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## FIELD MEASUREMENTS OF HANGING FLIGHT AERODYNAMICS IN THE KESTREL *FALCO TINNUNCULUS*

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### Summary

Hunting kestrels were observed to hang, almost without wing-flapping, in fixed positions over a sea dike. The height and position with respect to the dike profile, the wind direction and velocity and the percentage of hunting time without wing beating were recorded in 429 cases.

The vertical wind angle,  $\theta$ , the wind speed and its horizontal direction were measured at 13 heights up to 8.8 m above the windward slope, the top and the leeward slope of the dike under various wind conditions in 225 cases. These wind profile measurements were used to estimate  $\theta$  and wind speed near the hanging birds.

Kestrels hanging more than 90% of the hunting time preferred a position  $6.5 \pm 1.5$  m (s.d.) over the windward slope with sea winds blowing at  $8.7 \pm 1.5$  m s<sup>-1</sup> (s.d.) perpendicular ( $\pm 30^\circ$ ) to the longitudinal dike axis. For these birds angle  $\theta$  was approximately 6–7°.

These angles are larger than expected from aerodynamic models and wind-tunnel measurements. The minimum gliding angle for a kestrel under steady conditions is estimated to be 5°.

Hanging kestrels save two-thirds of the energy used during normal windhovering but have to spend 1.6 times more time to catch the same number of voles.

### Introduction

The metabolic costs of flight in the kestrel are extremely high. Masman and Klaassen (1987) found an expenditure of 14.6 W for directional flight and windhovering in free-living kestrels *Falco tinnunculus* L. using doubly-labelled water techniques. This figure is 16 times the basal metabolic rate (BMR) and it probably explains why this species devotes little time to flight-hunting: from 1.7 h day<sup>-1</sup> during winter to 4.6 h day<sup>-1</sup> for males during the nestling phase of the season. Kestrels economize on hunting costs in a number of ways. Videler *et al.* (1983) showed how approximately one-quarter of the maximum costs during windhovering are saved by alternating flapping flight with short gliding bouts. A more substantial cost reduction is obtained by hunting from a perch (Masman *et al.*

Key words: kestrel, hanging, updraught, aerodynamics, *Falco tinnunculus*.

1988). However, the yield from perching is only 0.3 voles per hour, which is substantially lower than the 6–7 voles per hour caught using windhovering (Masman *et al.* 1989). The same paper presents yield figures for yet another low-cost hunting technique. Kestrels make use of updraughts, in hilly environments (Village, 1983) or over hedgerows and dikes, where they can hang almost motionless with stretched wings in a fixed position with respect to the ground. From this position they scan the ground and detect moving prey to swoop down on. One pair of kestrels yielded on average slightly less than 4 voles per hour by hanging in the updraught over a high sea-dike bordering a polder.

Kestrels, gliding in a fixed position over the ground in an upward wind, fly at aerodynamic equilibrium, which offers an excellent opportunity to study gliding performance. Several studies have used a tilting wind tunnel to create the required wind conditions for this type of gliding flight. Pennycuik (1968) and Biesel *et al.* (1985) tested pigeons (*Columba livia*) under these experimental conditions. Tucker and Parrott (1970) and Tucker and Heine (1990) studied the aerodynamic characteristics of birds of prey (the laggar falcon, *Falco jugger*, and Harris' hawk, *Parabuteo unicinctus*, respectively), gliding at equilibrium in a tilted wind tunnel. Wind tunnels, however, have some serious drawbacks if they are used to measure the performance of living birds. Noise and limited space are the most significant.

Dikes along the sea-shore usually offer relatively undisturbed wind conditions and kestrels frequently hang motionless in the updraughts. We wanted to study gliding performance of kestrels under these conditions and to compare the aerodynamic characteristics with predictions from aerodynamic theory (Pennycuik, 1989; Tucker, 1987; Tucker and Parrott, 1970) and wind-tunnel measurements. We measured wind characteristics over a dike and studied how kestrels use these to save energy.

