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Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed

ANDERS HEDENSTRÖM

Department of Ecology, Theoretical Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden

SUMMARY

Birds migrating over land use either of two basic flight strategies, i.e. flapping or gliding/soaring flight. In soaring flight the birds gain altitude mainly by circling in thermals, i.e. rising air, and then they glide off until another thermal is encountered. Powered flapping flight is energetically much more expensive than gliding flight. This leaves us with the question why do not most birds adopt the soaring strategy rather than flapping flight on migration? I present optimization criteria, based on flight mechanical theory, for (i) energy-selected migration and (ii) time-selected migration, for flapping and soaring flight migration, respectively. These are evaluated in relation to general body size and rate of climb in thermals. I also consider the effects of wing morphology and horizontal winds. The general conclusion is that minimization of transport costs probably cannot be the only critical selective factor. In time-selected migration the size range of birds for which flapping flight is advantageous over thermal soaring flight, is significantly larger than in energy-selected migration, and this is in better agreement with what is found in real birds. Therefore, resulting migration speed probably constitutes an important selective force in bird migration. I also evaluate criteria for mixed strategies, i.e. when birds should use soaring flight when thermals are available and proceed by flapping flight otherwise. Finally, I also discuss some other factors, e.g. sensitivity to crosswinds, abundance of thermals and topography, which may affect the evolution of migration strategy.

1. INTRODUCTION

Birds migrate over vast distances to exploit different resources for breeding and survival. The distances covered and speeds achieved are indeed remarkable. Among birds three main flight strategies can be distinguished. Over land, birds adopt either powered flapping flight or soaring, mainly by using thermal updrafts to gain altitude and then descend by gliding flight until another thermal is encountered. Seabirds flying over the oceans extract energy from the wind speed gradient by the principle of dynamic soaring (Lord Rayleigh 1883; Idrac 1924) and from upcurrents close to the sea surface (Wilson 1975).

In this paper I address the question why birds migrating over land use either thermal soaring or flapping flight. Migration may be optimized either by energy or time minimization criteria, and I evaluate the efficiency with respect to these two optimization criteria for soaring and flapping flight migration in relation to general body size and wing morphology and wind velocity.

Pennycuik (1972) noted that energy expenditure in powered flapping flight increases steeply with increased body size ($P_{\text{mr}} \propto M^{7/6}$, where P_{mr} is the power at maximum range speed and M is the body mass), while gliding and soaring flight is relatively cheap and consumes only a low multiple (Baudinette & Schmidt-Nielsen 1974) of the basal metabolic rate ($P_s \propto M^{3/4}$, where P_s is the power during pure soaring/

gliding flight). This dichotomy between flapping and soaring flight results in relatively larger energy savings by using soaring flight with increasing size of the bird. However, even relatively small birds, for example an 8 g warbler, would save energy by soaring compared to flapping flight (Pennycuik 1972). Therefore, the energy hypothesis cannot explain why soaring is found mainly among larger species. A disadvantage of soaring flight is a comparatively slow cross-country speed and hence it may be that choice of flight strategy depends on the trade-off between energy economy and speed (Pennycuik 1989). A crude comparison of flight speeds between flapping and soaring flight is misleading as overall migration speed also includes time needed for energy deposition. The overall resulting migration speed includes time for stopover as well as actual flight, and must not be confused with flight speed. However, as discussed later there may be selection pressures to increase overall migration speed as well as flight speed. Recently, Alerstam & Lindström (1990) predicted optimal flight speeds associated with maximum overall migration speed, taking into account the rate of energy deposition at the stopover sites. By adopting the same approach also for soaring migration it is possible to evaluate the effects of size and morphology on the different migration strategies. In this paper I compare theoretical predictions about energy minimization and time minimization (speed maximization) for flapping and soaring flight migration in relation to general size. Other

Table 1. *List of symbols*

b	wing span
BMR	basal metabolic rate
DEE_{\min}	minimum daily energy expenditure
E_F	transport cost in flapping flight
E_S	transport cost in soaring flight
M	body mass
P	power
\hat{P}	resulting power when thermal availability is limited
P_{dep}	rate of energy deposition at stopover
P_{mr}	power at maximum range speed
P_{mt}	power at flight speed for minimum migration time
P_S	power in gliding/soaring flight
q_s	fraction of time used for soaring flight
q_{th}	fraction of time when thermals are available
S	wing area
V	airspeed; optimal airspeed in gliding flight
\hat{V}	resulting flight speed when thermal availability is limited
V_c	climb rate in thermals
V_{cc}	cross country speed when soaring
$V_{\text{migr,F}}$	overall speed of migration for flapping flight
$V_{\text{migr,S}}$	overall speed of migration for soaring flight
V_{mp}	minimum power speed
V_{mr}	maximum range speed
V_{mt}	flight speed for minimum migration time
V_w	wind speed
V_z	sink speed in gliding flight

aspects are also discussed, such as sensitivity to crosswinds, abundance of thermals and topography. All may have influenced the evolution of different flight strategies in migrating birds.

2. THEORY

A number of symbols are needed for the analyses developed in the following text. These are listed in table 1.

(a) *Aerodynamical theory of bird flight*

There is a well established theoretical framework for animal flight (Pennycuick 1969, 1975, 1989; Tucker 1973, 1974; Greenewalt 1975; Rayner 1979, 1986; Norberg 1990), the backbone of which relates power in flight to airspeed. This study uses Pennycuick's theory, but the general conclusions are independent of which version of flight theory is used.

