewalt (1975).

Fig. 7 compares the three approaches, using data from the chosen kestrel. The
curves are strikingly similar and show that a minimum power of less than 2 W is
required at a velocity of slightly more than 7 m s$^{-1}$. The power curves are flat for wind
speeds between about 4 and 11 m s$^{-1}$. Rough calculations based on the data from this
kestrel and on the available aerobic muscular power (Weis Fogh & Alexander, 1977)
indicate savings in the order of 25–40 % over the range of observed windhovering
speeds. The lower curve in Fig. 7 shows the average power required for this mode of
intermittent flapping and gliding, recalling that this is mainly due to the restoration
phase. Muscular tensions during gliding, adding slightly to the energy required, are
neglected. (Further details of the calculation of the power required for intermittent
windhovering are available from the authors, upon application.)

Obviously, this saving in the average power expenditure is not fully realised in cases
where the non uniformity of the wind precludes the use of gliding for most of the time.
On the other hand, prolonged gliding, and hence greater gains, are possible in up-
draughts. Such gains would encourage the use of gliding-restoration cycles in wind-
hovering whenever possible. In the filmed sequence where 21 % of the time was spent
gliding, the estimated saving in energy is about one quarter of the theoretical
maximum.

### DISCUSSION

Economizing on the cost of locomotion by intermittent movements is a widely used
strategy among flying and swimming animals. For example, two modes of intermit-
tent flight have been described by Rayner (1977): 1. Undulating flight, where birds
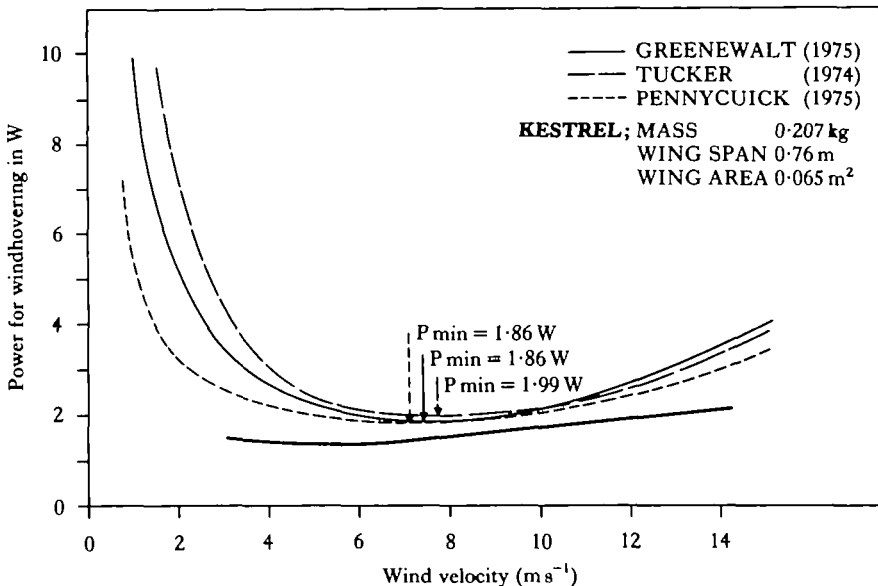glide down and regain height by flapping flight; and 2. Bounding flight, a strategy



Fig. 7. Comparison of three models for calculating power of windhovering as a function of windspeed.

sed by small birds, folding the wings during the unpowered phase in which they lose velocity rather than height. Fish with negative buoyancy can make use of the principle used in undulating flight (Weihs, 1973). Neutrally buoyant fish profitably coast between bouts of active movements because the drag on a straight fish body is much lower than the drag on a swimming fish (Weihs, 1974; Videler & Weihs, 1982). Intermittent gliding by windhovering kestrels is unique among these strategies because the head of the animal remains in a steady position with respect to the ground and moves at wind speed in a direction opposite to the wind. It is an impressive example of precise dynamic station keeping.

We have analysed this flight pattern for one bird for which conditions and morphology were precisely known. It can be anticipated that the frequency of gliding will change with wind velocity. At low wind speeds, where lift is small, gliding may not be possible. At high wind speeds drag will reduce the limit to gliding episodes and extra costs for a compensating speed increase may become prohibitive for true gliding under these circumstances. In hilly countrysides birds may selectively make use of updrafts, and it is known that kestrels' windhovering sites are concentrated on the windward side of Scottish hills (Village, 1982). In such conditions gliding may have a much larger share in the kestrel's hunting flight. In the flat area where our data were collected, intermittent gliding is expected to reduce the cost of windhovering, especially at intermediate ranges of wind speed. The Pennycuick-Tucker-Greenewalt curves predicting minimum costs at $7–8\ \mathrm{m\,s^{-1}}$ flight speed for kestrels, would then become even more markedly U-shaped if we apply them to the cost of windhovering at different wind speeds. It is remarkable that the intermediate range of minimum cost is also the range of wind speeds where average duration of windhovering bouts was maximal (Fig. 3). It also coincides with the range of wind speeds where flight hunting (in hours/day) attains a maximum frequency (Dijkstra, Vuursteen, Daan & Masman, 1982). We suggest that these wind speeds represent an optimum for kestrel flight hunt and that higher and lower wind speeds set energetic limitations to this behaviour, both by increased aerodynamic power output in flapping flight and by reduced chances for intermittent gliding. For analysis of the ecological implications, precise measurements of metabolic costs under different wind speeds are currently being made.

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