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FLIGHT PERFORMANCE DURING HUNTING EXCURSIONS IN ELEONORA'S FALCON *FALCO ELEONORAE*

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Summary

Among birds, falcons are high-performance flyers, in many cases adapted for aerial hunting and hence suitable targets for investigating limits to flight performance. Using an optical range finder, we measured flight tracks of Eleonora's falcon (*Falco eleonorae*), a species breeding in the Mediterranean region and specialised for hunting autumn passage bird migrants, when commuting between their nesting colony and offshore hunting areas (straight transportation flight) and when searching for prey (transecting and searching flight). Airspeed during searching flight was significantly slower than during straight transportation and transecting flight, but there was no significant difference in airspeed between the latter two flight modes. Straight transportation flight was significantly faster than predicted minimum power speed. Also, during straight transportation flight, the falcons responded to head- and tailwinds by increasing their airspeed when flying into the wind. However, they did not show any significant airspeed adjustments with respect to the angle between the track and the heading, as would be expected in birds trying to maintain a constant track direction. Mean sustainable climb rate (during ⩾240 s) was 1.4±0.31 m s^{-1} (mean ± S.D., *N*=13), which is rather a high rate for a bird the size of an Eleonora's falcon. The climb rate was used to calculate maximum load-carrying capacity and maximum sustained horizontal flapping flight speed. The mean wingbeat frequency during powered climbing flight was 4.68 Hz, which was used to estimate the mass-specific muscle work.

When falcons were leaving the colony for offshore hunting, they gained altitude by slope-soaring when there was an onshore wind. We formulated a simple criterion for the required gliding-flight rate of climb during an initial slope-soaring episode when minimizing the energy cost of reaching a certain altitude far out over the sea (which is where the prey is to be found). This climb rate was 0.36 m s^{-1}, and our observations indicated that the falcons experienced climb rates above this value when soaring in slope-lift.

Key words: flight speed, climbing rate, wind response, load-carrying, maximum speed, soaring, *Falco eleonorae*, Eleonora's falcon.

Introduction

Limits to bird flight performance are notoriously difficult to estimate because they rely on accurate measurements of animals challenged to perform at their maximum capacity. Nevertheless, birds show impressive and sometimes superior capacity compared with man-made micro air vehicles (*sensu* Spedding and Lissaman, 1998) for aspects of flight such as manoeuvrability, operational range (long-distance migration without refuelling), rate of climb and load-carrying capacity. Among birds, falcons are recognised as high-performance flyers adapted for aerial hunting and long-distance migration, as manifested in the high-impact stoops of peregrine falcons *Falco peregrinus* and one-way migration distances of 8600 km (Rudebeck, 1950–1951; Alerstam, 1987; Tucker, 1998; Peter and Kestenholz, 1998; Fuller et al., 1998). Eleonora's falcon *Falco eleonorae* has its breeding season adjusted to coincide with peak autumn bird migration, an adaptation shared only with the closely related sooty falcon *Falco concolor* (Walter, 1968, 1979a,b). The breeding colonies of Eleonora's falcon are scattered around the Mediterranean region and the east Atlantic, where many migrants pass on their way to tropical Africa between August and October. The falcons look out for flying migrants and they chase suitable prey in spectacular aerial hunts that usually involve several falcons (Walter, 1979a; Rosén et al., 1999). In strong winds (>10 m s^{-1}), the falcons mainly remain close to the colony, wind-hovering ('standing flight' according to Walter, 1979a) and waiting for passing migrants. Hence, a colony of Eleonora's falcons is an efficient death trap for migrants (Alerstam, 1990). In weak winds (0–7 m s^{-1}), the falcons are more mobile and make long (on average up to 24 km) offshore excursions to intersect migrants (Rosén et al., 1999). During hunting, they also climb to altitudes where the passing migrants fly. The falcons seem to be very flexible when it comes to adjusting their flight strategy in relation to wind during hunting. The hunting flight performance of these falcons provides an ideal opportunity to measure flight performance in a rarely studied falcon and to test predictions about flight behaviour from optimality theory and flight mechanics (Alerstam and Hedenström, 1998). We studied the flight performance of Eleonora's falcons by means of optical tracking of falcons hunting over the sea at a breeding colony.

Predictions from flight mechanical theory

Flight mechanics provides a framework for calculating the mechanical power of flight, characteristic flight speeds and adaptive responses in relation to wind (e.g. Pennycuick, 1975, 1989; Hedenström and Alerstam, 1995). Generally, mechanical power shows a U-shaped relationship with airspeed, with minimum power (V_{mp}) and maximum range (V_{mr}) speeds. These speeds maximise the time airborne on a given amount of energy (V_{mp}) and the maximum distance covered (V_{mr}). Optimal flight speeds different from V_{mp} and V_{mr} can be derived using alternative 'currencies', such as maximizing the rate of energy transport to young in a nest from a distant food patch (Norberg, 1981) or maximizing foraging efficiency (Welham and Ydenberg, 1993; Ydenberg et al., 1994; Hedenström and Alerstam, 1995; Houston, 1995). The optimal flight speed associated with the maximum rate of energy transport in central-place foraging depends on the flight power and the rate of self-feeding, which yield an optimal flight speed higher than V_{mr} (Norberg, 1981), while maximizing foraging efficiency is associated with V_{mr}. Birds looking out for food should generally fly at speeds intermediate between V_{mp} and V_{mr} (Hedenström and Alerstam, 1995).

The total mechanical power P_{tot} during climbing flight is given by the forward speed and the rate of climb from the relationship:

$$P_{tot} = P_{ae}(V) + m\boldsymbol{g}V_z\,, \tag{1}$$

where $P_{ae}(V)$ is the mechanical power for flapping flight (equation 3.11 in Pennycuick, 1989), m is body mass, $\boldsymbol{g}$ is the acceleration due to gravity and V_z is the vertical speed (positive upwards). Equation 1 is a simplistic model for climbing flight because it assumes that profile and induced power remain constant when the wings increase thrust for climbing. However, the total power during climbing flight derived according to equation 1 provides a lower estimate of the maximum power available (see Hedenström and Alerstam, 1992). By measuring forward airspeed and rate of climb, we can estimate P_{tot}, which in turn can be used to estimate flight performance characteristics such as load-carrying capacity and maximum speed (V_{max}).

