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Published in:
Evolutionary Ecology Research

2001

[Link to publication](#)

Citation for published version (APA):

Weber, T., & Hedenström, A. (2001). Long-distance migrants as a model system of structural and physiological plasticity. *Evolutionary Ecology Research*, 3(3), 255-271. <http://www.evolutionary-ecology.com/issues/v03n03/ccar1239.pdf>

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Long-distance migrants as a model system of structural and physiological plasticity

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ABSTRACT

Several migratory bird species show active cycles of hypertrophy and atrophy of nutritional organs and selected muscle groups. We develop a model for nutritional organs to identify the conditions under which such a pattern of structural change is optimal. Migrants may choose the size of two components of lean mass: a constant component that they carry throughout the entire migration period and a component just deposited during stopover. The benefit of depositing and subsequently discarding additional tissues in nutritional organs during stopover is an increased fuelling rate and a decrease in flight costs; the cost of hypertrophy and atrophy is a time cost.

The predicted pattern depends strongly on the lean mass with which the migrants enter the migratory period. Time-selected migrants flying between widely separated stopover sites should show the highest degree of structural plasticity if they commence migration with a lean mass below maximum. If stopovers are possible everywhere along the migratory route, cycles of hypertrophy and atrophy are still possible but less likely.

We also discuss the consequence of using different currencies in the optimization procedure. Only if duration of migration is a component of fitness can structural changes be expected. If the energy cost of transport is minimized, there is no unique prediction about active changes in lean mass. For short migration distances, it may be optimal to burn the lean mass deposited at the start of the stopover as fuel instead of discarding it before departure.

Keywords: avian migration, flight range, organ dynamics, stopover ecology, time minimization.

INTRODUCTION

The bodies of animals are highly dynamic systems in both the short and long term (Piersma and Lindström, 1997; Secor and Diamond, 1998). The long-term perspective, concerned with the often irreversible changes of investment in body functions, such as growth versus reproduction or age-dependent investment in somatic repair (Cichon, 1997), is the realm of classical life-history theory. Experimental and theoretical work on short- or medium-term reversible structural changes in body composition has mainly been concerned with the storage of adipose tissue to support periods of high energy demands, such as during winter or migration (Haftorn, 1989; McNamara *et al.*, 1994; Weber and Houston, 1997;

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Weber *et al.*, 1994, 1998a), or with reversible changes in the digestive system in response to a new diet (Piersma *et al.*, 1993; Starck, 1999) or a single large meal (Secor and Diamond, 1998, 1999).

Long-distance migration of birds is one of the most energy-demanding activities in the animal kingdom. For a long time the paradigm was that non-fat components are nearly constant and that only fat is deposited on stopovers and burned during the subsequent flights (Odum *et al.*, 1964; Blem, 1990). Recently, it has become clear that other body components change as well (Åkesson *et al.*, 1992; Lindström and Piersma, 1993; Biebach, 1998; Lindström *et al.*, 1999; Piersma *et al.*, 1999; Battley *et al.*, 2000). Most attention has been directed to changes in muscle mass (Dietz *et al.*, 1999; Lindström *et al.*, 2000) and nutritional organs. It has been shown that migrants, after having completed a long flight during which they apparently have to metabolize some protein, need some time to build up digestive structures, such as the stomach, intestine and liver (Karasov and Pinshow, 1998; Lindström *et al.*, 1999).

It would appear, however, that some migrants show a considerable active restructuring of their bodies during stopover that goes beyond the simple replacement of protein and fat used during flight (Jehl, 1997; Piersma and Gill, 1998; Piersma, 1998). For example, the Black-necked Grebe, *Podiceps nigricollis*, undergoes several cycles of hypertrophy and atrophy of muscles and digestive organs each year (Jehl, 1997). During fat accumulation, the nutritional organs are well developed and the flight muscles are atrophied. Just before departure, the birds decrease their nutritional organs by 50% – but surprisingly also their fat by 30%. Bar-tailed Godwits, *Limosa lapponica*, also show a similar pattern under some circumstances: birds flying southwards from Alaska to New Zealand – a 10,000 km flight with probably no stopover opportunities – discard nutritional organs before departure, whereas northbound birds in the Dutch Waddensea facing a shorter flight do not show a reduction in lean mass (Piersma, 1998).

We are interested in defining the conditions for such active, adaptive changes in body components of migrants. We need to distinguish these changes from processes that occur during endurance locomotion, such as the amounts of fat and protein metabolized during flight and the adaptation of muscle size to changing demands. It is possible that some protein needs to be metabolized together with fat and that, during endurance flight, protein is taken from tissues that are of no immediate use, such as the stomach and the intestines, and that the pectoral muscles decrease in size during flights when body mass decreases significantly (Lindström *et al.*, 2000). Some aspects of these metabolic processes can certainly be subjected to an optimality analysis (Weber, 1987; Pennycuick, 1998), but they are conceptually different from the problem we analyse here. We take the need to metabolize some protein during flight as a constraint (Jenni and Jenni-Eiermann, 1998) and consider the deposition of additional protein during stopover and the discarding of the added mass before departure as the strategic option of interest: Protein may be deposited in amounts beyond the amounts required to replenish structures used as fuel during the flight. We are thus analysing just one aspect of the complex metabolism of protein during periods of high physiological demands.

We show that migrants can offer a general model system for the study of adaptive physiological and structural plasticity. A combination of field studies, feeding experiments, wind tunnel studies and theoretical approaches allows the elucidation of physiological mechanisms and the placement of the observed changes in a broader life-history perspective. For example, some controversy surrounds the choice of a realistic currency for optimal

decision-making during migration. The main contenders for a surrogate measure of fitness are duration, the total energy cost of migration, the energy cost of transport and survival (Hedenström and Ålerstam, 1997). So far, the empirical support for any of the alternative currencies is questionable, but the available evidence seems to champion a significant role of time, a factor in the first two currencies (Weber *et al.*, 1999). The following treatment will also place the structural changes of migrants in this context.

