

CLIMBING PERFORMANCE OF MIGRATING BIRDS AS A BASIS FOR ESTIMATING LIMITS FOR FUEL-CARRYING CAPACITY AND MUSCLE WORK

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Summary

Sustained climb rates and airspeeds in flapping flight were measured by radar tracking fifteen species of migrating birds ranging in body mass between 10 g and 10 kg. There was an inverse correlation between body size and climb rate: the lowest mean climb rate, 0.32 m s^{-1} , was observed in the mute swan and the highest mean value, 1.63 m s^{-1} , in the dunlin. Some dunlin flocks achieved sustained climb rates exceeding 2 m s^{-1} , up to 2.14 m s^{-1} . Assuming that the migrants expend maximum sustained power during their climbs, the climbing power can be used as a conservative estimate of the power margin. Estimates of climbing power for the species tracked by radar were used, in conjunction with aerodynamic theory, to calculate the amount of extra load the migrants should be able to carry if their power margin was used for load transportation rather than for climbing. Calculated ratios of total body mass with maximum load to lean body mass ranged between 1.28 and 2.75, showing an overall negative correlation with body size. There was a broad agreement with maximum fuel loads observed among free-living birds, indicating that the upper limits of fuel-carrying capacities and flight ranges in migrating birds are determined by power margin constraints in sustained flapping flight. Markedly reduced climb rates have been recorded for shorebirds departing with very large fuel reserves from W. Africa and Iceland, supporting the calculated trade-off between climb rate and fuel load. Total power consumption was estimated as the sum of calculated aerodynamic power for forward flight and climbing power. The ratio of total power to the expected minimum aerodynamic power was 1.1–1.3 in the three largest species, increasing to 2–4 in the smallest species. Medium- and small-sized species seem to allocate power in excess of the minimum aerodynamic power not only for climbing but also for maintaining a forward speed faster than the minimum power speed. Given provisional estimates of flight muscle masses and wingbeat frequencies, the mass-specific sustained muscle work for the different climbing bird species was calculated to be in the range 16–41 joules per kilogram muscle mass, showing a significant positive correlation with body mass.

Key words: bird flight, climbing performance, flight power, fuel load, load carrying, muscle work.

Introduction

The range of operational possibilities for a bird in flight, e.g. to fly at an extra fast speed, to climb steeply or to travel with a heavy fuel burden, is ultimately determined by the difference between the maximum power that can be developed by the flight muscles and the power required to fly unladen at standard speed. Pennycuick (1969, 1975) predicted that the relative power margin should decrease with increasing bird size, because the power required to fly increases more rapidly with body size than does the power available from the flight muscles.

Migrating birds store large reserves of fuel (mainly fat) and cross vast ecological barriers in long non-stop flights. Are the largest fuel reserves regularly observed among migrating birds of different sizes, and hence the associated maximum flight ranges, determined by the constraints set by the power margin or are they explained by other physical or ecological factors? To answer this question and to predict the maximum amount of extra load a flying bird can tolerate to the extent of having used up its power margin completely requires estimates of flight power and muscle capacity.

Pennycuick (1969) suggested that a vertebrate locomotor muscle may achieve a mass-specific work capacity of about 57 joules per kilogram muscle for maximal sprint exertion. This is in accordance with estimates of muscle work by one of the largest flying birds, the Kori bustard *Ardeotis kori* (58 J kg^{-1} ; Pennycuick, 1969) and during maximal sprint performance by Harris' hawks *Parabuteo unicinctus* climbing with added loads (50 J kg^{-1} ; Pennycuick *et al.* 1989).

Assuming the above-mentioned value for muscle work capacity, Pennycuick (1969) used his theory for flight power calculations to predict the total load that birds of different sizes should be able to carry. Hence, the Kori bustard with a body mass of 12 kg was regarded as the heaviest bird able to fly by flapping flight. With a zero power margin, it will not be able to carry any significant extra load. Bird species of decreasing body masses will show successively larger relative power margin and load capacity, and birds with a mass of about 1.5 kg will be able to carry an extra load as heavy as their own fat-free body mass. Still smaller birds would theoretically have an even higher load capacity, but Pennycuick (1969) assumed that there are other limiting structural factors that prevent small birds from putting on fuel reserves much heavier than their lean body mass. However, the above considerations refer to the sprint performance of birds. This restriction also applies to the measurements of maximum load-lifting during take-off by birds, as reported by Marden (1987, 1990).

The muscle capacity for prolonged work must be considerably lower than that for maximal sprint exertion, and Pennycuick and Rezende (1984) and Pennycuick (1989) suggest an expected mass-specific level for sustained muscle work of about 21 J kg^{-1} or somewhat lower, depending on the volume of mitochondria in the muscle tissues. Hence, cruise rather than sprint performance may be of prime interest in judging the constraints on load-carrying capacity set by the power margin in migrating birds, but there are few data about birds' operational scope in sustained flight.

In this paper we present measurements obtained by radar tracking of sustained climb rates and airspeeds of a selected number of migrating bird species, ranging in body mass from about 10 g (siskin) up to 10 kg (mute swan). On the assumption that the migrants expend maximum sustained power during their climbs, the observed climbing power can be used as a conservative estimate of the power margin. We have used the estimated power margins for calculating, on the basis of flight mechanical theory, the amount of extra load the migrants should be able to carry if their power margin was used for load transportation rather than for climbing. Comparisons with maximum fuel loads observed among free-living migrating birds allow us to decide whether it is likely that these fuel loads are indeed determined by power margin constraints.

Furthermore, the total power output by the climbing migrants is estimated by adding the aerodynamic power, derived by theoretical calculation (Pennycuick, 1989), to the climbing power. This makes it possible, after taking the predicted wingbeat frequency (Pennycuick, 1990) into account, to make a provisional estimate of the level of sustained muscle work for the climbing migrants.

