


Benefits of the destinations, not costs of the journeys, shape partial migration patterns

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Summary

1. The reasons that lead some animals to seasonally migrate, and others to remain in the same area year-round, are poorly understood. Associations between traits, such as body size, and migration provide clues. For example, larger species and individuals are more likely to migrate.

2. One explanation for this size bias in migration is that larger animals are capable of moving faster (movement hypothesis). However, body size is linked to many other biological processes. For instance, the energetic balances of larger animals are generally more sensitive to variation in food density because of body size effects on foraging and metabolism and this sensitivity could drive migratory decisions (forage hypothesis).

3. Identifying the primary selective forces that drive migration ultimately requires quantifying fitness impacts over the full annual migratory cycle. Here, we develop a full annual migratory cycle model from metabolic and foraging theory to compare the importance of the forage and movement hypotheses. We parameterize the model for Galapagos tortoises, which were recently discovered to be size-dependent altitudinal migrants.

4. The model predicts phenomena not included in model development including maximum body sizes, the body size at which individuals begin to migrate, and the seasonal timing of migration and these predictions generally agree with available data. Scenarios strongly support the forage hypothesis over the movement hypothesis. Furthermore, male Galapagos tortoises on Santa Cruz Island would be unable to grow to their enormous sizes without access to both highlands and lowlands.

5. Whereas recent research has focused on links between traits and the migratory phases of the migratory cycle, we find that effects of body size on the non-migratory phases are far more important determinants of the propensity to migrate. Larger animals are more sensitive to changing forage conditions than smaller animals with implications for maintenance of migration and body size in the face of environmental change.

Key-words: allometry, animal migration, bioenergetics, *Chelonoidis*, dynamic programming, energetic, insular dwarfism

Introduction

Migratory behaviour has evolved in a wide diversity of taxa (Alerstam, Hedenstrom & Akesson 2003). The selective forces that lead some, but not all, species to migrate are

expected to also drive patterns in partial migratory populations, in which only some individuals migrate (Alerstam, Hedenstrom & Akesson 2003). Identifying these selective forces, however, is difficult because of the complex life histories of migratory animals. Studies of the association of individual or species traits, such as body size, with migration can provide clues. However, a given trait can often be linked to multiple biological processes and shaped by

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various selective forces. Identifying the primary selective forces that drive migration ultimately requires quantifying fitness impacts over the full migratory cycle. Understanding these selective forces is important because migratory populations are especially threatened by global environmental change (Berger 2004; Wilcove & Wikelski 2008) and play a vital role in linking communities and ecosystems across the globe (Bauer & Hoye 2014).

Among species that swim or run, larger species are more likely to migrate (Alerstam, Hedenstrom & Akesson 2003). Similarly, within those populations where some individuals migrate and others do not, larger individuals are more likely to migrate than smaller ones (Blake *et al.* 2013; Yackulic *et al.* 2014). Explanations for these links between body size and the propensity to migrate have focused on the positive relationships between body size and migration speed and efficiency (Peters 1983; Alerstam, Hedenstrom & Akesson 2003). According to this ‘movement hypothesis’, larger animals can move faster, minimizing the direct and indirect costs of migration (e.g. lost opportunities to forage) and allowing them to migrate greater distances (Hein, Hou & Gilgooly 2012). However, processes associated with the migratory destinations also scale with body size. In particular, the amount of time it takes individuals to convert food into energy (i.e. the handling time) scales negatively with body mass, M , typically with a power of c. $-3/4$, and handling rates can limit the foraging rate of many animal species (Yodzis & Innes 1992).

