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Abstract

Overall migration speed is likely to be a trait under selection pressure in animals migrating annually between habitats for reproduction and survival. A general expression was used for migration speed (V_{migr}), accounting for energy accumulation and transport, and derive how V_{migr} scales with body mass for three types of migratory locomotion: running, swimming and flying (powered and soaring flight). Migration speed is predicted to increase with increasing body mass in animals that run ($\propto m^{1/11}$), swim ($\propto m^{1/24}$) and fly by soaring ($\propto m^{0.22}$), whereas in animals migrating by powered flight it decreases ($\propto m^{-1/4}$). How the relative duration of fuel accumulation to that of migratory locomotion scales with body mass is also derived. This proportion should increase in animals that run and fly, but should remain unaffected by body size in swimmers. The suggestion is made that in runners and swimmers, selection for enhanced migration speed could provide an explanation to Cope's rule, i.e. the observation that body size gradually tends to increase over time.

Key words: migration speed, biomechanics, locomotion, body mass, Cope's rule

INTRODUCTION

Many animal species migrate annually between reproduction and survival areas. Besides breeding (and moult in birds), migration is a major life-history event to be accommodated within the annual cycle in temperate regions. Locomotion energetics differs between modes of transport (Schmidt-Nielsen, 1972) and so the occurrence and distance of migration may differ between animals that run, swim or fly (Tucker, 1975). Alexander (1998) investigated how fast animals can migrate using these different modes of locomotion. His analysis assumed that the animals had stored energy to fuel the entire migration. Many long-distance migrants have to refuel repeatedly during the migration, which will slow down their overall rate of travel. Animals that have the capacity to cover their migration in one go without refuelling en route must spend time fuelling before the onset of movement. In principle, this fuelling time, before the onset of the first migratory movement, should be included in the time for migration when calculating the overall migration speed (Hedenström & Alerstam, 1998). In this paper I present a scaling analysis of the overall migration speed for animals using either of three main modes of locomotion. The theoretical analysis is based on biomechanical considerations and empirical measurements of locomotion energetics to calculate how migration speed scales with body mass. The findings are also discussed in an evolutionary context of animal migration and body size.

CALCULATING MIGRATION SPEED

Migration over long distances comprises alternate phases of stopover, when energy (fuel) is deposited, and transport, when fuel is converted into distance covered. During stopovers the animal remains in an area suitable for energy accumulation, but the time spent fuelling for the next transportation stage is part of the migration process. Even if the migratory transport consists of one stage only then the 'pre-migratory' fuelling time should be included in the total migration time. Hence, the overall rate of migration is considerably lower than the actual speed of transport between consecutive stopovers. The total time of migration T_{migr} is the sum of transport time T_{transp} and the energy deposition time T_{dep}. For a total migration distance D at a speed of transport V (speed of running, swimming or flying), the time of transport is $T_{transp} = D/V$. Let P_{transp} represent the rate of energy expenditure at the transport speed V, and let P_{dep} represent the net rate of energy deposition. Then the time required for accumulating the energy to cover the total distance D is $T_{dep} = (D/V)(P_{transp}/P_{dep})$. By using these quantities we can derive an expression for the overall speed of migration

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V_{migr}, as the total migration distance divided by the total time of migration, i.e. D/T_{migr}, which after rearrangement gives the equation:

$$V_{migr} = \frac{V P_{dep}}{P_{transp} + P_{dep}}. \qquad (1)$$

This is the fundamental expression for the overall migration speed, which is used in this paper to derive how speed of migration scales with body mass for different modes of locomotion. From the two rates P_{dep} and P_{transp} and transportation speed one can determine the migration speed in any animal and even if we cannot estimate the maximum migration speed, equation (1) can be used to investigate how V_{migr} scales with body mass. Crucial to estimating V_{migr} is the rate at which energy can be deposited. Animals exhibit some maximum level of metabolic scope (Kirkwood, 1983; Hammond & Diamond, 1997), usually considered as some multiple of the basal metabolic rate (K $= \alpha \cdot$ BMR). During fuelling the animal must pay a metabolic cost for its way of living, including maintenance and locomotion, which is the field metabolic rate (FMR); FMR is also some multiple of BMR, i.e. FMR $= \beta \cdot$ BMR. Theoretically, the rate of energy accumulation must be allocated from the margin between the metabolic scope and FMR, hence $P_{dep} = \gamma \cdot$ BMR where $\gamma = \alpha - \beta$. Even if it has not yet been shown in all animal groups, I shall assume that the rate of energy deposition is proportional to BMR. For scaling purposes the magnitude of the factor γ will not affect the scaling relationships obtained.