The total power for a bird in horizontal flight is given by

$$P = \alpha + \beta V^{-1} + \gamma V^3, \quad (1)$$

where P is power, V is flight velocity and α , β and γ represent coefficients that vary due to the bird's body mass, morphology, drag coefficient and air density. The quantity α represents the sum of profile power and the basal metabolic rate (BMR throughout). The profile power is the component needed to overcome the drag of the flapping wings which is assumed to be independent of flight velocity. The second term on the right hand side of equation (1) is the power required to support the weight, known as induced power. The third term in equation (1) is the parasite power, which

is the power needed to propel the bird's body, excluding the wings, through the air. By flapping the wings the bird generates a forward thrust to overcome the drag of the body. At constant flying speed these forces, drag and thrust, must balance. The sum of the power components expressed as a function of speed gives a U-shaped curve (figure 1). From this relationship we can find two characteristic velocities. First, by solving $dP/dV=0$, the minimum power speed, V_{mp} , is obtained as the lowest point on the power curve. At this speed the energy expenditure per unit of time is minimized. Secondly, by solving $dP/dV=P/V$, the maximum range speed, V_{mr} , is obtained (figure 1). At this speed the energy expenditure per unit of distance is minimized. Graphically, this speed can be found by drawing a tangent from the origin to the power curve (see figure 1).

The overall process of migration includes, besides the actual flight, the time necessary for accumulation of energy reserves to be used during flight. By combining these quantities the optimal flight speed can be found if the bird maximizes the overall migration speed (Alerstam & Lindström 1990). The optimal flight speed, V_{mt} , is found by solving $dP/dV=(P+P_{\text{dep}})/V$, where P is given by equation (1) and P_{dep} is the rate of energy deposition at intermediate stopover sites. Graphically, this solution is obtained by drawing a tangent to the power curve from a point on the extended ordinate, representing the rate of refuelling (figure 1).

In gliding flight the counterpart to the power curve for flapping flight is the so-called glide polar, which relates sink speed to forward gliding speed (Pennycuick 1975, 1989). At higher speeds the glide ratio can be improved by reducing the wing span by flexing the wings (Tucker & Parrott 1970). The superpolar is defined as the envelope of separate fixed-span polars (Tucker 1987; Pennycuick 1989).

Soaring flight can be defined as gliding flight through rising air which counteracts the sink during gliding flight. Rising air can be produced in a number of ways, but most important to migrant birds travelling over land is thermal convection (Pennycuick 1972; Kerlinger 1989). By circling in thermals the birds gain altitude and then glide off in the migration direction until a new thermal is encountered (Pennycuick 1975). This requires a certain abundance of thermals as a new one has to be encountered before the bird descends to the ground. The maximum resulting cross country speed in thermal soaring and gliding flight is given by

$$V_{\text{cc}} = VV_c/(V_c - V_z), \quad (2)$$

where V is the optimal gliding speed as calculated from the superpolar and rate of climb, V_z is sink speed (negative downwards) at the optimal glide speed and V_c is climb rate in thermals (Pennycuick 1972, 1975, 1989; Tucker 1987).

The cost of gliding flight is generally assumed to be a constant multiple of BMR. Hence, the power for soaring flight is a constant irrespective of the resulting cross-country speed, which in turn is closely dependent on the strength of thermals.

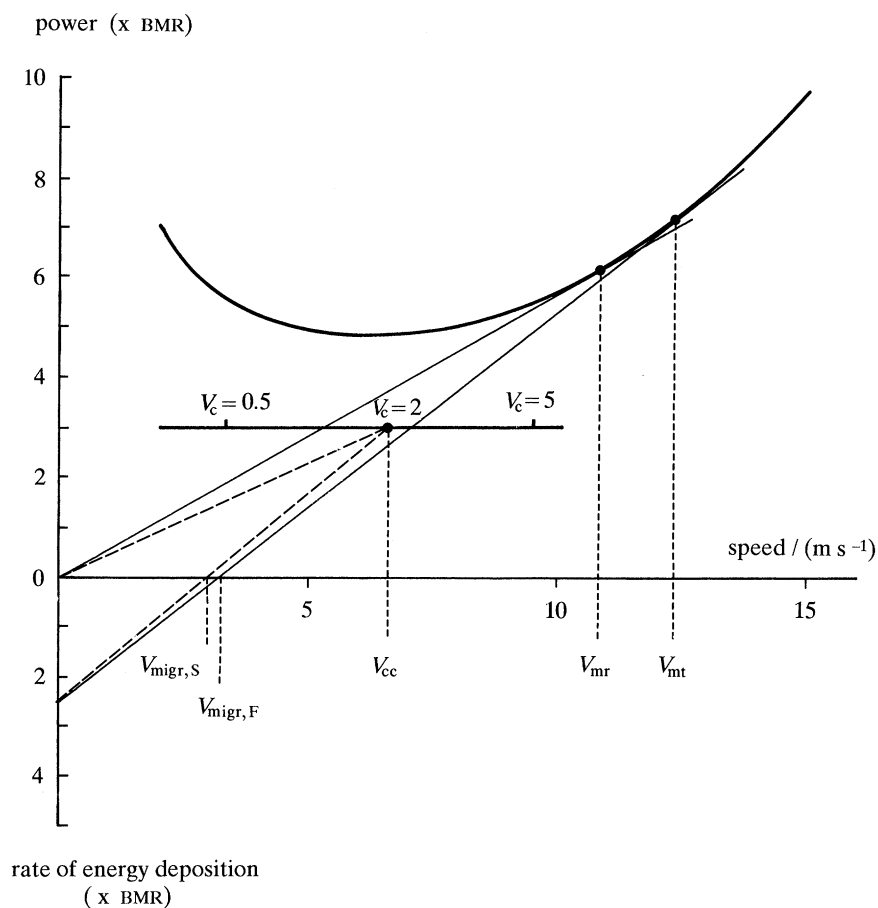


Figure 1. Graphical representation of currency and optimization criteria for flapping flight migration (U-shaped curve) and soaring flight migration under different thermal conditions giving different resulting cross-country speeds (horizontal line). The power curve is calculated for a 50 g passerine at sea level with wing-span according to the average allometric relation given by Rayner (1988). Characteristic flight speeds are indicated; V_{cc} , cross-country speed in soaring migration (in this case with rate of climb in thermals, i.e. $V_c = 2 \text{ m s}^{-1}$); V_{mr} , flapping flight maximum range speed; V_{mt} , optimal flapping flight speed between stopovers in time-selected migration; $V_{migr,S}$, overall migration speed in soaring migration; $V_{migr,F}$, overall migration speed in flapping flight migration. The extended ordinate represents rate of energy accumulation at stopover. The illustrated situation ($V_c = 2 \text{ m s}^{-1}$) shows a situation where the bird should soar from an energy minimization point of view ($P_S/V_{cc} < P_{mr}/V_{mr}$), but migrate by flapping flight from a time minimization point of view ($V_{migr,S} < V_{migr,F}$).