MODEL AND RESULTS

We model the optimal levels of lean mass and fuel for a migrant minimizing time or the total energy cost of migration (Ålerstam and Lindström, 1990; Hedenström and Ålerstam, 1997). Piersma and Gill (1998) and Piersma (1998) suggested that long-distance migrants might discard lean mass just before departure to increase the value of the deposited fuel by saving flight costs. To allow us a more quantitative account of this hypothesis, we assume that the lean mass of the migrant consists of three components: a minimum lean mass M_{\min} which is necessary for survival, an extra constant component M_0 which supports fuel deposition, and a component M_L which is deposited during migratory stopovers and increases the fuel deposition even more and is discarded before departure (see Fig. 1; all model parameters and variables are summarized in Table 1). Lean mass is of course a continuous variable, but the division into three components allows us to model the pattern in a more straightforward manner.

The mass components above the minimum mass should be considered as enlargement of the bird's gastrointestinal and metabolic capacity (rate of digesting food). The cost of adding and subsequently discarding lean mass during stopover is a loss of time during which no or hardly any fuel deposition is possible. The benefit is an increased fuelling rate and an increase in flight range for a given stopover time. We put an upper limit on the total extra lean mass – that is, $M_0 + M_L = \text{constant}$. Our analysis will treat the constant extra lean mass M_0 in two ways, first as a given constraint and then as a strategic choice. This

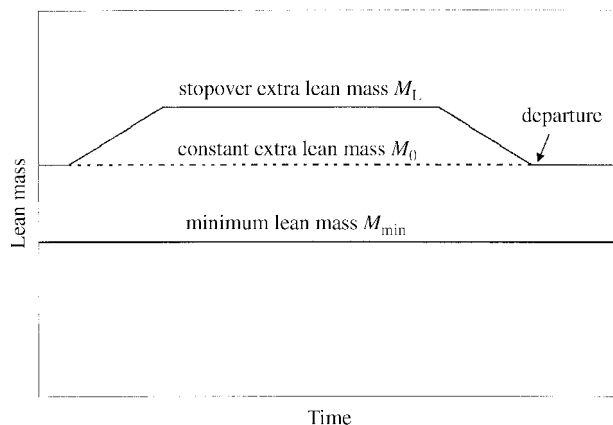


Fig. 1. Schematic representation of the three components of lean body mass. Both the minimum lean mass M_{\min} and the constant extra lean mass M_0 do not change with time. The stopover extra lean mass M_L is only deposited at the start of the stopover and is discarded before departure.

Table 1. Model parameters

Parameter or variable	Baseline value	Description
M_{\min}	180/10	minimum lean mass (g)
M_0		mass of constant lean tissue supporting fuel deposition (g)
M_L		mass of disposable lean tissue supporting fuel deposition (g)
t_e	2	search/settling cost at stopover (days)
Y		flight range (km)
f		fuel load (g)
C	300,000/50,000	constant in flight range equation ($\text{g}^{0.5} \cdot \text{km}$)
k_L		rate of accumulating lean mass ($\text{g} \cdot \text{day}^{-1}$)
k_f		fuel deposition rate ($\text{g} \cdot \text{day}^{-1}$)
k_d		rate of discarding lean mass before departure ($\text{g} \cdot \text{day}^{-1}$)
\bar{k}_h		harmonic mean rate of k_d and k_L ($\text{g} \cdot \text{day}^{-1}$)
t_L		time needed for depositing and discarding lean mass (days)
t_b		time depositing lean mass during stopover (days)
t_f		time for fuel deposition (days)
T		total stopover time (days)
D	2000/6000	distance between stopover sites (km)
a	1.25/0.35	constant in equation relating fuelling rate to lean mass ($\text{g}^{1-b} \cdot \text{day}^{-1}$)
b	0.67	exponent in equation relating fuelling rate to lean mass
E		total energy cost of migration (J)
V		flight speed ($\text{m} \cdot \text{s}^{-1}$)
P		power required for flight ($\text{J} \cdot \text{s}^{-1}$)
P_{dep}		maximum fuel deposition rate ($\text{J} \cdot \text{s}^{-1}$)
x		field metabolic rate
E_{flight}		energy cost of flight
K		metabolic ceiling
a		ratio of field metabolic rate and basal metabolic rate
β		ratio of fuel deposition rate and basal metabolic rate
γ		ratio of metabolic ceiling and basal metabolic rate

component of lean mass could well be kept below maximum by selective pressures outside the migration period, such as the physiological and behavioural costs of supporting a high metabolic rate. If M_0 is already set to a certain value when the migration period commences, then the birds can only choose a component M_L that maximizes the fitness currency. On the other hand, birds might be free to choose both M_0 and M_L . This distinction has to be kept in mind when interpreting the results.

We assume a rather simple model of the events during stopover and fuel deposition. A stopover consists of four phases: a possible search/settling phase t_e , then a period where lean mass M_L is built up, then fuel deposition and a final phase where the previously built up lean mass is discarded. The fuel deposition rate is positively correlated with the lean mass above the minimum lean mass. Discarding lean mass before take-off decreases flight costs. Pennycuik (1998) modelled the adaptive mass loss of flight muscles during flight; however, we do not consider flight muscles explicitly by including them in the fuel component. Houston (1998) modelled the advantage of a bird to increase stomach size during the entire

migratory period, but did not consider the time investment for deposition and discarding. Finally, we compare our results with an alternative strategy: birds do not discard lean mass before departure but during flight by using it as fuel.

Flight range

Flight range Y (km) is a function of fuel load f (g) and lean mass $M_0 + M_{\min}$ (g) at departure (which is the same as the lean mass at arrival):

$$Y(f, M_0, M_{\min}) = C(M_0 + M_{\min})^{-0.5}(1 - (1 + f(M_0 + M_{\min}))^{-0.5}) \quad (1)$$

The constant C ($\text{g}^{0.5} \cdot \text{km}$) includes all parameters that affect the flight range but are not altered by fuel deposition, such as energy conversion efficiency, flight speed and the body drag coefficient (Alerstam and Hedenström, 1998).