When evaluating how V_{migr} scales with body mass, we have to find how characteristic travel speed (V) and the associated rate of energy expenditure (P_{transp}) scale with body mass. I will start by evaluating these variables using simple biomechanical relationships. Only a fraction of the total energy used by a muscle is converted to useful mechanical work and much of the energy consumed is released as heat (e.g. Pennycuick, 1992). I will assume that the energy conversion efficiency remains constant across body size, even though some studies indicate that conversion efficiency increases with increasing body size (Casey, 1992).

How the equation for V_{migr} scales with body mass by using published relationships of the scaling of power input and speed with respect to body mass is also explored. These relationships are generally based on measurements of whole animal metabolism and therefore circumvent the problem of variable conversion efficiency.

SCALING OF MIGRATION SPEED

Runners

The energetics of running is notoriously difficult to analyse (cf. McGeer, 1992). Kram & Taylor (1990) proposed a simple model for energy cost of running, based on the time that the foot applies force to the ground during each stride. The running rate of energy cost can be written as $P(V) = (c \cdot mg \cdot V)/L$, where c is a cost coefficient, m is body mass, g is acceleration due to gravity, V is velocity and L is the step length. Step length is defined as the distance travelled while each foot is in contact with the ground. It is assumed that step length is proportional to leg length (Alexander & Jayes, 1983), which is $\propto m^{1/3}$ in isometrically scaled animals. Following Alexander & Jayes (1983), I will assume that animals will travel at the same typical Froude number, and hence travelling speed is $V \propto m^{1/6} \cdot g^{1/2}$. The Froude number is defined as $F = V^2/gl$, where l is a characteristic length such as leg length (Alexander & Jayes, 1983). Evaluating how power of running scales with body mass and gravity yields $P(V) \propto m^{5/6} \cdot g^{3/2}$. Measurements of BMR are invariably close to $\propto m^{3/4}$ (Kleiber, 1961; Ricklefs, Konarzewiski & Daan, 1996). Now, evaluating equation (1) using these scaling relationships gives

$$V_{migr} \propto \frac{k_1 m^{\frac{1}{6}}}{k_2 m^{\frac{1}{12}} + 1}, \qquad (2)$$

where k_1 and k_2 are constants. The overall body mass scaling exponent depends on the magnitude of k_2; if $k_2 \ll 1$ the denominator of equation (2) is approximately one and the overall scaling is $V_{migr} \propto m^{1/6}$, while if $k_2 \gg 1$ the denominator is approximately proportional to $m^{1/12}$ and $V_{migr} \propto m^{1/12}$. Hence, the true scaling exponent (exp) is in the interval $1/12 < \exp < 1/6$, depending on k_2 as determined by the ratio P_{transp}/P_{dep}. Using available published data (Kleiber, 1961; Kram & Taylor, 1990), I obtained an estimate as $k_2 = 8$ and used this value to evaluate equation (2) numerically in the size range 1–1000 kg, which resulted in the relationship $V_{migr} \propto m^{1/11}$.

An alternative approach is to use published relationships for the scaling of running energetics and speed (cf. Alexander, 1998). For runners, Taylor, Heglund & Maloiy (1982) found that the rate of energy consumption is $P(V) = 10.7 \cdot m^{0.68} \cdot V + 6.0 \cdot m^{0.70}$ (W), and Heglund, Taylor & McMahon (1974) found that $V = 1.52 \cdot m^{0.24}$ (m/s) in mammals ranging in size from mice (0.03 kg) to horses (680 kg). For a mammalian BMR $= 3.3 \cdot m^{0.76}$ (W) (Kleiber, 1961) and assuming that $P_{dep} = 0.5 \cdot$ BMR, I obtained the relationship

$$V_{migr} = 9.31 \cdot m^{0.12} \text{ (km/day).} \qquad (3)$$

Hence, the scaling based on mechanical considerations and the one based on empirical data yield similar scaling exponents (1/10 and 0.12) for migration speed as a function of body mass.

