

LETTER

Energetic and biomechanical constraints on animal migration distance

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Abstract

Animal migration is one of the great wonders of nature, but the factors that determine how far migrants travel remain poorly understood. We present a new quantitative model of animal migration and use it to describe the maximum migration distance of walking, swimming and flying migrants. The model combines biomechanics and metabolic scaling to show how maximum migration distance is constrained by body size for each mode of travel. The model also indicates that the number of body lengths travelled by walking and swimming migrants should be approximately invariant of body size. Data from over 200 species of migratory birds, mammals, fish, and invertebrates support the central conclusion of the model – that body size drives variation in maximum migration distance among species through its effects on metabolism and the cost of locomotion. The model provides a new tool to enhance general understanding of the ecology and evolution of migration.

Keywords

Allometry, biomechanics, dispersal, ecomechanics, ecophysiology, energetics, migration, movement ecology, scaling, spatial ecology.

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INTRODUCTION

Each year, diverse species from around the planet set out on migrations ranging from a few to thousands of kilometres in length (Dingle 1996; Egevang *et al.* 2010; Hedenström 2010). Biologists have long hypothesised that this variation in migration distance among species might be governed by differences in basic species characteristics such as morphology and body size (Dixon 1892). Although much progress has been made in understanding how these characteristics are related to the mechanics of locomotion and to the migratory capabilities of individual species (e.g. Pennycuik & Battley 2003; Alexander 2005), success in understanding variation in migration distance among species has been limited. This is because current models often require detailed information on the morphology and behaviour of migrants (e.g. Alerstam & Hedenström 1998; Pennycuik & Battley 2003). This requirement has precluded a quantitative analysis to determine the extent to which shared functional characteristics such as body size could be responsible for observed variation in migration distances among species. As a result, the need for general theory and cross-species analyses of migration has been strongly emphasised in recent years (Bauer *et al.* 2009; Milner-Gulland *et al.* 2011).

Herein, we present a model to describe constraints on animal migration distance. Our model expands on past approaches (Alexander 1998; Hedenström 2003; Pennycuik 2008) by incorporating (1) the body mass-dependence of the cost of locomotion, (2) dynamic changes in the body masses of migrants as they utilise stored fuel and (3) scaling of morphological characteristics and maintenance metabolism among migrants of different body masses. In contrast to past approaches, the model assumes that the number of refuelling stops made by migrants is unknown and may vary substantially among species. This facilitates prediction of statistical patterns of migration

distance among species, even when the details of migratory behaviour of individual species are unknown.

MODEL DEVELOPMENT

We treat migration as a process in which a migrant travels a distance of Y_i (km) by breaking the journey into a series of N legs of length Y_i ($i \in 1, 2, \dots, N, N \geq 1$, Fig. 1A). Describing variation in migration distance among species, thus, requires describing the processes that determine Y_i , while accounting for among-species variation in N . To accomplish this, we begin by making four simplifying assumptions (see Appendix S1 in Supporting Information for detailed derivation and alternative assumptions). We assume (1) that the total rate of energy use by a migrating animal, P_{tot} (W), is the sum of the rate of energy use for general maintenance, P_{mtn} and that required for locomotion, P_{loc} (i.e. $P_{tot} = P_{mtn} + P_{loc} = -dG/dt$, where G = Joules of stored fuel energy), (2) that migrants using a particular mode of locomotion are geometrically similar, such that linear morphological characteristics (e.g. lengths of appendages) are proportional to $M^{1/3}$ and surface areas are proportional to $M^{2/3}$ (where M is body mass (kg), Peters 1983), (3) that migrant metabolism provides the power required for locomotion and (4) that the number of refuelling stops made by individuals of each species is independent of body mass.

Distance travelled on a single migratory leg

During any given leg of a migration, the rate of change in migration distance per unit change in body mass can be expressed as

$$dY_i/dM = (dY_i/dt)(dt/dG) = -vc/(P_{mtn} + P_{loc}),$$

where v is travel speed (m s^{-1}) and c is the energy density of stored fuel (Joules kg^{-1}). The distance travelled on a particular leg can be

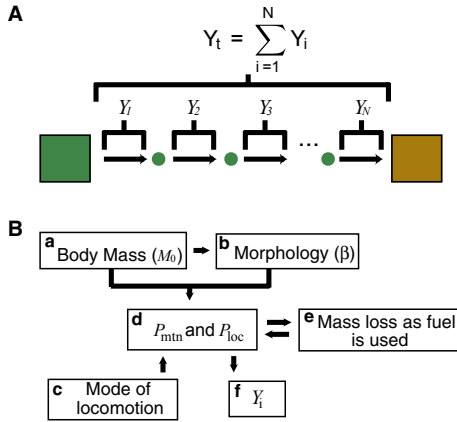


Figure 1 (A) Total migration distance is the sum of the distances travelled on each of N migratory legs. (B) Migration distance on a single migratory leg. Body mass (a), morphology (b) and mode of locomotion (c) govern the rate at which a migrant uses stored fuel energy (d). This rate changes as migrant loses fuel mass (e), and determines the maximum distance covered during a single leg (f, eqn (1)). The relationship between a and b is governed by the mass-dependence of morphology. Total rate of energy use (d) is determined by the mass-dependence of maintenance metabolism and by the biomechanics of locomotion (eqns 3–5).

obtained by integrating this expression from initial mass at the beginning of the leg, M_0 (kg), to final mass after all fuel energy has been used, $M_0(1 - f)$, where f is the ratio of initial fuel mass to M_0 ,

$$Y_i = \int_{M_0}^{M_0(1-f)} \frac{-v(M, \beta) c}{P_{min}(M) + P_{loc}(M, \beta)} dM \quad (1)$$

Here, v , P_{min} and P_{loc} have been rewritten to show their dependence on body mass and on a small set of morphological traits, β (lengths and surface areas, e.g. wingspan, body cross-sectional area), which determine the energetic cost of locomotion. This formulation allows for changes in speed and rate of energy use, as the migrant loses stored fuel mass.