Materials and methods

Radar observations of climbing performance

The flight of migrating birds was recorded by mobile short-range tracking radar (X-band, 40 kW peak power, pulse duration $0.3 \mu\text{s}$, pulse repeat frequency 1800 Hz, 2.2° pencil beam width). Range, elevation and bearing to the target were read manually (data from 1980) or by computer (data from 1981 to 1986) every 60 s (1980) or 10 s (1981–1986) from the radar, which was operating in automatic tracking mode. The radar is equipped with $9\times$ and $18\times$ binoculars, and identity of targets, flock sizes and other visual observations were reported to a tape recorder simultaneously with the radar registrations.

Winds at different altitudes were measured within 1 h before or after radar registration of a bird target, by releasing and tracking a hydrogen balloon carrying an aluminium foil reflector. Horizontal wind direction and speed were averaged over tracking intervals corresponding to altitude strata of about 150 m (1980) or 75 m (1981–1986). Horizontal airspeeds of birds were calculated by vector subtraction of wind velocity at the altitude stratum in which the birds were flying from the birds' flight vector in relation to the ground (track direction/ground speed). Mean horizontal airspeed for a bird flock ascending through a series of altitude/wind strata is the average of successive calculations for each such stratum traversed by the birds. The climb rate is equal to the vertical speed of the birds (any allowance for the possible effect of vertical winds on the climb rate could not be made).

All trackings used in this paper refer to birds migrating in flocks. The flocks were normally tracked at distances of 0.5–5 km from the radar. Maximum tracking error for a target in high-speed linear motion at 1 km distance is 0.7° in elevation and azimuth and 12 m in range.

Table 1. Fat-free body mass (m_0), actual fuel factor (h_0), wing span (b) and aspect ratio (Λ) for 15 bird species tracked by radar during climbing flight

Number	Species	m_0 (kg)	h_0	b (m)	Λ
1	Mute swan <i>Cygnus olor</i>	9.6	1.1*	2.23	9.2
2	Greylag goose <i>Anser anser</i>	3.25	1.1*	1.64	8.5
3	Eider <i>Somateria mollissima</i>	1.63	1.1*	0.94	8.4
4	Red-throated diver <i>Gavia stellata</i>	1.24	1.1*	1.11	12.2
5	Brent goose <i>Branta bernicla</i>	1.24	1.1*	1.15	10.7
6	Curlew <i>Numenius arquata</i>	0.72	1.1*	0.90	6.7
7	Wigeon <i>Anas penelope</i>	0.65	1.1*	0.80	8.2
8	Wood pigeon <i>Columba palumbus</i>	0.49	1.1*	0.78	6.5
9	Oystercatcher <i>Haematopus ostralegus</i>	0.48	1.1*	0.83	8.7
10	Arctic tern <i>Sterna paradisaea</i>	0.11	1.1*	0.80	11.2
11	Song thrush <i>Turdus philomelos</i>	0.061	1.08†	0.34	6.0
12	Dunlin <i>Calidris alpina</i>	0.042	1.19†	0.40	11.0
13	Swift <i>Apus apus</i>	0.037	1.1*	0.45	13.2
14	Chaffinch <i>Fringilla coelebs</i>	0.019	1.16†	0.26	5.3
15	Siskin <i>Carduelis spinus</i>	0.010	1.14†	0.21	5.9

* Assumed fuel factor.

† Average fuel factor found for migrating birds trapped in the relevant season and region.

For this analysis, we use data from a selection of fifteen species for which we have repeated trackings of climbing flight and, moreover, where the selected species cover a wide spectrum of body sizes (Table 1).

The tracking results are from different study sites in South Sweden. The climbing flights of swans, geese, ducks, divers, shorebirds and terns (species no. 1–7, 9, 10 and 12 in Table 1) refer to departures across land at the Baltic Sea coast of Scania (55°42'N, 14°12'E, radar 30 m above sea level) during the autumn migration period (July–October). Landbird species, such as the wood pigeon, song thrush and chaffinch (species no. 8, 11, 14), were tracked when departing and climbing in spring (March–April) across the Baltic Sea from the northernmost tip of Öland (57°22'N, 17°05'E, radar 10 m above sea level). However, the data for the siskin (species no. 15) refer to autumn (September–October) climbing flights across the sea and the shoreline at the coastal site in Scania (see above). In contrast to other species, the data for the swift (species no. 13) do not refer to migratory flights, but to the dusk ascent when swifts assemble into flocks and climb to high altitudes where they spend the night in flight (see Bruderer and Weitnauer, 1972). The climbing swifts were recorded in July and August at two different inland sites (55°39'N, 13°37'E, radar 45 m above sea level, and 60°05'N, 15°55'E, radar 185 m above sea level).

The data refer to tracking intervals of at least 4 min duration (often much longer, see below) showing a relatively uniform rate of continuous ascent. In cases where birds changed climbing rate during the tracking, we distinguished intervals

of relatively constant climb rates, and used the interval, of at least 4 min duration, with the highest ascent rate. This means that, for long trackings, our data reflect the steepest phase of climb not incorporating reduced climb rates which often occur when the birds reach high altitudes (see Alerstam, 1985). However, the mean climb rates given must be conservative estimates of maximum sustained climb rates, because in many cases radar tracking did not start until the target flock had reached a considerable altitude, and the steepest part of the climb may possibly have been missed.

All data refer to birds climbing by flapping flight, without any elements of gliding in thermals. Still, the birds' climb rates may be affected to an unknown extent by vertical winds. Measured climb rates may be biased on the high side if the birds could locate and fly in rising air (associated with thermals, slope winds or lee waves) while climbing. Such conditions of rising air are unlikely at the observation site on Öland. However, the relief of south Sweden is probably sufficient to create lee waves at the coastal site in Scania when the winds blow from land, i.e. from westerly directions (most common wind directions). In contrast, when the winds blow from the sea, lee waves would be unlikely. Instead, local slope winds probably prevail at the shoreline in the latter situation, but probably mainly at low altitudes below the flight levels of the birds tracked by radar (C. J. Pennycuick and B. Larsson, personal communication).

