

Optimal flight behavior of soaring migrants: a case study of migrating steppe buzzards, *Buteo buteo vulpinus*

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This article presents tests of the theoretical predictions on optimal soaring and gliding flight of large, diurnal migrants using Pennycuick's program 2 for "bird flight performance." Predictions were compared with 141 observed flight paths of migrating steppe buzzards, *Buteo buteo vulpinus*. Calculations of cross-country speed relative to the air included bird's airspeeds and sinking rates in interthermal gliding and climbing rates in thermal circling. Steppe buzzards adjusted interthermal gliding airspeed according to their actual climbing rate in thermal circling. By optimizing their gliding airspeed, the birds maximized their cross-country performance relative to the air. Despite this general agreement with the model, there was much scatter in the data, for the model neglects horizontal winds and updrafts during the gliding phase. Lower sinking rates due to updrafts during the gliding phases allowed many birds to achieve higher cross-country speeds than predicted. In addition, birds reacted to different wind directions and speeds: in side and opposing winds, the steppe buzzards compensated for wind displacement during soaring and increased their gliding airspeed with decreasing tailwind component. Nevertheless, cross-country speed relative to the ground, which is the important measure for a migratory bird, was still higher under following winds. This study shows that Pennycuick's program 2 provides reliable predictions on optimal soaring and gliding behavior using realistic assumptions and constants in the model, but a great deal of variation around the mean is generated by factors not included in the model. **Key words:** *Buteo buteo vulpinus*, bird flight performance, cross-country speed, flight behavior, gliding flight, soaring flight, steppe buzzard. [*Behav Ecol* 8:288–297 (1997)]

Different flight styles of birds have evolved under strong selective forces constrained by biometrical, ecological, and energetic factors. Active powered flight is the most common style, but larger species use a gliding flight because energy consumption for mechanical power in flapping flight increases steeply with body mass [power at maximum range speed $\propto (\text{body mass})^{7/6}$] (Pennycuick, 1972). For a large raptor like the white-backed vulture (*Cyps africanus*; mean body mass 5450 g; del Hoyo et al., 1994), energy consumption is about 30 times higher in flapping flight than in gliding flight (Pennycuick, 1972). Soaring and gliding require about twice the resting metabolic value in herring gulls (*Larus argentatus*; Baudinette and Schmidt-Nielsen, 1974), which corresponds to 3.1 times the basal metabolic rate (BMR) according to Lustick et al. (1978) and Ellis (1984) and 4 times the BMR according to Lasiewski and Dawson (1967). Because mass-specific BMR decreases with increasing body mass [nonpasseriformes: $\log(\text{body mass}) = \log 78.3 + 0.723 \log \text{kJ} \cdot \text{day}^{-1}$; Lasiewski and Dawson, 1967], soaring and gliding flight becomes more economical with increasing body mass. The switch from flapping to soaring–gliding flight is profitable at a relatively low body mass: assuming an energy consumption of 4 times BMR in gliding flight and a climbing rate in thermals of 1 m/s, soaring and gliding become less expensive than flapping at about 132 g for a time-minimizing bird (i.e., when flapping it flies with maximum range speed; when soaring–gliding it maximizes cross-country speed) (Hedenström, 1993).

Larger raptors migrate mainly by soaring and gliding. Flight altitude is potential energy that birds can transform into distance by gliding. Thermal convection is the most important

source of potential energy (Kerlinger, 1989), and birds usually gain altitude by circling in these thermals. Energy consumption (kJ/h) in soaring–gliding flight is independent of flight speed and increases linearly with flight duration. To minimize energy consumption per distance, a soaring and gliding migrant should therefore maximize its cross-country speed by adjusting its gliding airspeed to the actual climbing rate in a thermal. Steppe buzzards, *Buteo buteo vulpinus* (Spaar, 1995), and steppe eagles, *Aquila nipalensis* (Spaar and Bruderer, 1996), react to different thermal conditions: they increase their interthermal gliding airspeed when circling in strong thermal convections. Both steppe buzzards and steppe eagles seem to be able to estimate their own climbing rate while soaring and to adjust a thermal-dependent gliding airspeed. By increasing their airspeed under favorable thermal conditions, they reach higher cross-country speeds. Are they therefore maximizing cross-country speed and minimizing time consumption by optimizing airspeed? Flight mechanical theory by Pennycuick (1989) predicts optimal gliding airspeed depending on the actual climbing rate if birds maximize their cross-country speed. We compare these predictions to optimal flight behavior with the empirical flight behavior of migrating steppe buzzards.

Wind is also an important factor for soaring migrants. In opposing winds, birds soaring in thermals drift against the migratory direction, and gliding groundspeeds are reduced. In following winds, birds profit while circling and gliding from an additional progress in the migratory direction. Do birds react to different wind conditions in soaring and gliding flight? According to flight theory, optimal soaring and gliding behavior is independent of wind direction (Pennycuick, 1989): soaring birds optimize their flight performance in relation to the air by maximizing cross-country speed in relation to the air; wind is considered as factor linearly reducing or enhancing cross-country speed in relation to the ground.

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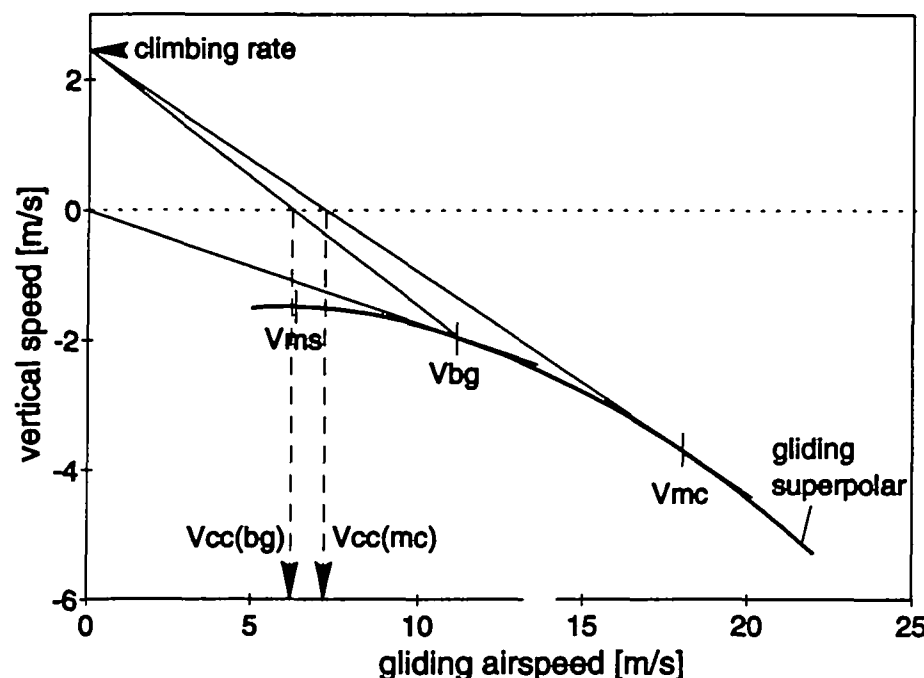


Figure 1

Theoretical relationship between the gliding superpolar and the resulting cross-country speed when adopting different airspeeds (after Pennycuik, 1989). Gliding superpolar: relation between airspeed and sinking rate while gliding. V_{ms} : gliding airspeed with the minimum sinking rate. V_{bg} : gliding airspeed with the best gliding to sinking ratio and, thus, with the smallest gliding angle (tangent from 0 vertical speed to the superpolar). V_{mc} : optimal airspeed if the cross-country speed is maximized; it depends on the actual climbing rate in thermal circling (tangent from climbing rate to the superpolar). $V_{cc(bg)}$: cross-country speed if gliding with V_{bg} between thermals. $V_{cc(mc)}$: maximum cross-country speed if gliding with V_{mc} between thermals.