Because the falcons performed consistent climbs, it would be possible to test whether they adjust their true airspeed in relation to decreasing air density with increasing altitude, which is to be expected if the birds were to maintain a constant equivalent airspeed. The true airspeed (V) relates to the equivalent airspeed (V_e) as $V=V_e(\rho/\rho_0)^{-1/2}$, where ρ_0 is air density at sea level and ρ is air density at flight altitude. For example, the true airspeed would increase by 2.4 % between 500 m and 1000 m altitude. We tested this prediction on a total of 30 trackings of climbing flights lasting for at least 180 s.

Recent results from birds flying in a wind-tunnel indicate that the default value for the body drag coefficient ($C_{D,par}$) used in Pennycuick (1989) is too high (Pennycuick et al., 1996). The previous default value for a bird with the dimensions of an Eleonora's falcon was $C_{D,par}$=0.36. Pennycuick et al. (1996) suggest that $C_{D,par}$=0.1 should be used and that values down to $C_{D,par}$=0.05 may be valid for birds with a streamlined body shape. Tucker (1990) constructed a smooth model body of a peregrine falcon and obtained a value of $C_{D,par}$=0.14, but recommended that $C_{D,par}$=0.18 be used as the mean of the smooth model and a frozen peregrine falcon body with feathers. Because of the uncertainty concerning $C_{D,par}$ in birds, we calculated our predictions and estimates for values of $C_{D,par}$ ranging from 0.4 to 0.05. Predicted V_{mp} and V_{mr} using Pennycuick's (1989) model for an Eleonora's falcon male are shown in Table 1. Note that the predicted speeds increase with decreasing body drag coefficient.

Another prediction concerns the flight speed in relation to wind; in order to fly at V_{mr} (or any other non-V_{mp} speed), a bird should increase its airspeed when flying into headwinds and reduce its speed when flying in tailwinds (Pennycuick, 1978). If a bird intends to maintain a constant track over the ground, it should also adjust its airspeed with respect to side-winds, independently of the head/tailwind decrement/increment (Liechti et al., 1994), where the condition for the optimal airspeed is given by:

$$\frac{\mathrm{d}P}{\mathrm{d}V} = \frac{P_{ae}(V)}{V_g}(\cos\alpha)^{-1}\,, \tag{2}$$

where $P_{ae}(V)$ is power according to the mechanical power equation (equation 3.11 in Pennycuick, 1989), V_g is ground speed and α is the angle between track and heading.

Materials and methods

Study site

We observed Eleonora's falcons *Falco eleonorae* Gené at a breeding colony on a rocky island of 51 km^2, Isola di San Pietro (39º09′N, 08º13′E), 6 km off the south-west coast of Sardinia, Italy. The colony is situated along a 7 km long stretch of the west coast of the island, holding approximately 115 pairs of Eleonora's falcons (Badami, 1998). The coast consists of near-vertical volcanic cliffs, facing west-northwest and ranging in height from 40 to 120 m. The flight tracks of the falcons were obtained from a plateau 112 m above sea level, which provided good views over a large part of the breeding cliffs. We made field measurements between 12 and 20 September 1997. During this period, there were light winds on 7 days (2.1±0.8 m s^{-1}; mean ± 1 S.D.), a brisk 9.3 m s^{-1} from north-northwest on 14 September and a moderate 4.8 m s^{-1} from northwest on 15 September.

Field measurements of flight tracks

We measured the tracks of flying Eleonora's falcons using

Table 1. *The effects of body drag coefficient on flight characteristics of Eleonora's falcon*

$C_{D,par}$*	V_{mp} ($m\,s^{-1}$)	V_{mr} ($m\,s^{-1}$)	$P_{ae}(V)$ (W)	P_{tot} (W)	h_{max}	V_{max} ($m\,s^{-1}$)	Q_m ($J\,kg^{-1}$)
0.4	7.5	12.5	4.86	9.67	1.60	20.0	29.5
0.36	7.7	12.9	4.57	9.38	1.63	20.5	28.6
0.24	8.5	14.3	3.69	8.50	1.71	22.7	25.9
0.2	8.9	15.0	3.38	8.19	1.75	23.8	25.0
0.18	9.1	15.4	3.22	8.03	1.77	24.5	24.5
0.14	9.7	16.4	2.89	7.70	1.82	26.3	23.5
0.1	10.6	18.0	2.54	7.35	1.88	29.1	22.4
0.05	12.6	21.5	2.04	6.85	2.00	36.2	20.9

$P_{ae}(V)$ during horizontal flapping flight was calculated according to Pennycuick (1989).

$P_{tot}=P_{ae}(V)+P_c$, where $P_c=m\boldsymbol{g}V_z$ (4.81 W), given by tracking falcons climbing for at least 4 min.

See text for further details.

$C_{D,par}$, body drag coefficient; V_{mp}, minimum power speed; V_{mr}, maximum range speed; $P_{ae}(V)$, mechanical power; P_{tot}, total power at maximum rate of climb; P_c, climbing power; m, mass; $\boldsymbol{g}$, acceleration due to gravity; h_{max}, maximum load-lifting capacity; V_{max}, maximum sustained flight speed; Q_m, muscle-mass-specific work; V_2, vertical speed; *Re*, Reynolds number.

*Characteristic values of $C_{D,par}$ that have been suggested for bird bodies in the literature are as follows: 0.4 is the default value for small birds (*Re*<50000) (Pennycuick, 1989), 0.36 is the default value for Eleonora's falcon (Pennycuick, 1989), 0.24 is the default value for large birds (*Re*>200000) (Pennycuick, 1989), 0.18 is the suggested value for a Harris' hawk *Parabuteo unicinctus* (Tucker, 1990), 0.14 is the measured value for a smooth-surfaced model body of a peregrine falcon (Tucker, 1990), 0.1 is a new default value suggested by Pennycuick et al. (1996) and 0.05 is a possible value for very streamlined bird bodies (Pennycuick et al., 1996).

