LETTER

Energetic and biomechanical constraints on animal migration distance

Andrew M. Hein,[1]* Chen Hou[1,2,3] and James F. Gilloofly[1]

[1]Department of Biology, University of Florida, Gainesville, FL 32611, USA
[2]Department of Systems and Computational Biology, Albert Einstein College of Medicine, Bronx, NY 10461, USA
[3]Department of Biological Science, Missouri University of Science and Technology, Rolla, Missouri 65409, USA

*Correspondence: E-mail: amhein@ufl.edu

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_t (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_{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

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

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
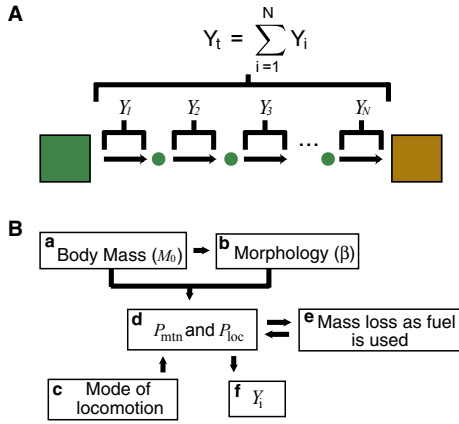
Figure 1 (A) Total migration distance is the sum of the distances travelled on each of N migratory legs. (B) Migration distance on a single migratory leg. Body mass (a), morphology (b) and mode of locomotion (c) govern the rate at which a migrant uses stored fuel energy (d). This rate changes as migrant 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,

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

Here, v, P_{mtn} 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 $v(M, \beta)$, $P_{mtn}(M)$ and $P_{loc}(M, \beta)$. We assume that P_{mtn} scales with body mass as $P_{mtn} = p_0 M^{3/4}$, 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_{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, $\overline{N}$. 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

$$Y_T = E\left[\sum_{i=1}^{N} Y_i\right] = \overline{N}\,Y_i \tag{2}$$

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

$$P_{walk} = \gamma \frac{gM}{L_c} v \tag{3}$$

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,

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

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

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

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 (Pennycuick 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 (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 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

$$Y_T = y_0 M_0^{0.34}, \tag{6}$$

swimming,

$$Y_T = y_0 p_0^{-0.64} M_0^{0.3} \tag{7}$$

and flying

$$Y_T = y_0 \ln \left[\frac{p_0 + k_1 M_0^{0.42}}{p_0 + k_2 M_0^{0.42}} \right] \tag{8}$$