Equation (1) can be used to predict how Y_i varies among species by specifying appropriate functions for $v(M, \beta)$, $P_{min}(M)$ and $P_{loc}(M, \beta)$. We assume that P_{min} scales with body mass as $P_{min} = p_0 M^{3/4}$, both within and among individuals, where p_0 is a normalisation constant that varies by taxon (Kleiber 1932; Hemmingen 1960). Biomechanics theory provides a means of expressing P_{loc} and v as functions of M and β for migrants using a particular mode of locomotion (see below).

Generalising to multi-leg migrations

Total distance travelled over the course of migration is given by the sum, $\sum_{i=1}^N Y_i$, where N is the number of migratory legs travelled by a given species (Fig. 1A). N is unknown for the majority of migratory species. To account for variation in N among species, we treat N as a random quantity with mean, \bar{N} . We treat Y_i as fixed for a given species because we are interested in maximum migration distance. Iterated expectation shows that the expected distance travelled over N migratory legs is

$$Y_T = E \left[\sum_{i=1}^N Y_i \right] = \bar{N} Y_i \quad (2)$$

where the operator, E , denotes the expected value (Rice 1995). Eqn (2) shows that Y_T is proportional to Y_i , which is given by eqn (1).

Parameterizing the model for walking, swimming and flying migrants

The model developed above is general and applies to migrants using any mode of locomotion. Herein, we parameterize the model for the three dominant modes of migratory locomotion (walking, swimming and flight) by using standard models of locomotion to describe the P_{loc} and v terms in eqn (1) (biomechanical models described in detail in Appendix S1). For walking migrants, P_{loc} can be described by

$$P_{walk} = \gamma \frac{gM}{L_c} v \quad (3)$$

where L_c is stride length (m), v is walking speed (m s^{-1}), γ is a cost coefficient (J N^{-1}) and g is the acceleration due to gravity (m s^{-2} , Kram & Taylor 1990). The only morphological variable in eqn (2) is L_c , which is proportional to leg length (Alexander & Jayes 1983). We assume that walking migrants travel at speeds, $v \propto M_0^{0.1}$ (Alexander 1998) and that they maintain these speeds over the course of migration.

The power required for swimming can be described by the resistive model,

$$P_{swim} = \delta \frac{A_b v^{2.8}}{L_b^{0.2}} \quad (4)$$

where δ is a dimensionless cost coefficient, A_b is body cross-sectional area (m^2), L_b is body length (m) and v is swimming speed (m s^{-1} , Alexander 2003). The set of relevant morphological variables, β , is A_b and L_b . We assume that migrants swim at speeds that minimise the ratio P_{tot}/v .

Power required for flight near minimum power speed can be described by the equation

$$P_{fly} = (1 + \kappa) \left[\varphi M^2 L_w^{-2} v^{-1} + \phi A_b v^3 \right] \quad (5)$$

where κ is a dimensionless profile power coefficient, φ and ϕ are cost coefficients (section 1.4 Appendix S1), A_b is body cross-sectional area (m^2), L_w is wingspan (m) and κ is proportional to A_w/L_w^2 , where A_w is wing area (Pennycuik 2008). The set of relevant morphological variables, β , is therefore A_b , L_w and A_w . We assume flying migrants travel at speeds that minimise P_{fly}/v_s (Pennycuik 2008).

Substituting eqns (3–5), corresponding migration speeds and the mass-dependence of maintenance metabolism into eqn (1) allows Y_i to be expressed as a function of initial mass M_0 , p_0 and β for each mode of locomotion. In each of the biomechanical models described above, the power required for locomotion depends, in part, on a set of morphological lengths and areas, β , that do not change as the migrant uses stored fuel to power migration. The dependence of Y_i on β can be eliminated by expressing morphological variables in terms of M_0 based on the assumption of geometric similarity (i.e. lengths $\propto M_0^{1/3}$, surface areas $\propto M_0^{2/3}$).

Substituting functions for Y_i (section 1 Appendix S1) into eqn (2) yields expressions for the expected maximum migration distances of walking

$$Y_T = j_0 M_0^{0.34}, \quad (6)$$

swimming,

$$Y_T = y_0 p_0^{-0.64} M_0^{0.3} \quad (7)$$

and flying

$$Y_T = y_0 \ln \left[\frac{p_0 + \kappa_1 M_0^{0.42}}{p_0 + \kappa_2 M_0^{0.42}} \right] \quad (8)$$

migrants. Herein, y_0 is a proportionality constant that varies by mode of locomotion, and κ_1 and κ_2 are empirical constants. Differences in the functional forms of eqns (6–8) are caused by differences in the way P_{bc} depends on mass in walking, swimming and flying migrants. In the case of eqn (8), the predicted relationship does not follow a simple power function in M_0 . This is because the cost of flight increases more rapidly with increasing body mass than does the cost of walking or swimming. The variable, p_0 , does not appear in the final form of the equation for walking migrants because here we only consider the distance travelled by walking mammals, for which p_0 is roughly constant (White *et al.* 2009).

The exponents of the mass terms in eqns (6–8) describe how maximum migration distance changes as a function of M_0 and reflect the mass-dependence of maintenance and locomotory metabolism. The constant, y_0 , describes effects of mass-independent factors, such as the number of migratory legs, that affect the absolute distances travelled by migrants but do not affect the scaling of migration distance with body mass. The metabolic normalisation constant, p_0 , and the morphological constants κ_1 and κ_2 can be estimated from empirical measurements (see Materials and Methods).