an optical range finder (Wild, 80 cm, 11.25×) furnished with azimuth and elevation scales (see Pennycuick, 1982). The azimuth and distance were aligned with the direction to a fixed object of known position determined by a Leica Geovid 7×42 BDA [measuring range 25–1000 m, accuracy (maximum absolute error): distance ±1 m, azimuth ±0.5]. The elevation scale was set to zero at the horizon. Fixes of flying falcons were read every 15 s. The accuracy (maximum absolute error) of the measurements was within ±10 m for a target at 500 m distance, ±20 m at 1 km and ±100 m at 2 km distance (Hedenström and Alerstam, 1996). The closest distance for the range finder was 300 m. Immediately after each track registration, we also noted information about flight behaviour, for example flapping/gliding/soaring flight or whether the falcon was under transport to/from a hunt or searching for prey, etc. To determine flight tracks in relation to the air, we measured wind direction and velocity by tracking ascending helium-filled weather balloons always within 30 min of tracking a bird. The tracking data obtained from the range finder (distance, azimuth and elevation angle) were converted into Cartesian coordinates (x, y, z), and we calculated the horizontal distance projected on the horizontal plane (x, y) between all readings. These data, together with the elapsed time between fixes, were used to calculate the horizontal ground speed vector between successive readings. The wind vectors, obtained using the same procedure, were then used to calculate the heading and airspeed by vector calculation of flight tracks and wind at relevant altitudes by matching wind and bird vectors at the same altitudes. The vertical speed was calculated similarly using the z (altitude) coordinate. Then, since the elapsed time interval between successive fixes was constant at 15 s, the mean airspeed, ground speed and vertical speed were calculated for entire trackings (when flight behaviour was the same) or for segments (⩾45 s) of trackings (when flight behaviour changed). When calculating means of speeds, we only used one track segment or the entire track for each bird. All tracks were plotted and compared with field notes to classify tracks into different behavioural categories, such as leaving, incoming or searching flight and active, gliding or soaring flight. We also separated flights into circling *versus* straight-line flight and finally also into climbing, level or descending flight. Level flight was defined as those tracks with a vertical speed of less than 0.5 $m\,s^{-1}$, i.e. $-0.5<V_z<0.5\,m\,s^{-1}$.

In total, 186 tracks of falcons flying in different situations were obtained, corresponding to 10 h of effective flight time. For analyses, we only included tracks with a minimum duration of 45 s; for analyses involving sustained flight performance, we only included tracks of at least 240 s (see Hedenström and Alerstam, 1992). When analyzing the potential speed adjustment in relation to side-winds, tracks with a duration of 180 s or more were used.

It appeared that the birds were prone to soaring in updraughts. Soaring is defined as any flight technique by which energy is extracted from air currents in the atmosphere and converted into potential or kinetic energy of the bird (Pennycuick, 1975). In the present study, birds soared mainly by gliding or by mixed gliding and flapping flight. The tracks could be divided into the following three main flight modes on the basis of behaviour (see Rosén et al., 1999).

Leaving for offshore hunting

This category includes falcons leaving the breeding colony for offshore hunting. The flight was in a constant direction. We tracked these falcons for distances of up to 2–4 km, where they became too small to see or were lost in haze. When track measurements ended, these birds invariably continued further still as checked by telescope. This category contains the majority of falcons in climbing flight, which often initially soared in slope-lift if wind conditions allowed.

Transecting flights

This category includes falcons that left the colony in straight-line flight, but at some distance out over the sea turned (within sight of the observers) and flew back to the colony, where they often turned again to fly out over the sea once more. This flight mode could be interpreted as systematic straight-line searching flight.

Searching flights

This category includes falcons flying in circuitous pattern, usually using slope updraughts, in quite close proximity to the colony. The birds were obviously searching for prey, because hunts occur where searching falcons are flying. During searching flight, the falcons often mix flapping, gliding and soaring.

Wingbeat frequency

To estimate the wingbeat frequency, we used a Panasonic MS-1 video camera to film falcons, mostly those leaving for offshore hunting. Wingbeat frequency was determined for each sequence of a falcon by counting an integer number of wing beats over approximately 2 s and recording the number of frames from the start to the end of each such sequence (each frame is 0.04 s).

Morphology

Wing span and wing area were measured from two dead Eleonora's falcons in fresh plumage from Sicily according to methods described by Pennycuick (1989). The two birds, one adult male and one immature female, had wing spans of 0.952 m and 0.946 m and wing areas of 0.1061 m^2 and 0.1020 m^2, respectively. These data give aspect ratios (wing span squared divided by wing area) of 8.54 and 8.77, respectively, for the two birds. Our data on wing span fall below the range 1.1–1.3 m given by Cramp and Simmons (1980), but within the range given by Noakes (1990). For aerodynamic calculations, we used the following biometrical data as representative for a male Eleonora's falcon: body mass 0.350 kg, wing span 0.95 m and wing area 0.1040 m^2 (Walter, 1979a).

Air density

We calculated a representative value of air density for each day of flight speed measurements from temperature, barometric pressure and altitude (see Pennycuick, 1989). We measured ground-level temperature during field work, and barometric pressure was obtained from published weather maps (European Meteorological Bulletin, Amtsblatt des Deutchen Wetterdienstes, ISSN 0341-2970). The weather during our field work remained quite stable, with a mean barometric pressure of 10.18 kPa (N=9 days, range 10.12–10.21 kPa), and a mean ground-level temperature of 22 °C (range 21–35 °C) during our measurements. These data gave a mean ground-level air density of 1.20 kg m^{-3} (range 1.19–1.21 kg m^{-3}). To calculate expected flight velocities from aerodynamic theory, we assumed an altitude of 500 m, which was a typical flight altitude for our trackings. Assuming that air temperature declines by 0.65 °C per 100 m altitude, we obtained an air density of 1.15 kg m^{-3} (range 1.14–1.16 kg m^{-3}) corresponding to 500 m altitude.

Results

General flight behaviour

Hunting flights were classified into one of three categories (see above). Falcons leaving the colony for offshore hunting generally departed in directions between north-northwest and northwest, with a mean track direction of 309±19.3 ° that differed significantly from a random distribution (mean ±1 angular S.D., N=85, r=0.94, P<0.001; Batschelet, 1981). Generally, there were small differences between track and heading directions in falcons departing for offshore hunting. On the day when a 9.3 m s^{-1} wind blew from north-northwest, there was a 22.1 ° difference between track and heading, indicating that the falcons did not compensate fully for wind drift when flying over the sea (Rosén et al., 1999). Transecting falcons departed in directions similar to those leaving for offshore hunting, but they turned at some distance from the colony and flew back along more or less the same track, while searching falcons showed circuitous flight tracks over the sea outside the colony.