The ducks and divers (species no. 3, 4, 7) fly around a lot while climbing at the coastal site in Scania, before finally departing inland. Hence, the possibility that they exploit a lee wave for extra lift seems more likely than for the other species which climb while flying long distances inland along rather straight flight paths (any use of lee waves or thermals in these cases would probably be incidental rather than deliberate). The climb rate of eiders was indeed a bit higher with winds blowing from land (mean wind speed at the altitudes where the birds were flying = 5.6 m s^{-1}) possibly creating lee waves (mean climb rate = 0.44 m s^{-1} , s.d. = 0.11, $N=19$) than with winds (of mean speed = 4.3 m s^{-1}) from the sea (mean climb rate = 0.38 m s^{-1} , s.d. = 0.07, $N=16$; the difference between means is statistically significant; $P < 0.05$, t -test). This comparison cannot be made for the red-throated diver, but significant lift assistance in lee waves may be involved because all instances of climbing except one were registered with winds blowing from land, and the wind speed was rather high (mean wind speed = 9.1 m s^{-1}).

Characteristic fat-free body mass, wing span and aspect ratio ($(\text{wing span})^2 / \text{wing area}$) for the fifteen selected species in Table 1 were estimated as follows. As an estimate of fat-free body mass we used the lowest monthly mean body mass given by Cramp and Simmons (1977, 1983) and Cramp (1985) (species no. 1–4, 6–10, 13); body mass before fat accumulation in spring in the brent goose (species no. 5), which is the lowest mass during the annual cycle, reported by Ebbinge (1989); and body mass data from Ottenby Bird Observatory ($56^\circ 12' \text{N}$, $16^\circ 24' \text{E}$) for birds with no fat according to a visual method (species no. 11–12, 14–15). Wing span (the distance between the wing tips on outstretched wings; Pennycuick, 1989) was taken from Cramp and Simmons (1977, 1983) and Cramp (1985, 1988) (species

no. 1–13) and our own unpublished data (species no. 14–15). Aspect ratio was taken from Rayner (1985a) (species no. 1, 3–4) or calculated from wing span and wing area, where wing area was taken from Greenewalt (1962) and corrected to include the area of the body between the wings (species no. 2, 6–10) or own unpublished data (species no. 5, 11–15).

For four species, body mass data for trapped migrants at Ottenby could be used to estimate the mean fuel load at the appropriate time of year when the radar data were registered. The location of Ottenby by the Baltic Sea not far from the relevant radar sites makes it likely that the estimated fuel loads reflect reliable means to be expected for the migrants tracked by radar. Mean fuel factors (h =ratio of total body mass to lean body mass) for these four species range between 1.08 and 1.19 (Table 1). For the other species, information about probable fuel loads are meagre, but data for mute swan (S. Mathiasson, personal communication) indicate low fat loads. There are no indications that any of the species travel with large fuel reserves in the region and seasons concerned, and we have provisionally used a value of $h=1.1$, which seems to fit literature data on body masses fairly well.

Climb rates and airspeeds

Observed average climb rates range between 0.32 m s^{-1} (mute swan) and 1.63 m s^{-1} (dunlin), while mean airspeeds of the climbing birds fall in the range between 9.9 m s^{-1} (arctic tern) and 20.3 m s^{-1} (wigeon) (Table 2). The highest climb rate recorded during a period of at least 4 min was achieved by a flock of ten

Table 2. Average sustained climb rates (V_z), horizontal airspeeds (V_h) and mean altitudes (above sea level) for migrating birds according to tracking radar registration

Number	Species	$V_z \pm \text{s.d.}$ (m s^{-1})	$V_h \pm \text{s.d.}$ (m s^{-1})	Mean altitude (m)	Number of trackings	Month
1	Mute swan	0.32 ± 0.15	16.7 ± 1.2	259	4	October
2	Greylag goose	0.46 ± 0.11	15.9 ± 1.3	351	6	September–October
3	Eider	0.41 ± 0.10	16.9 ± 1.7	276	35	July, September–October
4	Red-throated diver	0.49 ± 0.17	17.9 ± 1.4	592	37	September–October
5	Brent goose	0.53 ± 0.18	16.4 ± 1.8	312	20	September–October
6	Curlew	1.07 ± 0.26	14.9 ± 1.1	770	5	July
7	Wigeon	0.90 ± 0.32	20.3 ± 2.3	451	12	September
8	Wood pigeon	0.68 ± 0.18	15.5 ± 1.4	322	46	March–April
9	Oystercatcher	0.86 ± 0.20	13.6 ± 0.8	704	4	July, September
10	Arctic tern	1.24 ± 0.22	9.9 ± 1.4	1074	15	July–September
11	Song thrush	1.00 ± 0.21	12.4 ± 1.5	733	10	March–April
12	Dunlin	1.63 ± 0.41	13.9 ± 1.4	717	10	July
13	Swift	1.34 ± 0.30	10.0 ± 0.8	783	7	July–August
14	Chaffinch	1.02 ± 0.33	11.2 ± 1.2	387	24	April
15	Siskin	0.84 ± 0.23	13.4 ± 1.2	529	7	September–October

The number of radar trackings and months of observation are also given.

dunlins, ascending steadily from an altitude of 425 to 1410 m above sea level in 7 min 40 s, giving a climb rate of 2.14 m s^{-1} (mean airspeed was 12.9 m s^{-1}). After that, the flock continued to climb, although at a reduced rate, and the total climb rate measured during the whole tracking time of 11 min 30 s was 1.98 m s^{-1} . The performance of this flock was not exceptional, however, as two further flocks of dunlins achieved a climb rate exceeding 2 m s^{-1} .