Lean mass and fuel deposition rate

The dynamics of body composition are governed by several rates; all rates have units of $\text{g} \cdot \text{day}^{-1}$ and lean mass deposition rates refer to wet protein. The rate k_L with which extra lean mass is deposited during stopover is constant. This deposited lean mass is given by $M_L = k_L t_b$, where t_b is the time invested in depositing lean mass. The fuel deposition rate k_f is a function of the total ‘excess’ lean mass that the birds carry during stopover:

$$k_f = a(M_L + M_0)^b, \quad a, b > 0 \quad (2)$$

We assume that the rate depends mainly on the surface area of the intestines, thus the exponent b is set to 0.67. Different organs in the nutritional system might require different exponents; if we consider the liver, a linear relationship could be the appropriate scaling. Other values for b , however, will not affect the qualitative details of the results. (For a review of mechanisms of digestive plasticity, see Karasov, 1996.) The constant a includes environmental and physiological parameters such as food availability and digestive efficiency.

The constant rate with which the birds discard the extra ‘depositing machinery’ M_L before departure is denoted by k_d . There is no empirical evidence showing how similar k_L and k_d are. Therefore, in the following analysis, we always use the harmonic mean \bar{k}_h of the two rates as a general specification of the build-up and discarding of lean mass. The harmonic mean is the inverse of the arithmetic mean of the inverse of the two rates. The total time needed to deposit and discard the extra lean mass during stopover is thus $t_L = 2M_L/\bar{k}_h$.

For both deposition and discarding of lean mass, we have chosen linear functions for simplicity. An exponential function might be a more realistic alternative for the build-up of lean mass. In the following, however, it will become clear that only the total time invested in building up and discarding lean mass is relevant. The exact shape of the functions describing the build-up and discarding of lean mass are not important in the current context.

We also assume that the deposition of lean mass and the deposition of fuel are not overlapping. The total amount of fuel deposited during the relatively short time while lean mass is built up or discarded will only be small. Including an overlap of lean mass and fuel deposition could lead to slightly broader conditions favouring the cyclical deposition of lean mass.

Minimizing time

Spatial arrangement of stopover sites

We analyse two situations that are representative for most migratory systems: discrete stopover sites and stopovers available in a continuous environment. Time-minimizing migrants maximize their speed of migration Y/T , where Y is the flight range and T the stopover time. In the first case, with discrete stopover sites, the fixed distance to the next site sets the departure load and thus stopover time T has to be minimized. Optimization has to be done with respect to M_0 and M_L ; that is, the birds choose an extra lean mass that they always carry and an extra lean mass they build up during stopover and discard before departure. In a continuous environment, the birds are free to choose their departure fuel load – and thus their range Y – as well. For simplicity, we only consider a case where all sites along the migratory route are identical with respect to feeding conditions and search/settling costs (global variation; see Houston, 1998; Weber *et al.*, 1999).

Discrete sites. The birds start their stopover with lean mass $M_{\min} + M_0$ and deposit more lean mass with rate k_L until they reach M_L ; they then achieve the fuel deposition rate $k_f = a(M_L + M_0)^b$. The time needed to deposit fuel depends on the distance to the next site. From equation (1) we find the fuel load f (g) required to cover distance D to the next site on the flyway:

$$f(D, M_0) = (M_0 + M_{\min}) \left(\frac{(C(M_0 + M_{\min}))^{-0.5}}{(C(M_0 + M_{\min}))^{-0.5} - D} - 1 \right) \quad (3)$$

The time needed to deposit the required fuel load is thus $t_f = f(D, M_0)/a(M_L + M_0)^b$. We have to find the combination of M_0 and M_L that minimizes the total stopover time T :

$$T = t_e + t_L + t_f = t_e + \frac{2M_L}{\bar{k}_h} + \frac{f(D, M_0)}{a(M_L + M_0)^b} \quad (4)$$

For a given M_0 we can find the optimal extra lean mass to be deposited during stopover by solving $\partial T/\partial M_L = 0$. Then we arrive at:

$$M_L^* = \left(\frac{2a}{f(D, M_0)b\bar{k}_h} \right)^{-1/(b+1)} - M_0 \quad (5)$$

In the following, we look at two cases: a moderately large bird with a minimum lean mass of 180 g, such as a medium-sized wader like the Bar-tailed Godwit (*Limosa lapponica*) migrating between widely separated sites, and a small bird with a minimum lean mass of 10 g, such as a passerine migrating between temperate breeding and tropical wintering sites and crossing the Sahara or the Gulf of Mexico on the journey.

Figures 2–4 show the time needed to complete one migration step and the corresponding combinations of the constant extra lean mass M_0 and the optimal stopover extra lean mass M_L^* . Figures 2 and 3 were calculated for a bird with a minimum lean mass of 180 g, three different rates of lean mass deposition and two different distances. We set the constant a in equation (2) to 1.25 and the maximum extra lean mass is 70 g. Here and in the following cases we have chosen the constant a so that the relative fuel deposition rate – daily gain in relation to total lean mass – never exceeds 0.06 for medium-sized birds and 0.08 for small birds (cf. Lindström, 1991). In both cases, time spent on migration is minimized if the birds carry the maximum possible lean mass throughout migration – that is, time is at

