PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Optimal Flight Speed of Birds

Anders Hedenstrom and Thomas Alerstam

Phil. Trans. R. Soc. Lond. B 1995 **348**, 471-487
doi: 10.1098/rstb.1995.0082

Optimal flight speed of birds

ANDERS HEDENSTRÖM[1] AND THOMAS ALERSTAM[2]

Theoretical Ecology[1] *and Animal Ecology*[2], *Ecology Building, S-223 62 Lund, Sweden*

CONTENTS

SUMMARY

The speed of birds in flapping flight is a behavioural attribute that, when interpreted in the light of optimization theory, may provide important implications about the limitations in time, energy and safety that affect birds in different situations. This study is an evaluation and review of optimal flight speeds of birds, based on foraging, migration and flight mechanical theory. Flight in different ecological contexts is considered, such as foraging flight, food transportation flight, migration flight and aerial display flight. Relevant optimization criteria and immediate currencies are identified for these flight situations, permitting the derivation of optimal flight speeds.

Foraging birds are expected to maximize foraging gain ratio (the ratio of gross energy intake rate to the cost of foraging in excess of the resting metabolism) when energy minimization is of imminent importance or when they are constrained by a metabolic ceiling. In other circumstances they are expected to maximize the net energy intake rate. Generally, optimal flight speeds are faster in the latter than in the former case. Thus when the foraging gain ratio is maximized the optimal flight speed between foraging patches is V_{mr} (speed of minimum energy cost per unit of distance flown), whereas it is faster than this, to a variable degree depending on the quality of and distance between patches, when net energy intake rate is maximized.

Birds should adapt their flight speed differently when transporting food or migrating as compared with flying in pure foraging situations. Cost of transport (energy/distance) or resulting speed of transport or of migration (distance/time) are the immediate currencies relevant for predicting optimal flight speeds depending on whether birds in food transportation flights are metabolically constrained or not and whether migrating birds are energy- or time-selected. Optimal flight speeds for maximizing the resulting speed of transport or of migration exceed V_{mr} to an increasing degree with an increasing rate of food/energy gain. Still other optimization criteria apply to further flight situations that are reviewed, and, in addition, flight speed is expected to vary with wind, load, altitude, climb rate and flock size.

Optimal flight speed theory provides a possibility to use flight speed measurements of birds in widely different situations for obtaining insights about crucial time and energy limitations.

1. INTRODUCTION

Birds fly in a multitude of different situations, searching for food, travelling between food patches, transporting food to their young and mates or to caches, migrating, displaying, etc. There exists a well developed theory of bird flight making it possible to calculate, e.g., the expected relation between flight power and velocity for a bird of given mass and dimensions in flapping flight (Pennycuick 1969, 1975, 1989; Tucker 1973; Rayner 1979, 1986; Spedding 1992). From this fundamental power function, significant flight velocities associated with minimum power (V_{mp}) or with the maximum range that can be flown on a given amount of energy (V_{mr}, which is the speed of minimum transport costs, i.e. energy costs per unit of distance flown) can be derived. It has become increasingly clear that, although these speeds sometimes represent the best choices for the birds, there also exist many cases where neither of these two significant flight speeds is likely to be optimal.

The optimal flight speed depends on which general criteria the birds are expected to optimize and which constraints are affecting them in different situations. In addition, the flight speed is expected to vary with a host of factors, like wind, load, height, climb rate and flock size. In fact, the question of optimal flight speed has turned out to be highly multifaceted.

In this paper we shall try to evaluate and review the most important criteria, constraints and other factors determining the optimal flight speeds of birds (see, for example: Ware 1975; Kacelnik 1984; Pyke 1984; Blake 1985; Schmid-Hempel *et al.* 1985; Stephens & Krebs 1986). To focus on such a narrow problem as bird flight speed may seem rather futile, not least in view of the complexity of the matter. However, this complexity also brings fascinating possibilities. Detailed measurements of birds' flight speeds are feasible by the use of optical instruments, radar and radio telemetry. If it emerges that birds really show a high degree of flexibility and adapt their flight speed to different situations, the flight speed may turn out to be a behavioural attribute with the richest ecological implications. It may constitute quite an extraordinary key variable, revealing a great deal about underlying selection pressures and constraints concerning the birds' fundamental energy and time economy.

We distinguish a number of flight situations, which are treated in sections 2–5. For each such situation we start by identifying different optimization criteria and immediate currencies that are relevant under different conditions of energy and time constraints (table 2). We then proceed by investigating the implications for the optimal flight speed of birds under these conditions. In section 6 we briefly review how the flight speed is predicted to vary with additional factors, like wind, load and height. Finally, we discuss studies and measurements of flight speeds in relation to the overall multiplex theory of optimal flight speed of birds.

2. FORAGING FLIGHT

A number of symbols are needed for the analyses developed in the following text. These are listed in table 1. Please note that to simplify equations, we have not introduced the energy assimilation efficiency i.e. the fraction of consumed food which is eventually turned into useful energy. In most cases our gross energy intake rate E must be multiplied by an appropriate assimilation efficiency. In some cases we treat energy collection rate and energy intake rate as interchangeable quantities further, unless otherwise stated, we assume that the bird maintains a balanced energy budget.

(*a*) *Optimization criteria*

Flight is an integral part of the foraging behaviour of many birds, which fly while searching for food and fly between food patches. To evaluate the optimal flight speeds associated with foraging, we must first consider which criteria are most likely to be optimized by foraging birds maximizing their fitness under different conditions. As seen from table 2, there are two immediate currencies of main importance in foraging. The birds are expected to behave so as to maximize either the *net energy intake rate* (which is the difference between gross energy gain from the food and the energy expenditure during foraging) or the *foraging gain ratio* (which is the quotient of gross energy gain and the energetic cost of foraging). The latter currency has usually been termed foraging efficiency, but we have refrained from using this wording to avoid confusion with the definition of foraging efficiency as the proportion of useful energy output from a given input. Which of these currencies applies depends on the interests and constraints affecting the foraging bird, and we distinguish six situations that are likely to be valid quite often (table 2). Ydenberg *et al.* (1994) evaluated the effects of limitations in time and assimilation capacity for the currencies of foraging animals. Such limitations are taken into account in the different foraging situations distinguished below.

(1) It may be most beneficial for a bird to minimize the necessary foraging time, because of risks associated with foraging, or because of the extra time that becomes available for alternative non-foraging behaviour. Consider a bird alternating between foraging during a fraction t of the time and using the remaining

Table 1. *List of symbols*

α	angle between track and heading
A	rate of non-foraging energy consumption; resting metabolism
C	rate of foraging energy consumption; inter-patch travelling cost; flight cost
C_{L}	lift coefficient
D	distance between foraging patches; migration distance
E	gross energy intake rate
E_{n}	rate of net energy gain
h	load factor
K	metabolic ceiling
m	body mass
P	power
P_{max}	power available
P_{mp}	power at minimum power speed
P'	first derivative of the power equation with respect to airspeed
R	generally used for currencies
r	relative turning radius
S	resulting speed of transport; wing area
T	time interval spent foraging to accumulate food or fuel
t	time fraction
t_{p}	patch residence time
t_{t}	travel time
V	airspeed
v	relative velocity
V_{g}	ground speed
V'_{g}	first derivative of ground speed with respect to airspeed
V_{max}	maximum airspeed
$V_{\mathrm{max,aer}}$	maximum sustainable airspeed
$V_{\mathrm{max,anaer}}$	maximum sprint airspeed
V_{migr}	resulting speed of migration
V_{mp}	minimum power speed
V_{mr}	maximum range speed
V_{mt}	flight speed for minimum migration time
$V_{z,\mathrm{max}}$	maximum vertical climb rate
V^*	optimal airspeed

time for an alternative behaviour (e.g. resting) with a rate of energy consumption equal to A. Energy balance will hold if

$$(E-C)\,t = A(1-t), \tag{1}$$

where E is the rate of gross energy intake from foraging and C is the rate of energy consumption during foraging. Both E and C are functions of the flight velocity in foraging, which we shall consider more closely when specifying conditions for the optimal flight speed in sections 2(*b*) and 2(*c*) below. From rearranging equation (1)

$$t = A(E-C+A)^{-1}, \tag{2}$$

which shows that t becomes minimal when *net energy intake rate* (E–C) is maximized. This applies when foraging time is minimized in favour of the time for any alternative non-foraging behaviour, as long as the birds is not constrained by a metabolic ceiling (cf. case 3 below).

(2) Minimization of the total energy consumption may be important under conditions of food scarcity. The total amount of energy consumed, R, is given by

$$R = Et. \tag{3}$$

Provided that energy intake and expenditure are in balance according to equation (1) and (2), it follows that

$$R = A[1-(C-A)\,E^{-1}]^{-1}, \tag{4}$$

where A now corresponds to the resting metabolism ($A < C$). This shows that R becomes minimal when the *foraging gain ratio*, i.e. $E(C-A)^{-1}$, is maximized. It should be noticed that it is the foraging costs in excess of the resting metabolism (i.e. $C-A$) that should be used in this currency. Only if $A \ll C$ will the foraging gain ratio calculated on the basis of the total foraging costs as E/C serve as a useful approximation.

(3) A bird may divide its time between foraging (during fraction t_1 of time), performing a coveted but costly non-foraging activity (e.g. display; during fraction t_2 of time, with rate of energy consumption A_2), and resting (with resting metabolism A). Resting is necessary, if the other activities are costly enough for the bird to be constrained by a metabolic ceiling, K, corresponding to a maximum rate of metabolizable energy intake (Drent & Daan 1980; Kirkwood 1983; Peterson *et al.* 1990; Weiner 1992). In this situation the overall rate of energy intake will accord with the level of the metabolic ceiling,

$$K = Et_1. \tag{5}$$

Assumption of an energy budget in balance gives the following equality between input and expenditure,

$$(E-C)\,t_1 = A_2\,t_2 + A(1-t_1-t_2). \tag{6}$$

Insertion of t_1 from equation (5) into this equation and rearrangement gives

$$t_2 = [K-A-K(C-A)\,E^{-1}]\,(A_2-A)^{-1}. \tag{7}$$

The fraction of time t_2 that can be devoted to the fitness-promoting activity will thus be maximal when the foraging gain ratio, i.e. $E(C-A)^{-1}$, is maximized for a bird constrained by a metabolic ceiling. However, without this constraint the appropriate immediate currency will be the net energy intake rate (cf. case 1 above).