Many of the flocks maintained climb rates given in Table 2 not just for 4 min, but for periods twice or three times as long, and occasionally much longer. By way of example, our data include one flock of eiders continuously climbing at a mean rate of 0.39 m s^{-1} for 25 min, red-throated divers climbing at 0.38 m s^{-1} for 37 min, wigeons at 0.83 m s^{-1} for 30 min, wood pigeons at 0.60 m s^{-1} for 37 min and song thrushes at 1.31 m s^{-1} for 20 min. This clearly indicates that the given climb rates reflect what the birds can achieve in sustained effort without incurring an oxygen debt. The only reservations apply to the mute swans and greylag geese, which did not climb to very high altitudes, and the data in Table 2 refer, with one exception, to climb periods lasting only between 4 min (seven of the ten flocks) and 7 min 40 s. The exceptional case is a flock of 26 greylag geese maintaining a 0.40 m s^{-1} rate of ascent for 11 min. This flock continued to climb for a further 9 min, achieving an overall climb rate of 0.32 m s^{-1} for 20 min.

As expected from flight mechanical theory (Pennycuick, 1975, 1978), there is an overall pattern of increasing climb rate with decreasing body mass of the bird species (Spearman rank correlation coefficient $r_s = -0.75$, $P < 0.001$, $N = 15$, Table 2). However, the negative correlation between climb rate and body mass is far from perfect, with the smallest species, the chaffinch and siskin, showing only moderate climb rates. The sample of 15 species includes five species from the family Anatidae and can therefore be regarded as taxonomically biased (see Pagel and Harvey, 1988). In order to check for this bias we also calculated the correlation for the other species excluding the Anatidae. The correlation between climb rate and body mass remained negative, although not significantly so ($r_s = -0.37$, $P > 0.05$, $N = 10$). Furthermore, there is a general positive relationship between airspeed and body mass of the different species ($r_s = 0.77$, $P < 0.001$), which also accords with predictions from aerodynamic theory (Pennycuick, 1969, 1975). However, this is again an imperfect correlation with many deviating cases, but the correlation is robust to taxonomic bias ($r_s = 0.66$, $P < 0.05$, $N = 10$).

Results and discussion

Estimates of fuel-carrying capacity

Calculation of maximum fuel loads

A flying object that is to gain height at a steady rate needs to expend a certain amount of mechanical power to raise its weight against gravity. The climbing power, P_c , for a bird of body mass m is:

$$P_c = mgV_z, \quad (1)$$

Table 3. Climbing power (P_c), aerodynamic power (P_{ae}), total power ($P_{tot}=P_c+P_{ae}$), maximum fuel factor (h_{max}), wing-beat frequency (f) and muscle mass-specific work (Q_m) calculated for 15 species of birds registered by tracking radar during sustained climbing flight

Number	Species	P_c (W)	P_{ae} (W)	P_{tot} (W)	h_{max}	f (Hz)	Q_m (J kg ⁻¹)
1	Mute swan	33	241	274	1.28	3.5	41
2	Greylag goose	16	64	80	1.43	3.8	32
3	Eider	7.2	48	55	1.30	7.0	24
4	Red-throated diver	6.6	28	34	1.42	5.5	25
5	Brent goose	7.1	25	32	1.48	5.0	26
6	Curlew	8.3	15	23	1.79	5.5	29
7	Wigeon	6.3	20	26	1.52	6.5	31
8	Wood pigeon	3.6	11	14	1.55	5.8	25
9	Oystercatcher	4.5	8.8	13	1.74	5.7	24
10	Arctic tern	1.5	1.0	2.5	2.75	4.1	28
11	Song thrush	0.65	1.3	2.0	1.72	10.1	16
12	Dunlin	0.80	1.0	1.8	2.22	8.1	26
13	Swift	0.40	0.43	0.83	2.56	6.8	16
14	Chaffinch	0.22	0.38	0.60	1.94	9.8*	16
15	Siskin	0.094	0.31	0.40	1.53	11.2*	18

Methods of calculation for each variable are given in the text.

* Effective wing-beat frequency estimated for species using bounding flight (see text).

where g is the acceleration due to gravity and V_z is the vertical component of speed (positive upwards). Estimated climbing powers for the 15 study species are given in Table 3.

The aerodynamic power, P_{ae} , required for horizontal flapping flight can be subdivided into three main components:

$$P_{ae} = P_{ind} + P_{par} + P_{pro}, \quad (2)$$

where P_{ind} is induced power, P_{par} is parasite power and P_{pro} is profile power (see Pennycuik, 1969, 1975). Assuming that the migrants expend maximum sustained power output, P_{max} , during their climbs, we can estimate this power as the sum of climbing and aerodynamic power for the migrants tracked by radar with body masses $m=h_0m_0$ (Table 1):

$$P_{max} = P_{tot} = P_c + P_{ae}. \quad (3)$$

An estimate of the maximum fuel factor in sustained flight (h_{max}) can be obtained by solving:

$$P_{ae}(m = h_{max}m_0) = P_{max} \quad (4)$$

with respect to h_{max} for the different species. Hence, we assume that the limiting fuel factor occurs when the aerodynamic power alone amounts to the maximum sustained power and the birds have no surplus power available for sustained climb. In these calculations we have furthermore made the simplifying assumption that

the birds do not change their horizontal airspeed (given for the different species in Table 2) with fuel load, which will lead to conservative estimates of h_{\max} . Air density was taken as the density of the standard atmosphere at the average mid-altitude of the trackings for each species.

It will be noticed that induced, parasite and profile power appear for the same bird (constant wing morphology and airspeed) with different fuel loads (i.e. different body mass and body frontal area) on both the left- and right-hand sides of equation 4. P_{ind} increases in proportion to body mass squared (i.e. $\propto h^2$), P_{par} varies in direct proportion to body mass ($\propto h$, see Pennycuick, 1975), while P_{pro} is independent of body mass. Thus, P_{pro} is equal on both sides in equation 4 and therefore needs no consideration. Formulae for P_{ind} and P_{par} were taken from Pennycuick (1975, 1989). The calculated estimates of h_{\max} for the study species are presented in Table 3.

Comparison with theoretical expectations and with maximum fuel loads in free-living birds

The maximum estimated fuel factors range between 1.28 for the mute swan and 2.75 for the arctic tern (Table 3). Generally, maximum fuel-carrying capacity decreases with increasing body mass ($r_s = -0.76$, $P < 0.001$; $r_s = -0.30$, $P > 0.05$ when the Anatidae are excluded).