### Aerodynamic theory of hanging flight

A flight-hunting kestrel keeps its head in a precisely fixed position with respect to the ground (Videler *et al.* 1983). A steady head position during gliding in an upwardly directed wind requires horizontal and vertical equilibrium of forces, with zero velocities in all directions. The ideal case is drawn in Fig. 1, where the wind blows steadily upwards at an angle  $\theta$  to the horizontal. The airflow generates a drag force component  $D$  on the bird in the direction of the wind and an obliquely upward lift force component  $L$  perpendicular to the wind direction. At equilibrium, the sum of these components counteracts the weight (mass times gravitational acceleration)  $W$  in the vertical direction.

Vertical equilibrium of forces demands that:

$$L\cos\theta + D\sin\theta = -W, \quad (1)$$

and horizontal equilibrium that:

$$\begin{aligned} D\cos\theta &= L\sin\theta \\ \text{or } D/L &= \tan\theta. \end{aligned} \quad (2)$$

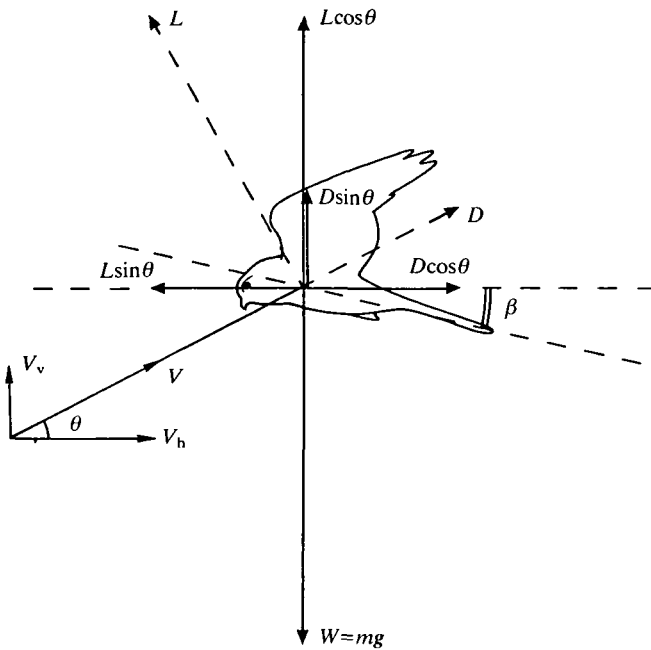


Fig. 1. Forces on a kestrel gliding at equilibrium in an updraught. The upwardly directed wind makes an angle  $\theta$  with the horizontal. The vertical ( $V_v$ ) and horizontal ( $V_h$ ) components of the wind speed  $V$  are indicated. The longitudinal body axis is kept at an angle  $\beta$  to the horizontal.  $L$  is the lift force component,  $D$  is the drag force component,  $W$  is the weight of the bird,  $m$  is its body mass and  $g$  is the acceleration due to gravity.

The lift and drag can easily be calculated once the mass of the bird and the angle  $\theta$  are measured. We used equations 1 and 2 and trigonometry to derive:

$$L = -W \cos \theta$$

$$\text{and } D = -W \sin \theta. \tag{3}$$

Gliding performance calculations are usually directed at calculations of glide polars, i.e. graphs of sinking speed as a function of forward speed, usually both relative to the ground. In our case and in tilting wind tunnels, the vertical component ( $V_v$ ) of the obliquely upward wind velocity ( $V$ ) replaces the sinking speed, and the horizontal component ( $V_h$ ) replaces the forward speed. Since we estimated  $\theta$  and  $V$  for hanging birds and

$$V_v = V \sin \theta$$

$$\text{and } V_h = V \cos \theta, \tag{4}$$

it was most convenient to use the angle  $\theta$  as a function of the wind speed  $V$  instead of the conventional glide polar where  $V_v$  is presented as a function of airspeed  $V$ .

We used the semi-empirical models of Pennycuick (1975, 1989), Tucker and

Parrott (1970) and Tucker (1987) and data from Tucker and Heine (1990) to compare the hanging behaviour of kestrels with predictions for maximum gliding performance and data obtained in tilting wind tunnels.