(4) In many situations it is of prime importance for a bird to accumulate surplus energy at the maximum possible rate. The energy surplus may be used either externally, like food delivered to young or hoarded for future use, or internally as reserves of, e.g., fat. The resulting accumulation rate of such surplus energy, R, will be

$$R = (E-C)\,t - A(1-t), \tag{8}$$

when fraction t of the time is used for foraging (with E the gross energy intake rate and C the rate of energy consumption) and the remaining time for resting (with A the resting metabolic rate). If the bird operates below its metabolic ceiling there are no further conditions and equation (8) shows that R becomes

Table 2. *Summary of flight situations and the associated relevant immediate optimization currencies*

flight situation	net energy intake rate	foraging gain ratio	resulting speed of transport/migration	energy cost of flight		
				transport	power	other
(*a*) foraging (foraging within/between food patches						
(1) minim. of foraging time	×					
(2) minim. of total energy consumption		×				
(3) maxim. of time for non-foraging activity (metabolic ceiling)		×				
(4) maxim. of internal/external energy accumulation rate	×					
(5) maxim. of internal/external energy accumulation rate (metabolic ceiling)		×				
(6) maxim. of stopover gain ratio on migration		×				
(*b*) food/energy transportation						
(1) maxim. of energy transport rate			×			
(2) maxim. of energy transport rate (metabolic ceiling)				×		
(*c*) migration						
(1) minim. of total migration time			×			
(2) minim. of energy cost				×		
(*d*) other						
(1) aerial display					×	×
(2) staying airborne					×	
(3) escaping predators						×
(4) attacking prey						×

maximal if all useful foraging time is exploited ($t_{\max}$) and if, during that time, the *net energy intake rate* ($E-C$) is maximized.

(5) The condition imposed by a metabolic ceiling on a bird accumulating excess energy will be different depending on whether the energy represents a surplus above the ceiling (external energy surplus) or is contained within the ceiling energy budget (internal energy deposition). In both cases the bird is obliged to rest during part of the time because of the metabolic constraints. In the former case the maximum rate of metabolizable energy intake, K, will be equivalent to

$$K = Ct + A(1-t), \tag{9}$$

and in the latter case the condition given in equation (5), i.e. $K = Et$, will hold. Insertion of t from these two relations into equation (8) gives the following two expressions, respectively:

$$R = (K-A)\,E(C-A)^{-1} - K, \tag{10}$$

$$R = K[1-(C-A)\,E^{-1}] - A. \tag{11}$$

These equations show that both the resulting external and internal energy accumulation rates become maximal when the *foraging gain ratio*, $E(C-A)^{-1}$, is maximized.

(6) The overall optimization criteria for birds transporting energy and for migrating birds (cf. sections 3 and 4 below), impose conditions not only for the actual transport and migration flights but also for the associated foraging interludes. In most cases the latter conditions will be directly related to the foraging situations discussed above. However, for a bird minimizing the total energy costs during its migratory journey, it emerges (cf. section 4*a* below) that maximization of overall stopover gain ratio (the quotient of the resulting stopover rate of gross energy intake, E_0, to the resulting stopover energy consumption rate, C_0) constitutes the relevant criterion for stopover foraging.

During stopover a migrating bird typically divides its time between foraging during fraction t of the time (with rates of energy gain E and costs C as defined in earlier cases) and resting during the remaining time (with resting metabolic rate A). Hence, the resulting stopover rates of energy intake and consumption become

$$E_0 = Et, \tag{12}$$

$$C_0 = Ct + A(1-t). \tag{13}$$

If the bird is not metabolically constrained the stopover gain ratio will be

$$E_0\,C_0^{-1} = Et[(C-A)\,t + A]^{-1}. \tag{14}$$

It is probably a common situation that the bird is restricted to foraging during approximately half of the stopover time (considering e.g. a daytime forager which is obliged to rest during the night). With $t = 0.5$ the stopover efficiency will be maximal when *foraging gain ratio*, here defined as $E(C+A)^{-1}$, is maximized. This divergent definition of foraging gain ratio probably represents the most useful approximation of immediate currency in this case. However, notice that this definition of foraging gain ratio is local to this case only, i.e. when maximizing the stopover efficiency when unrestricted by a metabolic ceiling. With t approaching unity or zero (extreme situations which are unlikely to hold in many cases), the corresponding immediate currencies will be the foraging gain ratio defined as EC^{-1} and the gross energy intake rate (E), respectively.

For a bird that during stopover operates at its metabolic ceiling (Lindström 1991), the overall stopover energy intake rate will be equal to this maximum limit of resulting metabolizable energy intake rate ($E_0 = K = Et$; cf. equation (5)). On the basis of this relation and equation (13), the stopover efficiency can be expressed as

$$E_0\,C_0^{-1} = K[K(C-A)\,E^{-1}+A]^{-1}. \qquad (15)$$

In this case the stopover efficiency will be maximal when the *foraging gain ratio*, i.e. $E(C-A)^{-1}$, is maximized.

As a generalization, we conclude that foraging gain ratio is the immediate currency that foraging birds are expected to maximize when energy minimization is of imminent importance or when they are constrained by their metabolic ceiling. In other cases, foraging birds are expected to maximize the net energy intake rate (table 2). These two currencies (and others as well) have been considered and also compared in evaluations of bird flight associated with foraging or food transportation (see, for example: Blake 1985; Houston 1987; Welham & Ydenberg 1988; McLaughlin & Montgomerie 1990; Welham & Ydenberg 1993). We shall now turn to the prediction of optimal flight speeds of a foraging bird maximizing either of these two currencies of key importance.

(*b*) *Flight speed while searching for food*

(i) *Currency: net energy intake rate*

General criteria for travel speed while foraging were given by Pyke (1981), who found that when net energy intake rate is maximized the optimal speed V^* should be greater than V_{mr} in most cases. If the goal for a foraging bird is to maximize the rate of net energy gain while foraging within a food patch, then the optimal flight speed is found when $R = E(V) - P(V)$ is at a maximum. Here $E(V)$ represents the energy intake rate which is a function of flight speed V (Alerstam *et al.* 1993). $P(V)$ is the power expenditure during flight which is also a function of flight speed. In flapping flight $P(V)$ is given by the well known flight power curve (see, for example, Pennycuick 1989). In the general case foraging success increases initially as flight speed increases but then decelerates (Charnov 1976; Kacelnik & Houston 1984; Alerstam *et al.* 1993). At increasing flight speeds the gain function may even decline owing to e.g. increasing difficulties to perceive cryptic prey items above a certain speed. In the general case the optimal flight speed, V^*, is found when (see figure 1)

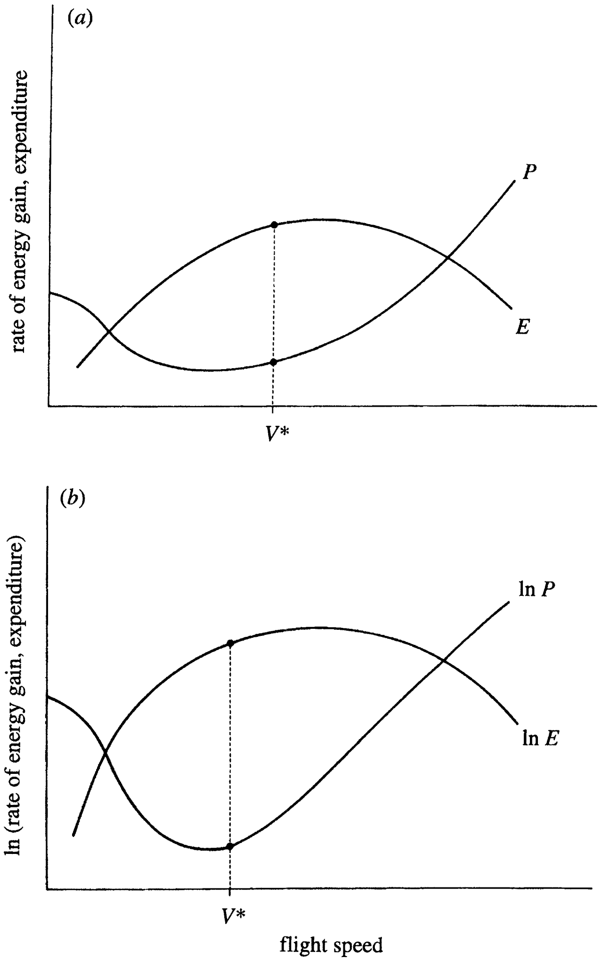

Figure 1. Optimal flight speed while searching for food when maximizing currencies (*a*) net energy intake rate and (*b*) foraging gain ratio. E is rate of energy gain and P is cost of foraging (flight). The gain function is of the form $E(V) = aV - bV^2 + c$ (where a, b and c are constants), which gives the general humped gain function in relation to flight speed. Flight power $P(V)$ refers to an ideal passerine bird *sensu* Pennycuick (1975). Notice that the solution for optimal flight speed in case (*b*) is analogous to that in case (*a*) when taking the logarithms of $E(V)$ and $P(V)$ of case (*a*), since $\log E(V) - \log P(V) = \log R$, where $R = EP^{-1}$ (see paragraph 2*b*(ii)). Optimal flight speed is faster in (*a*) than in (*b*).

$$\mathrm{d}E/\mathrm{d}V = \mathrm{d}P/\mathrm{d}V. \qquad (16)$$

The gain curve may also take the shape of a number of special cases (Alerstam *et al.* 1993). In 'fly and wait' foragers the energy gain is supposedly independent of flight speed ($E(V)$ constant). Ecological situations where this may apply are wind-hovering birds (e.g. kestrel *Falco tinnunculus* and osprey *Pandion haliaetus*) or frigate birds *Fregata* spp. loafing at a sea-bird colony waiting for incoming birds to kleptoparasitize. These birds maximize their net energy gain by flying at V_{mp} (Videler *et al.* 1983; Alerstam *et al.* 1993). A consequence of this is that wind-hovering foragers should seek an altitude where the wind speed is V_{mp}, hence where they can fly at the lowest possible cost with no net movement over ground.