In offshore wind conditions, falcons leaving the colony did so using flapping flight directly from the nesting cliffs. However, when there was an onshore wind, slope-lift was present immediately beyond the cliffs as well as above the island (see Bradbury, 1995). This slope-lift was frequently exploited by the falcons, which soared in the lift to gain altitude before switching to flapping flight when departing from the vicinity of the island (see below).

Flight speeds

Summary statistics for flight speeds of falcons leaving the colony for offshore hunting, transecting and searching flight are shown in Table 2. There were no significant differences in airspeed between climbing and level flapping flight, either in falcons leaving for offshore hunting (t=1.02, d.f.=92, P>0.05; Table 2) or during transecting flight (t=0.19, d.f.=27, P>0.05; Table 2). Values for climbing and level flight were therefore combined when comparing flight modes. There were no significant differences in airspeed between falcons leaving for offshore hunting and transecting falcons (P>0.05, GT2-test; Sokal and Rohlf, 1995), but both these flight modes showed significantly faster airspeeds than those of falcons during flapping searching flight (P<0.05, GT2-test).

When testing the effects of head/tailwind on falcons leaving for offshore hunting, we included only trackings lasting at least

Table 2. *Observed flight speeds and rates of climb for Eleonora’s falcons at San Pietro, Italy*

Mode of flight	Flight type	N	V_g (m s^{-1})	V_a (m s^{-1})	V_z (m s^{-1})
Leaving, straight flight	Active climb	85	11.4±3.08	13.1±2.35	1.3±0.48
	Active level	9	11.3±2.40	12.2±3.77	0.2±0.21
Transecting	Active climb	23	9.9±3.45	11.9±2.32	1.6±0.90
	Active level	6	8.6±3.65	11.7±1.98	0.2±0.21
Searching	Active climb	6	6.4±2.99	7.3±2.33	1.9±0.52

Leaving birds are flying to offshore hunting areas, transecting birds are looking out for prey in straight-line flight, and searching refers to mixed flapping and gliding circuitous flight.

N, number of observations; V_g, ground speed; V_a, airspeed; V_z, climb speed.

Values are means ± S.D.

180 s (i.e. based on at least 13 fixes) to exclude possible measurement errors for short tracks. We analysed the effect on airspeed of the wind increment/decrement (V_g–V_a) and of the side-wind angle as 1/cosα, where α is the difference between track and heading (see equation 2). There was a significant relationship between airspeed and V_g–V_a (Fig. 1; linear regression, F=17.8, d.f.=26, P<0.001), as well as between airspeed and 1/cosα (F=7.48, d.f.=26, P<0.012). However, a multiple regression of airspeed on V_g–V_a and 1/cosα showed that only the effect of wind increment/decrement was significant (t=3.05, P<0.006). Hence, an effect of side-wind (equation 2) could not be demonstrated on the basis of the present data.

Climbing active flight

The mean rates of climb of falcons leaving for offshore hunting were 1.3±0.48 m s^{-1} (mean ± 1 S.D., N=85), 1.6±0.90 m s^{-1} (N=23) during transecting flight and 1.9±0.52 m s^{-1} (N=6) during searching flight (Table 2). These trackings had a duration of at least 45 s. To estimate the sustained climb rate, we included only trackings lasting at least 240 s (see Hedenström and Alerstam, 1992). The mean sustained rate of climb was 1.4±0.31 m s^{-1} (N=13) for birds leaving for offshore hunting, ranging from 0.9 m s^{-1} to 1.9 m s^{-1} (Fig. 2). Note that one falcon had a mean climb rate of 1.6 m s^{-1} over 795 s (i.e. >13 min).

Out of 30 trackings of 180 s or longer, 15 showed increasing airspeed with increasing altitude, 11 showed decreasing airspeed and four showed unchanged airspeed with increasing altitude (P>0.05, binomial test; Siegel, 1956). Hence, we found no support in our data for an increased airspeed in relation to decreasing air density during climbs.

To compare the sustained rate of climb of Eleonora’s falcon with those of other birds, we analysed the data for 15 species during climbing flight presented by Hedenström and Alerstam (1992). The birds ranged in body mass from the siskin *Carduelus spinus* (10 g) to the mute swan *Cygnus olor* (9.6 kg). These data on rate of climb *versus* body mass are plotted together with data for Eleonora’s falcon in Fig. 3. We calculated the regression line for the 15 species excluding Eleonora’s falcon to estimate the expected climb rate for a bird of body mass 0.35 kg (representing Eleonora’s falcon),

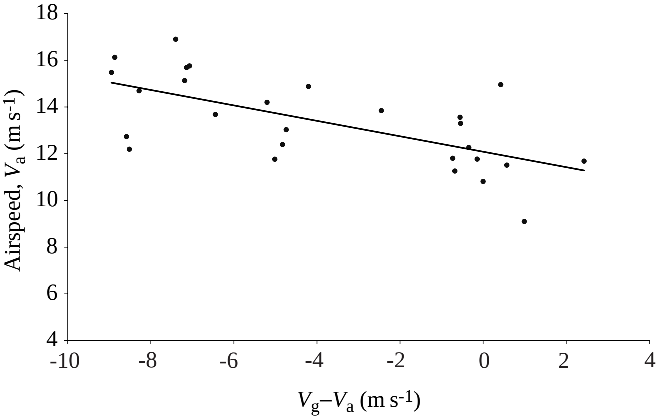

Fig. 1. Airspeed (V_a) in relation to tail- or headwind increment/decrement (V_g–V_a, where V_g is ground speed) in Eleonora’s falcons tracked for 180 s or more when leaving the breeding colony for offshore hunting. The linear regression equation is V_a=12.1–033(V_g–V_a) (P<0.001, r^2=0.42, N=27).