Thus, if soaring birds behave according to the theory, they should react similarly regardless of different winds. This study analyzes the flight performance of steppe buzzards under differing wind conditions.

MATERIALS AND METHODS

Theory on optimal soaring and gliding flight after Pennycuik (1989)

The gliding performance of a bird depends on biometric characteristics (body mass, wing span, wing area, and aspect ratio of the wings) and on physical constraints like gravity and air density. Gliding performance is described by the "gliding superpolar," which gives the relationship between the bird's airspeed and the sinking rate while gliding (Figure 1). At the airspeed V_{ms} (ms, minimum sink), a bird glides with the minimum sinking rate. By flexing the wings, reducing both wing span and area, it increases airspeed and sinking rate while gliding. The bird reaches the best ratio between airspeed and sinking rate at the airspeed V_{bg} (bg, best glide), and thus covers the maximum distance per unit height. V_{bg} is defined by a tangent from zero vertical speed at the ordinate to the gliding superpolar. If birds maximize their cross-country speed, they have to adjust their gliding airspeed to the actual thermal conditions and glide with the optimal airspeed V_{mc} (mc, maximum cross-country speed). V_{mc} is found by drawing a tangent from the point of the actual climbing rate in thermal circling on the ordinate to the gliding superpolar. Corresponding cross-country speeds are at the intersection of the tangent and the line of zero vertical speed. The cross-country speed, $V_{cc(bg)}$, is achieved when gliding with V_{bg} between thermals; the maximum cross-country speed, $V_{cc(mc)}$, accordingly when gliding with V_{mc} .

Observation sites and recording of data

Raptor migration was studied in southern Israel at two observation sites: in the Negev Highlands near Sede Boqer, and in the Arava Valley near Hazeva. In the autumn of 1991, obser-

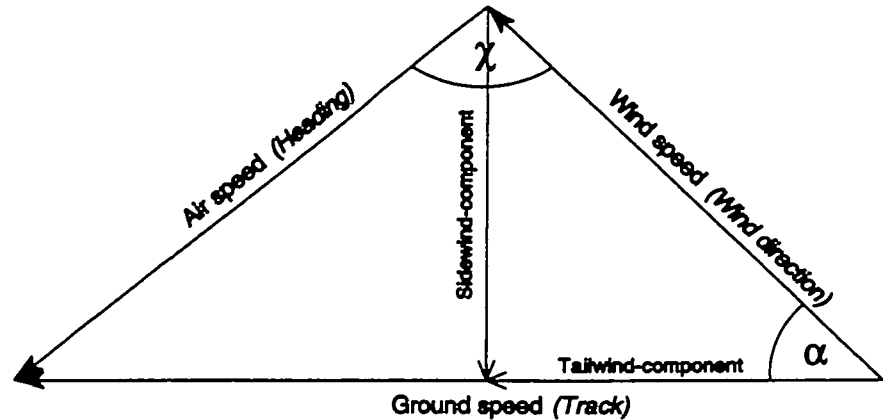
vations were carried out from 10 September to 31 October at both sites, mainly during the morning until 1100 h and in the late afternoon from 1600 h onward. In spring 1992, observations took place from 1 March to 20 May in the Arava Valley, and from 1 to 30 April in the Negev Highlands. In autumn 1992, observations were restricted to the Arava Valley, from 10 August to 18 September. Most flight paths analyzed in this paper were from the spring.

"Superfledermaus" radars were used. Bird tracking is possible up to distances of about 8 km in a half sphere around the radar for a bird of the size of a steppe buzzard. Each second the radar transmitted the position of the bird (distance ± 10 m; azimuth and elevation $\pm 0.06^\circ$; Bruderer et al., 1995) and transformed the polar coordinates into Cartesian x, y, and z coordinates which were recorded in a computer; the track was visualized on the computer screen. Simultaneously, an experienced observer identified the tracked target through a 12.4 \times telescope mounted parallel to the radar beam. Each bird was observed visually during its tracking time to obtain information on wing beats, flock sizes, and flock compositions. Pilot balloons, released and tracked every 4 h, gave information on wind speed and direction at all flight levels. For further information see Bruderer et al. (1995).

Analysis of tracks

The raptor tracks were subdivided into intervals of 10 s. Complete gliding and soaring phases were marked interactively at the computer screen. A complete soaring phase was defined from the end of a gliding phase to the start of the next when the bird was circling in a thermal. At the end of thermal phases, when the birds started gliding, they often had positive vertical speeds, gliding slowly for several s until they left the updraft zone. The situation before they started circling in the thermal was similar. We excluded these parts of the tracks when calculating vertical and horizontal speeds. Gliding direction is considered the preferred migratory direction. Statistics are based on Sokal and Rohlf (1981) and Sachs (1984), and circular statistics are based on Batschelet (1981).

Figure 2
Calculation of gliding airspeed from gliding groundspeed and wind by Equation 1 (see text). Correspondingly, cross-country speed in relation to the ground can be calculated by Equation 5.



Calculation of gliding airspeeds and cross-country speeds relative to air and ground

We calculated airspeed while gliding by subtracting the wind vector from the track vector by the cosine law (Figure 2):

$$V_a = \sqrt{V_g^2 + V_w^2 - 2 \cdot V_g \cdot V_w \cdot \cos \alpha}, \quad (1)$$

where V_g is the gliding groundspeed, V_w is the windspeed, and α is the angle between track (i.e., gliding) and wind direction. Model and variables for calculating the cross-country speed relative to the air (V_{cra}) are explained in Figure 3: without any wind influence, cross-country speed relative to the air can be calculated as follows:

$$V_{cra} = \frac{t_g \cdot V_g}{t_g + t_s}, \quad (2)$$

where V_g is the gliding airspeed, t_g is the duration of interthermal gliding, and t_s is the duration of thermal circling. If the height differences (Δh) in thermal circling and interthermal gliding are equal, the following equation is valid:

$$t_s = \frac{t_g \cdot V_g}{V_s}, \quad (3)$$

where V_s is the climbing rate in thermal circling and V_g is the sinking rate in interthermal gliding. By substituting t_s in Equation 2, the final formula for the cross-country speed relative to the air is obtained:

$$V_{cra} = \frac{V_g \cdot V_s}{V_s + V_g}. \quad (4)$$

This equation contains flight parameters that can be mea-

sured with the tracking radar. These flight parameters allow a reliable calculation of the cross-country speeds relative to the air. Cross-country speed relative to the ground (V_{crg}) is calculated from V_{cra} and the wind vector as follows (Figure 2):

$$V_{crg} = \sqrt{V_a^2 + V_w^2 - 2 \cdot V_a \cdot V_w \cdot \cos \chi} \quad (5)$$