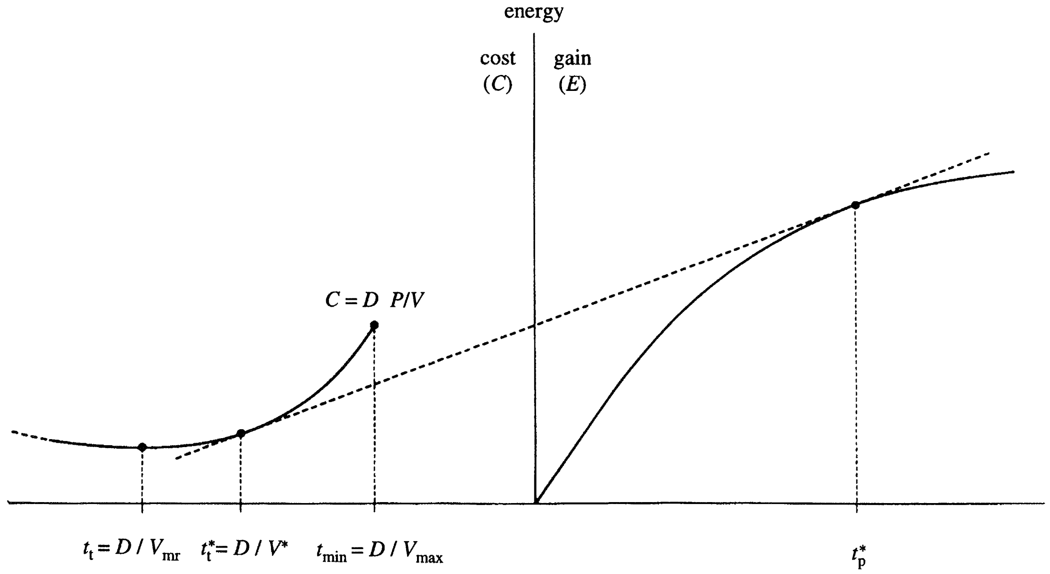

Figure 2. Graphical solution of optimal flight speed between foraging patches when maximizing net energy intake rate. The right side of the figure illustrates an arbitrary energy gain function while feeding in the patch (energy gain in relation to time in the patch) and the left side illustrates the transport cost between patches (energy cost in relation to transport flight time between patches; equation (17)). The transport time (t_t) increases from the origin towards the left, and the cost curve shows a minimum when flight speed is V_{mr}. The net energy intake corresponds to the slope of a line between points on the gain and cost curves, respectively. This is maximized for the combined tangent of the gain and cost curves as illustrated. The illustrated example is calculated for an ideal passerine bird (see figure 1).

(ii) *Currency: foraging gain ratio*

In most cases when foraging gain ratio is the relevant immediate currency it is $E(C-A)^{-1}$ that is to be maximized, where A is the resting metabolic rate (cf. above). For a bird the rate of energy cost of flying is the sum of the aerodynamic power components and metabolic power. Hence, since power consumption during flight includes the basal metabolic rate (BMR) and if A is a low multiple of BMR the currency will be approximately $R = E(V)/P(V)$, where $E(V)$ is the energy gain function and $P(V)$ is the aerodynamic power expenditure. The optimal flight speed for maximizing foraging gain ratio is compared in figure 1 with the situation of maximal net energy intake rate. The optimal solution of foraging gain ratio becomes analogous to the case of net energy intake rate if we use the logarithms of $E(V)$ and $P(V)$, because $\log E(V) - \log P(V) = \log R$. For an identical power curve and gain function we see that maximization of foraging gain ratio yields a lower optimal flight velocity compared with when net energy intake rate is maximized (figure 1).

(*c*) *Flight speed between food patches*

Food in nature often has an aggregated distribution (MacArthur & Pianka 1966), which imposes the need to travel between patches of abundant food. Most previous work is concerned with optimal rules about when to leave a foraging patch (Charnov 1976; Pyke *et al.* 1977; Pyke 1984).

(i) *Currency: net energy intake rate*

Houston (1986, 1992) formulated a criterion for optimal inter-patch flight speed under the maximization of the net energy intake rate criterion. He found that the optimal velocity should decrease with distance between patches and increase with increasing patch quality. We have extended Houston's (1986) solution to the general graphical representation in figure 2. The gain function is a decelerating function of patch residence time. Travel time between patches varies in relation to flight speed, with the shortest time obtained at V_{max}. The associated energy cost varies from relatively high cost at V_{max}, declining to a minimum at V_{mr} and then increasing again at still slower flight speeds. Travelling energy cost between patches can be written as

$$C = PV^{-1}D, \qquad (17)$$

where V is flight speed, P is the associated power (a function of V) and D is distance between patches. The cost is a U-shaped function drawn in relation to travel time ($t_t = DV^{-1}$) on the extended abscissa in figure 2. Finding the flight speed that maximizes the overall net energy gain is equivalent to seeking the maximum of

$$R = (E_n - C)(t_p + t_t)^{-1} \qquad (18)$$

where E_n is the net energy gain function while foraging in the patch, C is the transport cost between patches, t_p is patch residence time and t_t is travel time. It should be noticed that both C and t_t are functions of flight speed and inter-patch distance. Graphically the optimal solution is given by drawing the combined tangent of the cost and gain functions (figure 2). From this solution we see that the optimal flight speed should decrease with increasing distance between the patches (figure 3*a*) and increase with increasing patch quality (figure 3*b*). Analytically the optimal solution is given when

$$\frac{dE_n}{dt_p} = -\frac{dC}{dt_t} = \frac{E_n - C}{t_p + t_t}. \qquad (19)$$

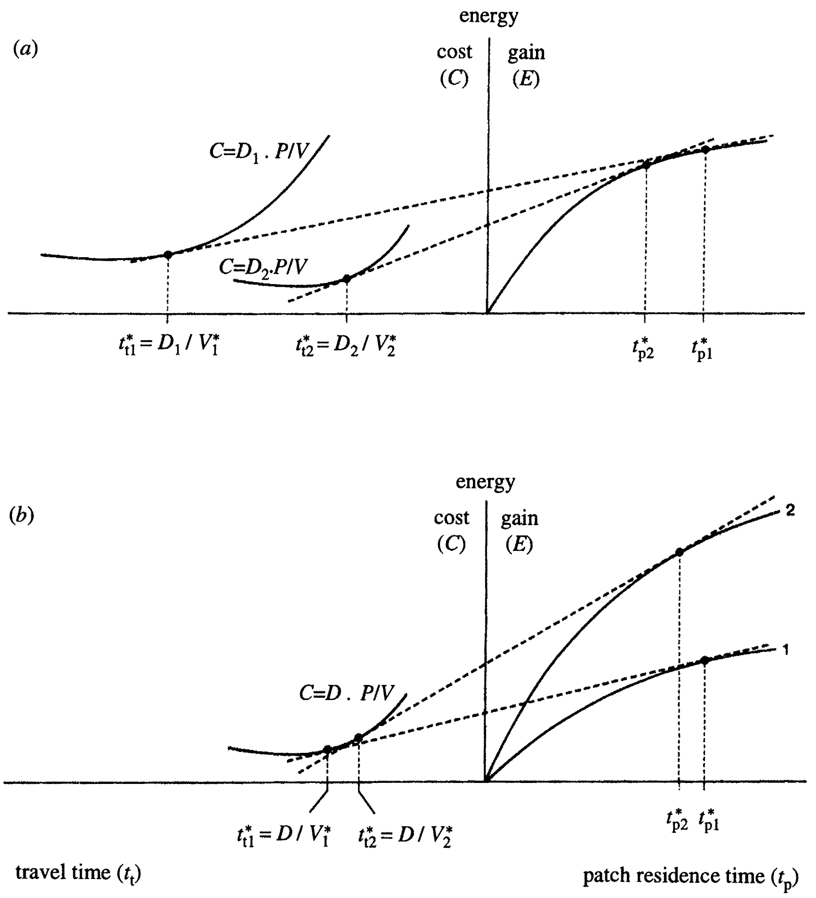

Figure 3. (*a*) Effect on inter-patch distance (and therefore travel time) on optimal flight speed between food patches. The optimal flight speed decreases, approaching V_{mr}, with increasing distance between patches. (*b*) Effect of patch quality on optimal flight speed between food patches, which increases with increasing patch quality (measured as rate of energy gain). Both situations refer to maximization of net energy intake rate.

If we assume a fixed net energy intake rate and a fixed patch residence time when foraging in a patch, we obtain the particular solution for the optimal flight speed $V*$ between patches as

$$V* = \frac{1}{P'}\left[\frac{E_{\mathrm{n}} - C}{t_{\mathrm{p}} + t_{\mathrm{t}}} + P\right], \tag{20}$$

where P' is the derivative of the power equation with respect to airspeed. It should be noticed that this solution contains the currency R and the optimal flight speed may be written as

$$V* = (R+P)/P'. \tag{21}$$

Assuming that the bird forages just to maintain itself at an energy budget without any energy accumulation, i.e. $R = 0$, we get the optimal flight speed condition as $\mathrm{d}P/\mathrm{d}V = PV^{-1}$. This gives the flight speed with minimum cost of transport, i.e. V_{mr}. The optimal flight speed will be faster than V_{mr} if $R > 0$, and it will increase with an increasing excess in the overall energy budget (defined in equation (18)).

(ii) *Currency: foraging gain ratio*

In most cases when foraging gain ratio is the relevant optimization currency $R = E_{\mathrm{n}}C^{-1}$ can be taken as an approximate currency (see section 2*b*ii above). However, when calculating the optimal inter-patch flight speed we can consider E_{n} as independent of this speed. Therefore, if R is to be maximized the transport cost must be at a minimum and, hence, the optimal flight speed between patches is V_{mr}.

3. FOOD/ENERGY TRANSPORT FLIGHT

(*a*) *Optimization criteria*

Birds transport energy when, e.g. flying back and forth between their nests and suitable feeding places, delivering and fetching food to their young, or flying to and from caches where food is hoarded. The birds' primary interest in these situations presumably is to attain the maximum possible energy delivery rate. We shall consider two main cases, when (1) the bird is free from metabolic constraints and (2) it is working at its metabolic ceiling, giving different immediate currencies for the transport flight behaviour (table 2). The former case was dealt with in the pioneering study by Norberg (1981).