Consider, for example, a simple model of the net energetic balance, E , of a consumer foraging according to a type-II functional response (Holling 1959) and subject to metabolic costs roughly proportional to mass taken to a $3/4$ power (Kleiber 1947):

$$E(M, n) = \tau sn / (1 + sn\theta M^{-3/4}) - \phi M^{3/4} \quad \text{eqn 1}$$

where τ is the efficiency with which ingested materials are converted to energy, s is the search rate, n is the resource

density, θ is a constant associated with the handling rate, and ϕ is a constant associated with the energetic cost of active metabolism. This simple energetic model implies that larger animals are able to run large energetic surpluses when resources are plentiful (Fig. 1a). However, it also suggests that larger animals are more sensitive to reductions in food availability, where sensitivity is defined formally as the derivative of the energetic balance with respect to food density (dE/dn):

$$\frac{dE}{dn} = \tau s / (1 + sn\theta M^{-3/4}) \quad \text{eqn 2}$$

As a result, the same difference in vegetation quantity between two potential migratory endpoints may translate to minimal differences in energetic balances for smaller organisms and substantial differences in larger organisms (Fig. 1), suggesting an alternate ‘forage hypothesis’ to explain size biases in migration. (*N.B.* Although we used a simple type-II functional relationship here, the same general finding that sensitivity increases with body size can be shown by similar logic to arise from type-III functional relationships, models that include interference competition and models that allow search rate to scale with a smaller absolute exponent than the handling rate.)

To test whether migration speed or sensitivity to food density is a more important driver of migratory patterns, we develop a full migratory cycle bioenergetics model. We parameterize the model and apply it to three species of Galapagos tortoises, including two species (*Chelonoidis porteri* and *Chelonoidis donfaustoi*) found on Santa Cruz Island that exhibit size-dependent altitudinal migration (Blake *et al.* 2013) and one sedentary species (*Chelonoidis hoodensis*) found on Espanola Island, a small, flat island without highlands. Within the two migratory species, infant and juvenile tortoises are found exclusively in the lowlands while most adult tortoises migrate to the highlands during the dry season (Blake *et al.* 2013; Fig. 2a). Galapagos tortoises provide a model study system because: (i) they exhibit

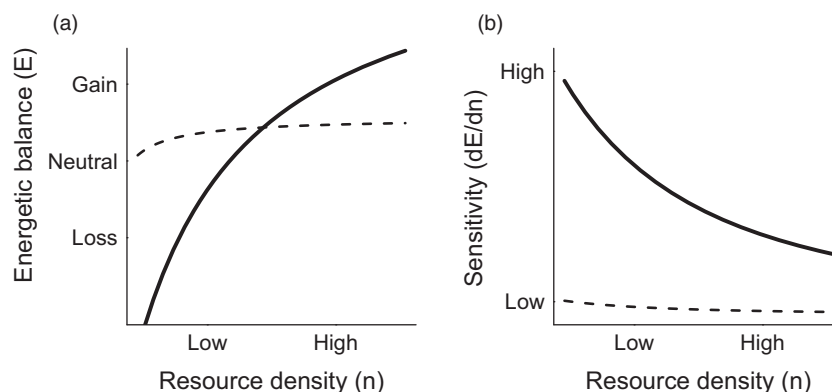


Fig. 1. Larger organisms are more sensitive to changes in resource density, which may give larger organisms a greater incentive to migrate and track seasonal changes in resource densities. (a) Larger organisms (solid line) foraging according to eqn (1) run larger surpluses than smaller organisms (dashed line) under high resource availability, however, at low resource densities, larger organisms run larger deficits than smaller organisms because of their higher metabolic demands. (b) Larger organisms are always more sensitive than smaller organisms to changing resource densities and both larger and smaller organisms are more sensitive at lower resource densities. Curves are based on eqns (1) and (2).