In this context it may be interesting to calculate how the maximum fuel load capacity scales with body mass across the species by an exponential curve fit. An 'ideal' bird (*sensu* Pennycuick, 1975) should have a scaling exponent of $-1/3$ (see Pennycuick, 1969). However, it is reasonable to assume that fuel accumulation does not affect the length of the bird; hence, the fuel factor is directly proportional to the body frontal area (Pennycuick, 1975, p. 20). The expected scaling exponent for an ideal bird becomes $-2/7$. The theoretical model for 'real' birds also takes into account that the body drag coefficient declines with increasing body size (Pennycuick *et al.* 1988), and this reduces the expected scaling exponent still further. We calculated the maximum fuel factors for our birds with constant mass-specific muscle work (an adapted version of Program 1A; Pennycuick, 1989), and obtained an expected scaling exponent of -0.19 . The observed scaling exponent of h_{\max} on body mass among our study species was -0.074 (s.e. = 0.024), which is significantly different from zero ($P < 0.01$), but also significantly smaller than the theoretically predicted values ($P < 0.001$). However, notice that this comparison assumes constant mass-specific muscle work, which we show below is not the case.

In order to compare the estimated maximum fuel loads calculated here with field data on large fuel loads in free-living birds, we extracted information on body masses from the literature (see Fig. 1 and Table 4). We selected maximum body masses for species prior to migrations across vast ecological barriers or otherwise the maximum body mass reported prior to migration for a species that undertakes long-distance flights. Body mass data for migrants that are known to migrate by short flights with small or moderate fuel reserves were not included, since our objective was to mirror the heaviest fuel loads that can be reached in nature

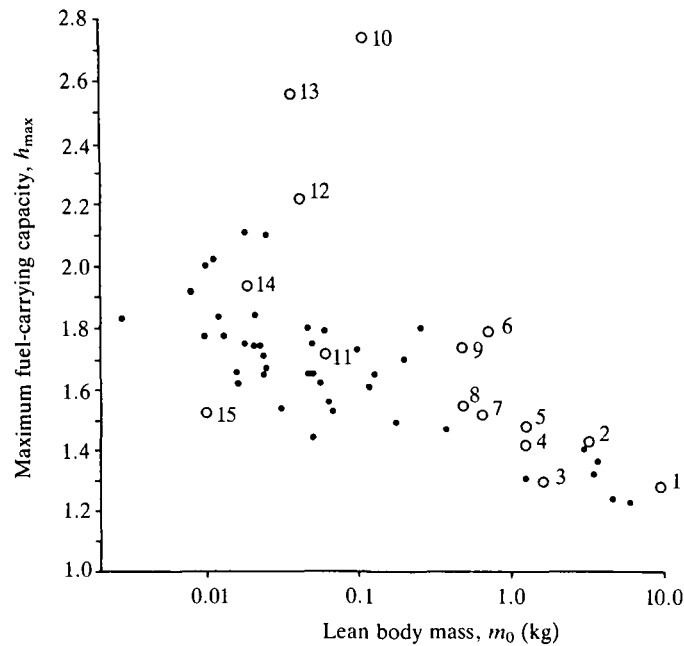


Fig. 1. Calculated maximum fuel-carrying capacities (h_{max}) for the study species (nos 1–15, Table 1) and maximum observed fuel factors in free-living birds in relation to lean body mass (m_0) ($r_s = -0.75$, $P < 0.001$, $N = 41$). The data on fuel factors and the methods of estimation for the 41 species in this figure are given in Table 4.

(Table 4). There is an overall agreement between our estimated maximum fuel capacities (Table 3) and field measurements of maximum body masses reached by migrants, but there is notable variation between the species (Fig. 1). The smallest of the investigated species (no. 15, siskin; Fig. 1) showed a surprisingly low fuel-carrying capacity. Partly, this can be explained by the high airspeed for siskins, which is 63% above the expected maximum range speed (Pennycuick, 1989; Program 1A). It is unclear why siskins should allocate so much of their total power to maintain a high airspeed (see below and Fig. 3). On the high side, we find three species (nos 10, 12 and 13) with fuel load capacities well above what is normally encountered in free-living birds (Fig. 1). These species have the largest relative wing spans, i.e. ratio of wing span to (body mass)³. A large wing span promotes flapping flight efficiency through a low induced power.

It seems that maximum fuel loads in birds are constrained by the power margin as estimated through climbing performance, but some species have an exceptionally high fuel-carrying capacity of which they have never been recorded to make full use (Fig. 1). Why, then, do not all free-living birds store fat up to the maximum capacity? A number of factors might explain this. First, it is impractical to gain fuel up to the ultimate possible limit because the birds then lose the valuable possibility of climbing at a reasonable rate (e.g. to cruising heights with

Table 4. Fat-free body masses (m_0) and maximum observed fuel factors (h_{obs}) in 41 bird species based on values in the literature