(1) An important factor for evaluating transport economy is the resulting speed of transport, taking into account not only the actual flying time but also the foraging time necessary to cover the energy costs for the transport flight. For a bird flying a transport distance D with velocity V, the flying time will of course be DV^{-1}. With a rate of energy consumption during flight P (P is a function of V according to the power curve

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

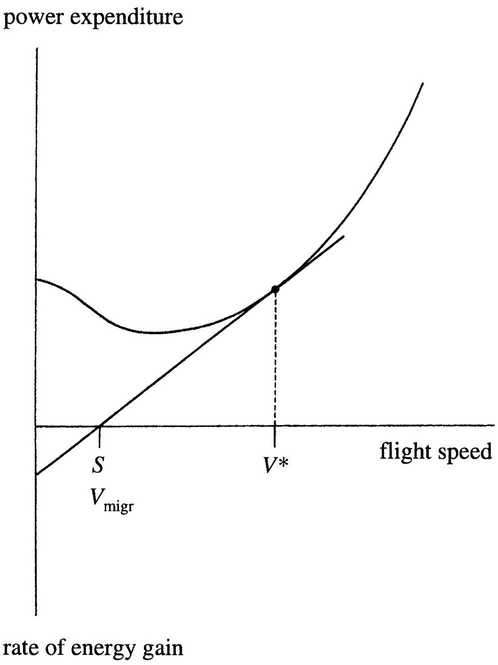

Figure 4. Graphical illustration of optimal flight speeds when maximizing the resulting speed of transport, S, or the resulting speed of migration, V_{migr}. Flight power expenditure is related to fligh speed according to the power curve for bird flight. The optimal flight speed is solved by drawing a tangent from the relevant rate of energy gain (on the extended ordinate, increasing downwards) to the power curve. The speed at which this tangent intercepts the abscissa shows the maximum speed of transport, S, or the maximum overall speed of migration, V_{migr}. The optimal flight speed will be faster than V_{mr}.

for flapping flight) and a rate of net energy gain E_{n1}, when the bird is foraging to cover its transport costs, the transport-related foraging time becomes $PD(VE_{n1})^{-1}$.

The rate of net energy gain is of course the difference between the gross energy intake rate and the rate of energy consumption during foraging, i.e. $E_{n1} = E_1 - C_1$. We have used a subscript 1 to keep in mind that these rates refer to the situation when the bird is foraging for itself, to cover its flight costs. The corresponding rates are not necessarily the same when the bird forages to accumulate food for its young or for caches (for these rates we shall use a subscript 2), although it seems likely that in general these two sets of rates are very similar (cf. Houston 1986, 1992).

Division of the transport distance D by the total time (for flight as well as transport-related foraging) gives the resulting speed of transport

$$S = VE_{n1}(P+E_{n1})^{-1}. \qquad (22)$$

For a bird that forages for its young during a typical time interval T and makes a transport flight over a total distance (return journey) D before resuming foraging for its young, the resulting energy delivery rate to the young, R, is the accumulated energy surplus divided by the total time

$$R = E_{n2}\, T(T+DS^{-1})^{-1}, \qquad (23)$$

where E_{n2} is the net energy accumulation rate when the bird is foraging for its young ($E_{n2} = E_2 - C_2$) as explained above. This relation shows that R becomes maximal when the *resulting speed of transport* as defined in equation (22) is maximized. (As regards the foraging behaviour, R will be maximal when the net energy intake rate is maximized, both when the bird is foraging for its young and for itself).

(2) Let us consider a bird operating at its maximum metabolic level, providing food for its young. It uses fraction t_1 of the time for foraging (both for its young and for itself, and we assume for simplicity that the same gross energy intake rate, E, and rate of energy consumption, C, apply in both situations) and t_2 for transport flights (with flight speed V and power P). Because of the constrained energy budget the bird is obliged to rest during the remaining time, consuming energy at its resting metabolic rate A. If the typical transport intensity is such that the bird covers a cumulated transport distance D during a total time interval T, it follows that

$$t_2 = DV^{-1}\,T^{-1}. \qquad (24)$$

The maximum rate of metabolizable energy intake, K, will be

$$K = Ct_1 + Pt_2 + A(1-t_1-t_2), \qquad (25)$$

and the resulting energy delivery rate to the young is

$$R = Et_1 - K. \qquad (26)$$

By combining equations (24)–(26) the resulting delivery rate may be expressed as

$$R = \frac{E}{C-A}\left[K - A - \frac{D(P-A)}{TV}\right] - K. \qquad (27)$$

This shows that R becomes maximal when the *cost of flight transport*, defined as $(P-A)\,V^{-1}$, is minimized. (As regards the foraging behaviour, R will be maximal when foraging gain ratio, i.e. $E(C-A)^{-1}$, is maximized.)

We conclude that birds should adapt their flight speed differently when transporting food as compared with when flying in pure foraging situations (e.g. flight between successive food patches). Energy cost of transport (energy/distance) or resulting speed of transport (distance/time) emerge as the immediate currencies relevant for predicting optimal transport flight speeds (cf. below) depending on whether the birds are metabolically constrained or not (table 2). As to the immediate currencies relevant for the associated foraging situations, foraging gain ratio and net energy intake rate are to be maximized in cases with and without metabolic constraints, respectively. This is in agreement with the generalizations about currencies related to foraging behaviour in section 2.

(*b*) *Transport flight speed*

We now turn to the optimal flight speed of flights involving transportation of energy. For a general account on central place foraging see Orians & Pearson (1979).

(i) *Currency: resulting speed of transport*

For a bird transporting food or energy it was found above that, when operating without a metabolic ceiling, the food delivery rate is maximized when the resulting speed of transport, S (equation (22)), is maximized. The associated optimal transport flight speed, V^*, is obtained from the condition

$$\frac{\mathrm{d}P}{\mathrm{d}V} = \frac{P+E_{\mathrm{n1}}}{V^*}, \tag{28}$$

where E_{n1} represents the rate of net energy gain when the bird forages to cover its transport costs. This solution was first derived by Norberg (1981). Graphically, the optimal flight speed can be solved by drawing the tangent to the power curve from a point on the extended ordinate, representing the rate of net energy gain while foraging (figure 4). Notice that the resulting speed of transport, S, is found where this tangent intersects with the abscissa (figure 4). With a positive net energy gain, the optimal flight speed will be faster than V_{mr}, and the bird should increase its flight speed as long as the concomitant flight cost increment is more than offset by the saved travel time in terms of additional foraging time. The higher the foraging intake rate (i.e. patch quality) the higher will the optimal transportation flight speed be.

If the bird forages on its wings when in the foraging patch, the foraging flight speed should be adjusted as to maximize the net energy intake rate (figure 1*a*).

(ii) *Currency: energy cost of transport*

If the bird is operating at its metabolic ceiling, the resulting energy delivery rate is maximized when the cost of transport flight is minimized. Hence, the associated optimal transport flight speed is found from the condition

$$\frac{\mathrm{d}P}{\mathrm{d}V} = \frac{P-A}{V^*}. \tag{29}$$

If A is close to BMR the optimal flight speed is V_{mr} as calculated from the aerodynamic power components.

During the actual foraging the flight speed should be adjusted so as to maximize the foraging gain ratio (figure 1*b*).

4. MIGRATION FLIGHT

(*a*) *Optimization criteria*

Following Alerstam & Lindström (1990) we distinguish two main optimization criteria for a migrating bird, namely, (1) minimization of the total duration of the migratory journey and (2) minimization of the total energy costs. The former criterion is expected to be relevant when it is of prime importance that the migrant arrives early at its destination, before its competitors, while energy saving is to be expected when food resources are scarce or there are risks (e.g. predation) associated with the energy intake. These two main criteria imply different immediate currencies to be considered when predicting optimal migratory flight speeds (table 2).

Before the initial migration flight and during stopover periods between successive migration flights, the bird deposits energy reserves to be used as flight fuel. Let E_0 be the overall stopover energy intake rate and C_0 the overall stopover rate of energy consumption during these fuel deposition periods. During the actual migration flights the bird will fly at speed V and power P according to the power curve for flapping flight.

(1) By analogy with the derivation of the resulting speed of transport (cf. section 3*a*) we can define an overall speed of migration, V_{migr}, where both the time for the actual migration flights and the time required for energy deposition are taken into account (Alerstam & Lindström 1990; Alerstam 1991):

$$V_{\mathrm{migr}} = V(E_0-C_0)\,(P+E_0-C_0)^{-1}, \tag{30}$$

where (E_0-C_0) is the resulting net energy accumulation rate at the fuel deposition stations along the migration route. Because the total time for the migratory journey is inversely proportional to the *resulting speed of migration*, V_{migr}, this will serve as the proper immediate currency to be maximized in time-selected migration.

As regards the stopover foraging behaviour, V_{migr} will increase with an increasing net energy accumulation rate (E_0-C_0) and the latter will be maximal when the bird maximizes its net rate of energy intake if operating below its metabolic ceiling, or maximizes its foraging gain ratio if metabolically constrained (cf. cases 4 and 5 in section 2*a*).

(2) Turning now to the case of energy-selected migration, we note that, for a bird migrating a total distance D, the associated time T_1 devoted to fuel deposition will be

$$T_1 = DPV^{-1}(E_0-C_0)^{-1}, \tag{31}$$

and the additional time spent in migratory flights will of course be DV^{-1}. The total energy expenditure R for the entire migratory journey, incorporating both flight and fuel deposition periods, is

$$R = T_1 E_0. \tag{32}$$

Insertion of T_1 from the earlier equation gives the relation

$$R = DPV^{-1}(1-C_0 E_0^{-1})^{-1}. \tag{33}$$

This shows that the total energy expenditure for migration becomes minimal when the *cost of flight transport*, defined as PV^{-1}, is minimized. As regards the stopover foraging behaviour, energy-selected migration will promote maximization of the overall stopover gain ratio, $E_0 C_0^{-1}$, and the relevant immediate currencies in this situation are evaluated in section 2*a* (case 6).

We conclude that birds should adapt their migratory flight speed to maximize the resulting speed of migration or to minimize the cost of flight transport, depending on whether migration is time- or energy-selected (table 2). These currencies are analogous to those valid for energy/food transport flights, and it is to be expected that birds under certain conditions fly at similar speeds on migration and during transport flights.

(*b*) *Migration flight speed*

Optimal flight speed during migration has long since been identified with maximum range speed V_{mr} (Pennycuick 1969). Recently, Alerstam & Lindström (1990) drew attention to the alternative currency of minimizing the time of migration.