(b) Energy minimization

To decide whether migration by flapping flight or thermal soaring/gliding is optimal when the objective is to minimize the energy cost per unit distance covered we can compare transport costs between strategies. For a given size and morphology the minimum value of this cost for flapping flight and soaring flight, respectively, gives the optimal strategy. For flapping flight the transport cost amounts to

$$E_F = P_{mr}/V_{mr}, \quad (3)$$

where P_{mr} is given by the power curve (equation 1) at the optimal flight speed V_{mr} . The cost of transport for soaring flight is

$$E_S = P_S/V_{cc}, \quad (4)$$

where P_S is the power expended in gliding flight and V_{cc} is the maximum cross country speed (equation 2).

Notice that these currencies are strictly energy cost of flight transportation over unit distance, while the costs of existence metabolism during the intervening stop-over periods are excluded. If the latter are included in

the energy cost of migration it follows that the total cost becomes related to the overall time of migration. Hence, minimizing the energy cost of migration to some extent also means to reduce the overall time of migration. However, from a strict energy minimization point of view the cost of existence metabolism should be disregarded, as this cost must be paid irrespective of whether the bird is migrating, has not yet started migration or already reached its destination. A strict currency for overall time of migration is given in the following paragraph.

(c) Time minimization

For birds using flapping flight the overall speed of migration is given by (Alerstam & Lindström 1990; Alerstam 1991):

$$V_{migr,F} = P_{dep} V_{mt} / (P_{dep} + P_{mt}), \quad (5)$$

where V_{mt} is the speed which is given graphically by drawing a tangent from the rate of energy accumulation (P_{dep} , on the extended ordinate, increasing

downwards) to the power curve (figure 1, equation 1). Graphically the overall speed of migration is found where this tangent intersects the abscissa.

The cross country speed will increase with increasing rate of climb in thermals, and rate of energy consumption will be constant during flight. Analogously to flapping flight the overall migration speed in soaring flight can be written as

$$V_{\text{migr, s}} = P_{\text{dep}} V_{\text{cc}} / (P_{\text{dep}} + P_{\text{s}}), \quad (6)$$

where P_{dep} is rate of energy accumulation, V_{cc} is cross-country speed (equation 2) and P_{s} is power expenditure in gliding flight. Graphically the migration speed in soaring migration is found when drawing a line from the rate of energy accumulation (figure 1, P_{dep} on extended ordinate, increasing downwards) to the relevant point on the (P, V_{cc}) -relation and noting the intercept on the abscissa. Hence, by increasing climb rate (V_{c}) and therefore also the cross-country speed, the overall mean migration speed increases. Everything else being constant, an increased energy deposition rate (P_{dep}) also results in an increased overall migration speed.

The optimal migration strategy, i.e. flapping versus soaring, will be the one with the maximum overall migration speed (equation (5) versus equation (6)).

3. EVALUATION OF THEORETICAL PREDICTIONS

(a) Procedure and parameter assumptions

To decide which flight strategy is the best, I have calculated the ratio of the currency measures (energy cost and overall migration speed, equations (3)–(6)) between flapping and soaring flight. By noting whether this ratio is larger or smaller than unity we can decide which strategy should be favoured. If the ratio equals unity there should be a switch between the strategies. Firstly, I will evaluate which is the best strategy in relation to general body size. It will be assumed that wing-span and wing area scale according to the allometric equations given by Rayner (1988), i.e. wing span $b = 1.165M^{0.394}$ (m) and wing area $S = 0.1576M^{0.722}$ (m²). The relations were evaluated separately for passerines and non-passerines since their basal metabolic rates are different (Lasiewski & Dawson 1967), i.e. $\text{BMR} = 6.25M^{0.724}$ (W) for passerines and $\text{BMR} = 3.79M^{0.723}$ (W) for non-passerines, respectively. Then, the effects of variation in wing morphology and wind velocity on efficiency of migration strategy will be assessed in separate paragraphs (see below).

The power consumption in gliding flight has been estimated in a few species. Baudinette & Schmidt-Nielsen (1974) obtained a value about $2 \times$ the resting metabolism in the herring gull *Larus argentatus*, which is $4 \times$ the predicted BMR according to Lasiewski & Dawson (1967), but only $3.1 \times$ the measured BMR in this species (Ellis 1984). Adams *et al.* (1986) estimated the gliding flight power to be $3 \times$ the predicted BMR in the wandering albatross *Diomedea exulans*. Although available data are restricted to seabirds, it seems that power consumption in soaring flight $P_{\text{s}} = (3 \times \text{BMR})$

(where BMR is calculated from the equation given by Lasiewski & Dawson (1967)) may be realistic. It may be somewhat higher so I have also calculated the quotients for $P_{\text{s}} = (4 \times \text{BMR})$.

In calculating the overall migration speeds for soaring versus flapping flight (equations (5) and (6)) we also need information on energy deposition rates at stopover sites. I have assumed that birds accumulate energy at their maximum rate possible, i.e. $P_{\text{dep}} = (2.5 \times \text{BMR})$ (Lindström 1991). In free-living actively foraging birds this rate is most certainly lower, but this will have only minor effects on the quantitative conclusions as the same energy deposition rate has been assumed for both migration strategies.