The framework described here uses body mass (Fig. 1B box a), morphology (Fig. 1B box b) and mode of locomotion (Fig. 1B box c) to determine migratory speed, and the metabolic costs of locomotory and maintenance metabolism (Fig. 1B box d). Equation (1) ensures that changes in speed and metabolism as the migrant uses stored fuel (Fig. 1B box e) are explicitly incorporated into the prediction of Y_i (Fig. 1B box f).

Model predictions

Equations (6–8) make several quantitative predictions that can be tested against data. First, each equation predicts that, after normalising for p_0 , a single curve can be used to describe expected maximum migration distance (in km) as a function of M_0 for species using each mode of locomotion. Second, each equation predicts how the number of body lengths travelled – a measure of relative distance (Alerstam *et al.* 2003) – varies with body mass. Migration distance and body length scale similarly with mass in walking and swimming animals (i.e. Y_T roughly proportional to $M_0^{1/3}$, body length $\propto M_0^{1/3}$) such that the number of body lengths travelled during migration, Y_{bl} , is described by $Y_{bl} = Y_T / (\text{body length}) \propto M_0^{1/3} / M_0^{1/3} \propto M_0^0$. Thus, after normalising for differences in p_0 , the number of body lengths travelled by walking and swimming animals should be approximately invariant with respect to M_0 . In flying animals, however, dividing eqn (8) by $M_0^{1/3}$ indicates that Y_{bl} should decrease with increasing mass for all but the smallest flying migrants.

MATERIALS AND METHODS

To evaluate the model, published measurements of maximum migration distances of terrestrial mammals, fish, marine mammals and flying insects and birds were collected. Data from studies that met

five criteria were included in the analysis: (1) reported movements could be considered to-and-fro migration or one-way migration (Dingle & Drake 2007), (2) individuals were directly tracked by mark-recapture, telemetry or other means, groups of individuals were tracked by repeated observation over the course of migration, or a reliable estimate of distance travelled could otherwise be established, (3) maximum travel distances, maps, tracks or other information that allowed direct calculation of minimum estimates of the distances travelled by individual animals were reported, (4) there did not exist strong but indirect evidence from other studies (e.g. sightings of unmarked individuals, stable isotope data) suggesting that the maximum reported migration distance was substantially shorter than true maximum migration distance and (5) in the case of flying species, studies reported migration distances of species that rely, at least partially, on flapping flight. The fifth criterion was imposed because the biomechanical model of flight used to derive our predictions applies most directly to flapping flight. Migration distance and body mass data were included from a large dataset (Elphick 1995) for which all of the selection criteria could not be verified for all species. Including these data did not qualitatively affect our conclusions (see Results).

We estimated the constants κ_1 and κ_2 in eqn (8) using empirical studies of the morphology of flying insects and birds; however, the general form of eqn (8) and the resulting predictions are not strongly affected by variation in the empirical values used to estimate κ_1 and κ_2 (section 2.2 Appendix S1). Empirical estimates of p_0 were used in eqns (7–8) (Appendix S1). Body mass data were used to estimate body lengths based on allometric equations (swimming mammals: Economos 1983; others: Peters 1983). Body lengths were used to convert migration distance (km) into units of body lengths.

To evaluate our first prediction, we fitted eqns (6–8) to migration distance data from walking ($n = 33$), swimming ($n = 32$) and flying migrants ($n = 141$). Eqns (6) and (7) were fitted to \log_{10} -transformed distance and body mass data using ordinary least squares. Eqn (8) was fitted to \log_{10} -transformed distance and body mass data using non-linear least squares (Gauss–Newton algorithm). Equations (6–8) have the general form: $Y_T = y_0 b(M_0^d p_0)$, where b is a known function, y_0 is a constant, and d is a scaling exponent. For each equation, two models were fitted: a model in which y_0 was fitted as a free parameter, but d was set to the predicted value (i.e. $d = 0.34, 0.3, 0.42$; for walking, swimming, and flying migrants respectively), and a model in which both y_0 and d were fitted. Model r^2 values reported below are based on the former method. The latter method was used to generate 95% profile confidence intervals for the d parameter. Prior to fitting, body mass values of swimming and flying animals were normalised to account for differences in p_0 according to the equations $M_{norm} = M_0^{0.3} p_0^{-0.64}$ and $M_{norm} = M_0^{0.42} p_0^{-1}$ respectively. To test our second prediction – that the number of body lengths travelled was invariant of mass in walking and swimming migrants, but decreased with mass in flying migrants – we fitted \log_{10} -transformed migration distance (in body lengths) as a function of \log_{10} -transformed body mass (kg) using a quadratic regression of the form, $\log_{10}(Y_{bl}) = \gamma_0 + \gamma_1 \log_{10}(Y_{bl}) + \gamma_2 \log_{10}(Y_{bl})^2$, where γ_i are regression coefficients (Venables & Ripley 1999). Species were separated based on mode of locomotion and by taxonomic groups differing in p_0 (i.e. walking mammals, fish, marine mammals, flying insects and passerine and non-passerine birds were fitted separately). Statistical analyses were implemented using the nlme package (Pinheiro *et al.* 2009) in R (2010).

RESULTS

Model predictions were evaluated using extensive data on maximum migration distances of animals from around the world ($n = 206$ species, Data S1). Consistent with our first prediction, maximum migration distance (km) varies systematically with body mass for walking, swimming and flying migrants (Fig. 2: $r^2 = 0.57, 0.65, 0.19$; for walking, swimming, and flying species respectively). The solid lines show predicted migration distance based on eqns (6–8). There is a tight correspondence between predicted relationships (solid lines) and fitted models that treat both y_0 and scaling exponents as free parameters (dashed lines and 95% confidence bands). In the case of walking and swimming animals, the data support model predictions of linear relationships in log-log space, with observed scaling exponents close to those predicted by eqns (6) and (7) (walking: predicted = 0.34, observed = 0.36 95%CI [0.25,0.48]; swimming: predicted = 0.3, observed = 0.34 [0.28,0.41]). In the case of flying animals, data support the prediction that the relationship is non-linear in log-log space reflecting the rapidly rising cost of flight with increasing mass (Fig. 2c). Again, the observed mass exponent is close to that predicted by eqn (8) (predicted = 0.42, observed = 0.43 [0.36,0.49]).