(i) *Currency: resulting speed of migration*

The optimal flight speed between successive stopover localities for a bird whose objective is to minimize the time of migration, or equivalently maximize the resulting overall speed of migration, is found by differentiating equation (30) with respect to flight speed V. This optimal flight speed is found from the condition

$$\frac{\mathrm{d}P}{\mathrm{d}V}=\frac{P+E_0-C_0}{V^*}, \tag{34}$$

where E_0-C_0 is the net energy accumulation rate in the stopover habitat (Alerstam & Lindström 1990). Graphically the optimal flight velocity is found by constructing a tangent from a point on the extended ordinate, representing the net fuel accumulation rate (E_0-C_0), to the power curve (figure 4). The resulting overall migration speed, V_{migr} (equation (30)), is found where this tangent intersects with the abscissa (Alerstam 1991). Notice the analogy with the case of optimal flight speed for energy transportation flight.

If the bird is operating below its metabolic ceiling the optimal foraging flight speed at stopovers should be adjusted so as to maximize the net energy intake rate (figure 1*a*), while a bird operating at its metabolic ceiling should choose a flight speed that maximizes its foraging gain ratio (figure 1*b*).

(ii) *Currency: energy cost of transport*

If the cost of transport, i.e. the energy cost per unit distance, is being minimized the optimal flight speed is the maximum range speed V_{mr} (Pennycuick 1969, 1975, 1978). This speed is immediately obtained from the flight power equation by the condition $\mathrm{d}P/\mathrm{d}V = PV^{-1}$. The value of V_{mr} should be chosen when energy rather than time constrains the migration. For instance, to successfully cross vast ecological barriers the most efficient use of the fuel load may be of crucial importance; hence V_{mr} is the optimal flight speed. Summing up the total energy expenditure during migration, including flight costs as well as existence costs at stop-over sites, it emerges that this is at a minimum at flight speed equal to V_{mr}.

At stopovers the immediate currency to be maximized is the foraging gain ratio; hence the flight speed while foraging should be adjusted accordingly (figure 1*b*).

5. OTHER SITUATIONS OF NON-FORAGING FLIGHT

(*a*) *Flight speed in aerial display*

Flight displays or song flight serve the function of attracting a mate and are probably used as a guide for the choosing sex to select the best possible mate. In species having song flight there are morphological adaptations improving the performance of the display (Hedenström & Møller 1992). Since flight is involved in the display as a part of the signal we also expect to find behavioural adjustments that improve the performance. In some species, e.g. the skylark *Alauda arvensis*, it seems that the length and rates of song flights are maximized (Møller 1991). This could reflect the general quality of the male or it could mirror the quality of his territory. In this case the flight speed should be V_{mp}, i.e. minimizing the energy expenditure per unit of time. Since territories are small and the birds do not need to cover any distance, it follows that the bird will seek the altitude where the wind speed equals V_{mp}. Aerial displays in many waders are acrobatic and manoeuvrability may be an important component of the performance (Jehl & Murray 1986; Jönsson 1987; Jönsson & Alerstam 1990). In these cases the optimal flight speed depends on which element of the manoeuvrability is to be maximized. If climb rate is important, it will be maximal (cf. equation (35)) when the horizontal airspeed is equal to V_{mp}.

(*b*) *Flight speed when staying airborne*

In some situations the goal is to stay on the wings for as long time as possible or to the minimum energy cost. One such case is birds staying aloft during the night when foraging is not possible, e.g. swifts *Apus apus* (Bruderer & Weitnauer 1972). This situation may be regarded as flight between temporally separated foraging patches. A patch becomes depleted at dusk, when the bird has to fly to the next patch, at which it arrives at dawn the next day. There is no net distance that has to be covered. The flight cost is $C = P(V)\,t_{\mathrm{t}}$, where t_{t} is travel time. Maximization of both the net energy intake rate and the foraging gain ratio yields V_{mp} as the optimal flight speed.

If birds on migration become disoriented when flying and there is no possibility of landing, e.g. if mist or a magnetic anomaly is encountered (Larkin & Sutherland 1977; Alerstam 1987*a*, 1990), the goal should be to stay airborne for as long time as possible or until enough orientation cues become available to allow continued migration. Also in this case V_{mp} is the optimal flight speed while disoriented.

(*c*) *Flight speed when escaping predator and attacking prey*

When a bird has been discovered by a predator and an attack has been initiated, it is of little significance whether the escape flight speed is chosen with respect to energy considerations or not. Primarily, the optimal flight speed is associated with the highest probability of surviving the attack. If there is a linear horizontal chase it should be best to accelerate as fast as possible to the maximum speed, $V_{\mathrm{max,\,anaer}}$, which is constrained by the ability of the flight muscles to deliver power anaerobically. However, if the sustained maximum speed, $V_{\mathrm{max,\,aer}}$, is greater than that of the predator, it could be best to fly at this speed until the predator gives up the chase because of fatigue.

If chased by a larger avian predator in the open air, the hunted bird may take advantage of its wider power margin (cf.: Pennycuick 1978; Andersson & Norberg 1981; Hedenström & Alerstam 1992) and outclimb the predator (Cade 1960). Hence, the maximum vertical climb rate is achieved at a horizontal flight speed of V_{mp}, according to the relation

$$V_{z,\,\max} = (P_{\max}-P_{\mathrm{mp}})\,m^{-1}g^{-1}, \tag{35}$$

where $P_{\max}$ is the available power from the flight muscles, P_{mp} is the power at V_{mp}, m is body mass and g is acceleration due to gravity.

Another escape strategy is to let the predator approach and then make a tight turn at an optimal moment before the predator reaches the prey (Howland 1974). For a successful escape the prey must consider the optimal time of initiation of its turn and the minimum closure distance of the predator. For the prey to escape from the predator in the turning gambit, Howland (1974) showed that the velocity of the prey relative to the predator, v, must be related to the relative turning radius of the prey to the predator, r, by the inequality

$$v > r^{\frac{1}{2}}. \tag{36}$$

If we use the aerodynamic expression for the minimum turning radius of birds (see, for example, Pennycuick 1975) and assume that the predator and prey species are isometrically scaled, the condition for successful escape can be written as

$$v > \left(\frac{m_2}{m_1}\right)^{\frac{5}{6}} \left(\frac{S_1\,C_{\mathrm{L}1}}{S_2\,C_{\mathrm{L}2}}\right)^{\frac{1}{2}}, \tag{37}$$

where m is body mass (subscripts: 1, prey; 2, predator), S is wing area and C_{L} is lift coefficient.

From an attacking predator's point of view the roles are now reversed and what matters is the regions of no escape. Hence, a bird of prey should try to keep its prey below and attack from above, thereby not letting the prey taking advantage of a higher capacity of climb rate. In the turning gambit, a successful outcome from the predator's horizon is given by changing 'greater than' to 'less than' in equation (37).

6. ADDITIONAL FACTORS AFFECTING FLIGHT SPEED

(*a*) *Wind*

Pennycuick (1978) showed by a graphical argument that to maximize the distance covered over ground, birds should adjust V_{mr} so as to increase airspeed into headwinds and reduce it with tailwind, respectively. Also the optimal flight speed associated with maximizing the overall migration speed, V_{mt}, is affected by winds in a similar way (Alerstam 1985). Flight speed for minimum power expenditure, V_{mp}, is not affected by wind speed. For birds encountering lateral winds the graphical argument by Pennycuick (1978) is not complete. Recently, Liechti (1992) and Liechti *et al.* (1994) showed that the optimal flight speed for minimizing the cost of transport of birds flying with sidewinds can be found from the condition

$$\mathrm{d}P/\mathrm{d}V = PV_{\mathrm{g}}^{-1}\,V_{\mathrm{g}}', \tag{38}$$

where V_{g} is the ground speed vector and V_{g}' is its derivative with respect to airspeed (V_{g}, V_{g}' and P are all functions of V). It appears that $V_{\mathrm{g}}' = (\cos\alpha)^{-1}$, where α is the angle between track and heading. Hence, since $V_{\mathrm{g}}' > 1$ for lateral winds the optimal airspeed will be higher than with due head- or tailwind.

For foraging flight the optimal flight speed is affected in qualitatively the same way. Thus, when searching for food birds should speed up into headwinds and slow down with tailwinds as compared with the zero wind situation (Alerstam *et al.* 1993). For flight between food patches (cf. section 2*c* and equation (21)) when the net energy intake rate is maximized the optimal flight speed can be found from

$$\mathrm{d}P/\mathrm{d}V = (R+P)\,V_{\mathrm{g}}^{-1}\,V_{\mathrm{g}}', \tag{39}$$

where R is the net energy intake rate and V_{g} is the ground speed. In sidewinds $V_{\mathrm{g}}' > 1$, which implies that the birds should speed up compared with the situations with due head- or tailwind (cf.: Liechti 1992; Liechti *et al.* 1994).

(*b*) *Load*

Birds carry loads in different situations. Before long migratory flights they have to accumulate fuel, mainly as fat, to be used as energy while flying. When feeding dependent young the parent birds have to transport food back to the nest. How does the extra load affect the optimal flight speeds derived above? First, we observe that extra load implies increased power to fly. Induced power increases owing to the weight *per se* and the extra volume of the load raises the parasite power. If the load is accumulated within the body, the body frontal area will increase in direct proportion to the load if we assume that the body length is unaffected by fat deposition (Pennycuick 1975; Hedenström 1992). If the bird carries a food item in its beak or in its talons, the effects on parasite power are difficult to estimate because the flow around the body may break up in a non-trivial way. Therefore, we analyse the effects of increased load for an ideal bird (*sensu* Pennycuick 1975) when parasite drag increases in direct proportion to the load.

Both V_{mp} and V_{mr} increase as $h^{\frac{1}{4}}$, where h is the load factor ($m = hm_0$, where m is the total body mass and m_0 is the lean body mass). Notice that flight speed will scale with $h^{\frac{1}{2}}$ if only induced (and not parasite) power is affected by the load, and the scaling will be more complicated if we also take into account the profile power. In time-minimization migration and energy transport flight the predicted optimal flight speeds, which are faster than V_{mr} (cf. figure 4), also increase when flying with added load. The effect of load on flight speed when searching for food is that optimal flight speeds increase with increasing load. This is valid for both of the currencies net energy intake rate and foraging gain ratio. However, the former currency yields a minute increase in optimal flight speed. When flying between foraging patches, the optimal flight speed when maximizing foraging gain ratio is V_{mr} (see section 2*c*), which increases with added load. In contrast to all other cases, the effect of load on optimal flight speed when maximizing net energy intake rate may be a decrease of flight speed with increasing load in small and medium sized birds up to the size of about 0.2 kg. However, this applies with the theoretical reservation that at very heavy loads, beyond the maximum load capacity of birds (Hedenström & Alerstam 1992), the optimum speed will increase with a further increase of load. Above the size of 0.2 kg the optimum flight speed increases immediately with an increase of load. Hence, a decrease of the optimal flight speed between foraging patches is not a general result, but it may arise depending on the size of the bird and the nature of the gain function.