(b) Energy minimization

The cross-country speed for soaring flight depends on the rate of climb while circling in thermals (equation 2). Therefore I have calculated for which body masses there is a switch between strategies over a range of climb rates for non-passerines and passerines respectively (figure 2*a,b*). Soaring migration is advantageous to the right of the curve showing the ratio 1.0 (figure 2*a,b*). I have also calculated isoclines for a range of ratios of energy cost in soaring flight to that in flapping flight migration (thin curves, figure 2*a,b*). For example, a ratio of 2 represents the body mass isocline where flapping has a twofold energetic advantage compared with soaring migration, whereas a ratio of 0.125 is the isocline where soaring has an eightfold energetic advantage as compared with flapping. Isocline ratios less than unity (i.e. when soaring flight has the lowest energy costs) can be interpreted as the magnitude of a detour in relation to the straight track between origin and destination of the migration that a soaring bird maximally can accept. If the bird needs to make a longer detour than the maximum acceptable, as represented by isocline ratios less than unity, then it pays to migrate by flapping flight along the shorter straight route instead. Birds normally encounter climb rates in the range $1\text{--}3 \text{ m s}^{-1}$ (Pennycuik 1972; Kerlinger 1989), and the switch points between strategies are displayed in table 2. As seen from this table, the body masses above which soaring becomes favourable are very low, e.g. 10 g for a passerine with $P_{\text{s}} = (3 \times \text{BMR})$ and strong thermals ($V_{\text{c}} = 3 \text{ m s}^{-1}$); a hypothetical non-passerine bird of only 2 g should migrate by thermal soaring flight. If the gliding flight cost is $P_{\text{s}} = (4 \times \text{BMR})$ the switch point between flapping and soaring flight becomes higher, but in strong thermals ($V_{\text{c}} = 3 \text{ m s}^{-1}$) it is still only 34 g for passerines and 7 g for non-passerines. In weak thermals ($V_{\text{c}} = 1 \text{ m s}^{-1}$) passerines heavier than 0.073 or 0.233 kg, depending on gliding flight cost, should migrate by thermal soaring flight rather than flapping flight.

(c) Time minimization

The curves in figure 3*a, b* show the ratio of the total migration speed achieved by flapping flight to that achieved by soaring flight, as calculated from equations (5) and (6). As in the case of energy minimization the thick curve in figure 3*a, b* represents the

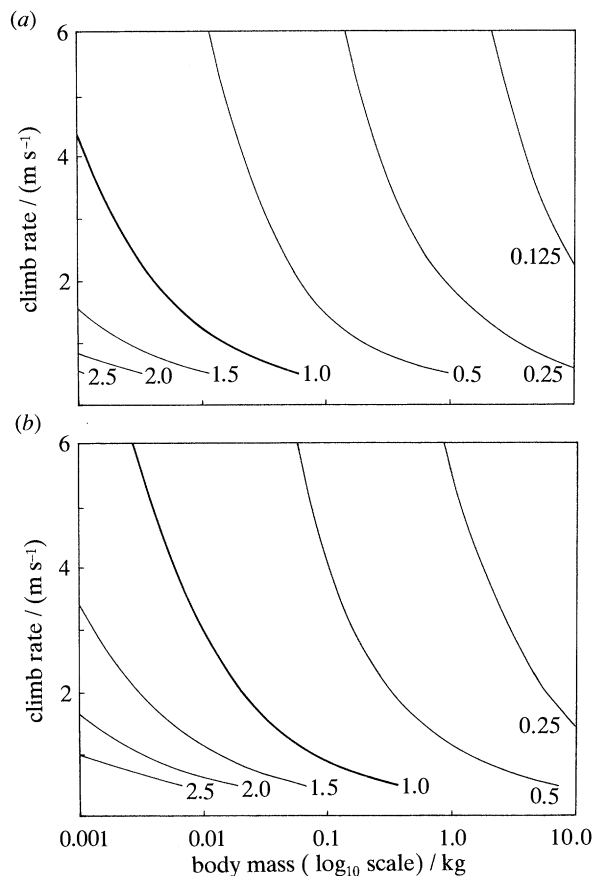


Figure 2. Curves for constant ratios of soaring flight transport cost divided by flapping flight transport cost in relation to climb rate in thermals and to body mass. The thick curve represents a ratio between strategies of unity, while the other curves represent ratios between the soaring and flapping strategies as denoted. Soaring is the most favourable strategy (lowest cost of transport) to the right of the thick curve with ratio = 1.0. Power consumption during soaring is $3 \times \text{BMR}$. (a) Non-passerines; (b) passerines.

situation when this ratio is one and the thin curves are isoclines for other ratios. As for energy minimizers the isoclines for ratios less than unity can be interpreted as the magnitude of acceptable detours for soaring migrants. Compared with energy minimization (figure 2*a,b*) the curves are translated to the right, i.e. it is advantageous for relatively larger birds to use flapping flight. The switch points between strategies for rates of climb normally encountered by birds are shown in table 2. In weak thermals ($V_c = 1 \text{ m s}^{-1}$) and $P_S = (3 \times \text{BMR})$, soaring becomes advantageous at a body mass of about 0.4 kg for passerines, whereas in non-passerines the corresponding body mass is about 60 g. With $P_S = (4 \times \text{BMR})$ these values become almost 1 kg and 0.13 kg, respectively. In strong thermals ($V_c = 3 \text{ m s}^{-1}$), the switch between strategies are lower and non-passerines ($P_S = 3 \times \text{BMR}$) of about 6 g should soar.

4. EFFECT OF WING MORPHOLOGY

Given one of the migration strategies, flapping or soaring flight migration, we may ask which effects variations in wing morphology have on the performance measures. This is to ask which adaptations are