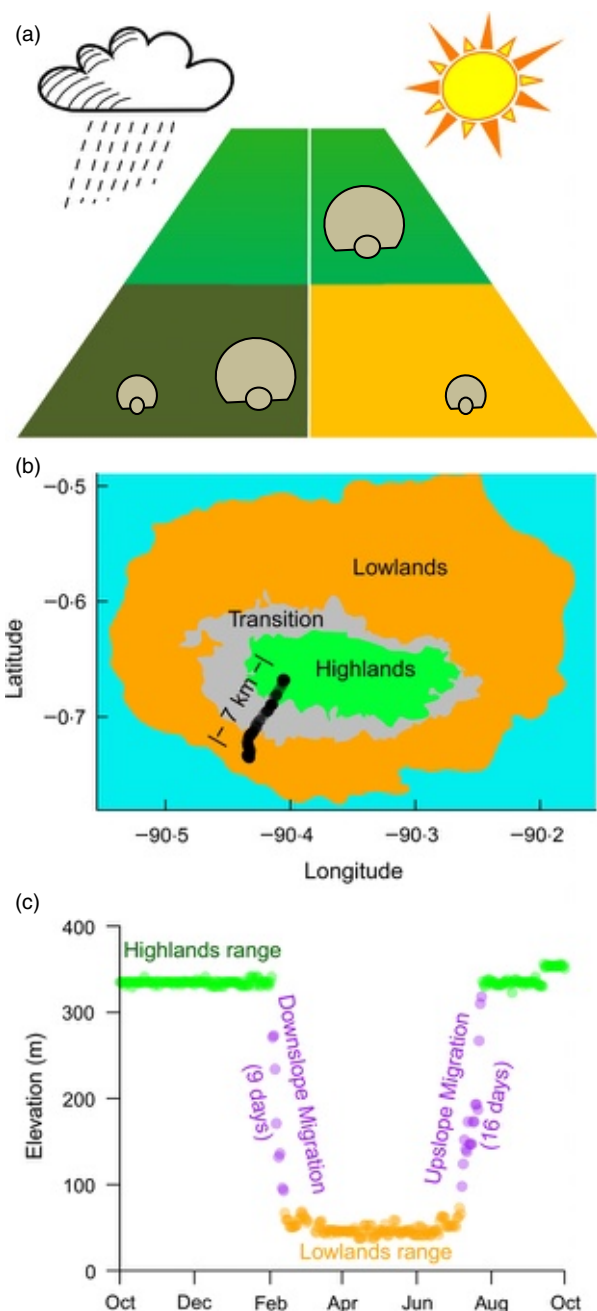


Fig. 2. Galapagos tortoises provide a model system to test the movement and foraging hypotheses. (a) Galapagos tortoises exhibit size-dependent partial migration. Both larger (>80 kg) and smaller tortoises (<50 kg) are found in the lowlands during the rainy season, but larger tortoises leave for the highlands during the dry season (Blake *et al.* 2013). (b) Migration routes between the lowlands and highlands are frequently direct and nearly linear. Overlapping black dots represent daily locations for a male (c. 240 kg) that migrates a linear distance of c. 7 km between its highland and lowland ranges on Santa Cruz Island. (c) Highland and lowland ranges are well-defined spatially and movement between ranges occurs on time scales of weeks. Data plotted here are for the same individual as depicted in panel b. We modelled migration speed based on previously published relationships between average daily speeds during migration and body size (Bastille-Rousseau *et al.* 2016). Tortoises are capable of faster rates, but often stop and forage as they migrate.

extreme intraspecific variation in body size; (ii) life stages larger than infants have no natural predators, which simplifies fitness calculations; (iii) nesting (lowland) and non-nesting (highland) habitats are well-defined (Fig. 2b), (iv) forage quantity in both habitats can be reliably estimated using a satellite derived proxy, the Normalized Difference Vegetation Index (NDVI; Huete *et al.* 2002); (v) diet data are available to estimate forage quality in the two habitats (Nagy, Henen & Vyas 1998; Blake *et al.* 2015a); (vi) growth data for three juveniles are available to estimate the search rate in terms of NDVI, and (vii) data on male and female body sizes and timing of migration exist to independently test the reliability of the model (Fig. 2c).

The model relies on an energetic definition of fitness (Brown, Marquet & Taper 1993) and determines when a migratory tactic confers greater annual energetic surpluses than remaining in either the nesting or non-nesting habitats year round (Fig. 3). The model is based on previously published relationships between body mass and biological processes. Many of these processes are proportional to M^b , where b takes values of c. $-3/4$ for handling rates, $3/4$ for metabolism, and between 0.1 and 0.3 for movement speeds across a range of species (Peters 1983; Yodzis & Innes 1992). Thus, while we apply the model to Galapagos tortoises and use the most appropriate parameters for these taxa, the underlying relationships are general. We begin by testing whether the model gives reasonable predictions of growth, the size at which migration begins, and the seasonal timing of migration as a function of body size. We then run scenarios in which the body size used to calculate migration speed and the body size used to calculate energetic balances differ, allowing us to tease apart the relative importance of the movement and foraging hypotheses in explaining observed migration patterns. Our work illustrates how full migratory cycle models can be used to identify the primary processes linking biological traits to migration patterns.