### Materials and methods

Tilting wind tunnels have the advantage that the two important parameters,  $\theta$  and  $V$ , are directly under the control of the investigator. In the field, the bird decides where it wants to hunt and which position offers suitable conditions for hanging or for a mixture of windhovering and hanging. We had to estimate  $\theta$  and  $V$  near a hanging bird. Therefore, we measured the height and the position of the bird with respect to the dike profile and recorded wind speed and direction simultaneously 1.5 m above the top of the dike at some distance from the bird. Separately we measured profiles of  $\theta$  and  $V$  across the dike for all prevailing wind directions and speeds at 13 heights between 1.5 and 8.8 m. Comparison between the wind conditions during a hanging bout and the wind profile data set provided estimates of  $\theta$  and  $V$  near the hanging bird.

#### *Location and dimensions of the dike*

The study area was a dike in the Lauwersmeer polder in the north-eastern part of the Netherlands (53°20'N; 6°10'E). The area is a sandy plain, separated from the Dutch Waddenzee by a dike in 1969. It was partly turned into dry land. It is now flat and open countryside where kestrels breed in nest boxes. We concentrated our measurements around a stretch of dike about 1 km east of the sea locks of Lauwersoog. The longitudinal axis runs WSW–ENE; the seaward slope faces north. Fig. 2 localizes the position of the dike and gives details of its dimensions. The top is at 8.35 m above average sea level. The slope facing the sea is 14° and that on the landward side is 16°. The slopes and top are covered with grass and offer a suitable habitat for common voles (*Microtus arvalis* L.), the kestrels' main prey items (Masman *et al.* 1988). Winds from the sea reach the dike undisturbed by obstacles. On the polder side there is a road along the foot of the dike, and a few shrubs across the road could cause some turbulence over the windward dike slope during southerly winds.

#### *Measurements of wind parameters*

We constructed a wind meter indicating both the average horizontal and vertical wind direction and the wind velocity ( $V$ ). A cup anemometer was mounted at one end of a 1 m long aluminium rod and a triangular horizontal wind vane at the opposite end. The centre of gravity of this apparatus, about half-way between the anemometer and the vane, was firmly attached to the horizontal shaft of a Sharp GP 1R52 rotary encoder (Sharp Electronics, Osaka, Japan). This encoder was mounted on top of a weathercock, consisting of a vertical aluminium pole fitted with a counterbalanced triangular vertical wind vane. The swivel joint between the weathercock and the earth-bound part of the wind meter as well as the cup

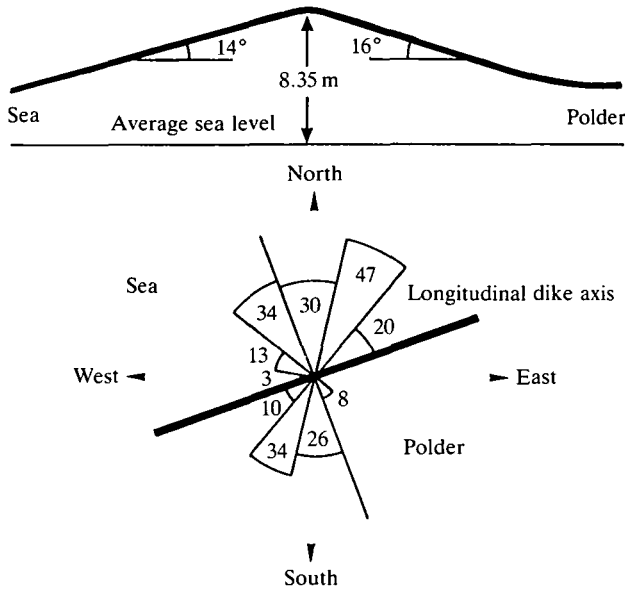


Fig. 2. (A) The dimensions of the sea dike near Lauwersoog (Netherlands) in cross-section. (B) The geographical orientation of the longitudinal dike axis. The horizontal wind directions during 225 wind profile measurements are indicated in the pie chart.

anemometer were originally parts of a VDO wind velocity and direction indicator used in yachting. The vanes were isosceles triangular aluminium plates. The span at the base and height of each triangle were 0.3 m.