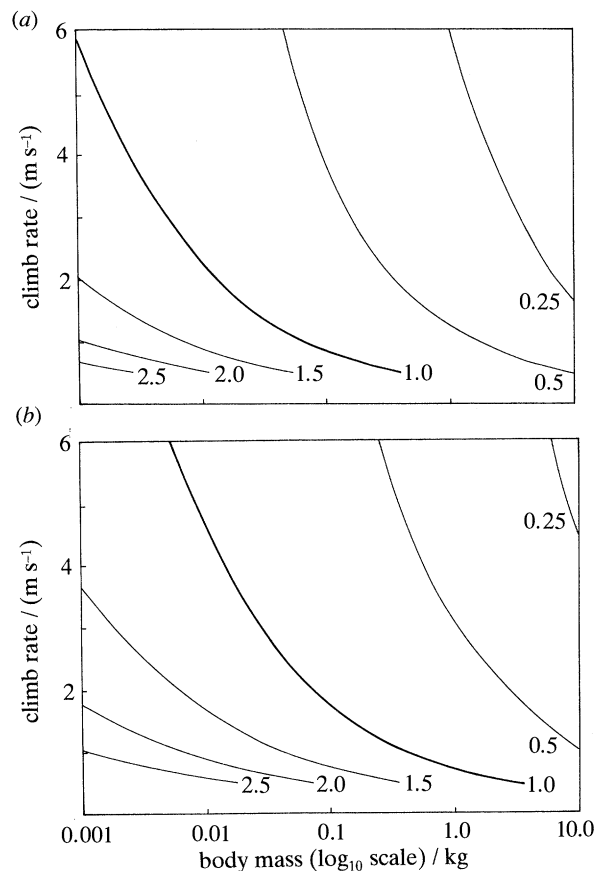


Figure 3. Curves for constant ratios of resulting migration speed by flapping flight divided by resulting migration speed by soaring flight in relation to climb rate in thermals and to body mass. The thick curve represents a ratio between strategies of unity, while the other curves represent ratios between the flapping and soaring strategies as denoted. Soaring is the most favourable strategy (shortest time for migration) to the right of the thick curve with ratio = 1.0. Power consumption during soaring is $3 \times \text{BMR}$. (a) Non-passerines; (b) passerines.

to be expected once a species has adopted flapping or soaring flight migration.

In flapping flight migration, an increased wing span reduces the energy cost for migration as well as it raises the migration speed. This is also the situation for soaring flight migration, but here the wing area should be minimized. Hence, especially for soaring migrants there should be selection for long but also thin wings, which is equivalent to an increased aspect ratio (wing span squared divided by wing area; e.g. Pennycuik 1989). However, the wings of many terrestrial soaring species have rather low aspect ratios, which may be an adaptation to requirements of take-off and landing performance (Pennycuik 1975). Broad wings, giving a low wing loading and low aspect ratio, may be a necessary adaptation in species using thermal soaring when patrolling to find food early in the morning when thermals are narrow and weak (Norberg 1990).

5. EFFECT OF WIND

For a migrant bird it is the distance covered over

Table 2. *Strategy switch points between flapping flight and soaring flight migration*

(Switches are body masses (kg) in allometrically scaled birds, P_S is power required to soar (\times BMR) and V_c is climb rate in thermals (m s^{-1}). For details about the strategy comparisons in the third panel see text. Soaring in thermals is more favourable than flapping flight above the body masses given in the first and second panels. Soaring in thermals is more favourable than the mixed strategy above the body masses given in the third panel (cf. text).)

energy minimization

	(\times BMR)	$V_c = 1$	$V_c = 3$
passerine	$P_S = 3$	0.073	0.010
passerine	$P_S = 4$	0.233	0.034
non-passerine	$P_S = 3$	0.014	0.002
non-passerine	$P_S = 4$	0.043	0.007

time minimization

	(\times BMR)	$V_c = 1$	$V_c = 3$
passerine	$P_S = 3$	0.388	0.029
passerine	$P_S = 4$	0.963	0.072
non-passerine	$P_S = 3$	0.061	0.005
non-passerine	$P_S = 4$	0.132	0.013

time minimization: mixed strategy versus pure soaring flight migration^a

	(\times BMR)	$V_c = 1$	$V_c = 3$
passerine	$P_S = 3$	33.5	5.8
passerine	$P_S = 4$	42.6	7.3
non-passerine	$P_S = 3$	6.2	0.9
non-passerine	$P_S = 4$	7.9	1.2

^a Thermals available 8 h per day, no energy accumulation en route possible.

ground that should be considered when calculating transport costs as well as resulting migration speed. Thus, in non-zero wind the calculation of the optimal flight speed must take into account the effect of wind velocity (Pennycuik 1969, 1978). Graphically this is accomplished by translating the power curve (figure 1) to the right in a tailwind and to the left in a headwind. Given a situation where powered flight is optimal compared to soaring flight in zero wind (where the point in the power-speed plane (figure 1) for the soaring strategy is to the left of the relevant tangent to the power curve), there is a tailwind increment when soaring becomes the optimal strategy. Analogously, if soaring flight is optimal compared to flapping flight in zero wind (where the point in the power-speed plane (figure 1) for the soaring strategy is to the right of the relevant tangent to the power curve), there is a headwind decrement when flapping flight becomes the optimal strategy. These results hold for both energy and time minimizers. Hence, we may expect to find a situation where a bird balances between flapping flight and soaring flight migration in zero wind, and therefore prefers to soar with following winds and flap into headwinds.

6. LIMITATIONS ON THERMAL AVAILABILITY

(a) *Energy accumulation along the flight route possible*

So far the evaluation of migration strategies with respect to size has incorporated no assumptions about restricted availability of thermals. However, in the real world convective thermals develop diurnally over land (Konrad 1970; Rowland 1973; Kerlinger & Moore 1989). There is also a topographical influence on the development rate and strength of thermal cells (Wallington 1977; Oke 1987). Furthermore, during the light hours thermal activity depends on time and weather (Kerlinger 1989). Hence, the abundance of convective thermals show clear restrictions both in space and time. For birds migrating by the soaring strategy this implies that only a fraction of the day (q_{th} , proportion of day when thermals are present) can be devoted to migration flight. The other time ($1 - q_{th}$) has to be spent either feeding, resting or on other activities.

For energy minimizers, the restriction on thermals has no consequence because the optimization criterion is energy cost per unit of distance covered without any time considerations. Thus, migration is undertaken when thermals are available and the other time is used to other ends.