Swimmers

Calculating the swimming speed associated with minimum cost of transport (V_{mr}), Weihs (1973) used a simple model relating power to speed, where $P(V) = P_{met} + a V^2/b$, where P_{met} is the metabolic rate at zero swimming speed and the second term is the parasite power; a is a constant including the surface area of the body and b is a constant relating mechanical efficiency to speed. I will

assume that $a \propto m^{2/3}$ and $b \propto m^0$. Weihs (1973) showed that $V_{mr} = (b \cdot P_{met}/a)^{1/2}$, which I used as a characteristic speed when calculating the migration speed. As before, I assumed that $P_{dep} = 0.5 \cdot BMR$. Evaluating equation (1) for swimmers thus yields

$$V_{migr} \propto m^{1/24}, \tag{4}$$

which is a rather slow increase of migration speed with increasing body mass.

I also used scaling relationships based on empirical data for fish analysed by Videler (1993). He found that $V_{mr} = 0.47 \cdot m^{0.17}$ and $P(V_{mr}) = 0.52 \cdot m^{0.79}$. For the resting metabolism I used the standard metabolic rate for fish reported by Peters (1983): $P_{met} = 0.16 \cdot m^{0.78}$. Using these empirical data in equation (1) gave

$$V_{migr} = 5.41 \cdot m^{0.16} \ (km/day), \tag{5}$$

which is a steeper increase of migration speed with increasing body mass than for the hydrodynamic equation (4). This could be due to varying energy conversion efficiency with increasing body mass (cf. Casey, 1992). Using allometric relationships of swimming energy costs for homoeothermic marine animals (Hind & Gurney, 1997), yield the alternative equation

$$V_{migr} = 9.79 \cdot m^{0.17} \ (km/day). \tag{6}$$

This equation indicates that homoeothermic animals migrate faster than fish but that the increase of migration speed with body mass is similar. If migration speed is selected for it will incur selection for increased body size in animals that swim.

Flyers

Scaling of migration speed in birds was analysed by Hedenström & Alerstam, (1998), who, using flight mechanics, derived that $V_{migr} \propto m^{-1/4}$ for powered flight and isometrically scaled birds, i.e. a negative exponent of body mass. Real birds are, however, not isometrically scaled (Rayner, 1988), which reduces the exponent to –0.19. With a $P_{dep} = 0.5 \cdot BMR$, as assumed also for runners and swimmers, and an allometric scaling of wing span on body mass ($b = 1.165 \cdot m^{0.394}$; Rayner, 1988) yield that

$$V_{migr} = 53.4 \cdot m^{-0.19} \ (km/day). \tag{7}$$

Hence, in flapping flight migration it should be advantageous to be small if migration speed is an important trait.

In thermal-soaring flight migration speed increases with increasing body mass in the size range of extant bird species (Hedenström & Alerstam, 1998). For allometrically scaled birds (wing span as above, wing area $S = 0.1576 \cdot m^{0.722}$; Rayner, 1988), with $P_{dep} = 0.5 \cdot BMR$, a climb rate while circling in thermals $V_c = 1$ m/s and restricted availability of thermals to 8 hours per day (Hedenström, 1993), the overall migration speed is

$$V_{migr} = 52.5 \cdot m^{0.22} \ (km/day). \tag{8}$$

This implies that there is a body mass where migration speeds are equal for both flapping and soaring-flight migration (Hedenström, 1993), which is at 1.04 kg for equations (6) and (7). The exact location of this body mass depends on the fuelling rate (P_{dep}) and rate of climb when soaring in thermals. Once a species has adopted soaring flight migration there should be selection for increased body size (Hedenström & Alerstam, 1998).

COMPARISON BETWEEN LOCOMOTION MODES

The scaling relationships derived from locomotion mechanics are given in Table 1, while the scaling proportionalities based on empirical data derived for runners (equation 2), swimmers (equation 5) and flyers (powered flight, equation 7; soaring flight, equation 8) are shown in Fig. 1. For aerial locomotion the curves have been extrapolated beyond the maximum body mass where flight is feasible (about 12–15 kg in birds using powered flight; Pennycuick, 1975), while animals that use soaring could evolve to a larger size than this. Also for terrestrial animals in cruising locomotion, mechanical