Consistent with our second prediction, the number of body lengths travelled by swimming and walking animals is independent of body mass (Fig. 3). On average, walking mammals travel 1.5×10^5 body lengths (Fig. 3a). The slope and curvature terms in the quadratic regression model does not differ from zero in walking mammals ($n = 33$, $P > 0.22$) indicating that the number of body lengths travelled is uncorrelated with body mass in this group. Swimming animals travel an average of 1.7×10^6 body lengths in a one-way migratory journey. The mean distance travelled by fish (triangles in Fig. 3b) exceeds that travelled by swimming mammals (squares in Fig. 3b) by a factor of 4 (fish: 2.1×10^6 body lengths; marine mammals: 5.3×10^5 body lengths, see Discussion), but the number of body lengths travelled is independent of mass in each of these groups (slope and curvature does not differ from zero, fish: $n = 20$, $P > 0.38$; swimming mammals: $n = 12$, $P > 0.43$). In flying migrants, the number of body lengths migrated declines clearly with increasing body mass (Fig. 3c). In non-passerine birds ($n = 80$), coefficients of linear and quadratic terms were both negative, and significantly different from zero ($\gamma_1 = -0.59$, $\gamma_2 = -0.19$, $P < 2.2 \times 10^{-5}$). In passerine birds ($n = 45$) and flying insects ($n = 16$), the γ_1 term was negative and distinguishable from zero (passerines: $\gamma_1 = -0.63$, $P = 5.4 \times 10^{-5}$; insects: $\gamma_1 = -0.16$, $P = 0.034$). Results for flying

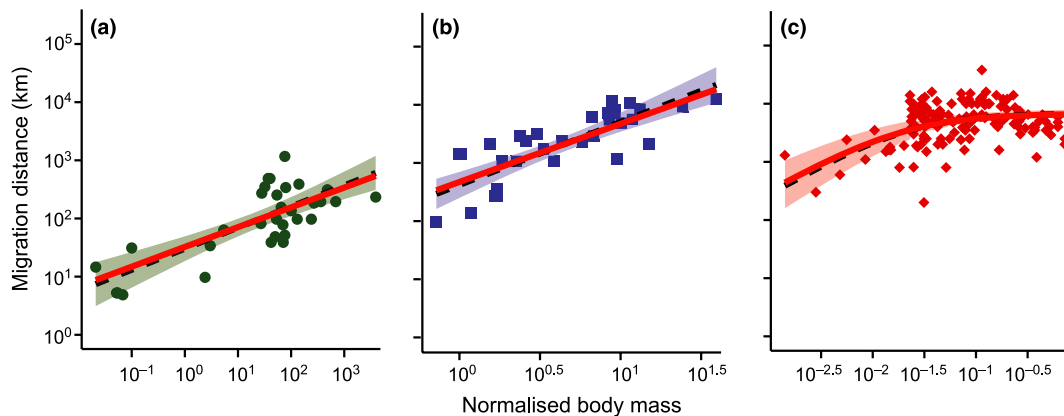


Figure 2 Maximum migration distance as a function of normalised body mass for (a) walking mammals, (b) swimming fish and marine mammals and (c) flying birds and insects. Solid lines are predicted curves based on fits of eqns (6–8) to data with y_0 fitted as a free parameter. Dashed lines and confidence bands represent best fit curves and 95% confidence intervals from linear (a, b) or non-linear regression (c) with y_0 and the mass scaling exponent fitted as free parameters. In panel (a), body mass is M_0 (kg). In panels (b) and (c), body mass is normalised according to the equations $M_{norm} = M_0^{0.3} p_0^{-0.64}$ and $M_{norm} = M_0^{0.42} p_0^{-1}$, respectively, to correct for differences in p_0 among groups. Data on walking animals are from mammals only and are therefore not corrected for p_0 .

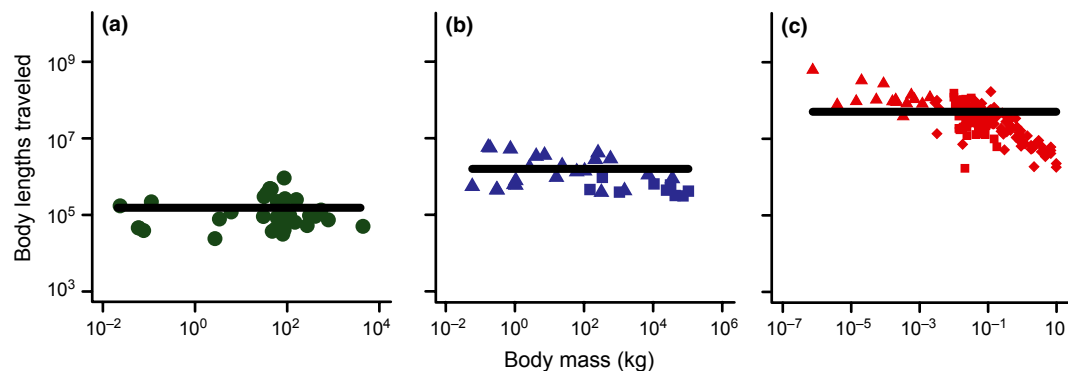


Figure 3 Number of body lengths travelled during migration by (a) walking mammals, (b) swimming fish (triangles) and mammals (squares) and (c) flying insects (triangles), passerine birds (squares) and non-passerine birds (diamonds). Lines denote mean number of body lengths travelled by species using each mode of locomotion.

migrants, confirm our prediction that larger flying migrants generally travel fewer body lengths over the course of migration. The number of body lengths travelled decreases with increasing mass such that the smallest insects and birds travel around 1.4×10^8 body lengths whereas the largest birds travel around 5.2×10^6 body lengths. In other words, the number of body lengths covered by moths, dragonflies and hummingbirds is roughly 25-times that travelled by the largest ducks and geese.