The situation is quite different for time minimizers. To maintain a balanced energy budget during migration, the energy accumulation at stopover must equal the amount of energy consumed during flight. This gives

$$q_s = P_{dep} / (P_S + P_{dep}), \quad (7)$$

where q_s is the fraction of time used for soaring, P_{dep} is rate of energy accumulation and P_S is power consumption during soaring flight. If the proportion of the day with thermals available is less than the ideal time spent soaring, $q_{th} < q_s$, it pays a time minimizer to continue migration flight by powered flight until the surplus energy ($P_S(q_s - q_{th})$) is used up. It should be noticed that this condition is valid irrespective of size. By way of example, with a maximum rate of energy accumulation of $P_{dep} = (2.5 \times \text{BMR})$ and a power consumption during soaring flight of $P_S = (3 \times \text{BMR})$, we get $q_s = 0.45$, which corresponds to about 11 h per day. The thermal availability in temperate regions generally does not exceed 8 h per day (Kerlinger 1989). With these figures we see that the optimal strategy for a time minimizer is to soar for 8 h and then continue with powered flight until the surplus energy is finished (if the rest of the daily time, $1 - q_{th}$, can be used for efficient energy accumulation). This may explain why some raptors, which normally migrate by soaring, occasionally have been observed migrating by flapping flight in night-time (Gatter 1984; Russel 1991). If the rate of energy accumulation is lower than the maximum possible also q_s becomes lower. Depending on the rate of energy accumulation we may have $q_s < q_{th}$, which concordingly may explain why so few observations of night migrating raptors have been reported.

(b) Energy accumulation along the flight route not possible

It is often not possible for migrating birds to feed and restore energy reserves wherever they land. Sometimes they have to cross vast ecological barriers such as deserts and seas, without the opportunity to feed at all. For other reasons migration across seemingly benevolent areas may be performed between distant stopover sites without refuelling inbetween (e.g. Gudmundsson *et al.* 1991). In such situations, the question for a soaring migrant is which is optimal when thermals are unavailable: to continue migration by powered flight or to seek shelter and burn as little energy as possible? For energy minimizers the situation is the same as when energy deposition is possible during the non-thermal time, i.e. only pure strategies are optimal.

A time minimizer has the option of adopting either a pure strategy, which is to soar as long as thermals are available (q_{th}) and then wait until the next day when thermals are again available, or adopting a mixed strategy by continuing migration by powered flight when the thermals are exhausted (after q_{th}). The switch between the pure and mixed strategies in relation to body mass can be evaluated by using the expressions for overall migration speed (equations (5) and (6)), but the resulting power and flight speed functions will be altered according to how non-thermal time is used, i.e. resting or migrating by powered flight. With a pure soaring strategy the resulting power becomes

$$\hat{P} = q_{th}P_S + (1 - q_{th})DEE_{min}, \quad (8)$$

where q_{th} is thermal availability, P_S is power consumption in flight and DEE_{min} is the minimum daily energy expenditure which I assume applies during the resting time. The resulting speed will be

$$\hat{V} = q_{th}V_{cc}, \quad (9)$$

where V_{cc} is cross country speed according to equation (2). The corresponding resulting power for the mixed strategy, i.e. soaring when thermals are available and powered flight at other times is

$$\hat{P} = q_{th}P_S + (1 - q_{th})P_{mt}, \quad (10)$$

where P_{mt} is power consumption at flight speed V_{mt} according to figure 1, and the resulting flight speed is

$$\hat{V} = q_{th}V_{cc} + (1 - q_{th})V_{mt}. \quad (11)$$

Using these expressions and assuming that thermals are available for 8 h per day ($q_{th} = 1/3$; Kerlinger 1989), I calculated the body masses where there are switches between the mixed strategy and the pure soaring strategy (table 2). As can be seen the body masses are now much higher than when pure strategies were compared without limitations on thermal availability (table 2). In the size range of passerine birds it should always be optimal with a mixed strategy, but for non-passerines with $P_S = (3 \times \text{BMR})$ and strong thermals ($V_c = 3 \text{ m s}^{-1}$) birds with body masses exceeding 0.92 kg should seek shelter and wait for the next day's thermals to develop.

7. DISCUSSION

The main question posed in this paper is which factor(s) determines whether a bird should migrate by flapping or soaring flight. To highlight this question I adopted an optimization approach by presenting a formal definition of currency measures (transport cost and resulting migration speed, respectively) for powered and soaring flight migration. The rate of climb while soaring in thermals has an effect on which strategy is optimal. Generally, thermal soaring migration is advantageous for larger birds, whereas flapping flight is preferable for small-sized birds. An increased rate of climb gives a decreased body size where soaring becomes advantageous compared to flapping flight migration. Furthermore, the size range where soaring migration becomes advantageous to flapping flight migration is highly dependent on whether migration is energy- or time-selected.

If the major objective for a migrating bird is to minimize the energy required to cover a given distance, the body size where soaring is advantageous compared to flapping is very small (table 2). Because the soaring strategy becomes more advantageous by a low basal metabolic rate (BMR) and passerines and non-passerines have different BMRs (Lasiewski & Dawson 1967), the body size where there is a switch from flapping to soaring is lower for non-passerines. The conclusion for energy-selected migration was that if energy minimization of the migration is the important selective factor, then also very small birds should use soaring flight when migrating (table 2). However, the masses where soaring becomes the best strategy are lower than the masses of many extant species adopting flapping flight on migration. Hence, to explain why many small bird species migrate by flapping flight, energy minimization is not a viable hypothesis and we must therefore look for other factors.