V_{crg} is at its maximum where V_{cra} is maximal. Therefore, if birds maximize cross-country speed according to flight theory, gliding airspeeds should be independent of horizontal wind. Tailwind component, T_{cw} , and sidewind component, S_{cw} , in relation to the gliding (track) direction are calculated by:

$$T_{cw} = V_w \cdot \cos \alpha \quad (6)$$

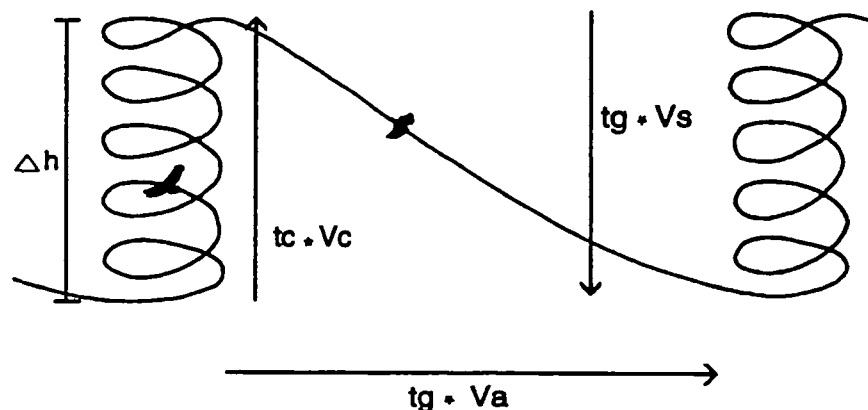
and

$$S_{cw} = V_w \cdot \sin \alpha. \quad (7)$$

Biometric data

Body mass, wing span, and wing area (or at least aspect ratio) are necessary to calculate the theoretical flight performance of a bird with program 2 (version 1.1) of Pennycuik (1989). Because no measurements of steppe buzzards were made for this study, biometric data of Mendelsohn et al. (1989) and Gorney and Yom-Tov (1994) were applied. Steppe buzzards caught in southern Israel at Eilat showed the following body masses: adults 579 ± 85 g ($n = 420$), immatures 529 ± 67 g ($n = 973$) (Gorney and Yom-Tov, 1994). Steppe buzzards measured in South Africa during the nonbreeding season had an average wing span of 118.8 ± 4.7 cm and an average wing area

Figure 3
Calculation of the cross-country speed relative to the air from measured flight parameters. V_s , climbing rate in thermal circling; V_g , gliding airspeed; V_s , sinking rate while gliding; t_s , soaring time; t_g , gliding time; α , gliding angle relative to the air; V_a cross-country speed.



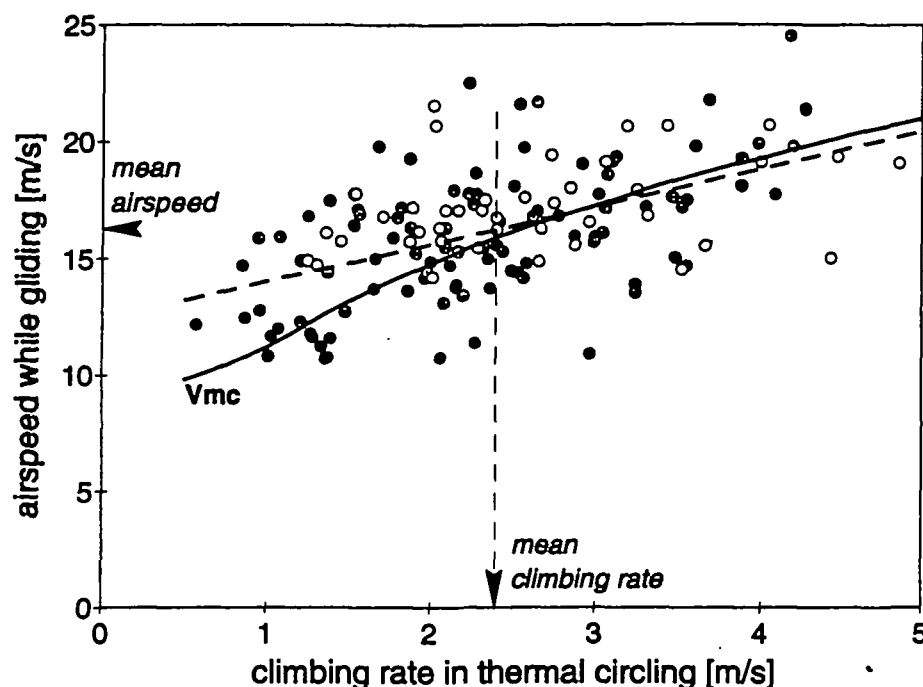


Figure 4
Climbing rate in thermal circling versus gliding airspeed. Each point represents one bird. The predicted line of optimal airspeed when maximizing cross-country speed (V_{mc} ; solid line) and the regression line of the observed data ($y = 2.41x + 12.13$, $n = 141$, $r = .62$, $p < .0001$; dashed line) are shown. Following winds (filled points): angle between gliding and wind direction is $0 \pm 60^\circ$. Side winds (shaded points): angle between gliding and wind direction is $90 \pm 29^\circ$. Opposing winds (open points): angle between gliding and wind direction is $180 \pm 60^\circ$. The solid line in the diagram indicates the predicted optimal airspeed V_{mc} for an average migrating steppe buzzard after Pennycuick (1989). The arrows indicate the means.

(two wings without body-part area) of $1872 \pm 197 \text{ cm}^2$ ($n = 17$) (Mendelsohn et al., 1989). However, for the calculation of the Pennycuick model, the body-part area has to be added to the area of the wings. The estimated body-part area after drawings of steppe buzzards in Porter et al. (1981) is about $11 \times 18 \text{ cm} \sim 200 \text{ cm}^2$. Thus, the wing-area inclusive body part of an average steppe buzzard is about 2070 cm^2 . The majority of the steppe buzzards returning from South Africa to their Palearctic breeding areas cross the Middle East (Shirihai and Christie, 1992). Therefore, the biometric measurements of wing span and wing area from South Africa should also be valid for Israel. The following values were entered in the flight calculation program of Pennycuick (1989) (see also Appendix): body mass 560 g, wing span 1.19 m, and wing area 2070 cm^2 .