The vertical vane of the weathercock rotated the vertical pole and pointed the balancing 1 m long rod, with the anemometer head on it, into the wind. The horizontal vane at the downwind end of the rod adjusted to the vertical angle of the wind, tilting the cup anemometer into the wind direction. The wind speed measured is indicated as  $V$  in Fig. 1.

The angle  $\theta$  between the horizontal and the 1 m rod was measured by the rotary encoder, consisting basically of an infrared light-emitting diode and a photodiode on opposite sides of a rotating disk fixed to a rotating shaft. We used a disk with 360 radial slits. With the rod in the horizontal position, the encoder was set to zero. The tilting rod rotated the shaft and the disk. The encoder counts and displays the number of slits that pass the diodes on rotation, indicating the tilting angle of the rod with a precision of  $1^\circ$ . Fast fluctuations during the measurements in the field made it necessary to take averages of 15 readings sampled every 2 s.

The analogue wind velocity indicator could be read with a precision of  $1 \text{ m s}^{-1}$ . We calibrated the wind velocity meter against pitot-tube manometer readings in a wind tunnel. The horizontal wind direction was read in points of the compass and calculated in degrees relative to the dike axis.

We mounted the wind meter on top of an extensible mast, which was used to vary the height where measurements were taken between 1.4 and 8.8 m. Six stays

supported the mast, which had to be precisely vertical for every measurement. The mast was extended manually, with the use of a ladder for the greatest heights.

We measured 225 wind profiles by taking series of readings of the compass bearing, vertical wind angle and velocity of the wind at 13 heights (1.4, 2.4 and 3.8 m and at increments of 0.5 m up to 8.8 m). These series of measurements were always successively taken at three locations: the windward slope, the top and the leeward slope of the dike. Fig. 2 indicates the horizontal wind direction with respect to the dike during these measurements. We measured predominantly northerly winds. During 64 wind profile measurements, a sea wind blew almost ( $\pm 30^\circ$ ) perpendicular to the dike. Land winds approximately perpendicular to the dike were measured in 34 cases.

#### *Observations of hunting behaviour*

The hunting behaviour of kestrels over the dike was recorded 429 times. In each case the total hunting time, defined as the time spent in one position with respect to the ground, and the percentage of that time spent hanging without oscillatory wing movements were estimated from stopwatch readings. Simultaneously, the position of the bird with respect to the dike profile was assessed. Estimating the height of the bird required special training and experience by the observer. We planted 4 m long measuring poles with 1 m marks at regular intervals along the dike and used the pole nearest to the hanging kestrel as a reference to get a first estimate of the height of the bird. In 60 cases a picture was taken using a camera mounted on a tripod equipped with a spirit level and an indication of the angle of elevation of the optical axis of the lens. The distance to the bird could be read from the calibrated lens after focusing. The kestrel's height above the ground was reconstructed from the distance and angle of elevation. We used a calibrated distance meter instead of the camera in cases where the birds were less than 100 m away. The accuracy of the height measurements decreased with increasing distance between the observer and the bird. However, first estimates and calculated heights were usually close enough to justify a height figure in metres to the nearest integer.

The horizontal direction and speed of the wind at 1.5 m over the top of the dike during each hunting bout were recorded.

## **Results**

### *The conditions preferred by hanging kestrels*

It was our aim to find the optimum conditions for hanging flight by studying the behaviour of the kestrels. We expected that most kestrels would exploit the most favourable wind conditions for prolonged hanging. We therefore scanned our data set to find out if this was the case. Table 1A summarizes the collected data by showing the numbers of kestrels observed hunting over the top and the leeward and windward sides of the dike. On 246 occasions the wind blew from the sea and we recorded 183 hunting bouts with the wind from the land. In more than 75 % of

Table 1. *Numbers of hunting kestrels in relation to position over a dike and wind direction*

Position	Wind directions		
	Sea	Land	All
A Total numbers of observations of dike-hunting kestrels			
Windward slope	166	166	332
Top	39	15	54
Leeward slope	41	2	43
Total	246	183	429
B Subset 1: windhovering kestrels			
Windward slope	3	5	8
Top	1	4	5
Leeward slope	17	2	19
Total	21	11	32
C Subset 2: kestrels hanging more than 90 % of hunting time			
Windward slope	113	25	138
Top	17	1	18
Leeward slope	0	0	0
Total	130	26	156

the 429 observations kestrels hunted over the windward slope; they hunted equally frequently over the seaward and the landward sides. Thirty-two kestrels did not attempt to hang at all. They were windhovering all the time (Table 1B). Seventeen of these did so over the leeward slope at an average height of  $9.1 \pm 2.8$  m (s.d.) against sea winds with an average velocity of  $9.0 \pm 3.4$   $\text{m s}^{-1}$  (s.d.).

