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.

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. Pennycuick & 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; Pennycuick & 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; Pennycuick 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 $Y_i$ ($i \in 1, 2, ..., N, N \geq 1$, 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, $P_{\text{tot}}$ (W), is the sum of the rate of energy use for general maintenance, $P_{\text{met}}$, and that required for locomotion, $P_{\text{loc}}$ (i.e. $P_{\text{tot}} = P_{\text{met}} + P_{\text{loc}} = -dG/dt$, 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 $M^{2/3}$ and surface areas are proportional to $M^{1/3}$ (where $M$ = 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

$$\frac{dY_i}{dM} = \frac{(dY_i/dt)(dt/dG)}{-v\epsilon (P_{\text{met}} + P_{\text{loc}})},$$

where $v$ = travel speed (m s$^{-1}$) and $\epsilon$ = the energy density of stored fuel (Joules kg$^{-1}$). The distance travelled on a particular leg can be...
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, \( M_f(1 - f) \), where \( f \) is the ratio of initial fuel mass to \( M_{0b} \):

\[
Y_i = \int_{M_0}^{M_f(1-f)} -r(M, \beta) \frac{r(M, \beta)}{P_{\text{mtn}}(M) + P_{\text{loc}}(M, \beta)} dM
\]  

(1)

Here, \( r, P_{\text{mtn}} \) and \( P_{\text{loc}} \) have been rewritten to show their dependence on body mass and on a small set of morphological traits, \( \beta \) (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 \( r(M, \beta) \), \( P_{\text{mtn}}(M) \) and \( P_{\text{loc}}(M, \beta) \). We assume that \( P_{\text{mtn}} \) scales with body mass as \( P_{\text{mtn}} = p_0 M^{n/4} \) both within and among individuals, where \( p_0 \) is a normalisation constant that varies by taxon (Kleiber 1932; Hemmingsen 1960). Biomechanics theory provides a means of expressing \( P_{\text{loc}} \) and \( r \) as functions of \( M \) and \( \beta \) 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

\[
Y_{\text{Tot}} = E\left[ \sum_{i=1}^{N} Y_i \right] = \bar{N} Y_i
\]  

(2)

where the operator, \( E \), denotes the expected value (Rice 1995). Eqn (2) shows that \( Y_{\text{Tot}} \) 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 \( P_{\text{mtn}} \) and \( r \) terms in eqn (1) (biomechanical models described in detail in Appendix S1). For walking migrants, \( P_{\text{mtn}} \) can be described by

\[
P_{\text{mtn}} = \frac{\gamma M}{L}
\]  

(3)

where \( L \) is stride length (m), \( r \) is walking speed (m s\(^{-1}\)), \( \gamma \) is a cost coefficient (J N\(^{-1}\)) and \( g \) is the acceleration due to gravity (m s\(^{-2}\)). The only morphological variable in eqn (2) is \( L \), which is proportional to leg length (Alexander & Jayes 1983). We assume that walking migrants travel at speeds, \( r \propto M_0^{1/4} \) (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,

\[
P_{\text{mtn}} = \delta M^{2.8} \frac{L}{T^2}
\]  

(4)

where \( \delta \) is a dimensionless cost coefficient, \( A_b \) is body cross-sectional area (m\(^2\)), \( L_w \) is body length (m) and \( r \) is swimming speed (m s\(^{-1}\)) (Kram & Taylor 1990). The only morphological variable in eqn (2) is \( L_w \), which is given by eqn (1). We assume that swimming migrants travel at speeds, \( r \propto M_0^{1/4} \) (Pennycuick 2008). The set of relevant morphological variables, \( \beta \), is \( A_b \) and \( L_w \). We assume that migrants swim at speeds that minimise the ratio \( P_{\text{mtn}} / r \).

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

\[
P_{\beta} = (1 + \kappa) \left( \phi M^2 L^{-2} r^{-1} + \phi A_b r^2 \right)
\]  

(5)

where \( \kappa \) is a dimensionless profile power coefficient, \( \phi \) and \( \varphi \) are cost coefficients (section 1.4 Appendix S1), \( A_b \) is body cross-sectional area (m\(^2\)), \( L_b \) is wingspan (m) and \( \kappa \) is proportional to \( k \cdot L_2 \), where \( k \) is wing area (Pennycuick 2008). The set of relevant morphological variables, \( \beta \), is \( A_b \) and \( L_b \). We assume that flying migrants travel at speeds that minimise \( P_{\beta} / r \) (Pennycuick 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 \( \beta \) 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, \( \beta \), that do not change as the migrant uses stored fuel to power migration. The dependence of \( Y_i \) on \( \beta \) 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

\[
Y_{\text{Tot}} = p_0 M_0^{0.34}
\]  