Materials and methods

THE MODEL

A general overview of the model is provided in Fig. 3. In the following sections we provide more details, including equations and references. Example R code is provided in Appendix S1, Supporting Information.

Forage intake

We assume that foraging rates in tortoises respond to forage quantity via a type II response (Holling 1959):

$$F(N_{x,y}, M, S) = \frac{sN_{x,y}}{1 + shN_{x,y}} \quad \text{eqn 3}$$

where F is the intake rate in units of kJ per day, $N_{x,y}$ is the resource density on the x th day in the y th habitat, M is the mass of an individual, s is the 'attack' or search rate and h is the

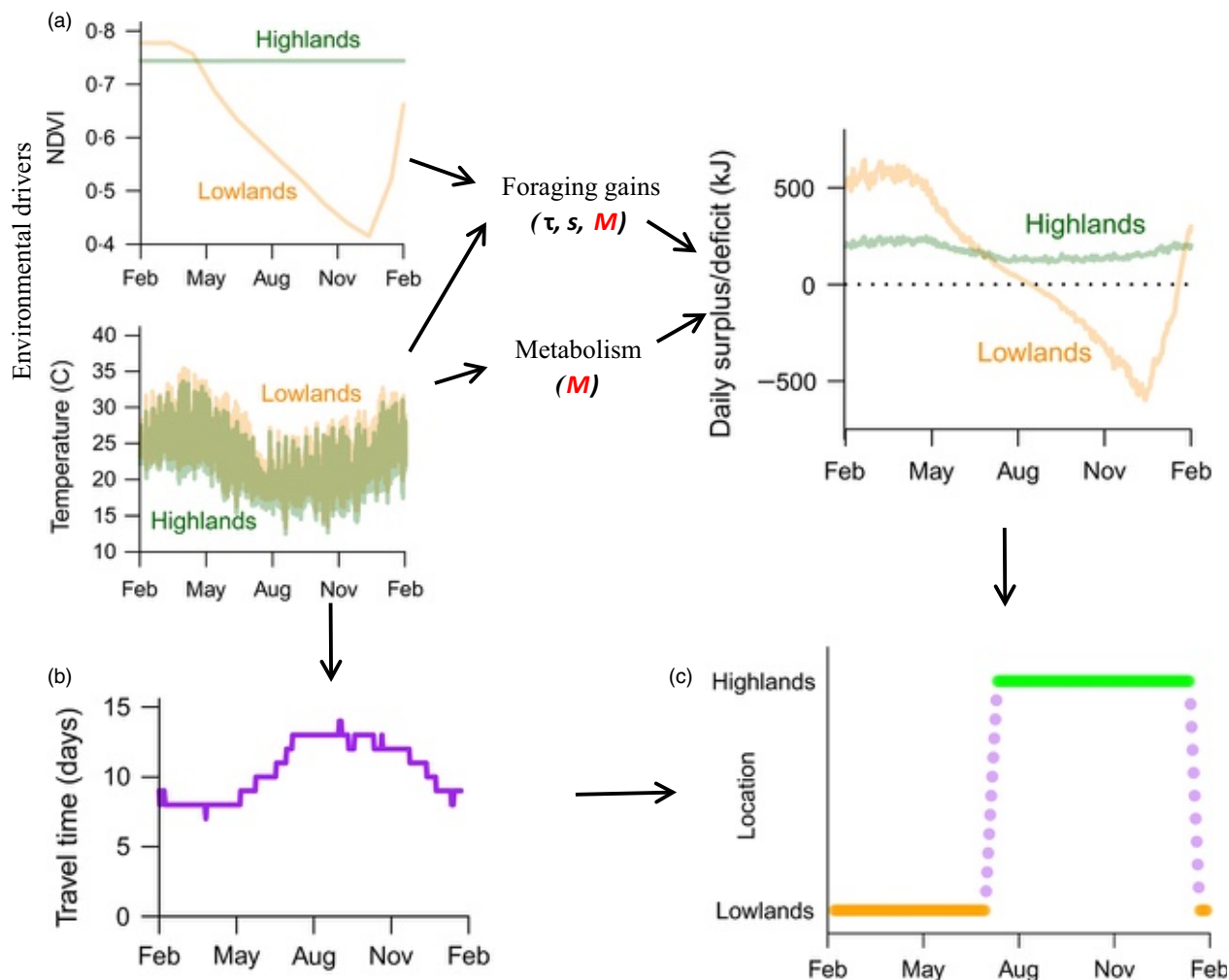


Fig. 3. Schematic representation of a full annual cycle bioenergetics model for Galapagos tortoises. (a) Foraging gains are calculated using a type II functional response (Holling 1959), where the assimilation efficiency, τ , is estimated from diet observations (Blake *et al.* 2015a) and studies in related taxa (Nagy, Henen & Vyas 1998), the handling time varies with body size, M (Yodzis & Innes 1992; Franz *et al.* 2011), the search rate, s , is estimated from the observed growth of three non-migratory juvenile tortoises in the field, and NDVI is used as a proxy for resource density. Basal and active metabolism are calculated based on a general allometric relationship for poikilotherms (Peters 1983). Both foraging gains and metabolism are modified based on daily internal temperatures, which are estimated from external shade temperatures (shown here) and body size, M . The net energetic balance in the highlands and lowlands is then calculated for each day by choosing the greater of: (1) the difference between foraging gains and cost of active metabolism (i.e. foraging with associated activity costs), or (2) the cost of basal metabolism (i.e. being inactive). (b) The model then calculates the number of days that would be required to migrate between habitats based on a relationship between body size and daily movement rates during migration derived from GPS-tagged tortoises (Bastille-Rousseau *et al.