A sensitivity analysis indicates that the agreement between model predictions and data are robust to deviations from geometric similarity and changes in the values of morphological and biomechanical parameters used to derive eqns (6–8) (see section 2.2 Appendix S1 and Table S2). In particular, the value of the exponent in metabolic scaling relationships has been a topic of much debate, with different authors reporting different exponents depending on the particular dataset and taxon studied and the method of analysis (e.g. White *et al.* 2009; Riveros & Enquist 2011). However, sensitivity analysis shows that the shape of our predicted relationships and the agreement between predictions and data are largely insensitive to changes in the value of the metabolic scaling exponent assumed (Appendix S1). Including data from Elphick (1995) did not significantly change the estimate of the mass exponent (0.36 95% CI [0.26,0.43] without data from Elphick (1995), 0.43 [0.36,0.48] with data from Elphick (1995)). Including data from Elphick (1995) decreased the model r^2 from 0.37 to 0.19.

DISCUSSION

When observed migration distances are plotted against predictions of eqns (6–8), points from all three groups cluster around a 1 : 1 line (Fig. 4). The data shown in Fig. 4 suggest that variation in maximum migration distances among species as distinct as Blue Whales (*Balaenoptera musculus*), Wildebeest (*Connochaetes taurinus*) and Bar-tailed Godwits (*Limosa lapponica*) appears to be driven, in part, by the basic differences in metabolism, morphology and biomechanics described by

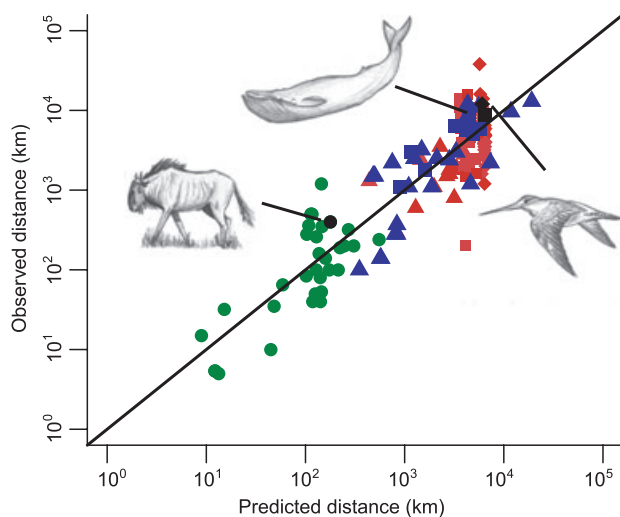


Figure 4 Observed and predicted migration distances for the walking, swimming and flying animals shown in Fig. 2. Data from walking mammals (green circles), swimming fish (blue triangles) and marine mammals (blue squares), and flying insects (red triangles), passerine birds (red squares) and non-passerine birds (red diamonds) are shown. Black points and illustrations show the well-studied migrants *Connochaetes taurinus* (Wildebeest), *Balaenoptera musculus* (Blue Whale) and *Limosa lapponica* (Bar-tailed Godwit). Solid line indicates 1 : 1 line.

our model. The variation explained by the model reflects the influence of constraints on energetics and biomechanics imposed by body mass. There is a large body of work describing how morphology (Peters 1983; Alexander 2003), biomechanics (Alexander 2003, 2005) and basic energetic properties such as maintenance metabolism (West *et al.* 1997; Banavar *et al.* 2010) are linked to body mass. Our model extends results of these studies by specifying how these quantities influence maximum migration distance of diverse species, thereby linking body mass to migration distance. Our results show that constraints imposed by body mass are detectable in migration distance data, despite variation in migration distance among species with similar body masses (i.e. variation about predicted relationships shown in Figs 2 and 4).

Migration distance data highlight the important role of basic differences in energetics in driving differences in migration distance among taxa. For example, the number of body lengths travelled during migration is independent of body mass within both swimming mammals and fish; however, fish travels an average of four times the number of body lengths travelled by swimming mammals. Equation (7) shows that the distances travelled by these groups depend on the metabolic normalisation constant, p_0 , which describes mass-independent differences in the maintenance metabolic rates of fish and marine mammals. In these groups, p_0 differs by a factor of roughly 9.1 ($p_0 \approx 3.9 \text{ W kg}^{-3/4}$ in marine mammals, $p_0 \approx 0.43 \text{ W kg}^{-3/4}$ in fish, see Appendix S1), whereas body length exhibits a similar relationship with mass in both groups ($l \approx 0.44M^{1/3}$) suggesting that the number of body lengths migrated by fish is greater by a factor of $(9.1)^{0.64} = 4.1$, which is very close to the observed factor of 4. Thus, the difference in the mean number of body lengths travelled by these groups may be driven by basic differences in the cost of maintenance metabolism. Data also reveal patterns that do not appear to be caused by the energetic and biomechanical factors considered here. For example, swimming is significantly less costly than flight in terms of the energy required to travel a given distance (Weber 2009), yet virtually all flying organisms travel distances that are as great or greater than those travelled by most swimming species (Fig 4). Whether this pattern is driven by differences in migratory behaviour or other ecological or evolutionary factors remains unknown and will likely be a fruitful area of future research.