RESULTS

Comparison between model and empirical data

Interthermal gliding airspeed was correlated with the climbing rate in thermal circling ($n = 141$, $r = .62$, $p < .0001$; Figure 4). The individual values are distributed along the predicted line of optimal airspeed, V_{mc} for an average steppe buzzard (see Materials and Methods) when maximizing cross-country speed. Thus, the steppe buzzards adjusted their gliding airspeed according to the climbing rate in thermal circling. Mean airspeed while gliding for all birds was $16.33 \pm 2.74 \text{ m/s}$ ($n = 141$), the mean sinking rate is $-1.70 \pm 0.70 \text{ m/s}$, and the mean climbing rate is $2.38 \pm 0.95 \text{ m/s}$.

In Figure 5 the cross-country speed is estimated by the graphical model according to Figure 1. The comparison between sinking rate in interthermal gliding and the theoretical gliding superpolar for an average steppe buzzard shows that the empirical values are scattered around the predicted gliding superpolar (Figure 5). The regression line of the observed data [expressed in a linear relationship: $-(\log y = 0.044x - 0.524)$, $n = 141$, $r = .63$, $p < .0001$] and predicted gliding superpolar [approximated: $-(\log y = 0.063x - 0.733)$] differed in slope and y-intercept (test for equality of slopes and

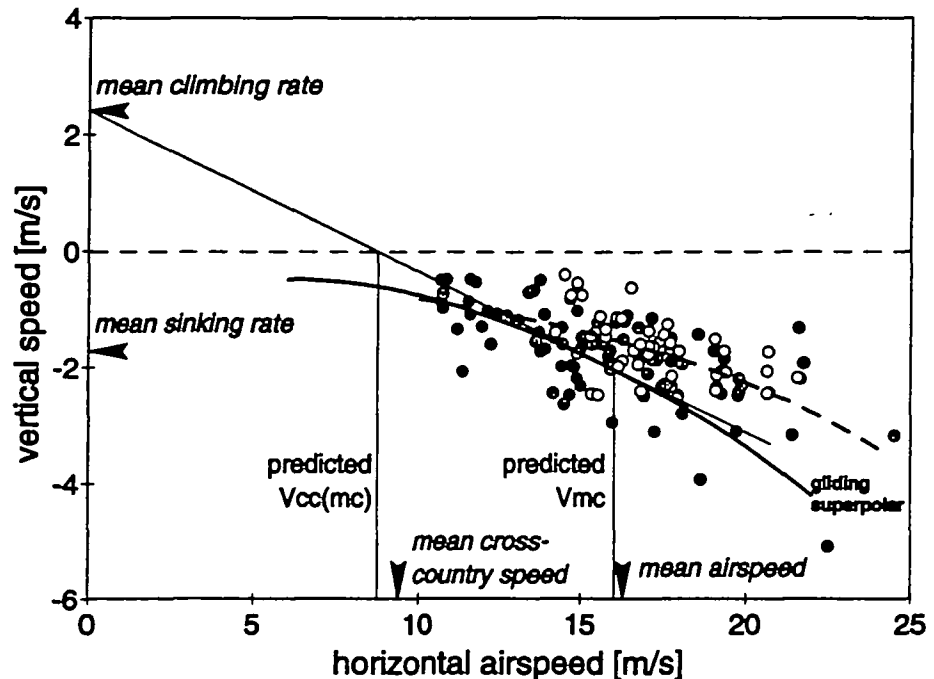
y-intercepts of a estimated and a observed regression line according to Sachs, 1984; Student distribution: slope, $t = 4.08$, $df = 139$, $p < .0001$; y-intercept, $t = 2.69$, $df = 139$, $p < .01$). The low sinking rates at high airspeeds in interthermal gliding indicate that the birds were gliding partially through updraft zones that reduced the overall sinking rate. Both mean interthermal gliding airspeed and cross-country speed relative to the air of the steppe buzzards were similar to the model prediction.

Figure 6 shows the relation between climbing rate in thermal circling and cross-country speed relative to the air for each bird according to Equation 4. If the birds glide with the best glide-to-sink ratio (i.e., they do not adopt their interthermal gliding airspeed according to the climbing rate), they reach the cross-country speed $V_{cst, \text{best}}$. The line of $V_{cst, \text{best}}$ is the predicted maximum cross-country speed reached by an average steppe buzzard if adopting an optimal airspeed V_{mc} according to the actual climbing rate in thermal circling. The scatter of the empirical values and the predicted line of maximum cross-country speed are in good agreement (Figure 6). The steppe buzzards maximized their cross-country performance. The regression line of the observed data (expressed in a linear relationship: $\log y = 0.47 \cdot \log x + 0.80$, $n = 141$, $r = .80$, $p < .0001$) and the predicted line of maximum cross-country speed $V_{cst, \text{best}}$ (approximated: $\log y = 0.46 \cdot \log x + 0.76$) are not different in slope (Student distribution; slope, $t = 0.56$, $df = 139$, ns), but have different y-intercepts ($t = 2.98$, $df = 139$, $p < .01$). Thus, steppe buzzards reached higher maximum cross-country speeds than predicted by the model. The predicted line of cross-country speed $V_{cst, \text{best}}$ when gliding with the best glide to sink ratio (approximated: $\log y = 0.24 \cdot \log x + 0.71$) and the observed data differ in both slope and y-intercept (Student distribution: slope, $t = 7.91$, $df = 139$, $p < .0001$; y-intercept, $t = 7.77$, $df = 139$, $p < .0001$).

Influence of wind

Gliding birds compensated for lateral drift and turned their heading into the wind (Figure 7). In following winds, the

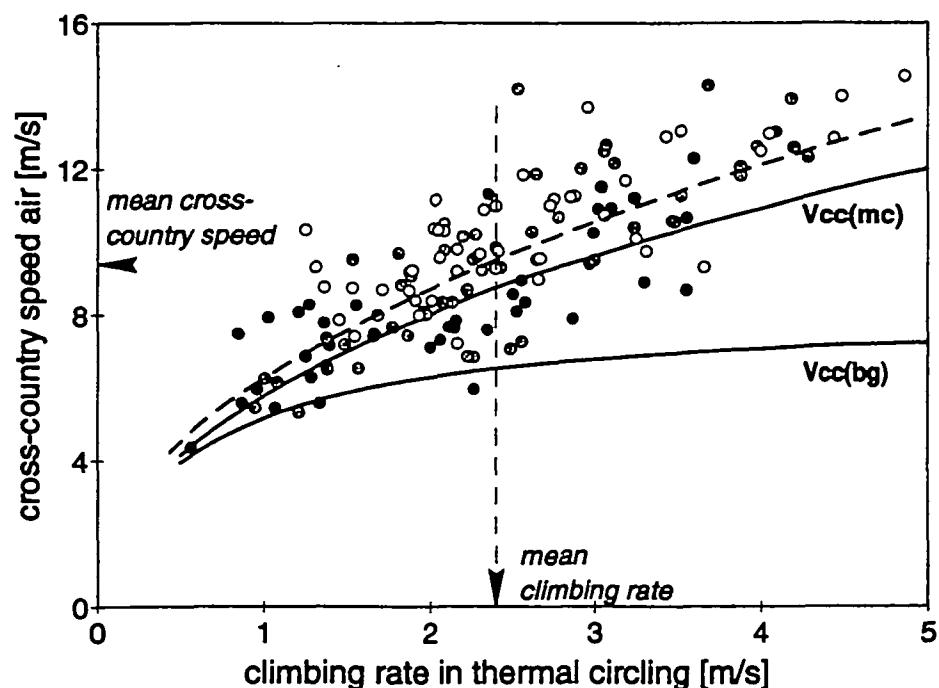
Figure 5
Graphical model to estimate cross-country speed after Pennycuik (1989). Each point represents the mean sinking rate and the mean gliding airspeed of one bird. (Filled points) following winds; (shaded points) side winds; (open points) opposing winds (for definition see Figure 4). The gliding superpolar (i.e., the relationship between gliding and sinking) is calculated for an average migrating steppe buzzard in southern Israel (see text). Arrows indicate the means of the field data.