* 2016), modified by the estimated internal temperature and assuming that habitats are separated by seven kilometres. (c) Using calculations of estimated net energy gains in the lowlands and highlands on each day of the year, the number of days required for migration and the energy gains or losses associated with migration, we then determine the optimal movement tactic over the course of the year, and the annual energy gains (or losses) associated with this tactic using deterministic dynamic programming (a commonly used method for finding the optimal sequence of decisions). All graphs are based on a 240 kg individual and thus comparable to Fig. 2c. For more information see Methods and Appendices S1–S3.

handling time, h can be estimated as the inverse of the consumption rate for an individual given food *ad libitum* (Yodzis & Innes 1992). In tortoises, fed *ad libitum*, Franz *et al.* (2011) estimates that maximum gross energy intake (I), in units of kJ per day, scales with body mass according to:

$$I(M) = 86.1M^{0.77} \quad \text{eqn 4}$$

Yielding a handling rate of $M^{-0.77}/86.1$ in units of days per kJ. In the absence of a direct measure of edible vegetation density we instead rely on NDVI estimates as a proxy for $N_{x,y}$ in the lowland

($y = 1$) and highland ($y = 3$) habitats (Blake *et al.* 2013) and did not directly estimate foraging while tortoises were migrating through the transition habitat ($y = 2$) dominated by trees. This leaves the search rate, s , as the only unknown parameter, which we estimate through model fitting based on the growth of three small non-migratory individuals (see the estimating search rate section).

Metabolic rate

Basal metabolism (in units of kJ per day) in poikilotherms is related to body size through the following equation (Peters 1983):

$$B(M) = 12 \cdot 1M^{0.75} \quad \text{eqn 5}$$

Active metabolism is c. 2–3 times basal metabolism, so we use an intermediate value of 2.5. We assume that tortoises metabolize according to this rate regardless of the activity (i.e. whether they are actively foraging, ingesting or digesting).