migrants. Herein, y_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_{loc} 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 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 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 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: 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: $Y_T = y_0 \, h(M_0^d \, p_0)$, where h 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 (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 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
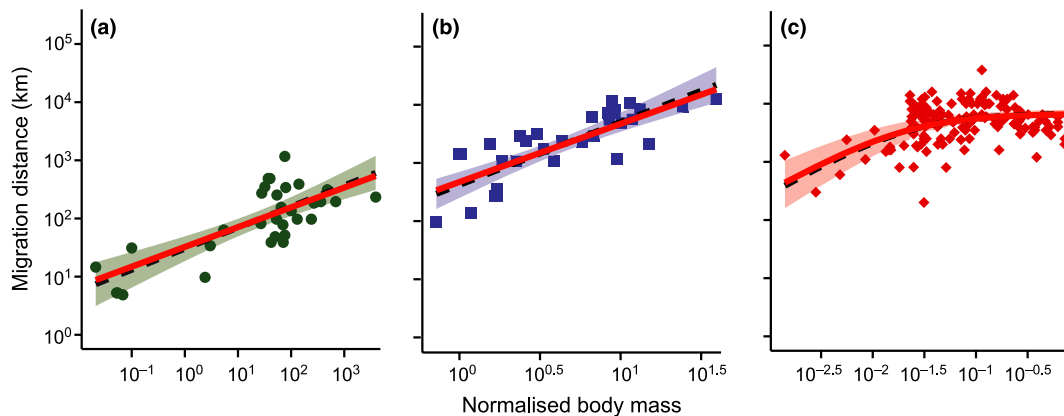
Figure 2 Maximum migration distance as a function of normalised body mass for (a) walking mammals, (b) swimming fish and marine mammals and (c) flying birds and insects. Solid lines are predicted curves based on fits of eqns (6–8) to data with y_0 fitted as a free parameter. Dashed lines and confidence 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 $M_{norm} = M_0^{0.3} p^{-0.64}$ 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.
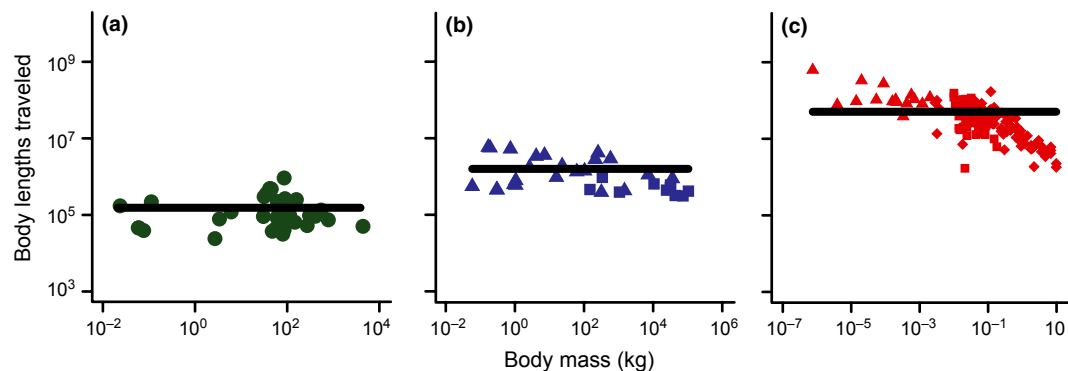
Figure 3 Number of body lengths travelled during migration by (a) walking mammals, (b) swimming fish (triangles) and mammals (squares) and (c) flying insects (triangles), passerine birds (squares) and non-passerine birds (diamonds). Lines denote mean number of body lengths travelled by species using 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
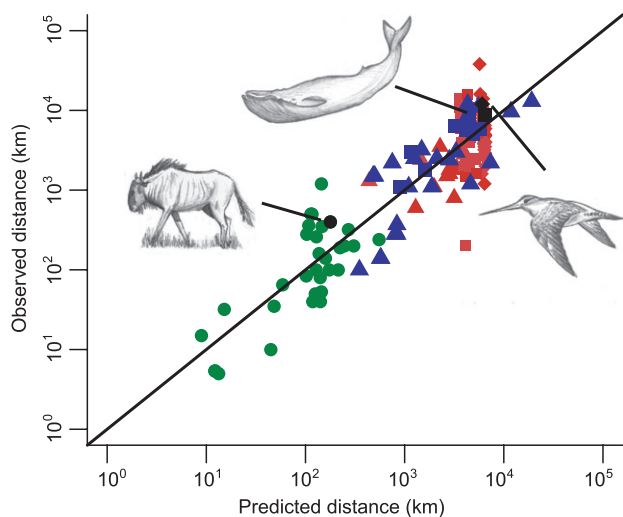
Figure 4 Observed and predicted migration distances for the walking, swimming and flying animals shown in Fig. 2. Data from walking mammals (green circles), swimming fish (blue triangles) and marine mammals (blue squares), and flying insects (red triangles), passerine birds (red squares) and non-passerine 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 ($p_0 \approx 3.9$ W kg$^{-3/4}$ in marine mammals, $p_0 \approx 0.43$ W kg$^{-3/4}$ in fish, see Appendix S1), whereas body length exhibits a similar relationship with mass in both groups ($l \approx 0.44 M^{1/3}$) 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 5×10^3 km$^1 \times 10^4$ 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 inter-specific 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.

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.

REFERENCES

Alerstam, T. & Hedenström, A. (1998). The development of bird migration theory. *J. Avian Biol.*, 29, 343–369.

Alerstam, T., Hedenström, A. & Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, 103, 247–260.

Alexander, R.M. (1998). When is migration worthwhile for animals that walk, swim or fly? *J. Avian Biol.*, 29, 387–394.