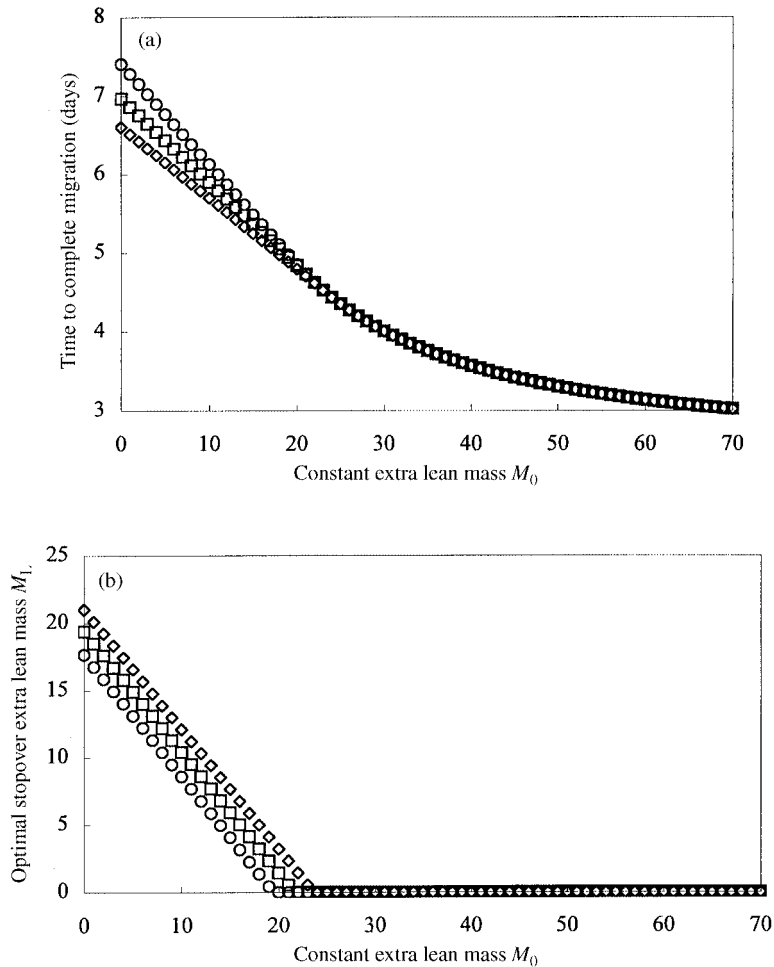


Fig. 2. (a) Time required to complete migration step (days) as a function of constant extra lean mass M_0 for a bird with a minimum lean mass of 180 g in an environment with discrete stopover sites and several mean rates \bar{k}_h for the acquisition and loss of lean mass (\circ , $\bar{k}_h = 12 \text{ g} \cdot \text{day}^{-1}$; \square , $\bar{k}_h = 14 \text{ g} \cdot \text{day}^{-1}$; \diamond , $\bar{k}_h = 16 \text{ g} \cdot \text{day}^{-1}$). The distance to the next site is 2000 km and the constant $C = 300,000 \text{ g}^{0.5} \cdot \text{km}$. (b) The corresponding optimal stopover extra lean mass M_L^* .

the minimum if $M_0 = 70 \text{ g}$ and thus $M_L = 0 \text{ g}$ (Figs 2b and 3b). The range of values for the constant extra lean mass M_0 where it is optimal to deposit and discard extra lean mass during stopover increases with the lean mass deposition rate \bar{k}_h and the distance to be covered. If the distance is 6000 km, the migrants deposit extra lean mass for nearly all values of M_0 .

Figure 4 shows an example for a small bird with a minimum lean mass of 10 g, a distance of 2000 km and four different lean mass deposition rates. The constant $a = 0.35$ and the maximum extra lean masses can be 6 g. The pattern is very similar to the corresponding case for a larger bird in Fig. 2. It is optimal to carry the maximum lean mass throughout migration and there is a small range of values for M_0 where it is optimal to deposit and to