(6)

swimming,
\[ Y_T = j_0 p_0^{-0.64} M_0^{0.3} \]  

(7)

and flying

\[ Y_T = j_0 \ln \left[ \frac{p_0 + k_1 M_0^{0.42}}{p_0 + k_2 M_0^{0.42}} \right] \]  

(8)

migrants. Herein, \( j_0 \) is a proportionality constant that varies by mode of locomotion, and \( k_1 \) and \( k_2 \) are empirical constants. Differences in the functional forms of eqns (6–8) are caused by differences in the way \( p_0 \) 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, \( j_0 \), 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 \( k_1 \) and \( k_2 \) 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 c) are explicitly incorporated into the prediction of \( Y_T \) (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 (Alarctam 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 \( M_0^{1/2} \), body length \( \propto M_0^{1/3} \)) such that the number of body lengths travelled during migration, \( Y_{bl} \) is described by \( Y_{bl} = Y_T / \text{(body length)} \propto M_0^{1/3} / M_0^{1/3} \propto M_0 \). 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 \( k_1 \) and \( k_2 \) 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 \( k_1 \) and \( k_2 \) (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: Economo 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 log10-transformed distance and body mass data using ordinary least squares. Eqn (8) was fitted to log10-transformed distance and body mass data using non-linear least squares (Gauss–Newton algorithm). Equations (6–8) have the general form: \( Y_T = j_0 b(M_0^{1/2} p_0) \), where \( b \) is a known function, \( j_0 \) is a constant, and \( d \) is a scaling exponent. For each equation, two models were fitted: a model in which \( j_0 \) 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 \( j_0 \) 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 \( M_{swim} = M_0^{0.34} p_0^{-0.64} \) and \( M_{swim} = M_0^{0.42} p_0^{-1} \) 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 log10-transformed migration distance (in body lengths) as a function of log10-transformed body mass (kg) using a quadratic regression of the form, log10(\( Y_{bl} \)) = \( y_0 + y_1 \log_{10}(Y_{bl}) + y_2 \log_{10}(Y_{bl})^2 \), where \( y_1 \) are regression coefficients (Venebles & 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 that 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 $1.5 \times 10^3$ body lengths (Fig. 3a). The slope and curvature terms in the quadratic regression model do 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 $1.7 \times 10^6$ 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: $2.1 \times 10^6$ body lengths; marine mammals: $5.3 \times 10^5$ 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 $\gamma_1$ 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 $M_{\text{norm}} = M_0^{0.34}$ for walking and flying species, 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 $1.4 \times 10^8$ body lengths whereas the largest birds travel around $5.2 \times 10^6$ 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 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 ($p_0 = 3.9$ W kg$^{-3/4}$ in marine mammals, $p_0 = 0.43$ W kg$^{-3/4}$ in fish, see Appendix S1), whereas body length exhibits a similar relationship with mass in both groups ($f = 0.44 M^{1/3}$) 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 $5 \times 10^3$ km$^3$ $\times 10^4$ 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 number of 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.

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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.
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

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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, \( P_{\text{tot}} \), speed, \( v \), and energy density, \( c \):

\[
Y_i = \int_{M_0}^{M_0(1-f)} \frac{-vc}{P_{\text{tot}}} dM \tag{S1}
\]

where \( P_{\text{tot}} = P_{\text{mtn}} + P_{\text{loc}} \), \( M_0 \) 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 \( P_{\text{mtn}}, P_{\text{loc}}, \) and \( v \). For \( P_{\text{mtn}} \), we assume \( P_{\text{mtn}} = p_0 M_0^{0.75} \) 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

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

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 \( v_{\text{walk}} \propto M_0^{0.1} \) among species but that it is fixed for an individual migrant (Alexander, 1998). Substituting these terms for \( L_c \) and \( v_{\text{walk}} \) gives an expression for the mass-dependence of \( Y_i \),

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

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, \( \ln[(p_0 + c_1 M_0^{0.02})/(p_0 + c_3 M_0^{0.02})] \approx \ln[(p_0 + c_1)/(p_0 + c_3)] M_0^{0.01} \). Thus, equation (S3) can be rewritten as a power function in \( M_0 \),

\[
Y_{i,\text{walk}} \propto y_w M_0^{0.34} \ln \left( \frac{p_0 + c_1}{p_0 + c_3} \right) \tag{S4}
\]