It is worth noting that other hypotheses may provide alternative explanations for some of the qualitative patterns observed in migration distance data. For example, the model predicts that migration distance (km) of larger flying species does not depend strongly on mass. An increase in mass from 10^{-6} kg to 10^{-3} kg, increases expected migration distance by a factor of more than 8, whereas an increase in mass from 10^{-2} kg to 10 kg increases expected migration distance by a factor of less than 2. This occurs because the energetic cost of flight increases rapidly with increasing mass to the degree that the increasing fuel mass that can be carried by larger migrants provides a diminishing increase in migration distance. An alternative explanation for this observation is that many subtropical and temperate habitats in the northern and southern hemispheres are separated by $5 \times 10^3 \text{ km}^1 \times 10^4 \text{ km}$ and that many flying migrants may not be under selection to migrate greater distances. In general, the relationship between the distances travelled by migrants and the global distribution of suitable migratory habitats is poorly known but may ultimately influence the distances travelled by many species.

While model predictions are supported by data, there is substantial unexplained variation in Figs 2 and 4. Investigating why particular species deviate from predictions may be an effective way to identify

ecological and evolutionary factors that drive differences in migration distance but are not currently included in our model. Our model ignores variation in fuel and morphology of species with similar masses and does not consider the possibility that some migrants may seek to minimise the time spent migrating. Two additional factors, in particular, are likely to contribute to observed residual variation. First, differences in the number migratory legs among otherwise similar species will lead to variation in migration distance among species as indicated by eqn (2). Second, species that interact strongly with abiotic currents during migration are likely to deviate from model predictions. The lack of information regarding the type and number of refuelling stops made by migratory species, and the lack of information about the manner in which many flying and swimming migrants interact with abiotic currents represents an important gap in current knowledge. In the case of some well-studied species such as the arctic tern (*Sterna paradisaea*), it is clear that these variables are important in facilitating extremely long-distance migrations. Individuals of this species stop at multiple highly productive foraging sites to refuel during migration (Egevang *et al.* 2010). This species is also known to track global wind systems thereby taking advantage of favourable air currents. In the case of species that migrate against abiotic currents, migration distances might be expected to be shorter than our model predicts. Indeed, many of the swimming migrants that fall below the predicted line in Fig. 2, are anadromous fish such as shad (*Alosa sapidissima*), alewife (*Alosa pseudoharengus*) and river lamprey (*Lampetra fluviatilis*) that swim against water currents during upriver migrations. Increased understanding of the interactions between migrants and abiotic currents and the number of migratory stopovers will allow for extensions of the model that could further improve our understanding of the reasons for interspecific differences in migration distance. In its current form, the model presented here provides a general expectation on maximum migration distance, which can be seen as a metric against which the distances travelled by particular species can be compared.

The body sizes of migratory animals vary by over 11 orders of magnitude. The model presented here makes specific quantitative predictions about how this variation in size drives patterns of migration distance among species. It attributes differences in the distances travelled by migrants to systematic differences in metabolism and morphological traits that are tightly coupled to body size, and to differences in the underlying mechanics of walking, swimming, and flight. In doing so, it provides an analytically tractable framework for studying the influence of energetics and biomechanics on migration distance that is consistent with data on species ranging from the smallest migratory insects to the largest whales.

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AUTHORSHIP

A.M.H., C.H. and J.F.G. conceived the study; A.M.H., C.H. and J.F.G. developed the model; A.M.H. compiled the data and performed analyses; A.M.H., C.H. and J.F.G. wrote the paper.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Model derivation, sensitivity and statistical analyses.

Data S1 Maximum migration distance and body mass data.

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Appendix S1. Model derivation, sensitivity, and statistical analyses

(Hein, Andrew M. et al; Energetic and biomechanical constraints on animal migration distance)

1 Derivation of migration distance equations

1.1 General distance equation

Here we provide a detailed derivation of the migration distance equations for walking, swimming, and flying migrants presented in the main text (equations 6-8). For each, we begin by expressing maximum migration distance on a single migratory leg, Y_i , as a function of total power, P_{tot} , speed, v , and energy density, c :

$$Y_i = \int_{M_0}^{M_0(1-f)} \frac{-v c}{P_{tot}} dM \quad (\text{S1})$$

where $P_{tot} = P_{mtn} + P_{loc}$, M_0 is initial mass at the beginning of the migratory leg, and f is the ratio of fuel mass to M_0 at the beginning of the leg. To solve for Y_i , we specify functions describing P_{mtn} , P_{loc} , and v . For P_{mtn} , we assume $P_{mtn} = p_0 M^{0.75}$ as described in the main text. Derivations of walking, swimming, and flying equations are given below. Constants in biomechanical equations (3-4) in the main text have been expanded to more explicitly show their physical basis.

1.2 Walking

To estimate the power required for walking, we use equation (3) described in the main text. Empirical evidence strongly supports the predictions of this model (Kram & Taylor, 1990; Roberts *et al.*, 1998). Combining this model with equation (S1) and integrating from initial to final mass gives

$$Y_{i,walk} = y_w L_c \ln \left(\frac{p_0 v_{walk}^{-1} + \gamma g L_c^{-1} M_0^{0.25}}{p_0 v_{walk}^{-1} + \gamma g L_c^{-1} M_0^{0.25} (1-f)^{0.25}} \right) \quad (\text{S2})$$

where y_w is a constant. Based on our assumption of geometric similarity, $L_c \propto M_0^{0.33}$, because stride length is typically proportional to leg length (Alexander & Jayes, 1983). We assume that $v_{walk} \propto M_0^{0.1}$ among species but that it is fixed for an individual migrant (Alexander, 1998). Substituting these terms for L_c and v_{walk} gives an expression for the mass-dependence of Y_i ,

$$Y_{i,walk} = y_w M_0^{0.33} \ln \left(\frac{p_0 + c_1 M_0^{0.02}}{p_0 + c_2 M_0^{0.02} (1-f)^{0.25}} \right) \quad (\text{S3})$$

where c_1 and c_2 are constants. The logarithmic component of equation (S3) contributes little to the shape of the function in the biologically relevant range of M_0 , and can be accurately approximated as, $\ln[(p_0 + c_1 M_0^{0.02}) / (p_0 + c_2 M_0^{0.02})] \approx \ln[(p_0 + c_1) / (p_0 + c_2)] M^{0.01}$. Thus, equation (S3) can be rewritten as a power function in M_0 ,

$$Y_{i,walk} \propto y_w M_0^{0.34} \ln \left(\frac{p_0 + c_1}{p_0 + c_2} \right) \quad (\text{S4})$$

For walking mammals, p_0 is roughly constant and so $Y_{i,walk} \propto M^{0.34}$.