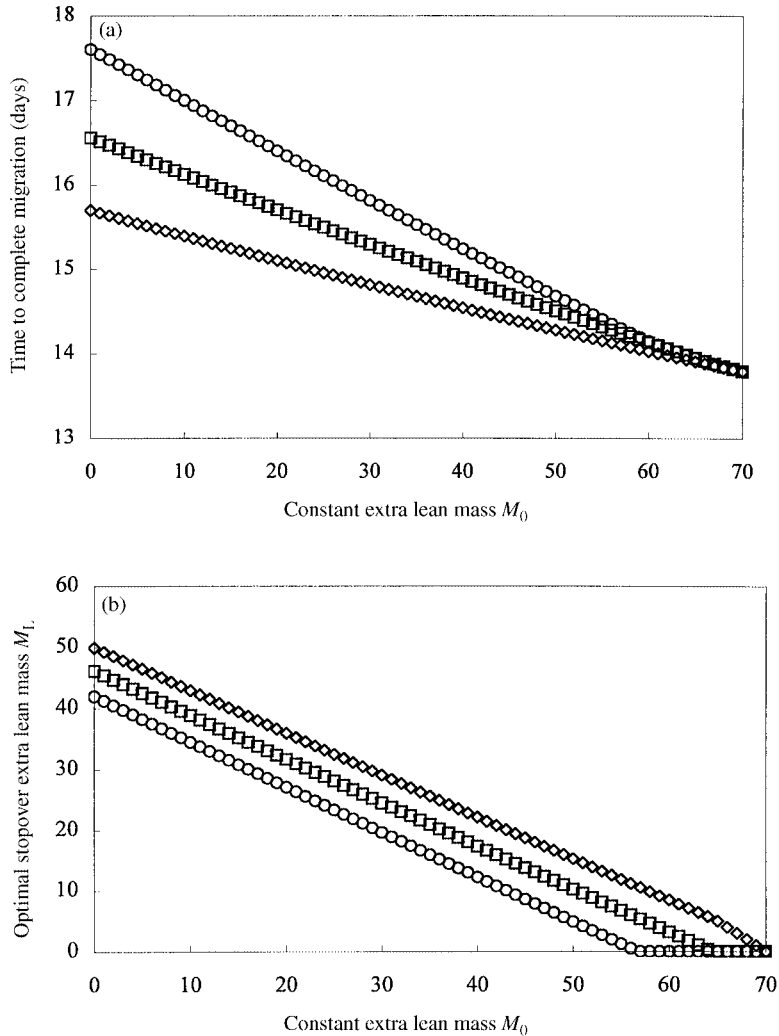


Fig. 3. (a) Time required to complete migration step (days) as a function of constant extra lean mass M_0 for a bird with a minimum lean mass of 180 g in an environment with discrete stopover sites and several mean rates \bar{k}_h for the acquisition and loss of lean mass (\circ , $\bar{k}_h = 12 \text{ g} \cdot \text{day}^{-1}$; \square , $\bar{k}_h = 14 \text{ g} \cdot \text{day}^{-1}$; \diamond , $\bar{k}_h = 16 \text{ g} \cdot \text{day}^{-1}$). The distance to the next site is 6000 km and the constant $C = 300,000 \text{ g}^{0.5} \cdot \text{km}$. (b) The corresponding optimal stopover extra lean mass M^*_L .

discard extra lean mass during stopover. Also, for larger distances, the pattern resembles the previous case of a larger bird.

Continuous environment. Also in this case we find the optimal solution by maximizing the rate of migration Y/T . The range Y is given by equation (1) where the fuel load $f = k_f t_f$. The total stopover time T is identical to equation (4) for discrete sites. We assume that time is discrete because migrants usually depart during a relatively short time-window around sunset and not at other times during the day (cf. Åkesson *et al.*, 1996).

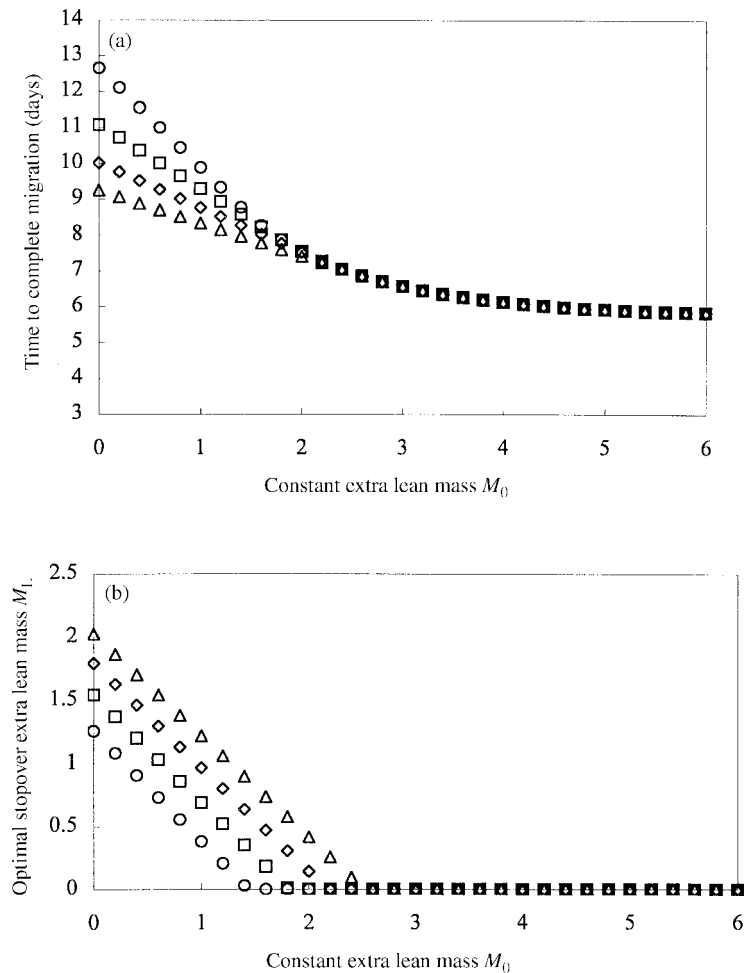


Fig. 4. (a) Time required to complete migration step (days) as a function of constant extra lean mass M_0 for a bird with a minimum lean mass of 10 g in an environment with discrete stopover sites and several mean rates \bar{k}_h for the acquisition and loss of lean mass (\circ , $\bar{k}_h = 0.5 \text{ g} \cdot \text{day}^{-1}$; \square , $\bar{k}_h = 0.7 \text{ g} \cdot \text{day}^{-1}$; \diamond , $\bar{k}_h = 0.9 \text{ g} \cdot \text{day}^{-1}$; \triangle , $\bar{k}_h = 1.1 \text{ g} \cdot \text{day}^{-1}$). The distance to the next site is 2000 km and the constant $C = 50,000 \text{ g}^{0.5} \cdot \text{km}$. (b) The corresponding optimal stopover extra lean mass M^*_L .

Figure 5a shows the maximum speed of migration as a function of the constant extra lean mass M_0 for a bird with a minimum lean mass of 10 g; Fig. 5b shows the corresponding optimal level of lean mass M^*_L deposited during stopover. The maximum extra lean mass can be 6 g at most, thus the maximum possible lean mass of the bird during stopover can be 16 g. The migrants deposit and discard lean mass at harmonic mean rates of 0.5–1.1 g per day. It is always best to carry the maximum constant lean mass if possible; speed of migration is highest if birds always carry 16 g of lean mass and do not deposit or discard lean mass during stopover. Only if the birds just enter the migration period with relatively low amounts of constant lean mass above the minimum (i.e. $M_0 \approx 1 \text{ g}$), is it worthwhile to deposit and discard extra digestive machinery during stopover. The range of constant extra