track directions of the gliding phases were closer to the wind directions than under other wind conditions. It seems that birds tried to keep the favorable winds from behind with little respect to gliding direction, as the directions of this group were more easterly than average. In opposing winds, they turned their headings into the wind, and gliding directions were concentrated to north-northeast. Mean track direction (Watson-Williams test: $F_{1,70} = 7.00$, $p < .05$) as well as the

scatter of the headings (Mann-Whitney U test: $z = 2.09$, $p < .05$) differed significantly between following and opposing winds. Furthermore, in following winds the birds chose a different mean heading direction than birds in sidewinds (Watson-Williams test: $F_{1,90} = 5.05$, $p < .05$). Table 1 shows the flight parameters of the steppe buzzards in following, side, and opposing winds; they are compared with both GT2 test and a nonparametric analysis of variance after Kruskal-Wallis

Figure 6
Climbing rate in thermal circling versus cross-country speed relative to the air. Each point represents the mean climbing rate in thermal circling and the cross-country speed air of one bird. (Filled points) following winds; (shaded points) side winds; (open points) opposing winds (for definitions see Figure 4). Solid lines show the predictions of the Pennycuik model (1989) for an average migrating steppe buzzard (see text): If the birds glide with the best gliding-to-sinking ratio, they reach the cross-country speed, $V_{cc(bg)}$ (expressed in a logarithmic term: $\log y = 0.24 \cdot \log x + 0.71$). If they adjust an optimal gliding airspeed according to the actual climbing rate, they reach the maximum cross-country speed, $V_{cc(mc)}$ (expressed in a logarithmic term: $\log y = 0.46 \cdot \log x + 0.76$). The dashed line corresponds to the logarithmic regression line of the field data ($\log y = 0.47 \cdot \log x + 0.80$, $n = 141$, $r = .80$, $p < .0001$).



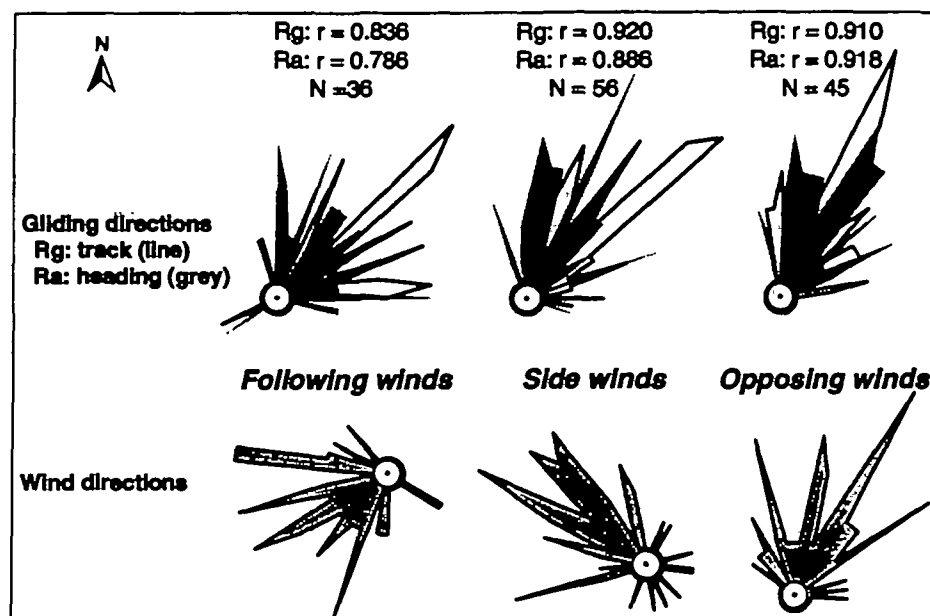


Figure 7
Percentual distribution of gliding and wind directions of the steppe buzzards migrating under different wind conditions; migratory birds in spring only (for definition see Figure 4). Track direction corresponds to the gliding direction over ground and heading direction to the orientation of the bird's body axis.

in Table 2. The climbing rates in thermals were significantly higher under both side and opposing winds than in following winds, indicating that under side and opposing winds, soaring conditions were generally better. A bird's airspeed while gliding was negatively correlated with the tailwind component ($y = 16.15 \cdot 0.97^x$, $n = 141$, $r = -0.55$, $p < .01$; Figure 8), but no significant correlation existed between airspeed and side-wind component ($n = 141$, $r = .04$, ns). The birds reduced their gliding airspeed in following winds and increased airspeeds in opposing winds. Consequently, these higher gliding airspeeds and higher climbing rates in thermals resulted in higher cross-country speeds in relation to the air in side and opposing winds (Tables 1 and 2). On the other hand, cross-country speeds in relation to the ground were highest in following wind situations and differed significantly between the three wind situations (Tables 1 and 2). Mean flight altitude of all birds was 475 ± 280 m above ground and was similar for the three groups.

Assuming that the soaring bird and the upcurrent airstream drift have the same velocity as the wind, soaring birds com-

pensated for the wind drift in side and opposing winds. In side winds, the horizontal displacement of the bird was on average 0.7 m/s below the wind speed (bird's horizontal speed 3.9 ± 2.4 m/s, wind speed 4.6 ± 2.2 m/s; paired t test, $df = 56$, $t = 2.38$, $p < .025$). Similarly, birds soaring under opposing winds (i.e., when thermals are drifted against the migratory direction) were on average 0.6 m/s slower than the windspeed (bird's horizontal speed 2.9 ± 1.9 m/s, wind speed 3.5 ± 1.6 m/s; paired t test, $df = 44$, $t = 2.1$, $p < .05$). In contrast, in following winds the birds' horizontal displacement and wind speed were of the same order (bird's horizontal speed 4.2 ± 2.6 m/s, wind speed 4.4 ± 2.7 m/s; paired t test, $df = 38$, $t = .98$, ns).