My next step was to invoke a time minimization criterion and calculate body size switch points between strategies in the same way as for the energy minimization criterion. The effect of BMR (passerine versus non-passerine) and climb rate are the same as for energy minimization, i.e. the soaring strategy becomes favourable at a lower body size in non-passerines as compared to passerines, and the soaring strategy is of course relatively more favourable with increased rates of climb. However, with a given BMR and rate of climb in thermals, the switch between flapping and soaring strategies occurs at a larger body mass in time-selected as compared to energy-selected migration (cf. table 2; figures 2 and 3). Thus, invoking time-minimization may help explain why soaring migration is not found among the smallest bird species. In weak thermals soaring becomes the favourable strategy in the body mass range where we find the smallest real bird species which regularly soar (e.g. corvids), whereas in strong thermals the switch from flapping to soaring is still at a lower mass than in real birds which never soar (e.g. thrushes). There are uncertainties as to which are the average thermal conditions that birds encounter on their migration,

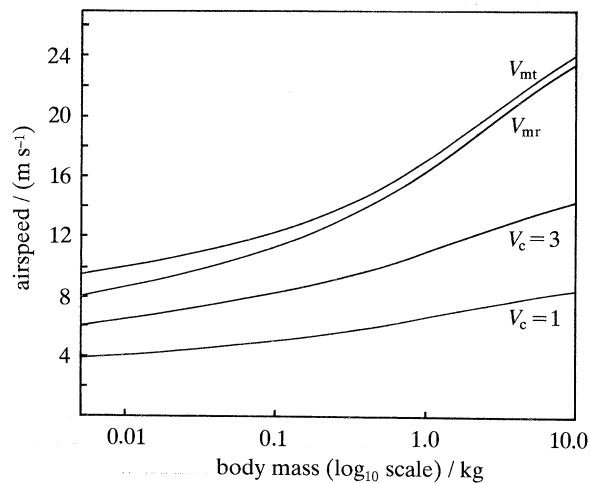


Figure 4. Air speed in relation to body mass in flapping flight migration (V_{mr} and V_{mt}) and in soaring migration in weak and strong thermals, respectively (V_c with $V_c=1$ m s^{-1} and $V_c=3$ m s^{-1} , respectively). Curves for powered flight refer to passerines, while cross-country speed in soaring flight is not affected by basal metabolic rate.

but the analyses suggest that time-minimization provides an important explanation to why larger birds soar and smaller birds flap when migrating.

So far the optimization of migration performance made no assumption about restricted thermal availability. By assuming a limited thermal availability it was found that a mixed strategy may be optimal if migration is time-selected. If energy accumulation is possible everywhere along the flight route it is always optimal for a soaring migrant to continue with flapping flight when thermals are unavailable and there is a surplus of energy. If there are ecological barriers or several flights are undertaken for other reasons before the energy reserves are renewed it is also optimal with a mixed strategy up to a size limit where pure soaring becomes optimal (table 2).

With this general analysis it is indicated that, to explain why the smallest birds do not use thermal soaring on migration, overall migration speed may be an important selective factor in bird migration. However, to make more precise predictions whether a certain species should use flapping or soaring on migration, we must also consider variations in BMR among taxa (see Ellis 1984; Kersten & Piersma 1987), wing morphology, horizontal wind velocity, distribution of thermals in time and space, and variations in the rate of energy accumulation at stopovers.

Throughout the analyses in this paper soaring has been taken as the overall flight strategy involving gliding flight within as well as between thermals. More generally soaring is defined as flying in such a way as to extract energy from the atmosphere, hence both gliding and flapping flight may qualify as soaring. A well known method of soaring used by glider pilots in straight line flight through alternative portions of rising and sinking air involves reducing speed when flying through rising air, and increasing speed in sinking air (Welch *et al.* 1977). It is possible also that birds migrating by flapping flight use this strategy (Nisbet 1962; Pennycuick 1989), and this

should be borne in mind when evaluating observations against the theoretical predictions given in the present paper.

I will conclude with a brief discussion of some other factors that might have influenced the evolution of flight strategy. These factors can be viewed as further constraints on the energy and time minimization hypotheses.

One disadvantage for small birds adopting soaring migration is that the resulting cross-country air speed while travelling becomes very low (figure 4). These resulting air speeds in soaring flight are in many cases only about half the airspeeds that the birds achieve if they use powered flight (V_{mr} and V_{mt} ; figure 4). Wind speeds below a bird's airspeed give a bird a 360° scope of orientation with respect to the resulting track direction, but when the wind speed (V_w) equals the airspeed of the bird (V) the scope of orientation drops to 180° . With even stronger winds ($V_w > V$) the scope of orientation declines with increasing wind speed as $\alpha = 2\arcsin(V/V_w)$ (e.g. Alerstam 1978). This implies that a soaring bird is more vulnerable to cross-winds and must either refrain from migration or accept a wind drift. Hence, flight speed per se may be an important selective factor for the evolution of flight mode in migrating birds.

A further disadvantage to small birds travelling by cross-country soaring is that their glide ratio (horizontal speed: vertical sink speed; Pennycuick 1971, 1975) is low. As a consequence they must rely on abundant thermals because after leaving a thermal they need to find a new one before they have descended to ground. Hence, topography and weather set a lower limit for being a practical soarer.

Still another topographical constraint is that thermals develop mainly over land (Wallington 1977). For both the energy and time minimization criteria the larger the bird the greater detour it can accept and still benefit from the soaring strategy (figures 2 and 3; Alerstam 1981). For a bird of a given size an energy minimizer shall accept a greater detour than a time minimizer (figures 2 and 3). For a normal-sized raptor it will be favourable to avoid extensive sea crossings by making detours over land that are 2–3 times longer than the direct overseas route (figure 3; Alerstam 1981). This explains why many obligate soarers migrating from Europe to Africa make detours to circumnavigate the Mediterranean Sea via Gibraltar or Bosphorous, a detour that may amount to $1.3 \times$ the straight route (Pennycuick 1972). Also, mountains obstructing the preferred migration direction make the birds circumnavigate them (Schmid *et al.* 1988), although mountain ridges oriented in the direction of migration can provide the birds with slope lift (Kerlinger 1989).

To conclude, the theoretical framework developed in this paper for the optimization of flapping and soaring flight migration can be tested by field studies of migrating birds. Data on recoveries of ringed birds of both categories can provide useful information on overall migration speed. Recent developments of satellite radio transmitters will open up a new field where migration behaviour of individual birds can be

monitored over great distances (e.g. Berthold *et al.* 1992).