1.3 Swimming

To estimate P_{loc} for swimming migrants, we use a standard resistive model of swimming locomotion (equation (4) in the main text, (Videler, 1993)). The cost of locomotion is proportional to drag times speed, so locomotory power can be expressed as

$$P_{swim} = \frac{\alpha}{\eta} D_t v \quad (S5)$$

where η is dimensionless conversion efficiency from stored fuel energy to muscle power output, and α is a dimensionless correction constant (Videler, 1993; Webb, 1992). We assume that boundary layer flow around the swimming migrants considered here is approximately turbulent (Vogel, 1994). Given this assumption, drag on a swimming migrant of total length, L_b , is given by $D_t = \alpha \frac{C A_b v^{1.8}}{L_b^{0.2}}$, where C is constant determined by water density and dynamic viscosity and A_b is a characteristic area (here taken to be body cross-sectional area, see (Videler, 1993; Alexander, 2003) for detailed discussion of this model). We take v to be the speed that minimizes P_{tot}/v (Videler, 1993), and assume that as a swimming migrant burns fuel, changes in body cross-sectional area, A_b , are small enough to be ignored. Substituting expressions for P_{mtn} , P_{swim} , and v_{swim} into equation (S1) gives,

$$Y_{i,swim} \propto \left(\frac{L_b^{0.2}}{A_b} \right)^{0.36} p_0^{-0.64} M_0^{0.52} [1 - (1 - f)^{0.28}] \quad (S6)$$

To recover the interspecific scaling equation from equation (S6), we note that $l \propto M_0^{0.33}$, $A_b \propto M_0^{0.67}$, and therefore

$$Y_{i,swim} = y_s p_0^{-0.64} M_0^{0.30} \quad (S7)$$

where y_s is a constant.

1.4 Flying

Locomotory power of an animal in steady horizontal flight can be expressed as the sum of three components: the power required to remain aloft (induced power, P_{ind}), the power required to overcome drag on the body (parasite power, P_{par}), and the power required to overcome drag on the wings (profile power, P_{pro})

$$P_{fly} = P_{ind} + P_{par} + P_{pro} \quad (S8)$$

where

$$P_{ind} = \frac{2\omega(Mg)^2}{\eta\pi L_w^2 \rho_a} v^{-1} \quad (S9)$$

$$P_{par} = \frac{\rho_a A_b C_d}{\eta 2} v^3 \quad (S10)$$

$$P_{pro} = \kappa(P_{ind} + P_{par}) \quad (S11)$$

, ω is a dimensionless induced power factor, g is the acceleration due to gravity, η is dimensionless conversion efficiency from stored fuel energy to muscle power output, ρ_a is the density of air, L_w is wingspan, C_d is a dimensionless drag coefficient, and A_b is body cross-sectional area (Pennycuick, 2008). This formulation expresses P_{pro} as a dimensionless profile power factor (κ) times the sum of the induced and parasite power (Pennycuick, 2008). We follow (Pennycuick, 2008) in assuming that $\kappa \propto A_w/L_w^2 = 1/\text{wing aspect ratio}$, where $A_w = \text{wing plan}$

area (Pennycuick, 2008). This model is discussed in detail in (Pennycuick, 2008). v is taken to be the speed that minimizes the ratio of induced and parasite power to speed. At this speed, locomotory power is described by the equation

$$P_{fly} = (1 + \kappa)1.05\eta^{-1} \left(\frac{\omega^3 g^6 A_b C_d M^6}{\rho_a^2 W^6} \right)^{0.25} = k_0 M^{1.5} \quad (\text{S12})$$

where k_0 is constant for an individual migrant. Before substituting P_{fly} and v into equation (S1), we make the additional assumption that, as a flying migrant burns fuel, changes in body frontal area, A_b , are small enough to be ignored (Alerstam & Hedenström, 1998). Under this assumption, maximum migration distance during a single leg is given by

$$Y_{i,fly} = y_f \ln \left(\frac{p_0 + k_0 M_0^{0.75}}{p_0 + k_0 (1 - f)^{0.75} M_0^{0.75}} \right) \quad (\text{S13})$$

where y_f is a constant. To recover the body mass scaling of maximum migration distance, we assume values for the constants and morphological variables that determine k_0 . Specifically, we assume $L_w = 1.1M_0^{0.33}$ (Greenwalt, 1962), $A_w = 0.16M_0^{0.67}$ (Greenwalt, 1962), $\eta = 0.23$ (Alexander, 1999), $\omega = 1.2$ (Pennycuick, 2008), $\rho_a = 0.98$ (Denny, 1993), $A_b = 0.0081M_0^{0.67}$ (Pennycuick *et al.*, 1988), $g = 9.8$, and $C_d = 0.2$ (Alexander, 2003), and $\kappa = 1.1$ (Pennycuick, 2008). Data on maximum fuel fractions of flying migrants prior to departure are available (Hedenström & Alerstam, 1992; Piersma *et al.*, 1997; Odum, 1960; Piersma & Gill, 1998; Battley *et al.*, 2001; Helms & Smythe, 1969; Mclandress & Raveling, 1981; Cockbain, 1961; Alonso-Mejía *et al.*, 1997; Wikelski, 2006), and indicate a mean value of $f = 0.59$ among species, assuming a mixture of 90% lipid and 10% protein is used as fuel (Weber, 2009). Substituting these values gives

$$Y_{i,fly} = y_f \ln \left(\frac{p_0 + k_1 M_0^{0.42}}{p_0 + k_2 M_0^{0.42}} \right) \quad (\text{S14})$$

where $k_1 = 60$ and $k_2 = 31$.