DISCUSSION

Theoretical predictions and empirical values

Theoretical predictions for an optimal soaring-gliding strategy were compared with a reliable set of data. The results

Table 1
Flight parameters in different wind situations (mean \pm SD)

Flight parameter	Following wind $0 \pm 60^\circ$ ($n = 39$)	Side wind $90 \pm 29^\circ$ ($n = 57$)	Opposing wind $180 \pm 60^\circ$ ($n = 45$)
Cross-country speed relative to the ground (m/s)	11.4 ± 2.5	9.7 ± 2.1	7.7 ± 2.0
Cross-country speed relative to the air (m/s)	8.0 ± 1.7	9.7 ± 2.3	10.4 ± 1.8
Climbing rate in thermal circling (m/s)	2.0 ± 0.9	2.5 ± 0.9	2.5 ± 0.9
Gliding groundspeed (m/s)	17.3 ± 2.5	16.4 ± 2.7	14.5 ± 2.1
Gliding airspeed (m/s)	14.3 ± 2.5	17.0 ± 2.8	17.2 ± 1.9
Gliding distance relative to the ground (m)	2435 ± 1300	2470 ± 1150	2140 ± 1055
Gliding distance relative to the air (m)	2025 ± 1185	2565 ± 1210	2495 ± 1140
Sinking rate while gliding (m/s)	-1.6 ± 0.8	-1.9 ± 0.7	-1.6 ± 0.6
Gliding angle relative to the ground ($^\circ$)	-5.1 ± 2.1	-6.5 ± 2.1	-6.5 ± 1.9
Gliding angle relative to the air ($^\circ$)	-6.1 ± 2.2	-6.2 ± 1.9	-5.4 ± 1.7
Mean flight altitude above ground (m)	495 ± 325	465 ± 260	465 ± 270
Wind speed (m/s)	4.5 ± 2.8	4.6 ± 2.2	3.3 ± 1.7

Following winds: angle between gliding and wind direction is $0 \pm 60^\circ$. Side winds: angle between gliding and wind direction is $90 \pm 29^\circ$. Opposing winds: angle between gliding and wind direction is $180 \pm 60^\circ$.

Table 2

Comparison of flight parameters in different wind situations (values from Table 1)

Flight parameter	GT2 test			Kruskal-Wallis analysis of variance
	Following wind/side wind	Following wind/opposing wind	Side wind/opposing wind	Following wind/side wind/opposing wind
Cross-country speed relative to the ground	**	**	**	***
Cross-country speed relative to the air	**	**	ns	***
Climbing rate in thermal circling	*	*	ns	*
Gliding groundspeed	ns	**	**	***
Gliding airspeed	**	**	ns	***
Gliding distance relative to the ground	ns	ns	ns	ns
Gliding distance relative to the air	ns	ns	ns	*
Sinking rate while gliding	ns	ns	ns	ns
Gliding angle relative to the ground	**	**	ns	**
Gliding angle relative to the air	ns	ns	ns	ns
Mean flight altitude	ns	ns	ns	ns
Wind speed	ns	ns	ns	*

Group differences tested by GT2 test and by Kruskal-Wallis nonparametric analysis of variance.

* $p < .05$; ** $p < .01$; *** $p < .001$.

show that steppe buzzards maximize their cross-country performance in soaring-gliding flight. According to the model, they adopted an optimal interthermal gliding airspeed, V_{opt} , according to the climbing rate in thermal circling, and thus reached maximum cross-country speed V_{opt} in relation to the air. There is considerable scatter around the predicted curves. Some variation had to be expected, since the theoretical curves are calculated for a steppe buzzard with average body characteristics. However, when calculating the flight performance for steppe buzzards of different body mass, wing span, and area (i.e., accounting for the natural variation in body characteristics; Gorney and Yom-Tov, 1994) according to Pennycuik, flight characteristics such as gliding superpolar, V_{opt} , and V_{opt} are similar. The following facts might explain the additional variation in the measured flight parameters: first, the comparison of the theoretical gliding superpolar and the actual gliding airspeeds and sinking rates revealed that the birds often had lower sinking rates than predicted. There are two possible reasons for this: either the gliding steppe buzzards had a better gliding performance than predicted, probably because they can reach high airspeeds by flexing the wings to a more minor extent than the model predicts (see "span factor" in Appendix), or, more likely, they did not glide through still air but often crossed zones with rising air. In Israel, this was also observed in steppe eagles, which are able to soar in a straight line gliding for several kilometers (Spaar and Bruderer, 1996). Gliding through rising air might be also the reason steppe buzzards reached higher maximum cross-country speeds than the model predicted (Figure 6).

Second, wind direction and wind speed were measured every 4 h at all flight levels; although winds were quite stable at the observation sites (Spaar R, Bruderer B, unpublished data), their short-term changes may explain some of the additional variation when calculating airspeeds by subtracting the wind vector from the track vector. This would, however, only increase scatter and not bias the data systematically.

Third, birds probably never adopt a certain behavior perfectly. Flight behavior during migration is only one of several selective forces influencing flight performance. A soaring bird that reacts to environmental conditions has to recognize and estimate the climbing rate or wind direction and wind speed. These estimations will guide the flight behavior such as the adjustment of an adequate airspeed or the direction of mi-

gration. Gliding behavior may also deviate strongly from optimality if a bird is searching for a roosting site or deciding whether to join other soaring birds in a good thermal. The assumption of the model about equal height differences in thermal circling and interthermal gliding is often not true, it seems that birds catch good thermals whenever they appear. However, birds migrating over long distances use a certain height band (Leshem and Yom-Tov, 1996), which is comparable to equal height differences.

Influence of wind

The steppe buzzards reacted to different wind situations: they reduced their gliding airspeeds in following winds. Airspeeds were about 3 m/s lower than in side or opposing winds. Nevertheless, gliding groundspeeds were still higher in following winds. Climbing rates were about 0.5 m/s lower in following winds. If adjusting optimal airspeeds according to the theory, average gliding airspeed should be only 1.4 m/s lower than in side and opposing winds. Why did the birds lower their airspeeds in following winds? One reason is that by gliding slower than V_{opt} (airspeed between V_{opt} and V_{opt}), birds reduce their gliding angles in relation to the ground (Table 2) and therefore cover longer distances over ground per unit height and lower the risk of not finding a good thermal. The results showed that the soaring conditions were worse in following winds than in side and opposing winds, but the flight altitudes were similar under the different wind situations. This may enhance the chance of finding suitable thermals under the weaker thermal conditions in following winds. Despite the lower climbing rates and gliding airspeeds, the resulting cross-country speed in relation to the ground was still higher in following winds than in side and opposing winds. A second possible reason is that the birds tended to achieve a certain groundspeed level, similar to passerines, which enhance airspeed in following winds and decrease airspeed in opposing winds (Liechti, 1992).