During the course of long distance migratory flights fuel is consumed with a concomitant decline of the body mass. Consequently, the optimal flight speed should decrease as body mass becomes reduced (Pennycuick 1978).

Various aspects of flight performance, e.g. roll acceleration, minimum turning radius, acceleration, maximum speed and rate of climb, become reduced by increased load (Hedenström 1992). Hence, the performance of attacked prey as well as attacking predators is best with as little extra load as possible.

In central place foraging birds are flying unloaded on the outward journey but carry a load on the inward journey. Hence, the optimal flight speed will be somewhat higher on the inward than on the outward flight.

(*c*) *Altitude*

There are two aspects of altitude that potentially might influence the flight speed of birds. First, flight speed is inversely related to the square root of air density, which in turn decreases with increasing altitude. Hence, characteristic flight speeds (e.g. V_{mp}, V_{mr} and V_{mt}) should increase with increasing altitude. The same result holds under the maximization of net energy intake rate and foraging gain ratio currencies of optimal flight speed both when searching for food and when flying between foraging patches. Second, when birds fly very low over a surface such as water, there will be an interference phenomenon with the surface resulting in a reduction of the induced power (Withers & Timko 1977; Blake 1983; Hainsworth 1988; Rayner 1991). It follows that the optimal characteristic speeds should be lower when flying with ground effect than when flying out of it (cf. flock formation flight below). A detailed theoretical analysis of the ground effect revealed that by reducing the speed by a factor of 0.95 a bird can obtain a reduction in cost of transport of about 10% (Rayner 1991). However, at speeds below V_{mp} the power increases sharply and soon even exceeds the power for flight out of ground effect (Rayner 1991).

(*d*) *Vertical flight speed*

Pennycuick (1975, 1978) proposed that during long distance migration flight one should expect a behaviour that he termed ‘cruise climb’. This effect is due to an increase of the resulting lift/drag ratio with decreasing air density (increasing altitude), hence making it favourable from a range maximization point of view to fly as high as possible. Physiologically the partial pressure of oxygen limits the rate at which oxygen can be absorbed by the lungs and the power available. Thus, the optimal cruising altitude becomes the highest one where the bird can maintain its characteristic flight speed, e.g. V_{mr} and V_{mt}. During a long flight the optimal cruising altitude will become progressively higher as body mass declines when fuel is used up; hence a bird should climb at a slow rate during the course of the flight.

An additional factor determining the cruising altitude, probably of greater importance than the effect due to air density, is where the bird finds the most favourable wind stratum. By flying with tailwind significant energy and time savings can be made. By minimizing the overall energy costs of a migratory flight, including the energy cost of climbing and the cost for horizontal flight, Hedenström & Alerstam (1994) derived a prediction of optimal rate of climb up to the cruising altitude.

(*e*) *Flying in flock formation*

By flying in a flock formation the induced drag becomes reduced and each bird experiences a reduction of the total power used to fly (Lissaman & Shollenberger 1970; Badgerow & Hainsworth 1981; Hummel 1983). Flight in less organized flocks may also give a reduction in flight power, although to a lesser extent than in formations (Higdon & Corrsin 1978). Hummel (1983) showed that the optimum speed for a flight formation is smaller than that of a bird flying singly. This result holds for optimum flight speed when cost of transport as well as overall time of migration is minimized. The overall migration speed V_{migr} will increase for birds migrating in flock formations as compared with solo flight migration.

Kshatriya & Blake (1992) derived an approximative formula for the reduction of induced power in formation flight, which is simply induced power for single flight divided by number of birds in the flock. By using their formula for power reduction in flock formations it is possible to calculate the effect on optimal flight speed in foraging flight for the different currencies. Generally, the optimal flock formation flight speed is lower than the corresponding single bird flight speed. This result holds for flight while searching for food, for flight between food patches and for central place foraging. Kshatriya & Blake (1992) calculated an optimal flock size during migration flights by using an efficiency currency, i.e. the ratio of net energy gain at stopover to energy expenditure while flying. However, such a currency is not relevant for migrating birds, which are expected to minimize either time or energy associated with migration (cf. section 4). If we use the formula for flight power reduction in formation flight according to Kshatriya & Blake (1992) and minimize the cost of transport or the overall time of migration, we find that there is no optimal flock size. Instead, the best flock size is the largest size possible.

7. DISCUSSION

Our study shows that there are many optimal flight speeds besides V_{mp} and V_{mr}, depending on which currency the birds are expected to optimize in different ecological situations. This means that field measurements of flight speeds do not allow any immediate critical tests of aerodynamic theory (as developed by: Pennycuick 1969, 1975, 1989; Tucker 1973; Greenewalt 1975; Rayner 1979, 1986; Spedding 1992), unless the optimization criteria for the observed flying birds are known. Consequently, discrepancies between V_{mr} predictions from different aerodynamic equations and observed airspeeds of free-flying birds, as found by e.g. Schnell & Hellack (1979) and Welham (1994), may be due to inadequate knowledge of valid optimization criteria rather than shortcomings in the aerodynamic theory.

However, this also means that uncertainties concerning the aerodynamic theory will propagate to affect the absolute quantitative predictions about flight speeds in various situations as evaluated in this paper. When analysing predicted and observed absolute flight speeds of birds, it will in many cases not be possible at our present state of knowledge to distinguish critically between the effects of birds adapting their speed according to different optimization criteria and the effects of uncertainties in the aerodynamic theory.

We think that there are at least two promising approaches to disentangle this problem. One such possibility, circumventing some of the complications arising from uncertainties in the aerodynamic theory, is to compare flight speeds of the same species (or ideally the same individuals) when flying in different ecological situations. Observed differences in flight speeds (rather than absolute speed levels) can be evaluated in a qualitative or semiquantitative way in the light of the theory in this paper. Such comparisons will also give important basic information about the degree of flexibility in the birds' regulation of their flight speed. An example of such a study concerns the speed of skylarks during song flight versus migratory flight (A. Hedenström & T. Alerstam, in preparation). The same approach could be adopted for many other situations.

Of course, uncertainties in the aerodynamic theory could also be solved if accurate information could be obtained on the power curve, or other performance data, of the species concerned (see, for example, Rothe *et al.* 1987; but also see Ellington 1991). We are presently planning experiments in a new advanced wind tunnel to investigate critical assumptions behind the theoretical power curve. More empirical data about the basic aerodynamics of bird flight will make it increasingly feasible to work out predictions about absolute speeds applicable for testing in the field, in the different situations considered in this paper.

The abovementioned complications serve to stress the necessity to take fully into account, not only the aerodynamic aspects, but also the ecological optimization situation, for an evaluation of the flight of free-living birds. It is of imminent importance in any study of flight speed that both bird and wind speeds are measured in a highly precise way (radar and other instruments admit such highly accurate measurements) in well controlled and defined situations, to reduce the errors inherent in the field data and to allow exploration of the rich ecological implications in the field of optimal flight speed theory.

With the present study we have aimed at developing a comprehensive new theory and overview of which optimization criteria and currencies might be appropriate in various ecological situations and their consequences for flight speed of birds. Generally, when foraging without any metabolic constraints birds should seek the policy that maximizes the net energy intake rate (see, for example: Pyke 1981; Houston 1986, 1992). However, when constrained by a metabolic ceiling (Drent & Daan 1980; Kirkwood 1983; Peterson *et al.* 1990; Weiner 1992) it emerges that maximization of the ratio of net energy gain to the energy costs in excess of resting energy expenditure, which we call the foraging gain ratio, gives the optimal policy. This result has been independently derived by Ydenberg *et al.* (1994). Apart from purely foraging situations there are a number of alternative currencies likely to be optimized depending on the ecological context, like energy transport, migration and other situations of non-foraging flight.

What is the empirical evidence supporting the assumption that birds really adjust flight speed as expected from the theoretical predictions outlined in this paper?

(*a*) *Foraging flight*

Optimal flight speed while searching for food is likely to be intermediate between V_{mp} and V_{mr} (Alerstam *et al.* 1993). In fact, this has often been observed in many species that are apparently looking out for food (see, for example: Schnell & Hellack 1979; Blake *et al.* 1990; Pennycuick & De Santo 1990; Alerstam *et al.* 1993). Schnell & Hellack (1979) suggested that resulting speeds observed in gulls, terns and skimmers loafing around a seabird colony could be a compromise between V_{mp} and V_{mr}, but if the birds were looking out for food we conclude that they probably selected flight speed so as to maximize foraging in terms of either of the currencies net energy intake rate or foraging gain ratio (cf. figure 1). Studying flight speed of foraging black skimmers *Rynchops nigra*, Blake (1985) compared observed speeds with predictions based on assumptions of (1) maximization of the foraging gain ratio and (2) maximization of a currency termed *daily energy budget*, defined as energy intake when foraging divided by the sum of flight costs when foraging and metabolic costs during non-foraging time. The latter currency gave predicted flight speeds in best agreement with observations. However, if the birds were accumulating energy for breeding, as Blake (1985) implies, we should expect the immediate currency to be either the net energy intake rate or the foraging gain ratio, depending on whether the birds were operating below or close to a metabolic ceiling. We do not see any logical justification for the currency termed daily energy budget by Blake (1985). The skimmers may have adapted their flight speed to maximize net energy intake rate, a currency not considered by Blake, and which gives higher optimal speeds compared to maximum foraging gain ratio. Kestrals use wind-hovering when looking out for food, a 'fly and wait' method where transport over ground presumably has little importance compared with actual search time.

In agreement with this kestrels showed the highest persistence of wind-hovering at wind speeds near their predicted V_{mp} (Videler *et al.* 1983; Masman & Klaassen 1987), when they could fly at minimum cost.