In contrast, none of the 156 kestrels that were hanging for more than 90 % of the hunting time (Table 1C) were flying over a leeward slope. A vast majority (113) used the windward slope during sea winds; only 18 were found hanging over the top of the dike. We will focus our attention on the wind conditions and flight altitude in these 113 cases. The horizontal direction of the wind, relative to the longitudinal dike axis, was  $90 \pm 30^\circ$  in 103 of the 113 cases. The wind blew at an angle between  $30$  and  $60^\circ$  onto the dike in the other 10 cases. The average wind speed for the 103 birds was  $8.7 \pm 1.5$   $\text{m s}^{-1}$  (s.d.) and the average height above the slope of the dike was  $6.5 \pm 1.5$  m (s.d.). We now need the wind profile measurements to estimate the vertical wind angle  $\theta$  under these conditions.

*Wind profile measurements*

Before examining the wind profiles above the windward slope during sea winds, we want to present briefly some general results from our 225 measurements of the vertical wind angle. We found large-scale turbulence, indicated by erratic direction and velocity readings, up to 6 m above the lower part of the slope on the



leeward side for horizontal wind directions at angles larger than  $30^\circ$  relative to the longitudinal axis of the dike.

The results of the measurements made 1.4 m above the top provided a positive correlation between the horizontal direction relative to the dike axis ( $\phi$ ) and the vertical angle  $\theta$  (for  $\phi$  between 0 and  $90^\circ$ ):

$$\theta = 1.18 + 0.03\phi \quad (N=142, r=0.37). \quad (5)$$

The angle  $\theta$  varied at that point between 0 and  $8.3^\circ$ , the average value was  $2.9^\circ$ , and we detected a significant negative correlation with the wind speed  $V$  in  $\text{m s}^{-1}$ :

$$\theta = 3.75 - 0.13V \quad (N=142, r=0.22). \quad (6)$$

These results indicate that we can expect the largest values of  $\theta$  when the wind blows at a low velocity perpendicular to the dike.

The kestrels showed a preference for hanging above the windward slope with sea wind blowing at an angle of  $90 \pm 30^\circ$  on to the dike. Measurements taken under these circumstances (Table 2) show a significant negative correlation between  $\theta$  and the height  $H$  above the windward slope in m:

$$\theta = 10 - 0.5H \quad (N=207, r=0.6). \quad (7)$$

The average value of  $\theta$  between 1.4 and 8.8 m was  $7 \pm 1.7^\circ$  (S.D.). The negative correlation between speed and  $\theta$  from equation 6 is only reflected in the averages for the windward slope and the top. The average value of  $V$  over the windward

Table 2. *Measurements of the vertical wind angle  $\theta$  and wind speed  $V$  at 13 heights over the windward slope, the top and the leeward slope of a sea dike*