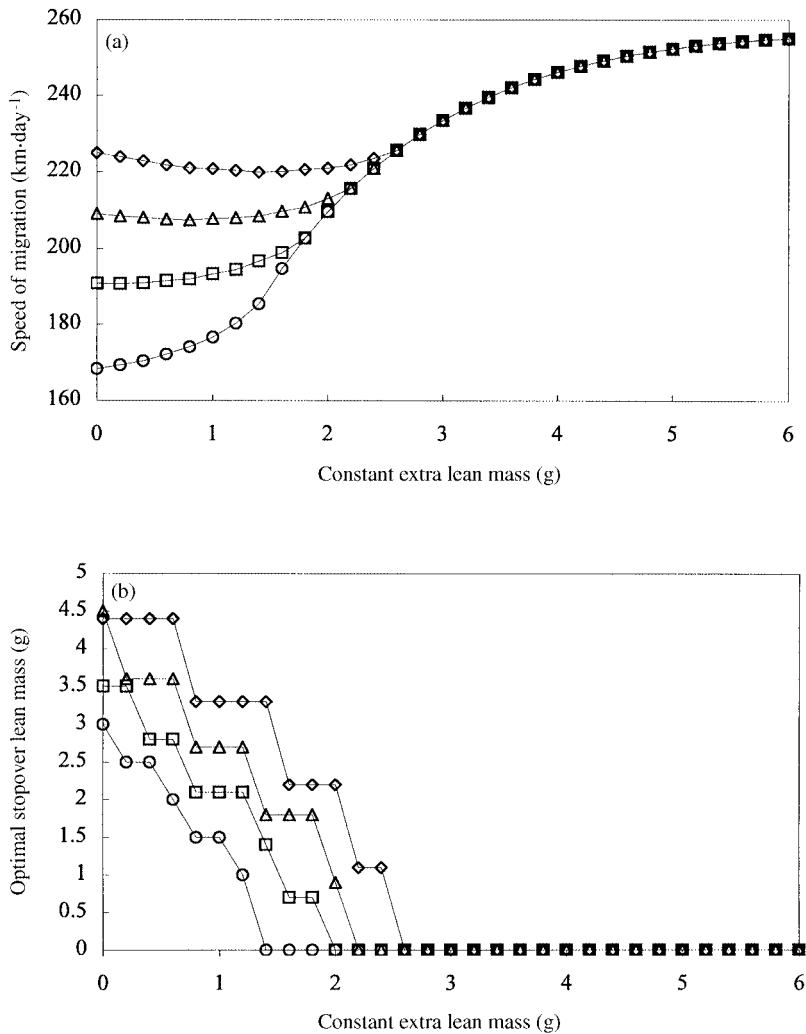


Fig. 5. (a) Speed of migration ($\text{km} \cdot \text{day}^{-1}$) as a function of constant extra lean mass M_0 for a bird with a minimum lean mass of 10 g in a continuous environment and several mean rates \bar{k}_h for the acquisition and loss of lean mass (\circ , $\bar{k}_h = 0.5 \text{ g} \cdot \text{day}^{-1}$; \square , $\bar{k}_h = 0.7 \text{ g} \cdot \text{day}^{-1}$; \triangle , $\bar{k}_h = 0.9 \text{ g} \cdot \text{day}^{-1}$; \diamond , $\bar{k}_h = 1.1 \text{ g} \cdot \text{day}^{-1}$). The constant $C = 50,000 \text{ g}^{0.5} \cdot \text{km}$. (b) The corresponding optimal stopover extra lean mass M_{L}^* .

lean masses M_0 where the deposition of extra nutritional organs during stopover is optimal increases with the mean rate \bar{k}_h .

Minimizing the total energy cost of migration

An alternative currency that migrants might be selected to optimize is the total energy cost of migration (Hedenström and Ålerstam, 1997), which can be written as:

$$E = \frac{PD}{V} \left(1 + \frac{x}{P_{\text{dep}}} \right) \quad (6)$$

where P is flight power (Pennycuick, 1975), D is the migration distance, V is flight velocity, P_{dep} is the rate of energy deposition at stopovers and x is the existence metabolism (field metabolic rate, FMR) over the entire stopover period. Flight power and speed are unaffected by the temporary accumulation of lean mass if it is discarded before flight. Hence, the trade-off applies to the situation during energy deposition. Since both FMR and fuel deposition rate are related to the basal metabolic rate (Nagy, 1987; Lindström, 1991), the accumulation of extra lean body mass will be advantageous if the increased fuelling capacity is off-setting the energy cost during accumulation and disposal of this mass. Using the same terminology as before, we may write the condition for accumulation of extra lean mass as:

$$E_{\text{flight}} \left(1 + \frac{x}{P_{\text{dep}}} \right) > E_{\text{flight}} \left(1 + \frac{x'}{P'_{\text{dep}}} + \frac{2M_L}{\bar{k}_h} \frac{x'}{E_{\text{flight}}} \right) \quad (7)$$

where E_{flight} is the energy cost of flight ($= PV/D$), x' is the modified field metabolic rate and P'_{dep} is the fuelling rate after the accumulation of extra lean mass. The FMR during the actual accumulation (and disposal) phase should be intermediate between x and x' ($x' > x$), but for simplicity we have assumed x' during this period. We have not included the energy cost of building the additional tissue, since it may be used for partly fuelling the existence metabolism during the disposal period. If $\text{FMR} = a\text{BMR}$ and the maximum metabolic ceiling is $K = \gamma\text{BMR}$ (Drent and Daan, 1980), then the maximum possible fuel deposition rate is $P_{\text{dep}} = \beta\text{BMR}$, where $\beta = \gamma - a$. With additional lean mass enhancing the metabolic capacity, the modified fuel deposition rate will be $P_{\text{dep}} = \beta'\text{BMR}$, where $\beta' = \gamma - a'$. Using these definitions we can rewrite inequality (7) as:

$$\frac{2M_L}{\bar{k}_h} < \frac{E_{\text{flight}}}{a'\text{BMR}} \left(\frac{a}{\beta} - \frac{a'}{\beta'} \right) \quad (8)$$

This inequality shows that additional mass M_L should be deposited if the effect of it is larger on the fuelling capacity than the increase of FMR. If this criterion is fulfilled, then birds selected to minimize the total energy cost of migration should adjust lean metabolic mass during stopover in a similar way to birds minimizing the overall time of migration. The restriction to accumulate extra lean mass is relaxed with increasing energy cost of flight E_{flight} according to inequality (8), which is directly related to the migration distance. Hence, also under this currency, long migratory flights promote the temporary accumulation of extra metabolic machinery.