Table 1. Scaling of body mass for animals that run, swim or fly (powered flight) for overall migration speed (V_{migr}, equation 1), performance number ($N = mgv/P$, where m is body mass, g is acceleration due to gravity, P is propulsive power and V is speed) and time for refuelling during migration (T_{dep})

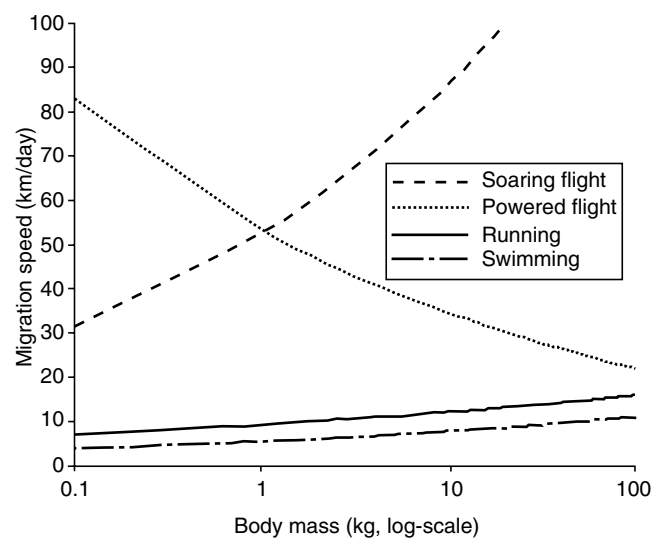| Measure	Runners	Swimmers	Flyers
V_{migr}	$m^{1/11}$	$m^{1/24}$	$m^{-1/4}$
N	$m^{1/3}$	$m^{1/4}$	m^0
T_{dep}	$m^{1/12}$	m^0	$m^{5/12}$

Fig. 1. Migration speed in relation to body mass for animal runners, swimmers and flyers (flapping flight and soaring flight). The scaling equations used are equations (3), (5), (7) and (8). Flyers using flapping flight are constrained by a maximum possible body mass of about 12 kg.

constraints set an upper limit for size given biological materials (Pennycuick, 1992), while swimmers moving in a medium of similar density as themselves are rather unrestricted by such constraints. The comparison in Fig. 1 indicates that if migration speed has a selective advantage then increasing size should be favoured, except in animals using flapping flight.

SCALING OF STOPOVER DURATION

In an analysis of time and energy currencies of bird migration, Hedenström & Alerstam (1997) showed that the relative time for transportation to that of accumulation of the necessary energy for the migration is $1 : P/P_{dep}$, where P is the power required for locomotion and P_{dep} is the rate of energy accumulation. This relationship is generally applicable to any locomotion mode for which the power required at the cruising speed is known. Using the same scaling functions as above, it follows that the relative stopover duration will scale with body mass as follows: runners $\propto m^{1/12}$, swimmers $\propto m^0$, and in flyers using powered flight $\propto m^{5/12}$ (Table 1). Hence, for animals that run or fly, progressively larger animals will use proportionally longer time for energy accumulation, while in swimmers the relative time between transportation and energy accumulation will remain unaffected by body size.

DISCUSSION

Many animal species live in seasonal environments where they move between different habitats for reproduction and survival. The ultimate goal – maximizing the reproductive output – is achieved by optimal management of time. Hence, the time available to migration should be used efficiently by maximizing the overall migration speed and survival during migration (cf. Alerstam & Lindström, 1990). Migration speed in this sense includes the time required for accumulating the necessary fuel energy and the transport time. This concept of travel speed also applies to other movements, such as transportation between food patches or commuting between foraging areas and nest or roost (cf. Norberg, 1981; Hedenström & Alerstam, 1995). In a classic paper, Schmidt-Nielsen (1972) introduced the cost of transport defined as $C = P_m/mgV$, where P_m is the metabolic rate of locomotion. He compared cost of transport between animals that run, swim or fly and showed that C decreases with increasing body mass. For the same body mass C was highest for animal runners, intermediate for flyers and lowest for swimmers. Pennycuick (1987) modified the cost of transport to the related dimensionless performance number $N = mgP/V$, where P is the mechanical power output rather than the metabolic power input. In the case of flight, N is the same quantity as the effective lift to drag ratio, while for running and swimming it measures the ratio between the weight and the average horizontal force needed to push the animal forward. The body mass scaling of the performance number are given for comparison in