For walking mammals, \( p_0 \) is roughly constant and so \( Y_{i,\text{walk}} \propto M_0^{0.34} \).
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

$$P_{swim} = \frac{\alpha}{\eta} D_t v$$  \hspace{1cm} (S5)$$

where $\eta$ is dimensionless conversion efficiency from stored fuel energy to muscle power output, and $\alpha$ 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 $D_t = \frac{\alpha C A_b v^{1.8}}{L_w}$, 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,

$$Y_{i,swim} \propto \left( \frac{L_0^{0.2} A_b^{0.36}}{A_b} \right) P_0^{-0.64} M_0^{0.52} [1 - (1 - f)^{0.28}]$$ \hspace{1cm} (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

$$Y_{i,swim} = y_s P_0^{-0.64} M_0^{0.30}$$ \hspace{1cm} (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, $P_{pro}$)

$$P_{fly} = P_{ind} + P_{par} + P_{pro}$$  \hspace{1cm} (S8)$$

where

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

$$P_{par} = \frac{\rho a A_b C_d}{\eta^2} v^3$$ \hspace{1cm} (S10)$$

$$P_{pro} = \kappa(P_{ind} + P_{par})$$ \hspace{1cm} (S11)$$

$\omega$ is a dimensionless induced power factor, $g$ is the acceleration due to gravity, $\eta$ is dimensionless conversion efficiency from stored fuel energy to muscle power output, $\rho_a$ 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 ($\kappa$) times the sum of the induced and parasite power (Pennycuick, 2008). We follow (Pennycuick, 2008) in assuming that $\kappa \propto A_w/L_w^2 = 1/$wing aspect ratio, where $A_w = $ 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

\[
P_{fly} = (1 + \kappa)1.05 \eta^{-1} \left( \frac{\omega^3 g^6 A_0 C_d M^6}{\rho_0^2 \omega^6} \right)^{0.25} = k_0 M^{1.5}
\]

(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

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

(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 \( L_w = 1.1 M_0^{0.33} \) (Greenwalt, 1962), \( A_w = 0.16 M_0^{0.67} \) (Greenwalt, 1962), \( \eta = 0.23 \) (Alexander, 1999), \( \omega = 1.2 \) (Pennycuick, 2008), \( \rho_a = 0.98 \) (Denny, 1993), \( A_b = 0.0081 M_0^{0.67} \) (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-Mejia 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

\[
Y_{i, fly} = y_f \ln \left( \frac{p_0 + k_1 M_0^{0.42}}{p_0 + k_2 M_0^{0.42}} \right)
\]

(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, \( p_0 \).
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 as 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.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>( p_0 ) value</th>
<th>reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>fish (20°C)</td>
<td>0.43</td>
<td>(Windberg, 1960)</td>
</tr>
<tr>
<td>marine mammals</td>
<td>3.9</td>
<td>Assumed</td>
</tr>
<tr>
<td>terrestrial mammals</td>
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<td>(Stahl, 1967)</td>
</tr>
<tr>
<td>birds (non-passerines)</td>
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<td>(Lasiewski &amp; Dawson, 1967)</td>
</tr>
<tr>
<td>birds (passerines)</td>
<td>6.3</td>
<td>(Lasiewski &amp; Dawson, 1967)</td>
</tr>
<tr>
<td>flying insects (40°C)</td>
<td>1.9</td>
<td>(Chown et al., 2007)</td>
</tr>
<tr>
<td>Taxon</td>
<td>Parameter</td>
<td>Parameter value</td>
</tr>
<tr>
<td>-----------</td>
<td>-----------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Walking</td>
<td>$L_c$</td>
<td>$L_c \propto M_0^{0.3}/M_0^{0.36}$</td>
</tr>
<tr>
<td></td>
<td>$v_{walk}$</td>
<td>$v_{walk} \propto M_0^{0.08}/M_0^{0.23}$</td>
</tr>
<tr>
<td></td>
<td>$P_{mtn}$</td>
<td>$P_{mtn} \propto M_0^{0.67}/M_0^{0.83}$</td>
</tr>
<tr>
<td>Swimming</td>
<td>$L_b$</td>
<td>$L_b \propto M_0^{0.30}/M_0^{0.36}$</td>
</tr>
<tr>
<td></td>
<td>$A_s$</td>
<td>$A_s \propto M_0^{0.6}/M_0^{0.74}$</td>
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<tr>
<td></td>
<td>$P_{mtn}$</td>
<td>$P_{mtn} \propto M_0^{0.67}/M_0^{0.83}$</td>
</tr>
<tr>
<td></td>
<td>$p_0$</td>
<td>0.39/0.47 (fish)</td>
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<td></td>
<td></td>
<td>3/6 (marine mammals)</td>
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<tr>
<td>Flying</td>
<td>$P_{mtn}$</td>
<td>$P_{mtn} \propto M_0^{0.67}/M_0^{0.83}$</td>
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<tr>
<td></td>
<td>$A_b$</td>
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<tr>
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<td>$A_w$</td>
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<td>$p_0$</td>
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<td></td>
<td>5.7/6.9 (passerines)</td>
</tr>
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</table>

* $d$ approximated as described in section 1.2 above.

References