In thermal updrafts, circling birds reduced the wind drift in side and opposing winds by 0.6–0.7 m/s (Figure 8). They compensated for the negative wind component in the direction of migration. Combined with the higher climbing rates in thermal circling and the higher interthermal airspeeds, they reached significantly higher cross-country speeds in re-

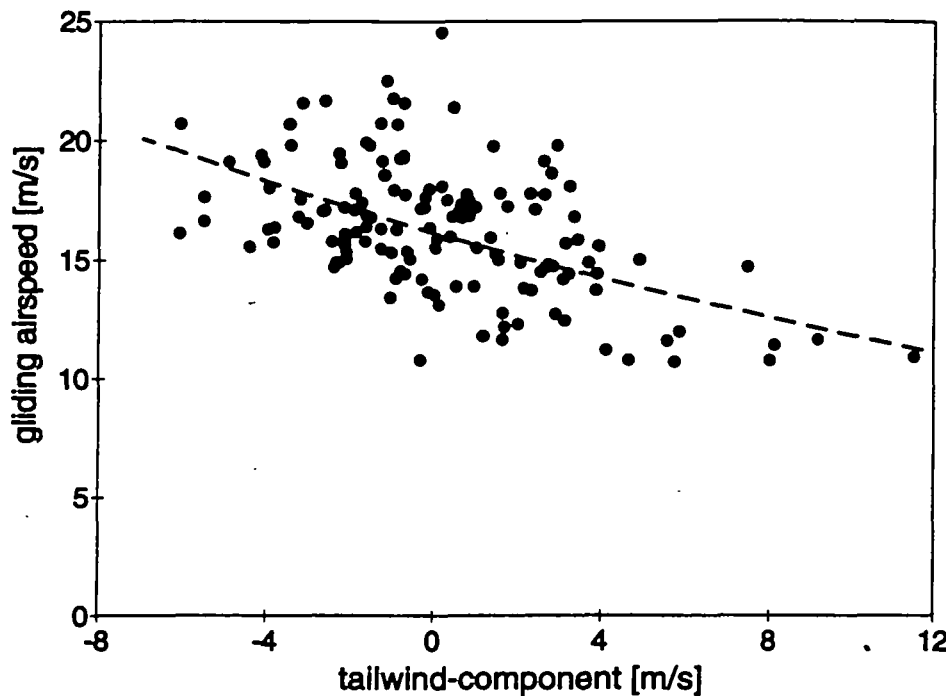


Figure 8
Gliding airspeed versus tailwind component. Each point represents the mean gliding airspeed of one bird. Tailwind component is calculated according to Equation 6. (Regression line: $y = 16.15 - 0.97x$, $n = 141$, $r = -0.55$, $p < .01$).

lation to the air. For steppe buzzards, the average soaring time in complete thermals was about 90 s (Spaar, 1995) and thus, by reducing the wind drift of 0.6–0.7 m/s, the horizontal compensation amounts to about 60 m. This indicates that the dimensions of thermals were such that soaring birds were able to move horizontally within the thermal to a certain extent, perhaps even accepting suboptimal climbing rates.

Flight theory after Pennycuik (1989)

The comparison of the theory with the field data showed a reasonable fit but wide scatter. The flight performance program of Pennycuik (1989) provides a useful method for calculating the gliding and cross-country performance for soaring and gliding birds as far as the assumptions are fulfilled. However, the model has some limitations: the calculations are based on the assumption that the birds gain altitude exclusively by soaring (circling) in thermals and that there is no vertical movement of the air during the interthermal glides. Neither assumption is necessarily valid, steppe buzzards often glided through vertically moving air masses (see above). Furthermore, climbing phases do not start or end with the bird's soaring (circling) in thermals. When entering or leaving a thermal, birds were often observed to climb by straight gliding for several s before they started soaring. This occurred predominantly in following winds, and birds reduced their airspeeds. Thus, during a part of their straight gliding, the birds have reduced sinking rates or even positive vertical speeds, which enhances the cross-country speed considerably. In this study the gliding airspeeds and sinking rates were calculated without these transitional parts of positive vertical speeds at the start and the end of the thermals. If transition parts before and after circling (cutting the phases when vertical speed became higher than 1 m/s) are included when calculating the gliding airspeeds, mean airspeed of the steppe buzzards is about 1.1 m/s lower and climbing rate 0.4 m/s lower than in this study (airspeed 15.2 m/s, climbing rate 2.0 m/s; Spaar, 1995). However, this methodical difference does not change the principle statement of optimal soaring-gliding behavior.

Interspecific comparison of optimal flight behavior

Optimized soaring and gliding flight was also found in other species. Steppe eagles reacted to the environmental conditions and adjusted their gliding airspeed according to climbing rate (Spaar and Bruderer, 1996). Furthermore, they soared in straight line gliding if linear arrays of thermals were available. They glided forward without losing and even gaining height, occasionally over several kilometers, and they reached high cross-country speeds in relation to the ground because they lost no time soaring in stationary thermals. Very often, steppe eagles combined soaring in thermals and in a straight line. Thus, maximizing cross-country speed in soaring and gliding flight not only involves adjustments to optimal airspeed but includes other behavioral reactions to environmental conditions such as timing of migration, flight direction in relation to the wind, and further profitable techniques such as soaring in a straight line. Pennycuik (1972) notes that birds use this strategy over tens of kilometers if thermal "streets" are available.

Interthermal gliding airspeed depends on several factors (Spaar, 1997). Besides the climbing rate, tailwind component, sidewind component, and flight altitude affect airspeed. Different species react differently to these factors: in 9 of 13 species analyzed airspeed was positively correlated with climbing rate (steppe eagle; lesser spotted eagle, *Aquila pomarina*; boot-eagle, *Hieraaetus pennatus*; Egyptian vulture, *Neophron percnopterus*; steppe buzzard; honey buzzard, *Pernis ptilorhynchus*; marsh harrier, *Circus aeruginosus*; levant sparrowhawk, *Accipiter brevipes*; and small falcons, *Falco* spp.). Tailwind component was negatively related and sidewind component was positively related to airspeed in most cases.

An interspecific comparison of harriers revealed fundamental differences within this group: marsh harriers adjusted their gliding airspeed according to the climbing rate, whereas pallid harriers, *Circus macrourus*, and Montagu's harriers, *Circus pygargus*, did not (Spaar, 1997; Spaar and Bruderer, 1997). Thus, marsh harriers behave more like typical soaring migrants. Montagu's and pallid harriers are less adapted to soar-

APPENDIX

Output of the flight performance calculation program 2 for an average migrating steppe buzzard in southern Israel after Pennycuik (1989)

Parameter	Assumed values
Empty body mass	0.56 kg
Payload mass	0 kg
All-up mass	0.56 kg
Span	1.188 m
Wing area	0.207 m ²
<i>g</i> (gravity)	9.81 ms ⁻²
ρ (air density)	1.23 kg/m ³
<i>G</i> (energy density of fat)	3.9E+07 J/kg
<i>k</i> (induced drag factor)	1.1
δ (slope of area vs. span line)	1
<i>cdw</i> (wing profile drag coefficient)	0.014
Body frontal area	0.00553 m ²
Body drag coefficient	0.334
Flat plate area	0.00184 m ²
Basal metabolic rate (chemical)	2.49 W
Type of bird: nonpasserine	