Species	m_0 (kg)	h_{obs}	Method	Source
<i>Ciconia ciconia</i>	3.03	1.42	2	Hall <i>et al.</i> (1987)
<i>Cygnus columbianus columbianus</i>	6.1	1.23	2	Limpert <i>et al.</i> (1987)
<i>C. c. bewickii</i>	4.66	1.24	2	Evans and Kear (1978)
<i>Anser anser</i>	3.45	1.32	2	Matthews and Campbell (1969)
<i>Brania canadensis maxima</i>	3.77	1.36	2	McLandress and Raveling (1981)
<i>B. bernicla</i>	1.24	1.31	3	Ebbinge (1989)
<i>Anas discors</i>	0.37	1.47	4	White <i>et al.</i> (1981)
<i>Porzana carolina</i>	0.050	1.44	4	Odum (1960)
<i>Charadrius hiaticula</i>	0.049	1.65	3	Clapham (1978)
<i>Pluvialis fulva</i>	0.117	1.61	1	Johnson <i>et al.</i> (1989)
<i>P. squatarola</i>	0.197	1.70	3	Prokosch (1988)
<i>Limosa lapponica</i>	0.254	1.80	3	Piersma and Jukema (1990)
<i>Xenus cinereus</i>	0.066	1.53	3	Summers and Waltner (1978)
<i>Tringa hypoleucus</i>	0.049	1.75	3	Summers and Waltner (1978)
<i>T. nebularia</i>	0.174	1.49	3	Summers and Waltner (1978)
<i>T. stagnatilis</i>	0.063	1.56	1	Pearson <i>et al.</i> (1970)
<i>Arenaria interpres</i>	0.099	1.73	3	Summers and Waltner (1978)
<i>Calidris alba</i>	0.047	1.80	3	Davidson (1984)
<i>C. alpina</i>	0.048	1.65	3	Goede <i>et al.</i> (1990)
<i>C. canutus</i>	0.129	1.65	3	Prater and Wilson (1972)
<i>C. ferruginea</i>	0.055	1.62	3	Barter (1986)
<i>C. maritima</i>	0.061	1.79	1	Atkinson <i>et al.</i> (1981)
<i>C. minuta</i>	0.021	1.84	3	Pearson (1987)
<i>C. pusilla</i>	0.021	1.74	4	Page and Middleton (1972)
<i>Jynx torquilla</i>	0.031	1.54	1	Hedenström and Lindström (1990)
<i>Archilochus colubris</i>	0.0028	1.81	4	Odum and Connell (1956)
<i>Motacilla flava</i>	0.016	1.62	1	Fry <i>et al.</i> (1970)
<i>Anthus trivialis</i>	0.022	1.74	1	Smith (1966); Ludlow (1966)
<i>Saxicola rubetra</i>	0.016	1.66	1	Smith (1966)
<i>Oenanthe o. leucorrhoa</i>	0.025	2.10	2	Ottosson <i>et al.</i> (1990)
<i>Acrocephalus shoenobaenus</i>	0.010	2.0	1	Gladwin (1963)
<i>Sylvia atricapilla</i>	0.018	1.75	1	Finlayson (1981)
<i>S. borin</i>	0.018	2.11	2	Ludlow (1966)
<i>S. curruca</i>	0.0096	1.77	1	Moreau and Dolp (1970); Moreau (1969)
<i>Ficedula hypoleuca</i>	0.012	1.83	1	Smith (1966)
<i>Muscicapa striata</i>	0.013	1.77	1	Moreau and Dolp (1970); Smith (1966)
<i>Piranga olivacea</i>	0.024	1.71	4	Odum (1960)
<i>P. rubra</i>	0.024	1.65	4	Odum (1960)
<i>Vermivora peregrina</i>	0.0080	1.92	4	Odum <i>et al.</i> (1961)
<i>Dendroica striata</i>	0.011	2.02	1	Murray (1979)
<i>Dolichonyx oryzivorus</i>	0.025	1.67	4	Odum (1960)

Methods for determination of fuel factor are (1) total body mass of the single heaviest individual related to the population mean of fat-free body mass (FFBM), (2) total body mass of the single heaviest individual in a specified size class related to the population mean of FFBM of that size class, (3) mean total body mass of fat individuals related to the population mean of FFBM and (4) maximum fat loads determined by chemical extraction of body constituents.

favourable winds). Second, heavy fuel burdens reduce manoeuvrability and maximum linear acceleration (see Andersson and Norberg, 1981), and hence the capacity to escape from a predator attack will become reduced with increasing fuel load. Consequently, optimal fuel loads, even in cases of extremely energy-demanding long-distance flights, are expected to balance below the maximum possible fuel-carrying capacity, giving the birds a safety margin with respect to climb, acceleration or manoeuvrability capacity. Furthermore, fuel loads might be kept low by energy savings through formation flight (Lissaman and Shollenberger, 1970; Hummel, 1983), which is likely to be of special importance among larger species where the power margin constrains fuel loads more tightly (Fig. 1). Interestingly, formation flight is found in most of the larger species in this study (nos 1–3, 5–7, 9, 10 and 12).

Effect of fuel load on climb rate

In theory there is a continuous trade-off between climb rate and fuel load for a bird flying at its maximum sustained power. Assuming that the climbing migrants recorded by radar in this study operate at this power, the expected relationship between climb rate and fuel load can be calculated for any of the species from the equation:

$$P_{ac}(m = hm_0) + hm_0gV_z = P_{max}, \quad (5)$$

where P_{max} is given according to equation 3. With increasing h , both the costs for horizontal flight and for climbing (the first and second terms in the above equation, respectively) will increase, and the climbing speed V_z must be reduced in order to diminish the climbing power and maintain the total power at the given maximum level. Of course, when the load has increased to the extent that the birds lose their climbing ability, equation 5 reduces to equation 4 with $V_z=0$ and $h=h_{max}$. The expected relationship between climb rate and fuel load is illustrated for the dunlin in Fig. 2. As before, calculations have been made with the airspeed held constant at the observed mean value given in Table 2.

Within-species comparisons of climb rates achieved by migrants with different fuel loads offer a possibility of judging the reliability of our estimates of maximum fuel load and of testing the assumption that the climbing migrants operate at a maximum power level. For the dunlin, climbing speed has been measured by optical range-finder for birds departing on long-distance spring migration flights from Mauritania in West Africa (Piersma *et al.* 1990). Before their departure, the birds accumulated large fuel reserves corresponding to $h=1.47$ (Zwarts *et al.* 1990). Their mean observed climb rate of 0.70 m s^{-1} is in reasonable agreement with what should be expected if they were to develop the same power as the dunlins climbing with much smaller fuel loads ($h=1.19$) during autumn migration in Sweden (Fig. 2).