Minimizing the energy cost of transport

Under this currency, the optimal fuel load only depends on the search/settling energy cost and is not affected by variation in the fuel deposition rate (Hedenström and Ålerstam, 1997). In the present framework, this means that migrants should just carry a constant lean mass that is as small as possible to minimize flight costs. Any extra lean mass deposited and discarded during stopovers will neither positively nor negatively affect fitness. Therefore, this currency makes no relevant, unique prediction about adjustments of nutritional organs.

Using protein as fuel instead of discarding it

Migrant birds might use another strategy to optimally manage the levels of lean mass in the gastrointestinal system: they could deposit lean mass, fuel up and then use the extra lean mass as a fuel component during flight instead of discarding it before departure. The birds then still have the benefit of an increased fuelling rate, but they do not save flight costs and they devalue their fuel stores because of an increased proportion of a component with low energy density fuel. For time minimizers, Figs 6a and 6b show the speed of migration and the corresponding optimal stopover extra lean masses as a function of the constant extra lean mass if the stopover lean mass is used as fuel instead of being discarded. Figure 6a does not differ from Fig. 5a as long as no extra stopover lean mass is deposited. Differences emerge under the conditions when the deposition of extra lean mass during stopover is optimal – that is, when M_0 is small. For low lean mass deposition rates, the strategy of burning extra lean mass as fuel is a better option than discarding it before departure. For high rates, the opposite is better.

For discrete sites the situation is different. If we look at birds with a constant lean mass M_0 which makes it optimal to store extra lean mass during stopover, the following pattern emerges. A bird weighing 200 g ($M_{\min} = 180$ g and $M_0 = 20$ g) and depositing lean mass at a rate of $12 \text{ g} \cdot \text{day}^{-1}$ should deposit and discard the extra lean mass if the distance to the next site is greater than 3800 km, and burn the lean mass during flight if the distance to the next site is less than 3800 km. This threshold distance depends, of course, on the lean mass deposition rate. Increasing values of this rate favour cycles of hypertrophy and atrophy even for shorter distances.

Here, we did not set separate values for the lean mass deposition rate k_L and the discarding rate k_d , and used the mean rate \bar{k}_n . It might be possible to investigate if differences in the two rates will favour discarding or burning previously deposited lean mass, but this is beyond the scope of the present paper. If the discarding rate is low compared to the deposition rate, burning of the lean mass may be advantageous under broader conditions.

DISCUSSION

Our results for time- and total energy cost-minimizers support the hypothesis of Piersma (1998) that migrants facing very long non-stop flights should show the highest structural plasticity. In a continuous environment, where relatively short flights are optimal, it is also possible that the nutritional organs show active cycles of hypertrophy and atrophy, but the conditions are more restricted and it could pay the birds to use the extra lean mass as fuel instead of discarding it. Some aspects of this pattern are analogous to that described by Secor and Diamond (1998, 1999), who demonstrated that Burmese pythons (*Python molurus*) consuming infrequent large meals also show large changes in digestive structures, whereas animals that frequently consume and digest small meals maintain the integrity of their guts.

Our results are not surprising in that we predict that always carrying the maximum possible lean mass leads to the maximum speed of migration. Whether any structural plasticity can be observed thus depends most critically on the lean mass with which the birds enter the migratory period. If the birds start with a lean mass well below the maximum, then cycles of lean mass deposition and subsequent discarding are likely to be observed. If birds have the chance to increase their lean mass before migration to the