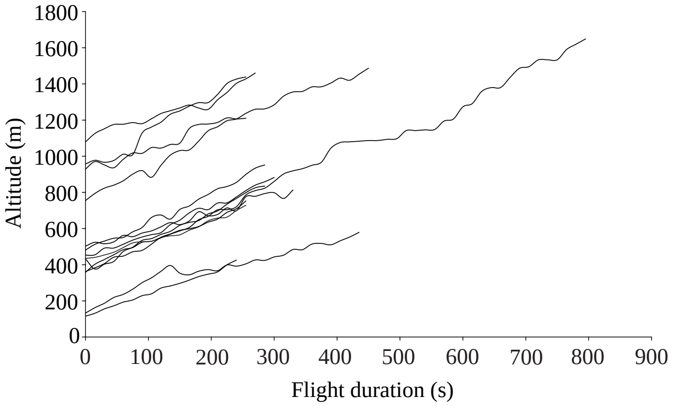

Fig. 2. Climbing flight profiles expressed as altitude *versus* time in actively flying Eleonora’s falcons tracked for more than 240 s. These tracks refer to sustained climb performance where the mean climb rate V_z is 1.4±0.31 m s^{-1} (mean ± S.D., N=13). The longest track is for a falcon showing a climb rate of 1.6 m s^{-1} over 795 s.

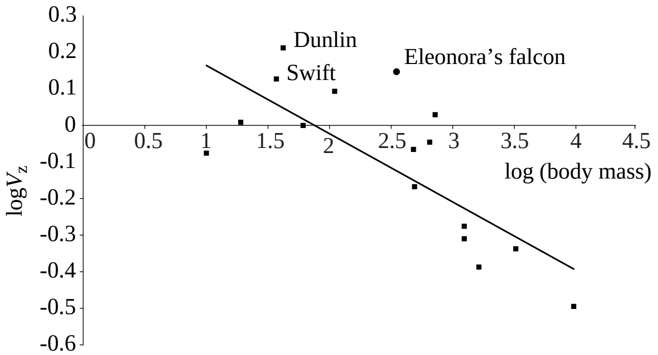

Fig. 3. Sustained rate of climb for at least 240 s (V_z; m s^{-1}) in relation to body mass (m; g) in 15 bird species (data from Hedenström and Alerstam, 1992) and Eleonora’s falcon (mean V_z 1.4 m s^{-1}). Note that the data have been log$_{10}$-transformed. The regression line has the equation $V_z=2.24m^{-0.19}$ ($P<0.001$, $r^2=0.63$, $N=15$) with the Eleonora’s falcon excluded.

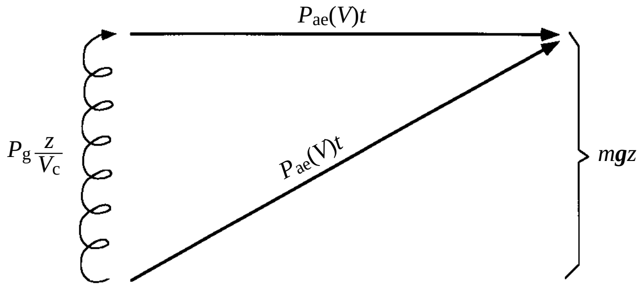

Fig. 4. A simple model for analysing the rate of climb in an initial soaring ascent that is required to yield an energetic advantage compared with a flapping-flight climb to an altitude z at some horizontal distance. During gliding flight, the bird expends a metabolic power P_g of 3BMR, where BMR is basal metabolic rate. V_c is the rate of climb when soaring, $P_{ae}(V)$ is mechanical power during flapping flight, t is the time required to fly the horizontal distance, m is body mass and $\boldsymbol{g}$ is the acceleration due to gravity. Note that t is the same for level flight and for active climbing flight because the airspeed did not differ between these flight modes. The criterion for an initial soaring ascent to be advantageous is given in equation 3.

which was 0.75 m s^{-1} (95 % confidence limits of estimate at 0.35 kg, 0.63 m s^{-1}, 0.89 m s^{-1}; Sokal and Rohlf, 1995). Hence, the observed mean sustained rate of climb of Eleonora’s falcon is well outside the confidence limit of the regression estimate. The sustained climb rate of Eleonora’s falcon is the largest positive residual from the regression line of the 15 species excluding Eleonora’s falcon, indicating that it has the largest capacity for climbing among all these 16 species when controlling for body size. In absolute terms, only the dunlin *Calidris alpina* shows a larger absolute sustained climb rate (mean 1.63±0.41 m s^{-1}, N=10) than Eleonora’s falcon (see Fig. 3), but the difference between the two species was not statistically significant (t=1.53, d.f.=21, $P>0.05$). The only other species showing a comparable rate of climb is the swift *Apus apus* (see Fig. 3; mean 1.34± 0.30 m s^{-1}, N=7).

Climbing soaring flight

In situations with onshore winds, we observed that many falcons soared in the updraughts created by the cliffs. After having gained altitude by soaring, the falcons left the vicinity of the colony using flapping flight and vanished over the sea as usual. When slope-lift was present, the falcons seemed to use this when departing almost by default, suggesting that they benefit from this ‘free ride’. To determine the magnitude of slope-lift required to be beneficial, we considered the alternative flight options showed in Fig. 4. The situation refers to departing falcons aiming to reach an altitude z at some horizontal distance over the sea. They can either choose active powered flight all the way or they can choose to soar initially in slope updraughts over the nesting cliffs until reaching the altitude z and then continue by horizontal flapping flight (Fig. 4). For this analysis, we assume that the birds soar exclusively using gliding flight. During soaring, the falcons expend a metabolic cost for gliding flight that has been estimated as approximately three times the basal metabolic rate (BMR) (Baudinette and Schmidt-Nielsen, 1974; Adams et al., 1986; Hedenström, 1993). This energy rate has to be converted into ‘mechanical power’ equivalents to be comparable with the mechanical power of flapping flight by multiplying the metabolic cost of gliding flight (P_g) by the conversion efficiency η, and so we can write the cost of gliding flight as $P_g=\eta\times3\times$BMR. We will assume that BMR=$3.79m^{0.723}$, where m is body mass, typical for non-passerines (Lasiewski and Dawson, 1967), and that the conversion efficiency is 0.23 (Tucker, 1972; Bernstein et al., 1973; Pennycuick, 1975). Alternatively, we could convert the estimated mechanical power of flapping flight into a metabolic rate, which would yield the same result as the calculation presented here. Flight speed during horizontal and climbing flight did not differ significantly (see above), and we therefore assumed that the aerodynamic power during horizontal and climbing flapping flight are the same (see Fig. 4). Note that the time t required to cover the horizontal distance will be the same during horizontal and active climbing flight. We can now formulate a criterion based on minimizing the energy cost of reaching an altitude z at some distance out over the sea as:

$$P_g\frac{z}{V_c}+P_{ae}(V)t\leqslant P_{ae}(V)t+m\boldsymbol{g}z\,, \tag{3}$$

where V_c is rate of climb during soaring using gliding flight and $P_{ae}(V)$ is the mechanical power of flapping flight (see Fig. 4). Rearranging and simplifying equation 3 yields:

$$V_c\geqslant\frac{P_g}{m\boldsymbol{g}} \tag{4}$$

for initial soaring to be energetically advantageous when

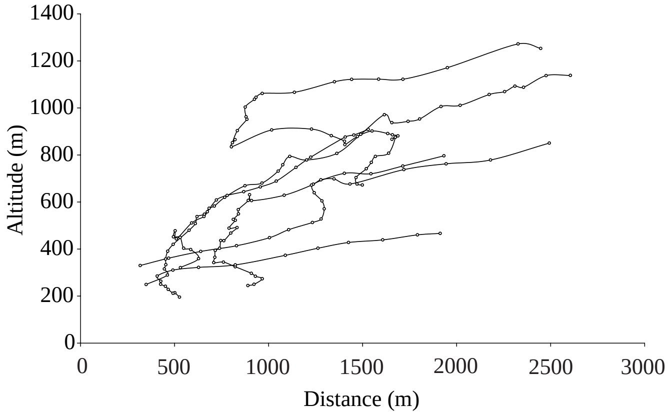

Fig. 5. A few typical tracks recorded from Eleonora's falcons with an initial soaring ascent using slope-lift close to the nesting cliffs followed by a continuing climb by active flapping flight. The distance on the abscissa is horizontal distance in the (*x*, *y*) plane from the bird to the observation point. The tracks illustrated had a mean climb rate of $1.49\,\mathrm{m\,s^{-1}}$ when soaring and $1.95\,\mathrm{m\,s^{-1}}$ when climbing using flapping flight, with an overall mean climb rate of $1.60\,\mathrm{m\,s^{-1}}$.

leaving the colony for offshore hunting. With a body mass m of 0.35 kg representing a male Eleonora's falcon (see above), equation 4 shows that it is advantageous to exploit the slope-lift when the rate of climb $V_c \geqslant 0.36\,\mathrm{m\,s^{-1}}$. Some studies have obtained lower estimates for the energy conversion efficiency η than 0.23 (e.g. Chai and Dudley, 1995) which, if true for Eleonora's falcon, would lead to a value of V_c lower than $0.36\,\mathrm{m\,s^{-1}}$.

In Fig. 5, a few tracks of departing falcons soaring initially are shown. Obviously they cannot reach their final hunting altitude solely from soaring, and they continue to climb by flapping flight after exiting the updraughts. However, an analysis similar to that given above for the two cases in Fig. 4, but assuming that the updraughts can only be used to reach an altitude z_0 (where $z_0 \leqslant z$), and where the remaining climb of $z - z_0$ has to be achieved by powered flight, results in the same criterion as equation 4 for exploiting initial slope-lift. Did the real falcons experience the required rate of climb when soaring?

Typically, falcons used a mixture of gliding and flapping when soaring, with an associated climb rate of $1.2 \pm 0.36\,\mathrm{m\,s^{-1}}$ (N=8). Circling active flapping flight was also used when climbing in updraughts with a climb rate of $1.9 \pm 0.29\,\mathrm{m\,s^{-1}}$ (N=7). However, the flight mode to compare with equation 4 is gliding flight when soaring, which was observed in only two departing falcons for at least 45 s; these birds showed climb rates of $1.2\,\mathrm{m\,s^{-1}}$ and $0.9\,\mathrm{m\,s^{-1}}$. Hence, it seems that the falcons exploiting updraughts reached climb rates well above the criterion of equation 4, and so they were gaining an energetic advantage from soaring compared with flapping-flight climbing.

Wingbeat frequency

Wingbeat frequency determined on 4 days did not differ significantly between wind situations (ANOVA; $F_{2,30}$=2.51, P>0.05), so all data were combined. Mean wingbeat frequency during departing and climbing flight was 4.68±0.20 Hz (N=33). Filmed birds were generally flying lower (<300 m above sea level) than those tracked by the range finder.

Discussion

We report flight speeds observed in Eleonora's falcons when commuting between their nesting cliffs and offshore hunting areas during the breeding season. To our knowledge, the flight behaviour and speeds of this species have not been studied before in any quantitative detail. Falcons are generally built for high-performance flight, including the legendary stoop of the larger species (Alerstam, 1987; Tucker et al., 1998). Eleonora's falcon is also capable of stooping and probably reaches terminal speeds comparable with those of the peregrine falcon, but we were not able to measure the speed of stooping Eleonora's falcons. Our measurements mainly refer to transportation flights when the falcons fly offshore to hunt passage bird migrants and when searching for prey over the sea. Generally, falcons searching for prey flew at slower airspeeds than those commuting to offshore hunting areas, which is compatible with theoretical expectations (Hedenström and Alerstam, 1995). When looking out for prey, the flight speed should be adjusted so that the net energy intake is maximized, which generally involves a compromise between flight costs and prey encounter rate (Hedenström and Alerstam, 1995). In birds commuting between a central place (e.g. the nest) and food patches, it can be argued that, to maximize the rate of energy delivered at the central place, they should fly at a speed $V^* > V_{\mathrm{mr}}$ (Norberg, 1981; Hedenström and Alerstam, 1995). During transecting flight, the optimal speed might be that which allows the bird to cover the maximum distance per unit energy, i.e. V_{mr}. But can we say at which alternative characteristic flight speed the commuting falcons were flying?