A similar provisional comparison of climb rates between birds with different fuel loads can be made for the knot *Calidris canutus*. During the radar studies in South Sweden, one mixed flock with six knots and six dunlins was tracked while

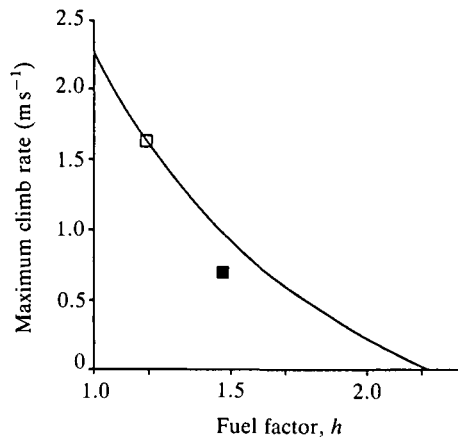


Fig. 2. Predicted maximum climb rate in relation to fuel factor for the dunlin based on the sustained climb rate and actual fuel factor recorded in this study (open square and curve). The filled square shows the mean climb rate recorded for dunlins departing from Mauritania with heavy fuel reserves corresponding to $h=1.47$ (Piersma *et al.* 1990; Zwarts *et al.* 1990). Intercepts of the curve on the ordinate and abscissa show the estimated maximum sustained climb rate (achievable without payload) and maximum fuel factor (h_{max} , see Table 3), respectively.

climbing at a uniform rate of 1.37 m s^{-1} for 7 min 20 s (airspeed= 15.8 m s^{-1}). According to trapping data from Ottenby, knots passing the Baltic region at the relevant time (end of July) carry very small fuel reserves, and h was probably close to 1.0. Piersma *et al.* (1990) report a mean climb rate of 0.91 m s^{-1} for knots departing on spring migration from Mauritania with $h=1.32$ (Zwarts *et al.* 1990). Furthermore, knots with even larger fuel reserves, $h=1.53$ (Gudmundsson *et al.* 1991), showed a mean climb rate of 0.72 m s^{-1} , measured by optical range-finder, when departing in straight-line flapping flight from Iceland in spring (Alerstam *et al.* 1990). The reduction in climbing speed and in climbing power with an increased fuel load, found in both the knot and the dunlin (Fig. 2), supports the notion that migrants in flapping flight gain height by climbing at their maximum sustained power or some constant fraction thereof, and indicates that our estimates of h_{max} may be realistic.

Estimates of muscle work

The balance between power for forward flight speed and power for climbing

Mechanical flight theory can be used to estimate the aerodynamic power required for horizontal flight at the observed airspeeds by the fifteen species in this study. The total power output by the migrants is the sum of this aerodynamic power P_{ac} and the climbing power P_{c} . We have used Pennycuick's (1989) theoretical framework to calculate P_{ac} according to his Program 1A (with the

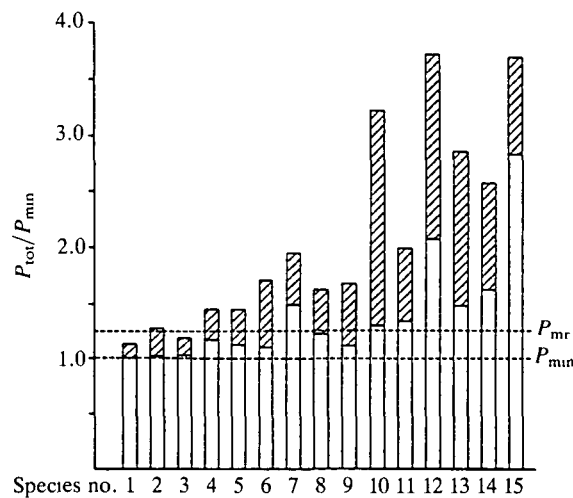


Fig. 3. Total mechanical flight power (P_{tot}) relative to minimum flight power (P_{min}) for the study species (nos 1–15, Table 1) in sustained climbing flight. Total power has been subdivided into aerodynamic and climbing (hatched) components (see Table 3). Minimum power (P_{min}) and maximum range power (P_{mr}) are indicated with horizontal lines. Calculations of aerodynamic power for the study species as well as their expected P_{min} and P_{mr} are based on Pennycuik (1989; Program 1A).

species' masses and measurements according to Table 1 and with air densities referring to the mean altitudes in Table 2). The results are given in Table 3.

Pennycuik's (1989) program also allows the estimation of expected minimum aerodynamic power P_{min} and the associated flight velocity (V_{mp}). While the mute swan showed an airspeed in close agreement with expected V_{mp} , observed airspeeds of all other species exceeded expected V_{mp} to a smaller or larger extent. This also means that their aerodynamic power exceeded the minimum power to a variable extent. In Fig. 3, the ratio of total power (with its components of aerodynamic and climbing power) to the expected minimum aerodynamic power is presented for the different species.

The maximum-range speed V_{mr} exceeds V_{mp} and is associated with minimum energy cost per unit of distance covered. Hence, V_{mr} represents the optimal flight speed for birds minimizing energy costs for the migratory journey. The associated flight power P_{mr} is expected to exceed the minimum power by about 25% according to Pennycuik (1989: Program 1A). It may be noted that the ratio of P_{mr} to P_{min} is not fixed but depends on the profile power ratio.

Fig. 3 indicates that there is an overall increase in total power relative to minimum flight power with decreasing body mass, up to a ratio approaching 4 for the smallest species. The power exceeding P_{min} represents a surplus that can be allocated for extra efforts such as increased speed and climb. The figure also indicates that observed climbing power is a conservative estimate of the power

margin, at least for the smaller species. By reducing their flight speed to V_{mp} , the small species may be able to climb at a significantly higher rate than that recorded or to carry larger fuel loads than those estimated in Table 3.

The three largest species (nos 1–3 in Fig. 3) fly with a power close to P_{min} and allocate all extra power for climbing. The calculations indicate that the mute swan does not have enough muscle power to fly at P_{mr} , and this power is only just achievable by the greylag goose and eider. Such severe power constraints in large-sized birds are in full agreement with predictions by Pennycuick (1969, 1975, 1989).

Medium-sized birds (nos 4–9) seem to allocate some of their extra power to increased forward speed while climbing, and their aerodynamic power falls between P_{min} and P_{mr} , or a bit higher (wigeon, see Fig. 3).