Height (m)	Windward slope		Top		Leeward slope	
	$\theta$ (degrees)	$V$ ( $\text{m s}^{-1}$ )	$\theta$ (degrees)	$V$ ( $\text{m s}^{-1}$ )	$\theta$ (degrees)	$V$ ( $\text{m s}^{-1}$ )
1.4	$8.6 \pm 1.1$	$5.6 \pm 3.0$	$3.9 \pm 1.9$	$8.6 \pm 0.9$	$3.5 \pm 3.0$	$2.3 \pm 2.2$
2.4	$8.4 \pm 1.1$	$5.6 \pm 3.0$	$3.5 \pm 1.7$	$7.9 \pm 0.4$	$0.8 \pm 1.5$	$4.4 \pm 2.9$
3.8	$8.4 \pm 1.4$	$5.8 \pm 2.8$	$4.8 \pm 2.0$	$8.7 \pm 1.2$	$2.4 \pm 1.9$	$5.2 \pm 2.5$
4.3	$7.9 \pm 1.2$	$5.7 \pm 3.1$	$4.9 \pm 2.4$	$8.8 \pm 1.1$	$3.0 \pm 1.5$	$5.4 \pm 2.2$
4.8	$7.2 \pm 1.2$	$5.7 \pm 3.2$	$5.6 \pm 2.3$	$9.0 \pm 0.5$	$3.2 \pm 1.8$	$5.3 \pm 1.7$
5.3	$7.0 \pm 1.3$	$5.9 \pm 3.2$	$5.0 \pm 2.5$	$8.9 \pm 1.0$	$3.5 \pm 2.4$	$6.4 \pm 2.0$
5.8	$6.8 \pm 1.5$	$5.8 \pm 3.4$	$4.8 \pm 2.0$	$8.8 \pm 0.8$	$3.5 \pm 1.8$	$6.6 \pm 1.9$
6.3	$6.6 \pm 1.5$	$5.9 \pm 3.3$	$4.0 \pm 1.9$	$8.6 \pm 0.9$	$3.4 \pm 2.2$	$7.0 \pm 1.9$
6.8	$6.4 \pm 1.5$	$6.1 \pm 3.2$	$4.5 \pm 1.9$	$8.7 \pm 1.0$	$3.8 \pm 2.2$	$6.7 \pm 2.3$
7.3	$6.0 \pm 1.4$	$6.1 \pm 3.4$	$4.1 \pm 1.8$	$8.8 \pm 0.9$	$3.7 \pm 2.0$	$6.8 \pm 2.2$
7.8	$5.7 \pm 1.5$	$6.2 \pm 3.6$	$3.9 \pm 1.8$	$8.6 \pm 1.0$	$4.0 \pm 1.9$	$7.0 \pm 2.2$
8.3	$5.4 \pm 1.3$	$5.4 \pm 3.1$	$3.0 \pm 0.8$	$8.6 \pm 1.1$	$3.5 \pm 1.0$	$6.7 \pm 2.4$
8.8	$4.4 \pm 1.8$	$5.2 \pm 3.3$	$2.8 \pm 1.3$	$8.5 \pm 1.1$	$3.0 \pm 0.8$	$5.9 \pm 2.6$

Winds are blowing from the sea side, perpendicular ( $\pm 30^\circ$ ) to the longitudinal dike axis. Values are mean (S.D.).

slope was  $5.9 \text{ m s}^{-1}$ , which was  $2.7 \text{ m s}^{-1}$  lower than the average wind speed over the top. The wind speed over the windward slope increased with height up to about 8 m and decreased higher up. This effect was not evident over the top of the dike, where average wind speeds did not change with height. Over the top,  $\theta$  increased with height up to about 5 m and decreased higher up. The data for the leeward slope are more erratic. These are of limited relevance here because kestrels hardly ever used that slope for hanging.

#### *The updraught and the positions of hanging kestrels*

Most of the kestrels hung over the windward slope when sea winds were blowing at approximately right angles to the dike axis. Their average height was 6.5 m above the sloping ground at an average wind speed of  $8.7 \text{ m s}^{-1}$  and the average value of  $\theta$  there was  $6.5^\circ$ . Note that the average wind speed at which these 103 kestrels were hanging more than 90 % of the time is  $2.7 \text{ m s}^{-1}$  higher than the average wind speed measured at that position. The average wind speed at which kestrels were hanging entirely without wing beats was  $10.6 \text{ m s}^{-1}$ ; the average values of  $\theta$  did not differ from the rest of the cases in which kestrels were hanging more than 90 % of the time. These data suggest that the birds prefer values of  $\theta$  between  $6$  and  $7^\circ$  and that higher wind speeds allow them to increase the percentage of time they spend not beating their wings.

### **Discussion**

#### *The wind parameters*

Owing to the boundary layer effect (Prandtl and Tietjens, 1934), the wind speed very close to the ground will be zero and it is expected to increase asymptotically to the free-flow value with increasing height. The thickness of the boundary layer is roughly inversely proportional to the square root of the wind velocity, but the real dimensions are hard to estimate in our case.