Let us consider the falcons leaving the colony using straight, active flight, which had a mean airspeed of $13.0 \pm 2.50\,\mathrm{m\,s^{-1}}$ (N=94, 95 % confidence limits $12.49\,\mathrm{m\,s^{-1}}$, $13.52\,\mathrm{m\,s^{-1}}$). This speed is similar to flight speeds of peregrine falcon and merlin (*Falco columbarius*) (Cochran and Applegate, 1986). In theory, we could calculate V_{mp}, V_{mr} or V^*, the optimal flight speed of central-place foraging, from flight mechanical theory and compare these values with the observed flight speed, but this approach requires a perfect theory (and exact morphological data for the birds involved). At present, there are uncertainties about some variables used when calculating aerodynamic power. Perhaps the most uncertain is the coefficient of parasite drag $C_{\mathrm{D,par}}$ (Pennycuick et al., 1996; Pennycuick, 1997). Recent findings suggest that, for reasonably streamlined birds, $C_{\mathrm{D,par}}$ should be 0.1 or even as low as 0.05 (Pennycuick et al., 1996). Reducing $C_{\mathrm{D,par}}$ has the effect of increasing V_{mp} and V_{mr}, as shown in Table 1. The observed speed of our falcons was significantly faster than all V_{mp} estimates except when $C_{\mathrm{D,par}}$ was 0.05 (Table 1), so the falcons probably did not fly at V_{mp}. If they flew at V_{mr}, $C_{\mathrm{D,par}}$ would need to be approximately 0.36 to match the observed speed (see Table 1), which is the default value used in the first programs issued by Pennycuick (1989). Be that as it may, Pennycuick (1997) argued that V_{mr} is a poorly defined optimum and that birds do not waste much transport economy from flying at sub-V_{mr} speeds. However, the adaptive wind response is expected only when birds are flying at non-V_{mp} speeds (Pennycuick, 1978, 1997; Hedenström and Alerstam, 1995). This behaviour was clearly present among the Eleonora's falcons, and we may therefore conclude that they were not flying at V_{mp}, but at a speed higher than V_{mp}.

We also tested for the predicted side-wind effect (Liechti et al., 1994), but failed to demonstrate that the falcons adjusted their speed to the angle between the track and heading directions. However, this effect would be expected if the birds were to maintain a constant track over the ground. The falcons were flying over the sea, and if they use the pattern of the sea surface as their frame of reference – the wavescape – some drift is inevitable because the entire coordinate system is moving (Alerstam and Pettersson, 1976). Another analysis showed that the Eleonora's falcons did not compensate fully for cross-winds; the hunting area at which the falcons are aiming may not be very well defined and, therefore, the incentive to keep a constant track is low (Rosén et al., 1999). Hence, the side-wind effect should perhaps not be very strong in this case.

We found no clear trend in airspeed during climbs with increasing altitude and hence decreasing air density, as would be expected if the birds were maintaining a constant equivalent airspeed. However, during a 500 m climb, the expected change in true airspeed is an increase of only 2.4 %. Most trackings refer to climbs of less than 500 m, and the predicted change may be to small to be detectable by our instruments.

By tracking falcons during sustained climbs, we can obtain an estimate of the lower boundary maximum performance (see equation 1; Hedenström and Alerstam, 1992). Because the falcons showed steady climb rates for more than 240 s, we take our observations as representing aerobic performance, further supported by the fact that one falcon maintained a climb rate of $1.6\,\mathrm{m\,s^{-1}}$ for more than 13 min (Fig. 2). A potential bias could be introduced if the birds were consistently flying in rising air, which would falsely overestimate the rate of climb. However, we think this is unlikely to be the case since our trackings refer to climbing flight well outside the slope-lift generated by the coastal cliffs in onshore winds. Also, the climb tracks show a rather homogeneous pattern among individuals (Fig. 2), indicating that the data represent true climbing rate in relation to the air since the trackings were obtained in different wind conditions.

Compared with another set of species also climbing for 240 s or longer (Hedenström and Alerstam, 1992; Piersma et al., 1997), Eleonora's falcon showed a comparatively high climbing rate (see Fig. 3). Pennycuick et al. (1989) measured climbing rates of up to $3\,\mathrm{m\,s^{-1}}$ in a 0.92 kg Harris' hawk (*Parabuteo unicinctus*), but these values were for very short (2–3 s) flights involving mainly anaerobic muscle work.

A mean climb rate of $1.4\,\mathrm{m\,s^{-1}}$ in an average male Eleonora's falcon of 0.35 kg gives a climb power P_{c} ($=m\boldsymbol{g}V_{\mathrm{z}}$) of 4.81 W. In addition, the bird exerts aerodynamic power which, among other things, depends on the value of $C_{\mathrm{D,par}}$. The total mechanical power available P_{tot} was calculated according to equation 1 for a range of values for $C_{\mathrm{D,par}}$ (Table 1). What can be said about these values? First, assuming that the estimated P_{tot} does represent the maximum power available, then we can calculate the maximum sustainable horizontal flight speed (V_{max}), simply by noting where the calculated power curve intersects a horizontal line representing P_{tot} (Pennycuick, 1968). Since P_{tot} depends on $C_{\mathrm{D,par}}$, V_{max} also varies with $C_{\mathrm{D,par}}$ (Table 1). For $C_{\mathrm{D,par}}$=0.18, V_{max}=$25\,\mathrm{m\,s^{-1}}$, and V_{max} increases to $36\,\mathrm{m\,s^{-1}}$ for $C_{\mathrm{D,par}}$=0.05 (Table 1). These speeds are well above the maximum observed speed, which was $19.4\,\mathrm{m\,s^{-1}}$ (A. Hedenström, M. Rosén, S. Åkesson and F. Spina, unpublished observations). For comparison, when stooping with partially folded wings, peregrine falcons are able to reach even higher speeds of approximately $50\,\mathrm{m\,s^{-1}}$ (Alerstam, 1987; Tucker et al., 1998; Peter and Kestenholz, 1998).

The mean wingbeat frequency observed (4.68 Hz) was significantly higher than that predicted (4.45 Hz at an air density α of $1.17\,\mathrm{kg\,m^{-3}}$ corresponding to an altitude of 300 m above sea level) from Pennycuick's (1996) formula for a male Eleonora's falcon in horizontal flapping flight (confidence limit test, $P<0.001$). However, the observed wingbeat frequency refers to climbing flight and, hence, gives further support for the idea that the falcons were working hard when climbing. On the basis of the observed wingbeat frequency and an assumed muscle mass fraction of 20 % of the lean body mass (see Greenewalt, 1962), we calculated the muscle-mass-specific work Q_{m} (Table 1). Again, this quantity will depend on the body drag coefficient. However, when compared with estimates from climbing birds (range $16\text{–}41\,\mathrm{J\,kg^{-1}}$) given by Hedenström and Alerstam (1992), the values for Eleonora's falcon are rather high.