Surprisingly fast airspeeds, exceeding V_{mr} , have been recorded for the smallest climbing birds (nos 12–15). There are a number of possible explanations for these fast speeds apart from sources of error related to the measurements and masses of birds used in the calculations or to the assumptions inherent in flight theory for birds. First, in addition to mechanical/aerodynamic energy costs for flight, other costs, such as the basal metabolism of the flying bird, should be taken into account for an accurate estimation of V_{mr} . Doing this (e.g. by using Program 1 in Pennycuick, 1989), gives higher estimates of V_{mr} than in the mechanical calculations, and the aerodynamic power P_{mr} required to meet these enhanced flight speeds will be slightly higher than indicated in Fig. 3. However, this factor alone is not sufficient to account fully for the discrepancy between observed airspeeds and V_{mr} . Second, the maximum-range speed is expected to increase with headwinds and decrease with tailwinds (Pennycuick, 1978). Most flocks of dunlins, swifts and chaffinches (nos 12–14) were indeed climbing into headwinds, and the average groundspeed was lower than the mean airspeed by between 2 and 4 ms^{-1} . However, the siskins (no. 15) were flying with neutral winds on the average, and their mean groundspeed equalled the mean airspeed. Third, it is of adaptive value for migrants to allocate extra power to maintain a speed in excess of V_{mr} if they are selected to minimize duration rather than energy costs for the migratory journey (Alerstam and Lindström, 1990).

To decide which of these and other possible explanations are relevant, we must await further empirical and theoretical clarification.

Mass-specific sustained muscle work

The mass-specific muscle work Q_m can be estimated by dividing the total power output by the flight muscle mass and the wingbeat frequency. Q_m is determined by the characteristic stress and strain prevailing in the muscle filaments, and the expected value for maximum efficiency in sustained work is about 21 J kg^{-1} for vertebrate aerobic muscles (Pennycuick and Rezende, 1984; Pennycuick, 1989).

The values of mass-specific muscle work given in Table 3 represent provisional estimates which we have calculated by assuming that the mass of the birds' pectoralis muscles amounts to 20% of their lean body mass, and by adopting wingbeat frequencies predicted by Pennycuick's (1990) equation. The estimations

of flight muscle mass and of wingbeat frequency are fraught with significant uncertainty.

As an average for all birds, pectoralis muscle mass relative to body mass amounts to 15 % (Rayner, 1988), while the total flight muscle ratio falls between 20 and 30 % for most bird species (Marden, 1987).

Comparing wingbeat frequencies predicted by Pennycuick's (1990) equation, as given in Table 3, with measured values that are available for some of the species (Bruderer *et al.* 1972; Bloch *et al.* 1981) gives a reasonable overall agreement, except for the chaffinch and siskin. According to radar registration, these two species fly with a wingbeat frequency of about 17 Hz (Bruderer *et al.* 1972). However, Pennycuick's (1990) predictions (Table 3) may represent a reasonable estimate of the 'effective' wingbeat frequency (wingbeat frequency multiplied by the fraction of time used for flapping) for these two species which travel by distinct intermittent flapping flight – so-called bounding flight (Rayner, 1985*b*). The fraction of time used for flapping may be expected to be higher for climbing than for level flight, where bursts of flapping typically last 30–50 % of the total time (Bruderer *et al.* 1972; Danielsen, 1988). The effective wingbeat frequencies in Table 3 for the chaffinch and siskin correspond to bounding flight with the flapping phase lasting 58–66 % of the total time, which may be realistic in climbing flight (these species were also observed to travel by distinct bounding flight when climbing). It is possible that divers, swans, ducks and waders have a higher wingbeat frequency than predicted by Pennycuick's (1990) equation because of the triangular pointed wings of these species. Observations on gyrfalcon *Falco rusticolus* and peregrine falcon *F. peregrinus* (which also have this wing shape) showed wingbeat frequencies about 30 % higher than predicted (C. J. Pennycuick, personal communication).

A further complication is the possibility that climbing birds increase wingbeat frequency in comparison with typical values in level flight. However, Pennycuick (1989) argues that the operating frequency of the flight muscles is expected to remain within narrow limits in sustained flight, so that maximum efficiency is maintained. Climbing carrion crows *Corvus c. corone* had an average wingbeat frequency that was only marginally higher (about 5 %) than that of birds in level flight (Althaus and Bruderer, 1982).

The overall mean mass-specific muscle work for the fifteen species in Table 3 is 25 J kg^{-1} , which is in reasonable accordance with the predicted level (Pennycuick, 1989). This is about half the level achieved in maximal sprint exertion (see Introduction), as has also been surmised by Pennycuick (1975). However, the scatter is rather wide, with estimated Q_m values ranging between 16 and 41 J kg^{-1} in the different species. For the majority of species, Q_m falls between 24 and 32 J kg^{-1} , with the mute swan deviating on the high side (41 J kg^{-1}) and the swift and the three passerine species on the low side ($16\text{--}18 \text{ J kg}^{-1}$).

There was a significant positive correlation between mass-specific muscle work and body mass ($r_s=0.69$, $P<0.01$; $r_s=0.61$, $P>0.05$ with the Anatidae excluded), which is at variance with Pennycuick's (1989) prediction of a rather constant level

of mass-specific muscle work independent of body mass. Partly, this positive correlation may be due to the fact that the lower the operating frequency (i.e. the frequency at which the flight muscle is adapted to operate in cruising locomotion) in birds of increasing mass, the lower the ratio of mitochondria to myofibrils, and hence the higher the stress and also the mass-specific work that the muscle can develop (C. J. Pennycuick, personal communication).

The high value for the mute swan reflects the extensive power requirements for flight by the largest birds. In contrast to the rest of the species, the swift and the three passerines fly by intermittent rather than continuous flapping flight. This makes the estimates of 'effective' wingbeat frequency (see above; this measure, taking into account the fraction of time used for flapping, must be used for a correct derivation of Q_m during the active flapping phase) particularly liable to error in these species, because little is known about how the balance between flapping and nonflapping phases is adjusted in climbing flight (see Renevey, 1981).

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