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REFERENCES

- Adams, N.J., Brown, C.R. & Nagy, K.A. 1986 Energy expenditure of free-ranging wandering albatrosses *Diomedea exulans*. *Physiol. Zool.* **59**, 583–591.
- Alerstam, T. 1978 A graphical illustration of pseudodrift. *Oikos* **30**, 409–412.
- Alerstam, T. 1981 The course and timing of bird migration. In *Society for Experimental Biology seminar series* (ed. D. J. Aidley), vol. 13, pp. 9–54. Cambridge University Press.
- Alerstam, T. 1991 Bird flight and optimal migration. *Trends Ecol. Evol.* **6**, 210–215.
- Alerstam, T. & Lindström, Å. 1990 Optimal bird migration: the relative importance of time, energy, and safety. In *Bird migration: physiology and ecophysiology* (ed. E. Gwinner), pp. 331–351. Berlin: Springer.
- Baudinette, R.V. & Schmidt-Nielsen, K. 1974 Energy cost of gliding flight in herring gulls. *Nature, Lond.* **248**, 83–84.
- Berthold, P., Nowak, E. & Querner, U. 1992 Satelliten-Telemetrie beim Weißstorch (*Ciconia ciconia*) auf dem Wegzug-eine Pilotstudie. *J. Ornithol.* **133**, 155–163.
- Ellis, H.I. 1984 Energetics of free-ranging seabirds. In *Seabird energetics* (ed. G. C. Whitow & H. Rahn), pp. 203–234. New York: Plenum press.
- Gatter, W. 1984 Nachtzug der Rohrweihe (*Circus aeruginosus*). *Vogelwarte* **32**, 309–311.
- Greenewalt, C.H. 1975 The flight of birds. *Trans. Am. Phil. Soc.* **65**(4), 1–67.
- Gudmundsson, G.A., Lindström, Å. & Alerstam, T. 1991 Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *C. alba* and turnstones *Arenaria interpres*. *Ibis* **133**, 140–152.
- Idrac, M.P. 1924 Etude théorique des manoeuvres des albatros par vent croissant avec l'altitude. *C. r. Séanc. Acad. Sci., Paris* **179**, 1136–1139.
- Kerlinger, P. 1989 *Flight strategies of migrating hawks*. University of Chicago Press.
- Kerlinger, P. & Moore, F.R. 1989 Atmospheric structure and avian migration. In *Current ornithology* (ed. D. M. Power), vol. 6, pp. 109–142. New York: Plenum Press.
- Kersten, M. & Piersma, T. 1987 High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* **75**, 175–187.
- Konrad, T.G. 1970 The dynamics of the convective process in clear air as seen by radar. *J. Atmos. Sci.* **27**, 1138–1147.
- Lasiewski, R.C. & Dawson, W.R. 1967 A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* **69**, 13–23.
- Lindström, Å. 1991 Maximum fat deposition rates in migrating birds. *Ornis Scand.* **22**, 12–19.
- Nisbet, I.C.T. 1962 Thermal convection and trans-saharan migration. *Ibis* **104**, 431.
- Norberg, U.M. 1990 Vertebrate flight. In *Zoophysiology*, vol. 27. Berlin: Springer-Verlag.
- Oke, T.R. 1987 *Boundary layer climates*. 2nd edn. London: Routledge.
- Pennycuik, C.J. 1969 The mechanics of bird migration. *Ibis* **111**, 525–556.
- Pennycuik, C.J. 1971 Gliding flight of the white-backed vulture *Gyps africanus*. *J. exp. Biol.* **55**, 13–38.
- Pennycuik, C.J. 1972 Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis* **114**, 178–218.
- Pennycuik, C.J. 1975 Mechanics of flight. In *Avian biology* (ed. D. S. Farner & J. R. King), vol. 5, pp. 1–75. New York: Academic Press.
- Pennycuik, C.J. 1978 Fifteen testable predictions about bird flight. *Oikos* **30**, 165–176.
- Pennycuik, C.J. 1989 *Bird flight performance: a practical calculation manual*. Oxford University Press.
- Rayleigh, Lord 1883 The soaring of birds. *Nature, Lond.* **27**, 534–535.
- Rayner, J.M.V. 1979 A new approach to animal flight mechanics. *J. exp. Biol.* **80**, 17–54.
- Rayner, J.M.V. 1986 Vertebrate flapping flight mechanics and aerodynamics, and the evolution of flight in bats. In *Bat flight* (ed. W. Nachtigall), Biona Report, vol. 5, pp. 27–74.
- Rayner, J.M.V. 1988 Form and function in avian flight. In *Current ornithology* (ed. R. F. Johnston), vol. 5, pp. 1–66. New York: Plenum Press.
- Rowland, J.R. 1973 Intensive probing of the clear convective field by radar and instrumented drone aircraft. *J. appl. Meteorol.* **12**, 149–155.
- Russel, R.W. 1991 Nocturnal flight by migrant 'diurnal' raptors. *J. Field Ornithol.* **62**, 505–508.
- Schmid, H., Steuri, T. & Bruderer, B. 1986 Zugverhalten von Mäusebussard *Buteo buteo* und Sperber *Accipiter nisus* im Alpenraum. *Ornithol. Beobachter* **83**, 111–134.
- Tucker, V.A. 1973 Bird metabolism during flight: evaluation of a theory. *J. exp. Biol.* **58**, 689–709.
- Tucker, V.A. 1974 Energetics of natural avian flight. In *Avian energetics* (ed. R. A. Paynter), pp. 298–334. Cambridge, Massachusetts: Nuttall Ornithological Club.
- Tucker, V.A. 1987 Gliding birds: the effect of variable wing span. *J. exp. Biol.* **133**, 33–58.
- Tucker, V.A. & Parrott, G.C. 1970 Aerodynamics of gliding flight in a falcon and other birds. *J. exp. Biol.* **52**, 345–367.
- Wallington, C.E. 1977 *Meteorology for glider pilots*, 3rd edn. London: John Murray.
- Welch, A., Welch, L. & Irving, F. 1977 *New soaring pilot*, 3rd edn. London: John Murray.
- Wilson, J.A. 1975 Sweeping flight and soaring by albatrosses. *Nature, Lond.* **257**, 307–308.

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