Optimum flight speeds between food patches should be faster than V_{mr} if net energy intake rate is maximized and equal to V_{mr} when the foraging gain ratio is maximized. In the latter case the bird is expected to be operating at its metabolic ceiling. Compared with this flight speed when foraging on aerial insects, swallows *Hirundo rustica* speed up well above predicted V_{mr} in what probably are transport flights between food patches (Blake *et al.* 1990). Trapline foraging in hummingbirds can be regarded as transport flight between discrete food patches. Gill (1985) measured such inter-patch flight speeds in the long-tailed hermit *Phaethornis superciliosus* of 1.6 time the expected V_{mr}. Ring-billed gulls *Larus delawarensis* foraging in the wake of tractors pulling cultivating devices showed flight speeds in agreement with the net energy intake rate currency, while observed patch residence times were rather in line with predictions from the foraging gain currency (Welham & Ydenberg 1988). In neither of these studies was the energetic scope for the birds measured and the observations should be regarded as suggestive of which currency the birds might be optimizing. The flight speed of pipistrelle bats *Pipistrellus pipistrellus* when commuting between their roost and feeding patch was significantly higher than the predicted maximum range speed (Jones & Rayner 1989), which suggests the bats were maximizing their net energy intake rate.

(*b*) *Food/energy transport flight*

When energy is transported, e.g. as food to nestlings or to a cache, birds should fly faster than V_{mr} if unrestricted by a metabolic ceiling in order to maximize the resulting speed of transport (Norberg 1981; Houston 1986). Otherwise they should minimize the cost of transport by flying at V_{mr}. McLaughlin & Montgomerie (1985, 1990) measured flight speeds of lapland longspurs *Calcarius lapponicus* feeding their young in a nest and found speeds in close agreement with V_{mr}. Measured flight speeds in black terns *Chlidonias nigra* when flying between the nest and foraging patches were best explained by the foraging gain ratio currency (Welham & Ydenberg 1993), although the calculated daily energy expenditure was only about 60–70% of the Kirkwood ceiling of maximum sustainable daily energy expenditure (Kirkwood 1983; Peterson *et al.* 1990; Weiner 1992). Hence, we should have expected them to fly at speeds maximizing the resulting speed of transport and why they seemed not to do that is unclear. For reliable estimates of daily energy expenditure one should ideally measure energy expenditure directly on the study birds. As an explanation Welham & Ydenberg (1993) suggest a number of constraints that could make parent birds inclined to work below the Kirkwood ceiling, such as reduced feather wear or requirements of a safety margin to protect against energy shortfall.

(*c*) *Migration*

For migration flights there are basically two alternative characteristic flight speeds, depending on whether overall migration speed is to be maximized (V_{mt}) or total energy expenditure for the migratory flights is to be minimized (V_{mr}). Observed flight speeds of migrating birds are often close to predicted V_{mr} (Alerstam 1981; Wege & Raveling 1984; Rayner 1985). Generally, the difference between V_{mr} and V_{mt} is quite small (Hedenström 1993), but rather observations indicate that some passerines tend to fly faster than their predicted V_{mr} during migration (Alerstam 1981; Hedenström & Alerstam 1992), and arctic terns *Sterna paradisaea* also showed flight speeds above their predicted V_{mr} during spring migration (Gudmundsson *et al.* 1992). The model of time minimization migration also generates a set of predictions concerning fuel deposition rules at stopovers (Alerstam & Lindström 1990), and field experiments in a few species have given data in support of the time minimization hypothesis (Lindström & Alerstam 1992).

(*d*) *Other flight situations*

Swifts roost on the wing during the night and flight speed is then adjusted close to V_{mp}, while swifts on migration fly much faster around their predicted V_{mr} (Bruderer & Weitnauer 1972). Emlen & Demong (1978) experimentally released white-throated sparrows *Zonotrichia albicollis* in the air and used radar to track them when flying off. Under clear skies they flew off in a seasonally appropriate direction at an airspeed very close to their expected V_{mr}, but when released under overcast skies, with presumed orientation difficulties, they showed no consistent direction and travelled slowly at airspeeds close to the expected V_{mp}.

Observations of flight speeds when escaping a predator or attacking a prey are meagre. Before stooping a peregrine *Falco peregrinus* was observed to accelerate by flapping flight to a speed well above the characteristic V_{mr} (Alerstam 1987*b*; but see Pennycuick *et al.* 1994).

Responses to tail- and headwinds are generally in agreement with predictions, i.e. that birds speed up into headwinds and slow down with tailwind (Tucker & Schmidt-Koenig 1971; Bloch & Bruderer 1982; Gudmundsson *et al.* 1992; Wakeling & Hodgson 1992). However, the complications of sidewinds as pointed out by Liechti (1992) and Liechti *et al.* (1994) have not been critically tested.

Videler *et al.* (1988) trained kestrels to fly in a corridor with and without extra load. Unloaded flight speeds were close to predicted V_{mr}, while extra mass had a decreasing effect on flight speed which approached V_{mp} with an extra mass of 61 g (40% of unloaded body mass). This is contrary to expectations for optimal characteristic speeds. However, since the birds were given a food ration at the ends of the corridor they could actually be regarded as flying between food patches. For maximization of the net energy intake rate the predicted optimal flight speed between food patches may be a decrease with increased load in the studied range of loads (cf. section 6*b*). In a study of brown-long-eared bats *Plecotus auritus* provided with extra loads, a decline of the flight speed in relation to load was also observed (Hughes & Rayner 1991).

That birds increase flight speed in relation to increasing altitude during migration, supposedly in relation to air density, has been indicated by some radar studies (Bergman & Donner 1964; Bruderer 1971).

Observations of birds during climbing flight on migration indicate that they expend their maximum power available and climb rate is reduced by heavy fuel loads (Hedenström & Alerstam 1992). Departing shorebirds studied on northwest Iceland indicated that the rate of climb was adjusted so as to minimize the energy cost for the migratory flight (Hedenström & Alerstam 1994).

As can be concluded from the various sources of measurements of flight speeds as summarized above, we find good evidence that birds actually adapt and optimize flight speed in different situations. A problem with many studies is that it is often unclear in which ecological context the birds were observed flying. An exception is the study of nest-feeding black terns by Welham & Ydenberg (1993), where the food abundance in the foraging patch was experimentally manipulated. To distinguish efficiently between different currencies and analyse the effects on flight speed selection we should like to forward a plea for comparative studies, preferably of the same species or individuals flying in different situations. Exploration of bird flight speeds seems to be a powerful tool for discriminating between different currencies and optimization rules, and it is a very promising field of future research.

We are grateful to Steffi Douwes for drawing the figures. We also thank C. J. Pennycuick and J. M. V. Rayner for comments that improved an earlier version of the manuscript. This project was financially supported by a grant from the Swedish Natural Science Foundation (T. A.).

REFERENCES

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: Cambridge University Press.

Alerstam, T. 1985 Strategies of migratory flight, illustrated by arctic and common terns, *Sterna paradisaea* and *Sterna hirundo*. In *Migration: mechanisms and adaptive significance* (ed. M. A. Rankin). Contr. mar. Sci. Suppl. **27**, 580–603.

Alerstam, T. 1987*a* Bird migration across a strong magnetic anomaly. *J. exp. Biol.* **130**, 63–86.

Alerstam, T. 1987*b* Radar observations of the stoop of the Peregrine Falcon *Falco peregrinus* and the Goshawk *Accipiter gentilis*. *Ibis* **129**, 267–273.

Alerstam, T. 1990 Ecological causes and consequences of bird orientation. *Experientia* **46**, 405–415.

Alerstam, T. 1991 Bird flight and optimal migration. *Trends Ecol. Evol.* **6**, 210–215.

Alerstam, T., Gudmundsson, G.A. & Larsson, B. 1993 Flight tracks and speeds of Antarctic and Atlantic seabirds: radar and optical measurements. *Phil. Trans. R. Soc. Lond.* B **340**, 55–67.

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.

Andersson, M. & Norberg, R.Å. 1981 Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15**, 105–130.

Badgerow, J.P. & Hainsworth, F.R. 1981 Energy savings through formation flight? A re-examination of the vee formation. *J. theor. Biol.* **93**, 41–52.

Bergman, G. & Donner, K.O. 1964 An analysis of the spring migration of the common scoter and the long-tailed duck in southern Finland. *Acta zool. fenn.* **105**, 1–59.

Blake, R.W. 1983 Mechanics of gliding in birds with special reference to the influence of the ground effect. *J. Biomech.* **16**, 649–654.

Blake, R.W. 1985 A model of foraging efficiency and daily energy budget in the Black Skimmer (*Rynchops nigra*). *Can. J. Zool.* **63**, 42–48.

Blake, R.W., Kolotylo, R. & De La Cueva, H. 1990 Flight speeds of the barn swallow, *Hirundo rustica*. *Can. J. Zool.* **68**, 1–5.

Bloch, R. & Bruderer, B. 1982 The air speed of migrating birds and its relationship to the wind. *Behav. Ecol. Sociobiol.* **11**, 19–24.

Bruderer, B. 1971 Radarbeobachtungen über Zug den Frühlingszug im Schweizerischen Mittelland. *Orn. Beob.* **68**, 89–158.

Bruderer, B. & Weitnauer, E. 1972 Radarbeobachtungen über Zug and Nachtflüge des Mauerseglers (*Apus apus*). *Rev. Suisse Zool.* **79**, 1190–1200.

Cade, T.J. 1960 *Ecology of the Peregrine and Gyrfalcon populations in Alaska*. Berkely: University of California Press.

Charnov, E.L. 1976 Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.

Drent, R.H. & Daan, S. 1980 The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**, 225–252.

Ellington, C.P. 1991 Limitations on animal flight performance. *J. exp. Biol.* **160**, 71–91.

Emlen, S.T. & Demong, N.J. 1978 Orientation strategies used by free-flying bird migrants: a radar tracking study. In *Animal migration, navigation, and homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 283–293. Berlin: Springer-Verlag.

Gill, F.B. 1985 Hummingbird flight speeds. *Auk* **102**, 97–101.

Greenewalt, C.H. 1975 The flight of birds. *Trans. Am. phil. Soc.* **65**, 1–67.

Gudmundsson, G.A., Alerstam, T. & Larsson, B. 1992 Radar observations of northbound migration of the Arctic tern, *Sterna paradisaea*, at the Antarctic Peninsula. *Antarctic Science, Wash.* **4**, 163–170.

Hainsworth, F. R. 1988 Induced drag savings from ground effect and formation flight in brown pelicans. *J. exp. Biol.* **135**, 431–444.