Alexander, R.M. (2003). *Principles of Animal Locomotion*. Princeton University Press, Princeton.

Alexander, R.M. (2005). Models and the scaling of energy costs for locomotion. *J. Exp. Biol.*, 208, 1645–1652.

Alexander, R.M. & Jayes, A.S. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool.*, 201, 135–152.

Banavar, J.R., Moses, M.E., Brown, J.H., Damuth, J., Rinaldo, A., Sibly, R.M. *et al.* (2010). A general basis for quarter-power scaling in animals. *Proc. Natl. Acad. Sci. USA*, 107, 15816–15820.

Bauer, S., Barta, Z., Ens, B.J., Hays, G.C., McNamara, J.M. & Klassen, M. (2009). Animal migration: linking models and data beyond taxonomic limits. *Biol. Lett.*, 5, 433–435.

Dingle, H. (1996). *Migration: The Biology of Life on the Move*. Oxford University Press, Oxford.

Dingle, H. & Drake, A. (2007). What is migration? *Bioscience*, 57, 113–121.

Dixon, C.A. (1892). *The Migration of Birds: An Attempt to Reduce Avian Seasonal Flight to Law*. Richard Clay and Sons, London.

Economos, A.C. (1983). Elastic and/or geometric similarity in mammalian design? *J. Theor. Biol.*, 103, 167–172.

Egevang, C., Stenhouse, I.J., Philips, R.A., Petersen, A., Fox, J.W. & Silk, J.R.D. (2010). Tracking of Arctic Terns *Sterna paradisaea* reveals longest animal migration. *Proc. Natl Acad. Sci. USA*, 107, 2078–2081.

Elphick, J. (1995). *Atlas of Bird Migration*. Random House, New York.

Hedenström, A. (2003). Optimal migration strategies in animals that run: a range equation and its consequences. *Anim. Behav.*, 66, 613–636.

Hedenström, A. (2010). Extreme endurance migration: what is the limit to non-stop flight? *PLoS Biol.*, 8, e1000362.

Hemmingsen, A.M. (1960). Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Sten. Mem. Hosp. Nord. Ins. Lab.*, 9, 6–110.

Kleiber, M. (1932). Body size and metabolism. *Hilgardia*, 6, 315–353.

Kram, R. & Taylor, R. (1990). Energetics of running: a new perspective. *Nature*, 346, 265–267.

Milner-Gulland, E.J., Fryxell, J.M. & Sinclair, A.R.E. (2011). *Animal Migration: A Synthesis*. Oxford University Press, New York.

Pennycuick, C.J. (2008). *Modeling the Flying Bird*. Academic Press, Amsterdam.

Pennycuick, C.J. & Battley, P.F. (2003). Burning the engine: a time-marching computation of fat and protein consumption in a 5420-km non-stop flight by great knots, *Calidris tenuirostris*. *Oikos*, 103, 323–332.

Peters, R.H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2009). nlme: linear and nonlinear mixed effects models. R package version 3.1-96. Available at: http://cran.r-project.org/web/packages/nlme/. Last accessed 30 October 2009.

R Development Core Team. (2010). *R: A Language and Environment for Statistical Computing*. R Development Core Team, Vienna, Austria.

Rice, J. (1995). *Methematical Statistics and Data Analysis*, 2nd edn. Duxbury, Belmont.

Riveros, A.J. & Enquist, B.J. (2011). Metabolic scaling in insects supports the predictions of the WBE model. *J. Insect Physiol.*, 57, 688–693.

Venebles, W.N. & Ripley, B.D. (1999). *Modern Applied Statistics with S-plus*, 3rd edn. Springer-Verlag, New York.

Weber, J.M. (2009). The physiology of long-distance migration: extending the limits of endurance metabolism. *J. Exp. Biol.*, 212, 593–597.

West, G.B., Brown, J.H. & Enquist, B.J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, 276, 122–126.

White, C.R., Blackburn, T.M. & Seymour, R.S. (2009). Phylogenetically informed analysis of the allometry of mammalian basal metabolic rate supports neither geometric nor quarter-power scaling. *Evolution*, 63, 2658–2667.

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.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organised for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.