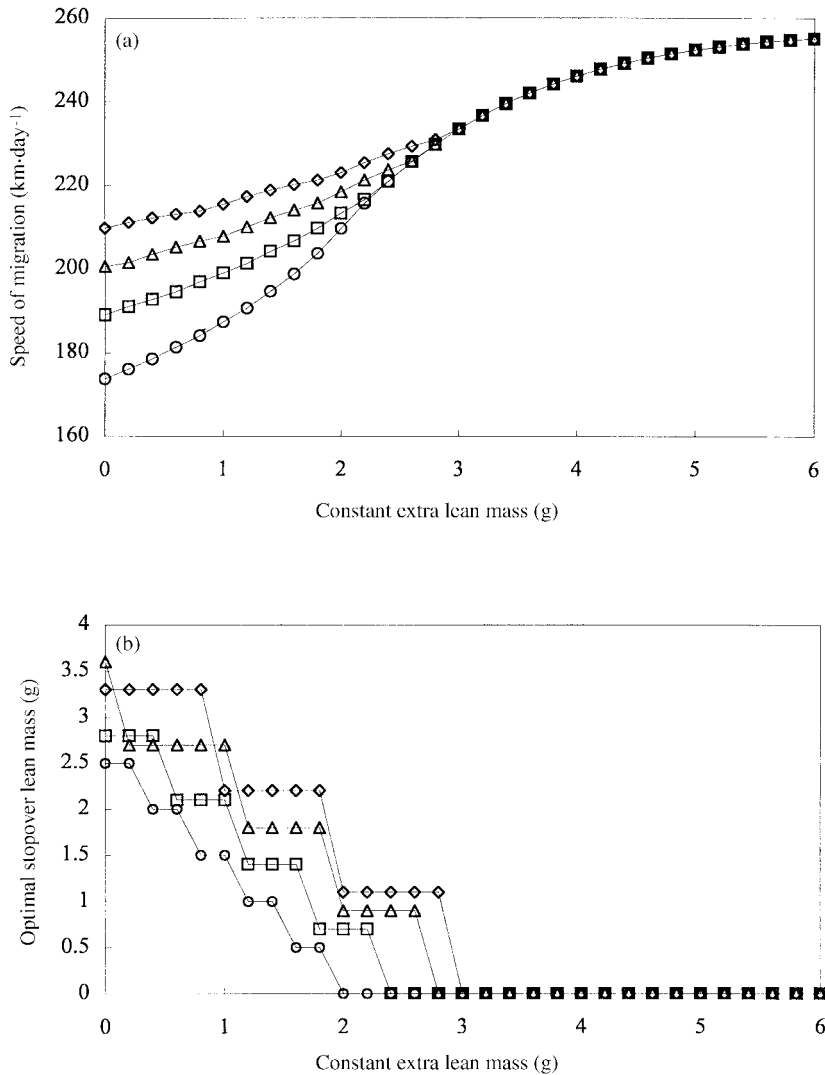


Fig. 6. (a) Speed of migration ($\text{km}\cdot\text{day}^{-1}$) as a function of constant extra lean mass M_0 for a bird with a minimum lean mass of 10 g in a continuous environment and several mean rates \bar{k}_L for the acquisition of lean mass (\circ , $\bar{k}_L = 0.5 \text{ g}\cdot\text{day}^{-1}$; \square , $\bar{k}_L = 0.7 \text{ g}\cdot\text{day}^{-1}$; \triangle , $\bar{k}_L = 0.9 \text{ g}\cdot\text{day}^{-1}$; \diamond , $\bar{k}_L = 1.1 \text{ g}\cdot\text{day}^{-1}$). Here the migrant burns the extra lean mass deposited at the start of the stopover during flight instead of discarding it before departure. The constant $C = 50,000 \text{ g}^{0.5}\cdot\text{km}$. (b) The corresponding optimal stopover extra lean mass M^*_L .

maximum or can keep it there, then no active cycles of deposition and discarding should be observed. If birds commence migration with a lean mass below the maximum value, cycles of deposition and discarding should occur in particular before long non-stop flights over ecological barriers. We believe that it is unlikely that birds carry the maximum amount of lean mass all year round. The optimal choice of lean mass during any activity, whether

breeding, moult or migration, will be subjected to some trade-offs. A large amount of lean mass will support energy acquisition and will thus enhance fitness in many contexts. A high energy turnover will, on the other hand, have a negative impact on other functions, for example immuno-competence, and thus influence fitness expectations. The optimal lean mass during the activities before migration could have an intermediate value. An analysis of optimal lean mass should consider the entire annual cycle (see Houston and McNamara, 1999). Such an analysis will probably show that different components of lean mass will be regulated on different time scales. The 'constant' lean mass M_0 might differ between breeding, wintering, moult and migration and the minimum lean mass M_{\min} will certainly differ between seasons. In addition to such perhaps more slowly changing levels may be superimposed short-term changes such as those modelled in the present paper.

Our analysis does not include the effects of wind on departure decisions. Rate-maximizing migrants in a continuous environment are expected to become sensitive to wind conditions after a few days of fuel deposition and then leave as soon as favourable winds occur (Weber *et al.*, 1998b). But what if favourable winds occur and the bird has not yet discarded all the surplus lean mass? Our model predicts that a flexible depositing machinery is quite likely if migratory flights extend over several thousand kilometres. Wind conditions at the departure site will probably not say very much about the conditions, say, at 2000 km or more further on and the net wind assistance over such large distances may be small or at least not very variable. Savings by discarding surplus lean mass may thus outweigh savings by leaving in favourable winds that are only used initially. But what about migrants in a continuous environment? We could identify some conditions under which migrants should deposit and subsequently discard lean mass in a continuous environment, but it is likely that winds have a far greater effect on the speed of migration than active changes in lean mass. Migratory step lengths are in the range of 100–500 km (Ellegren, 1993) and even modest tailwinds can increase the speed of migration significantly.

Our analysis suggests that, under the assumptions of our models, the patterns of structural plasticity as observed by Piersma and Gill (1998) and Piersma (1998) will be expected. These results indicate that predictions concerning reversible changes in nutritional organs depend strongly on the currency used and thus on other aspects of the life history. It is hard to imagine a scenario for migrants where pure minimization of transport costs could be appropriate. In temperate and Arctic latitudes, breeding success depends strongly on time of arrival and even early arrival on the wintering grounds seems to be important (Marra *et al.*, 1998). We did not consider the consequences of including mortality in the fitness measure. If fitness is a combination of time of arrival and mortality during the journey, it should be possible to find conditions where cycles of hypertrophy and atrophy of lean mass are optimal. This should be the case in particular if mortality occurs during flight. Reducing lean mass in the gastrointestinal tract will increase manoeuvrability and thus decrease predation risk (Hedenström, 1992). In a dynamic optimization model of Western Sandpiper (*Calidris mauri*) spring migration, Clark and Butler (1999) used the reproductive success of current and future years as the fitness currency. Such a measure is certainly more closely linked to fitness, but surrogate currencies such as time and energy cost of migration are also likely to be important components of fitness and often allow a first and sometimes analytically tractable insight into expected patterns.

Analyses of animal structures are often performed within the context of symmorphosis (Weibel *et al.*, 1991; Weibel, 2000). This hypothesis simply states that structures should match demands; analyses within that framework, however, often seem to rely implicitly on

efficiency as a currency. Investigations of animal structure–function relationships need to go beyond this concept and consider how, for example, energy is acquired, used and how exactly it contributes to fitness. Besides Burmese pythons (Secor and Diamond, 1998), avian migrants seem to be another promising model system to study structural and physiological regulation in vertebrates.

ACKNOWLEDGEMENTS

T.P.W. was supported by the Deutsche Forschungsgemeinschaft through grant WE2200/1–2 and A.H. by the Swedish Natural Science Research Council. We wish to thank Alasdair Houston, Åke Lindström and an anonymous referee for detailed comments on the manuscript.

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