Table 1 for the three locomotion types, showing that N increases for isometrically scaled runners and swimmers while it remains unaffected by body mass in flyers. Pennycuick (1987) used an alternative mechanical model for swimmers and therefore derived that N is unaffected by body size also in swimmers, while the model used here (Weihs, 1973) leads to a size dependence. Overall, if performance number is a measure related to fitness we should expect selection for increasing body size in runners and swimmers, but not in animals using flapping flight. The performance number is associated with fuel economy of migration and so is a high overall migration speed, because if the animal is using small amounts of energy per unit distance it will cover a long distance, resulting in high migration speed compared to a more wasteful use of energy. However, in flying animals the optimal flight speed associated with maximum migration speed is somewhat higher than the maximum range speed (V_{mr}), which is the optimal flight speed associated with the minimum energy cost of transport (Hedenström & Alerstam, 1995).

In animals performing annual migrations we will expect selection for time minimization migration, i.e. maximizing the overall speed of migration (Alerstam & Lindström, 1990; Hedenström & Alerstam, 1998; Houston, 1998). This is associated with selection on body size according the allometric equations derived in this paper (cf. Fig. 1; Table 1). In birds using flapping flight long distance migrations is favoured by small size, and in this group we find small passerines, shorebirds and, in particular, the arctic tern *Sterna paradisaea* as species migrating the longest distances. In large species using flapping flight, body size might constrain the round-trip migration distance that can be achieved. The migrations of the three species of European swans (*Cygnus olor*, *C. cygnus* and *C. columbianus*) is a possible illustration of this, where migration distance is inversely related to body mass (Cramp & Simmons, 1977). Intercontinental long-distance migration in large birds is invariably associated with soaring flight; thermal soaring by eagles and storks are examples. Satellite telemetry studies of migrating large raptors show that they exhibit a higher overall migration speed than birds using powered flight (Hedenström & Alerstam, 1998). Wandering albatrosses *Diomedea exulans* are large birds (10 kg) using dynamic soaring and wave slope-soaring, and show impressive foraging flights of up to 15 000 km at speeds of about 450 km/day (Jouventin & Weimerskirch, 1990), while their migration flights may be even more impressive (Prince *et al.*, 1997).

In terrestrial animals we find the longest migration distances in relatively large animals, such as caribou *Rangifer tarandus* exhibiting annual round-trip migrations of up to 6000 km (S. Couturier, pers. comm.). Likewise, in swimming animals long-distance migrations are found among the largest species that ever evolved, with return migration distances up to 11 000 km in whales (Lockyer & Brown, 1981), e.g. humpback whales *Megaptera novaeangliae* migrate between Hawaii and Alaska (Darling & McSweeney, 1985). Southern elephant seals *Mirounga leonina* perform impressive seasonal

migrations between breeding sites and non-breeding feeding areas (McConnell & Fedak, 1996). Recent tracking studies of white sharks *Carcharodon carcharias* show that individuals may migrate up to 3800 km (one-way) between Californian and Hawaiian waters (Boustany *et al*., 2002).

The proportion of time spent accumulating energy reserves for migration to that spent in actual transport should increase with body mass in animals that run and use powered flight, while it should be unaffected by body size in swimmers. In small birds this proportion should be 7 : 1 (Hedenström & Alerstam, 1997), which is consistent with available data on warbler migration (cf. Fransson, 1995). The predicted scaling in runners and swimmers remains to be tested. Because the time of migration spent on fuelling and transport differ it may be suggested that selection for efficient fuelling should be stronger than that of efficient locomotion. Houston (2000) offers a general approach for deriving the relative strength of selection between fuelling and efficient locomotion, which depends on the ratio P/P_{dep}, but also on the curvature of these functions in the neighbourhood of their respective optima.

In animals using terrestrial and aquatic locomotion there should be a selection towards increasing body size for improved overall migration speed. There might naturally be opposing selection pressures for reasons other than migration performance. However, a low but steady selection pressure on increased body size in animals where migration or foraging transport is important could be an explanation to Cope's rule, i.e. the observation that over evolutionary time there is a gradual overall increase in average mass (e.g. Alroy, 1998). For example, in the horse clade there is a well documented increase in body size (Simpson, 1944), which has previously been interpreted in the context of locomotion (Thomason, 1991).

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