Hedenström, A. 1992 Flight performance in relation to fuel load in birds. *J. theor. Biol.* **158**, 535–537.

Hedenström, A. 1993 Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Phil. Trans. R. Soc. Lond.* B **342**, 353–361.

Hedenström, A. & Alerstam, T. 1992 Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. exp. Biol.* **164**, 19–38.

Hedenström, A. & Alerstam, T. 1994 Optimal climbing flight in migrating birds: predictions and observations of knot and turnstone. *Anim. Behav.* **48**, 47–54.

Hedenström, A. & Møller, A.P. 1992 Morphological adaptations to song flight in passerine birds: a comparative study. *Proc. R. Soc. Lond.* B **247**, 183–187.

Higdon, J.J.L. & Corrsin, S. 1978 Induced drag of a bird flock. *Am. Nat.* **112**, 727–744.

Houston, A.I. 1986 The optimal flight velocity for a bird exploiting patches of food. *J. theor. Biol.* **119**, 345–362.

Houston, A.I. 1987 Optimal foraging by parent birds feeding dependent young. *J. theor. Biol.* **124**, 251–274.

Houston, A. 1992 Optimization of locomotion. In *Mechanics of animal locomotion* (ed. R. McN. Alexander), *Adv. comp. environ. Physiol.* **5**, 277–300.

Howland, H.C. 1974 Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. theor. Biol.* **47**, 333–350.

Hughes, P.M. & Rayner, J.M.V. 1991 Addition of artificial loads to long-eared bats *Plecotus auritus*: handicapping flight performance. *J. exp. Biol.* **161**, 285–298.

Hummel, D. 1983 Aerodynamic aspects of formation flight in birds. *J. theor. Biol.* **104**, 321–347.

Jehl, J.R. & Murray, B.G. Jr 1986 The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. *Curr. Ornithol.* **3**, 1–86.

Jones, G. & Rayner, J.M.V. 1989 Optimal flight speed in pipistrelle bats, *Pipistrellus pipistrellus*. In *European bat research* (ed. V. Hanák, I. Horácek & J. Gaisler), pp. 247–253. Prague: Charles University Press.

Jönsson, P.E. 1987 Sexual size dimorphism and disassortative mating in the dunlin *Calidris alpina schinzii* in southern Sweden. *Ornis Scand.* **18**, 257–264.

Jönsson, P.E. & Alerstam, T. 1990 The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. *Biol. J. Lin. Soc.* **41**, 301–314.

Kacelnik, A. 1984 Central place foraging in starlings (*Sturnus vulgaris*). 1. Patch residence time. *J. Anim. Ecol.* **53**, 283–300.

Kacelnik, A. & Houston, A.I. 1984 Some effects of energy costs on foraging strategies. *Anim. Behav.* **32**, 609–614.

Kirkwood, J.K. 1983 A limit to metabolisable energy intake in mammals and birds. *Comp. Biochem. Physiol.* **75A**, 1–3.

Kshatriya, M. & Blake, R.W. 1992 Theoretical model of the optimum flock size of birds flying in formation. *J. theor. Biol.* **157**, 135–174.

Larkin, R.P. & Sutherland, P.J. 1977 Migrating birds respond to project seafarer's electromagnetic field. *Science, Wash.* **195**, 777–779.

Liechti, F. 1992 Flugverhalten nächtlich ziehender Vögel in Abhängigkeit von Wind und Topographie. Ph.D. thesis, University of Basel, Switzerland.

Liechti, F., Hedenström, A. & Alerstam, T. 1994 Effects of sidewinds on optimal flight speed of birds. *J. theor. Biol.* **170**, 219–225.

Lindström, Å. 1991 Maximum fat deposition rates in migrating birds. *Ornis Scand.* **22**, 12–19.

Lindström, Å. & Alerstam, T. 1992 Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *Am. Nat.* **140**, 477–491.

Lissaman, P.B.S. & Shollenberger, C. 1970 Formation flight of birds. *Science, Wash.* **168**, 1003–1005.

MacArthur, R.H. & Pianka, E.R. 1966 On optimal use of a patchy environment. *Am. Nat.* **100**, 603–609.

McLaughlin, R.L. & Montgomerie, R.D. 1985 Flight speeds of central place foragers: female lapland longspurs feeding nestlings. *Anim. Behav.* **33**, 810–816.

McLaughlin, R.L. & Montgomerie, R.D. 1990 Flight speeds of parent birds feeding nestlings: maximization of foraging efficiency or food delivery rate? *Can. J. Zool.* **68**, 2269–2274.

Masman, D. & Klaassen, M. 1987 Energy expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunculus*). *Auk* **104**, 603–616.

Møller, A.P. 1991 Influence of wing and tail morphology on the duration of song flight in skylarks. *Behav. Ecol. Sociobiol.* **28**, 309–314.

Norberg, R.Å. 1981 Optimal flight speed in birds when feeding young. *J. Anim. Ecol.* **50**, 473–477.

Orians, G.H. & Pearson, N.E. 1979 On the theory of central place foraging. In *Analysis of ecological systems* (ed. D. J. Horn, G. R. Stairs & R. D. Mitchell), pp. 155–177. Columbus: Ohio State University Press.

Pennycuick, C.J. 1969 The mechanics of bird migration. *Ibis* **111**, 525–556.

Pennycuick, 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.

Pennycuick, C.J. 1978 Fifteen testable predictions about bird flight. *Oikos* **30**, 165–176.

Pennycuick, C.J. 1989 *Bird flight performance: a practical calculation manual.* Oxford: Oxford University Press.

Pennycuick, C.J. & De Santo, T. 1989 Flight speeds and energy requirements for white ibises on foraging flights. *Auk* **106**, 141–144.

Pennycuick, C.J., Fuller, M.R., Oar, J.J. & Kirkpatrick, S.J. 1994 Falcon versus grouse: flight adaptations of a predator and its prey. *J. avian Biol.* **25**, 39–49.

Peterson, C.C., Nagy, K.A. & Diamond, J. 1990 Sustained metabolic scope. *Proc. natn. Acad. Sci. U.S.A.* **87**, 2324–2328.

Pyke, G.H. 1981 Optimal travel speeds of animals. *Am. Nat.* **118**, 475–487.

Pyke, G.H. 1984 Optimal foraging theory: a critical review. *A. Rev. Ecol. Syst.* **15**, 523–575.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. 1977 Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* **52**, 137–154.

Rayner, J.M.V. 1979 A new approach to animal flight mechanics. *J. exp. Biol.* **80**, 17–54.

Rayner, J.M.V. 1985 Flight, speeds of. In *A dictionary of birds* (ed. B. Campbell & E. Lack), pp. 224–226. Calton: T & A. D. Poyser.

Rayner, J.M.V. 1986 Vertebrate flapping flight mechanics and aerodynamics, and the evolution of flight in bats. In *Biona report* no. 5, *Bat flight – Fledermausflug* (ed. W. Nachtigall), pp. 27–74. Stuttgart: Gustav Fischer.

Rayner, J.M.V. 1991 On the aerodynamics of animal flight in ground effect. *Phil. Trans. R. Soc. Lond.* B **334**, 119–128.

Rothe, H.-J., Biesel, W. & Nachtigall, W. 1987 Pigeon flight in a wind tunnel II. Gas exchange and power requirements. *J. comp. Physiol.* B **157**, 99–109.

Schmid-Hempel, P., Kacelnik, A. & Houston, A.I. 1985 Honeybees maximize efficiency by not filling their crop. *Behav. Ecol. Sociobiol.* **17**, 61–66.

Schnell, G.D. & Hellack, J.J. 1979 Bird flight speeds in nature: optimized or a compromise? *Am. Nat.* **113**, 53–66.

Spedding, G.R. 1992 The aerodynamics of flight. In *Mechanics of animal locomotion* (ed. R. McN. Alexander), *Adv. comp. eniron. Physiol.* **5**, 51–111.

Stephens, D.W. & Krebs, J.R. 1986 *Foraging theory.* Princeton: Princeton University Press.

Tucker, V.A. 1973 Bird metabolism during flight: evaluation of a theory. *J. exp. Biol.* **58**, 689–709.

Tucker, V.A. & Schmidt-Koenig, K. 1971 Flight speeds of birds in relation to energetics and wind directions. *Auk* **88**, 97–107.

Wakeling, J.M. & Hodgson, J. 1992 Optimisation of the flight speed of the little, common and sandwich tern. *J. exp. Biol.* **169**, 261–266.

Ware, D.M. 1975 Growth, metabolism, and optimal swimming speed of a pelagic fish. *J. Fish Res. Bd Can.* **32**, 33–41.

Wege, M.L. & Raveling, D.G. 1984 Flight speed and directional responses to wind by migrating canada geese. *Auk* **101**, 342–348.

Weiner, J. 1992 Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. *Trends Ecol. Evol.* **7**, 384–388.

Welham, C.V.J. 1994 Flight speeds of migrating birds: a test of maximum range speed predictions from three aerodynamic equations. *Behav. Ecol.* **5**, 1–8.

Welham, C.V.J. & Ydenberg, R.C. 1988 Net energy versus efficiency maximizing by foraging ring-billed gulls. *Behav. Ecol. Sociobiol.* **23**, 75–82.

Welham, C.V.J. & Ydenberg, R.C. 1993 Efficiency-maximizing flight speeds in parent black terns. *Ecology* **74**, 1893–1901.

Videler, J.J., Weihs, D. & Daan, S. 1983 Intermittent gliding in the hunting flight of the kestrel, *Falco tinnunculus* L. *J. exp. Biol.* **102**, 1–12.

Videler, J.J., Vossebelt, G., Gnodde, M. & Groenewegen, A. 1988 Indoor flight experiments with trained kestrels. I. Flight strategies in still air with and without added weight. *J. exp. Biol.* **134**, 173–183.

Withers, P.C. & Timko, P.L. 1977 The significance of ground effect to the aerodynamic cost of flight and energetics of the black skimmer (*Rhyncops nigra*). *J. exp. Biol.* **70**, 13–26.

Ydenberg, R.C., Welham, C.V.J., Schmid-Hempel, R., Schmid-Hempel, P. & Beauchamp, G. 1994 Time and energy constraints and the relationships between currencies in foraging theory. *Behav. Ecol.* **5**, 28–34.

Received 2 June 1994; revised 16 December 1994; accepted 4 January 1995