The shape of the dike in cross-section will compress the streamlines in a perpendicular steady air flow. According to Bernoulli's theorem, the highest air speed (and lowest pressure) can be expected close to the ground over the top of the dike. The boundary layer effect and the Bernoulli effect counteract each other and a precise match could probably explain the observation of similar wind speeds at different heights above the windward slope and the top of the dike (Table 2).

The largest values of  $\theta$  are expected close to the surface of the dike near to the top over the windward slope. From there we would expect  $\theta$  to decrease gradually with height until the wind is horizontal in the free undisturbed flow. These expectations are met by the values for the windward slope (Table 2): the largest angle is  $8.6^\circ$  at 1.4 m and the smallest is  $4.4^\circ$  at 8.8 m. Equation 7 predicts that the wind should be horizontal at about 20 m above the dike. Near the windward surface the wind will follow the slope with an upward angle of  $14^\circ$ , which means that it decreases by  $5.4^\circ$  over the first 1.4 m. This decrease is steeper than the decrease between 1.4 and 8.8 m, indicating that the angle does not change in a

linear way. For our purpose, however, equation 7 provides an easy to use rule of thumb.

#### *Comparison with tilting wind tunnel results*

Tucker and Parrott (1970) and Tucker and Heine (1990) showed how birds of prey, gliding in a tilted wind tunnel, adjust the lift/drag ratio for different wind speeds by varying their wing span. Both papers use the same drawing of a bird in the gliding position. The longitudinal axis of the animal runs parallel to the direction of the wind (the angle between the longitudinal axis of the bird and the horizontal is equal to the upward wind angle  $\theta$ ). Our Fig. 1 suggests that free-flying kestrels use an additional possibility to control lift and drag forces by changing the angle  $\beta$  between the longitudinal body axis and the horizontal, independently from the wind angle  $\theta$ . Drag forces can reach minimum values if  $\beta = \theta$ .

We also observed that kestrels spread and close their tail during hanging bouts. They obviously use three methods to adjust the lift/drag ratio and the magnitude of these forces while keeping their head in a fixed position in an earth-bound frame of reference. Birds in wind tunnels apparently only use wingspan alterations. This difference is probably directly related to differences in wind conditions. These are steady in a wind tunnel, whereas our kestrels have to deal with unsteady gusty winds in the updraughts.

#### *Aerodynamic models*

A comparison between our data and model predictions is made in Fig. 3, where angle  $\theta$  is shown as a function of wind speed. We calculated three models using data from a female kestrel (Videler *et al.* 1988a,b). The mass of the animal was

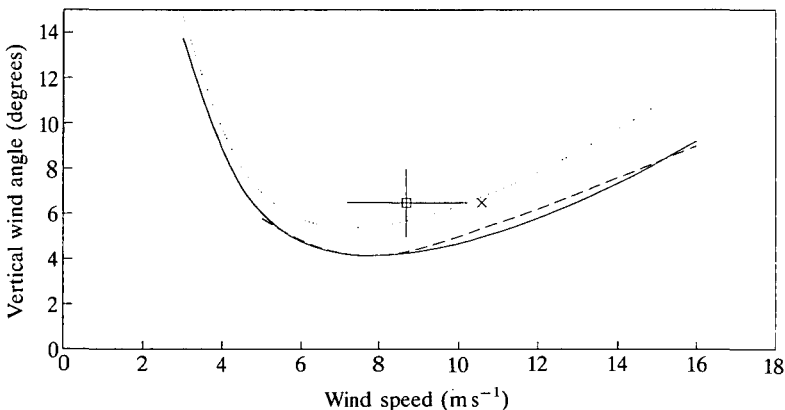


Fig. 3. Theoretical hanging polars, based on Pennycuick (1989) (dashed line), Tucker (1987) (solid line) and Tucker and Parrott (1970) (dotted line) and the actual vertical wind angles  $\theta$  used by kestrels. The square with standard deviations represents the data collected for birds hanging more than 90% of the time and the cross indicates the average value for birds hanging 100% of the time, both over the windward slope while winds blew from the sea.