2 Parameter estimation and model sensitivity

2.1 Estimation of p_0

The metabolic normalization constant, p_0 varies among broad taxonomic groups (Peters, 1983). We used published estimates of p_0 for walking mammals, swimming fish, flying insects, non-passerine birds, and passerine birds (Table S1). For swimming mammals, we assume that p_0 is equal to that observed in terrestrial mammals. For fish, the estimate of p_0 given in Table S1 is based on body temperatures of 20°C. We did not have data on fish body temperatures during migration so we did attempt to correct for deviations from this temperature. Flying insects exhibit core body temperatures between 33°C and 45°C, even during short flights (May, 1995; Alexander, 1999). We assume that flying insects operate at body temperatures of 40°C during migration flights. We therefore corrected p_0 given by (Chown *et al.*, 2007) from 25°C to 40°C following the UTD correction described in (Gillooly *et al.*, 2001).

Table S1. Empirical values of the normalization constant, p_0 .

Taxon	p_0 value	reference
fish (20°C)	0.43	(Windberg, 1960)
marine mammals	3.9	Assumed
terrestrial mammals	3.9	(Stahl, 1967)
birds (non-passerines)	3.6	(Lasiewski & Dawson, 1967)
birds (passerines)	6.3	(Lasiewski & Dawson, 1967)
flying insects (40°C)	1.9	(Chown <i>et al.</i> , 2007)

2.2 Sensitivity analysis

The derivation of equations for walking, swimming, and flying animals described above requires assuming values and body mass dependencies of a number of morphological and biomechanical parameters. An analysis of the sensitivity of migration distance equations to the particular parameter values assumed in the derivation is given in Table S2. In particular, the sensitivity analysis focused on two important properties of distance equations: the predicted body mass scaling exponent, d , and the r^2 statistic computed after fitting the equation to data. From Table S2, it is apparent that changes in the scaling of morphological variables and maintenance metabolism, and changes in the value of p_0 have only minor effects on the predicted mass dependence of maximum migration distance and the model r^2 .

To evaluate sensitivity, each parameter tested was individually increased or decreased by 10% relative to the value used in the original derivation of distance equations. In the case of some parameters, larger changes in parameter values were explored based on values reported in the literature. r^2 statistics were computed by fitting equations to maximum migration distance data assuming homoscedastic errors as described in the *Statistical analysis* section above. In the case of the flying equation, assuming departures from geometric similarity in body frontal area (A_b), wingspan (L_w), or wing plan area (A_w) result in changes in the functional form of equation (8) (main text) with respect to M_0 . However, these changes in functional form cause only minor changes in the shape of the predicted function, and consequently result in only minor changes in the agreement between the model and data as indicated by r^2 values. Because of changes in functional form, the scaling exponent, d , is no longer the only variable affecting the mass-scaling of Y_T , and it is therefore omitted from Table S2. Parameters that only affect the y_0 term in equations (6-8) (main text) were omitted from the sensitivity analysis. Additionally, increasing or decreasing the value of f , C_d , A_b , W , A_w parameters by 10% did not change the predicted mass dependence of the equation for flying animals, and did not result in detectable changes in r^2 values relative to the values used in the original derivation of the flight equation described above (i.e. $r^2 = 0.19$ for all parameter combinations).

Table S2. Sensitivity of distance equations to variation in input parameters. The **Parameter value** column shows minimum and maximum value of the corresponding parameter used to determine sensitivity. The **r^2** column indicates the r^2 value computed after increasing or decreasing the corresponding parameter and fitting the new equation to data. The **d** column indicates the value of the body mass scaling exponent after increasing or decreasing the corresponding parameter.

Taxon	Parameter	Parameter value min/max	r^2 min/max	d min/max
Walking	L_c	$L_c \propto M_0^{0.3}/M_0^{0.36}$	0.57/0.57	0.35/0.33*
	v_{walk}	$v_{walk} \propto M_0^{0.08}/M_0^{0.23}$	0.57/0.57	0.33/0.39*
	P_{mtn}	$P_{mtn} \propto M_0^{0.67}/M_0^{0.83}$	0.57/0.56	0.38/0.3*
Swimming	L_b	$L_b \propto M_0^{0.30}/M_0^{0.36}$	0.65/0.65	0.30/0.31
	A_s	$A_s \propto M_0^{0.6}/M_0^{0.74}$	0.66/0.61	0.32/0.27
	P_{mtn}	$P_{mtn} \propto M_0^{0.67}/M_0^{0.83}$	0.66/0.56	0.35/0.25
	p_0	0.39/0.47 (fish)	0.66/0.61	-
		3/6 (marine mammals)		
Flying	P_{mtn}	$P_{mtn} \propto M_0^{0.67}/M_0^{0.83}$	0.15/0.15	0.5/0.34
	A_b	$A_b \propto M_0^{0.6}/M_0^{0.74}$	0.16/0.2	-
	L_w	$L_w \propto M_0^{0.3}/M_0^{0.36}$	0.2/0.1	-
	A_w	$A_w \propto M_0^{0.6}/M_0^{0.74}$	0.15/0.21	-
	p_0	1.7/2.1 (insects)	0.19/0.18	-
		3.5/4.2 (non-passerines) 5.7/6.9 (passerines)		

* d approximated as described in section 1.2 above.

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