True airspeed (m/s)	Span factor	Sinking speed (m/s)	Glide ratio
5	1	0.510	9.81
6	1	0.484	12.4
7	1	0.499	14.0
8	1	0.549	14.6
9	1	0.633	14.2
10	1	0.753	13.3
11	0.977	0.908	12.1
12	0.870	1.090	11.0
13	0.782	1.290	10.1
14	0.708	1.510	9.26
15	0.646	1.760	8.81
16	0.593	2.030	8.53
17	0.547	2.320	7.89
18	0.507	2.640	7.32
19	0.472	2.990	6.35
20	0.440	3.370	5.94
21	0.413	3.770	5.57
22	0.388	4.210	5.23

Parameter	Computed value
Stall speed (<i>Cl</i> = 1.6)	5.19 m/s
Minimum sink	0.484 m/s at 6.1 m/s
Best glide ratio	14.6 at 8 m/s (= <i>V_g</i>)
Circling radius	7.72 m at 24° bank and <i>Cl</i> 1.4

Optimum interthermal gliding speed (*V_{int}*) and cross-country speed

V_{int} versus climbing rate in thermals.

V_{int} is cross-country speed if bird flies at *V_{int}* between thermals.

V_g is cross-country speed if bird flies at *V_g* between the thermals.

V_g = 8 m/s (best glide speed).

Fat consumption for zero wind [based on 2 × basal metabolic rate and *V_{int}*]

ing and gliding flight, reflecting their higher propensity to flapping flight. The profitability of soaring-gliding flight increases with increasing body mass, and thus differences in flight behavior may be due to the interspecific differences in body mass. Further, pallid and Montagu's harriers have narrower and more pointed wings than marsh harriers.

Kerlinger (1989) showed that sharp-shinned hawks (*Accipiter striatus*), broad-winged hawks (*Buteo platypterus*), red-tailed hawks (*Buteo jamaicensis*), and ospreys (*Pandion halia-*

APPENDIX

Continued

Climb (m/s)	<i>V_{int}</i> (m/s)	<i>V_{int}</i> (m/s)	<i>V_g</i> (m/s)	Fat consumption (ground) (g/km)
0.5	9.8	4.13	3.93	0.0309
1	11.2	5.78	5.17	0.0221
1.5	13.2	7.01	5.86	0.0182
2	14.8	8.01	6.29	0.0160
2.5	16.2	8.90	6.58	0.0144
3	17.3	9.60	6.77	0.0133
3.5	18.4	10.3	6.93	0.0124
4	19.3	10.9	7.04	0.0117
4.5	20.2	11.5	7.14	0.0111
5	21.0	12.0	7.21	0.0106
5.5	21.8	12.5	7.28	0.0102
6	22.5	13.0	7.34	0.00984

tus) behave similarly by adjusting their airspeeds according to the lift. For data on birds flying less than 90 m above ground along a ridge, lift was derived by calculating the vertical deflection of the wind at this ridge, and wind speed was measured 3 m above ground (Kerlinger, 1989). Since the theory of optimal soaring and gliding flight is based on the availability of vertical thermal updrafts and interthermal glides, these results do not directly support the theory. Nevertheless, Kerlinger's results reveal that birds optimize their airspeeds also while gliding at low flight altitudes.

The data for the steppe buzzard were collected when the Swiss Ornithological Institute was engaged in an environmental impact study about the potential hazard of a large radio antenna system in southern Israel. We are grateful to all those who worked at the radar stations for their field assistance. F. Liechti, M. Kestenholz, H. Stark, and D. Peter led the radar stations. T. Steuri developed the radar computer software, which was indispensable for the recording and analysis of the bird tracks. F. Liechti contributed important comments about the influence of different wind directions on cross-country speeds in soaring and gliding flight. S.C. Stearna, L. Schifferli, and M. Kestenholz made valuable suggestions on the manuscript.

REFERENCES

- Batschelet E, 1981. Circular statistics in biology. New York: Academic Press.
- Baudinette KV, Schmidt-Nielsen K, 1974. Energy cost of gliding flight in herring gulls. *Nature* 248:83–84.
- Bruderer B, Steuri T, Baumgartner M, 1995. Short-range high-precision surveillance of nocturnal migration and tracking of single targets. *Isr J Zool* 41:207–220.
- del Hoyo J, Elliott A, Sargatal J (eds), 1994. Handbook of the birds of the world, vol 2. New World Vultures to Guinea-fowl. Barcelona: Lynx Edicions.
- Ellis HI, 1984. Energetics of free-ranging seabirds. In: Seabird energetics (Whitow GC, Rahn H, eds.). New York: Plenum Press.
- Gorney E, Yom-Tov Y, 1994. Fat, hydration condition, and moult of steppe buzzards *Buteo buteo vulpinus* on spring migration. *Ibis* 136: 185–192.
- Hedenström A, 1993. Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Phil Trans R Soc Lond B* 247:183–187.
- Kerlinger P, 1989. Flight strategies of migrating hawks. Chicago: University of Chicago Press.
- Lasiewski RC, Dawson WR, 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23.
- Leshem Y, Yom-Tov Y, 1996. The use of thermals by soaring migrants. *Ibis* 138:667–674.

- Liechti F, 1992. Flight behaviour of nocturnal migrants in relation to wind and topography (PhD dissertation) [in German]. Basle: University of Basle.
- Lustick S, Battersby B, Kelty M, 1978. Behavioral thermoregulation: orientation towards the sun in Herring Gulls. *Science* 200:81–83.
- Mendelsohn JM, Kemp AC, Biggs HC, Biggs R, Brown CJ, 1989. Wing areas, wing loadings and wind spans of 66 species of African raptors. *Ostrich* 60:35–42.
- Pennycuik CJ, 1972. Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis* 114:178–218.
- Pennycuik CJ, 1989. Bird flight performance: a practical calculation manual. Oxford: Oxford University Press.
- Porter RF, Willis I, Christensen S, Nielsen BP, 1981. Flight identification of European raptors. Calton, UK: Poyser Limited.
- Sachs L, 1984. *Angewandte Statistik*. Berlin: Springer-Verlag.
- Shirihai H, Christie DA, 1992. Raptor migration at Eilat. *Br Birds* 4: 141–193.
- Sokal RR, Rohlf FJ, 1981. *Biometrics: the principle and practice of statistics in biological research*, 2nd ed. New York: Freeman.
- Spaar R, 1995. Flight behaviour of steppe buzzards *Buteo buteo vulpinus* during spring migration in southern Israel: a tracking radar study. *Isr J Zool* 41:489–500.
- Spaar R, 1997. Flight strategies of migrating raptors: a comparative study of interspecific variation in flight characteristics. *Ibis* 139 (in press).
- Spaar R, 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.
- Spaar R, Bruderer B, 1997. Migration by flapping or soaring: flight strategies of marsh, Montagu's and pallid harriers in southern Israel. *Condor* 99:458–469.