0.2 kg, with a wing span of 0.72 m and a wing area of 0.0598 m<sup>2</sup>. We assumed an air density of 1.23 kg m<sup>-3</sup>, an induced drag factor of 1.1, a wing profile drag coefficient of 0.389 and a body frontal area of 0.00278 m<sup>2</sup>.

Pennycuick's (1989) model predicts a far better performance than is shown in our measurements. At the relevant range of wind speeds, kestrels should be able to hang motionless with values of  $\theta$  slightly over 4°. However, the average value of  $\theta$  was 6.5°. The angle predicted by the model would allow the kestrel to hang even higher than the height recorded during windhovering over the leeward side. Tucker's (1987) constant span model gives virtually the same results as Pennycuick's model if we use the same variables to calculate  $\theta$ . Tucker and Parrott's (1970) semi-empirical model, evaluated using the same data set and a  $K$  value (the ratio between the parasite drag of the bird and that of a flat plate) of 2.4, provides a better match to our data, although the predicted vertical angles are slightly lower than the actual ones. Our data for 100% hanging fit this model exactly.

Our data set of 103 bouts of more than 90% hanging does not, of course, reflect the best possible performance, mainly because of the unstable wind conditions. Videler *et al.* (1988*a,b*) trained kestrels to fly between two falconers in a windless corridor. At the end of each flight the kestrels glided before landing. Analysis of the gliding kinematics showed that the kestrels were only losing speed, on average from 9.5 to 7.2 m s<sup>-1</sup>, and not height. The maximum  $L/D$  ratio there was 11.7, which would be the equivalent of a gliding angle of 5° if the birds were losing height instead of velocity. Tucker and Heine (1990) flew a 0.7 kg Harris' hawk in a tilted wind tunnel. This bird showed a maximum  $L/D$  ratio of 10.9 or a glide angle of 5.2°, at speeds between 8 and 14.7 m s<sup>-1</sup>. Pennycuick's (1989) model predicts 13.9 as the best glide ratio for a 0.2 kg kestrel at 7.7 m s<sup>-1</sup>. The preferred wind speed for hanging was 1 m s<sup>-1</sup> higher on average and the predicted glide ratio at that speed is 11.5, which is in good agreement with the corridor measurements and probably reflects the best possible performance of kestrels under steady conditions.

Kestrels seem to prefer a fairly narrow range of wind speeds during straight forward flapping flight, windhovering and hanging. The cruising speed of unloaded kestrels in the corridor was slightly over 9 m s<sup>-1</sup> and the preferred range of wind speeds for windhovering was between 5 and 11 m s<sup>-1</sup> (Videler *et al.* 1983). The wind velocities during the hanging sequences varied between 7 and 12 m s<sup>-1</sup> (8.7 m s<sup>-1</sup> on average). The models of Tucker (1974), Pennycuick (1975) and Greenewalt (1975) predict U-shaped relationships between the cost of flapping flight and flight speed. Gliding models predict U-shaped relationships between the vertical wind angle  $\theta$  and the wind speed. The extreme values for flapping flight costs and the extreme values of  $\theta$  required for gliding at the lower and higher ranges of speed (below 5 m s<sup>-1</sup> and over 11 m s<sup>-1</sup>) are probably the reason why kestrels are never observed under these conditions.

#### *How much energy is saved by hanging?*

Masman and Klaassen (1987) assume the metabolic cost of hanging to be 10%

of the cost of windhovering or active flight. This would be 1.46 W if we use their figure for the metabolic cost of flight. A kestrel hanging for more than 90 % of the hunting time would use about 2.8 W and would gain 11.8 W on the expenditure side of the energy balance. The yield per hour, however, is 2 voles less than during windhovering. One hour of windhovering yields about 6.5 voles and the energy required to catch these is 52.5 kJ. This amount of energy would allow a kestrel approximately 5 h of more than 90 % hanging flight with a yield of 20 voles. The time it takes to catch a certain number of voles is 1.6 times longer if the kestrel uses more than 90 % hanging instead of windhovering, but it requires only one-third of the energy.

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