For an aerial hunter, it should be advantageous to have a wide power margin, $P_{\mathrm{tot}}-P_{\mathrm{ae}}(V)$, that gives room for high maximum speed flight, acceleration and load-carrying capacity. Hedenström and Alerstam (1992) used radar measurements from climbing birds to calculate potential load-carrying capacity in 15 species. These estimates assumed a P_{tot} according to equation 1, and the total mass (empty mass + load) was then increased until the aerodynamic power alone reached P_{tot}. This total mass allows the bird just to maintain horizontal flight and leaves no room for climbing or manoeuvring. We repeated this analysis for Eleonora's falcon and calculated the maximum load factors h_{max} given in Table 1. The load factor relates empty mass (m_0) to maximum total mass m_{max} as $m_{\mathrm{max}}=h_{\mathrm{max}}m_0$. Again, the estimates depend on $C_{\mathrm{D,par}}$: reduced body drag coefficient gives an increased maximum load factor (Table 1). This estimate assumes that the extra load can be accommodated within the body (internal load), such as when birds accumulate fat before migratory flights (Hedenström, 1992), and increases the body frontal area without affecting the length of the bird (body frontal area $S_b \propto hS_{b0}$, where S_{b0} is the empty body frontal area and h is the load factor). The estimated h_{max} for Eleonora's falcon is comparable with values presented by Hedenström and Alerstam (1992) with a $C_{D,par}$ of 0.36 (Table 1). However, with the new recommendation of $C_{D,par}=0.1$ for streamlined birds (Pennycuick et al., 1996), an average male Eleonora's falcon would be capable of carrying a load of almost its own weight, i.e. $h_{max}=1.9$ (Table 1). This cannot be directly applied to prey load-carrying capacity, which involves two bird bodies interconnected by the talons holding the prey. Small prey items are held tucked up against the tail and are usually difficult for a human observer to detect. When the prey is of similar size to the falcon, a first-order approximation would be that the body frontal area is simply increased by a factor of 2, with an interaction term for the foot/prey junction. This interaction term is unknown but, because the prey has no profile drag, we assume that the terms are of the same magnitude and do not consider this complication further. With this assumption of body frontal area, $h_{max}=1.64$ for $C_{D,par}=0.1$, giving an estimate of the sustained load-carrying capacity of an Eleonora's falcon with an external mass held in the talons. This also assumes that the prey is aligned with the airflow, which is usually the case with prey (A. Hedenström, M. Rosén, S. Åkesson and F. Spina, unpublished observations). Admittedly, this is a first very crude estimate, and the aerodynamics of prey transportation in birds certainly needs to be examined more closely.

Walter (1979a) listed the prey taken by Eleonora's falcons, and the heaviest bird species were Manx's shearwater (*Puffinus puffinus*) weighing 0.45 kg and chukar (*Alectornix chukar*) weighing 0.39 kg (body mass data from Dunning, 1993). These species would represent load factors of 2.29 and 2.11, which are near the maximum estimates for internal loads (Table 1), but we do not know whether these birds were transported over long distances and, hence, whether these flights qualify as sustained load-lifting flights. However, such prey are exceptional; the usual prey mass is below the estimate for external load (see Walter, 1979a). In particular, at our study colony, the bulk of prey (out of a total sample of over 2000 birds; Spina et al., 1987) consisted of songbirds with mean body masses ranging between 10 and 20 g; the most frequent large prey were swift, hoopoe *Upupa epops*, wryneck *Jynx torquila* and golden oriole *Oriolus oriolus* (all less than 100 g).

Our measurements for climbing Eleonora's falcons and estimated V_{max} and load factors indicate that this species really is a high-performance micro air vehicle in some senses (see Spedding and Lissaman, 1998). This is no surprise for a species adapted for the aerial hunting of smaller birds. The relationship between rate of climb and body mass has a negative slope (see Fig. 3; Hedenström and Alerstam, 1992), and so the usual prey should be able to outclimb a pursuing Eleonora's falcon if the prey is at equal height when pursued. Interestingly, most small birds fold their wings and dive vertically when attacked (Walter, 1979a; A. Hedenström, M. Rosén, S. Åkesson and F. Spina, unpublished observations). In our observations, they also tried to escape by flying towards the island. However, the swift (a prey taken in quite high numbers at San Pietro compared with other colonies; Walter 1979a; Spina et al., 1987) is the only species that regularly tries to escape by outclimbing an attacking Eleonora's falcon. Considering Fig. 3, this seems a reasonable strategy for swifts. It may also be that the long wings of the swift are awkward to fold against the body, making them inefficient when diving. It is interesting to note that swift remains found in the nests of Eleonora's falcons were almost exclusively of juvenile birds (Walter, 1979a). Usually, Eleonora's falcons do not stoop on their quarry, as is common practice by the peregrine falcon, but instead chases are by active flight, in which the prey makes turning manoeuvres to escape the approaching falcon. Such a tactic should be advantageous if the prey bird has a low turning radius compared with that of the predator (Howland, 1974). Minimum turning radius is proportional to wing loading (Pennycuick, 1975) and, although Eleonora's falcon has a rather low wing loading ($33.0\,\mathrm{N\,m^{-2}}$) compared with that of the peregrine falcon and lanner falcon (*Falco biarmicus*) ($57.2\,\mathrm{N\,m^{-2}}$ and $42.1\,\mathrm{N\,m^{-2}}$, respectively; Jenkins, 1995), its wing loading is larger than that of most small passerines (see Greenewalt, 1962; Norberg, 1990).

The fact that the falcons almost invariably used slope-soaring in onshore wind conditions when departing for offshore hunting indicates that they save energy in this way when climbing to altitudes where they are likely to encounter migrating birds (see Rosén et al., 1999). Observed rates of climb were above the minimum rate of climb at which this strategy is favourable (equation 4). However, the birds often climbed using a mixture of gliding and flapping flight when soaring in rising air, suggesting that they also take the time required to climb into account when hunting. This is an interesting situation to which optimality considerations may apply, where the cost of flight (and the flight mode of the climb) is traded against improved prey density with increasing altitude.

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