Daily change in energy reserve while foraging or inactive at a reference temperature of 25.5 °C

In our model, tortoises that are not in the process of migrating (i.e. tortoises in either the lowlands, $y = 1$, or highlands, $y = 3$) choose to either forage or become inactive. The change in energy reserves associated with foraging ($\Delta E_{x,y}^F$) on the x th day in the y th habitat or inactivity (ΔE^I) are given by the following equations:

$$\Delta E_{x,y}^F = \tau_y * F(N_{x,y}, M, S) - 2.5 * B(M) \quad \text{eqn 6}$$

$$\Delta E^I = -B(M) \quad \text{eqn 7}$$

where τ_y is the efficiency of energy uptake from ingested foods in the y th habitat and all values are in units of kJ per day. We estimate τ_y based on two sets of observations: (i) Roughly 60% of the lowland diet and 30% of the highland diet are comprised of forbs, with the remaining portions consisting of lower quality forage, including grasses (Blake *et al.* 2015a); (ii) the efficiency of energy uptake in a sister taxa, desert tortoises, varies from 0.7 to 0.5 depending on whether they were fed higher quality forage consisting of forbs or lower quality forage consisting of grasses (Nagy, Henen & Vyas 1998). Taken together, these observations suggest that overall energetic efficiency is 0.62 in lowland habitat and 0.56 in the highland habitat.

We assume that tortoises that are not migrating chose between foraging and inactivity optimally so that the expected energy change for a non-migrating individual (ΔE_{nm}) is given by:

$$\Delta E_{x,y}^{nm} = \max(\Delta E_{x,y}^F, \Delta E^I) \quad \text{eqn 8}$$

Daily change in energy reserve while migrating

Tortoises are known to forage as they migrate, including sometimes stopping for multiple days in certain locations (e.g. Fig. 2c), and are in good physiological condition at the end of migrations, so we assumed a neutral energetic balance during migration. We also tested a model in which daily energetic change while migrating was calculated as the average of predictions for lowlands and highlands on that day, however this model predicted migration at a much smaller size than are observed.

Modelling internal temperature

We assume a two layer (surface and core) heat diffusion model, similar to the model described by Stevenson (1985), to estimate how external temperatures measured every 4 h over the course of the year and body mass interacted to determine core temperature. For more details see Appendix S2.

Converting core temperature into activity multiplier

Many of the allometric relationships we rely upon are derived from laboratory experiments during which temperatures were held constant. In order to account for the difference between this temperature and those experienced by tortoises in the field, we calculated an activity multiplier (Ψ) for each 4 h period in each day within each habitat by dividing the expected metabolic activity associated with the internal core temperature of the tortoise, $T^C(t)$, during that 4 h period, by the metabolic activity associated with 4 h at a constant temperature of 25.5 °C. In converting between temperature and metabolic activity (Ω), we relied on the empirical relationship detailed by Gillooly *et al.* (2001).

$$\Psi = \int_0^{14400} \frac{\Omega(T^C)}{\Omega(25.5)} dt = \int_0^{14400} \frac{e^{\zeta/(T^C+273.15)}}{e^{\zeta/(298.65)}} dt \quad \text{eqn 9}$$

where $\zeta = -8780$ K for reptiles.

Calculating temperature-adjusted daily net change in energy

We calculated the net change in energy associated with not migrating ($\omega_{x,y}^{nm}$) for the x th day in either the lowlands ($y = 1$) or highlands ($y = 3$) as:

$$\omega_{x,y} = \Delta E_{x,y}^{nm} \sum_{k=1}^{k=6} \frac{\Psi_{x,y,k}}{6} \text{ km per day} \quad \text{eqn 10}$$

where $\Psi_{x,y,k}$ is the activity multiplier for the x th day, y th habitat, and k th 4 h interval within the day.

Calculating the travel time between lowlands and highlands

We calculated daily movement rates, D_x , as:

$$D_x = 0.186 * M^{0.267} * \sum_{k=1}^{k=6} \frac{\Psi_{x,2,k}}{6} \text{ kJ per day} \quad \text{eqn 11}$$

where the scaling relationship is derived from free-ranging Galapagos tortoises in the process of migrating (Bastille-Rousseau *et al.* 2016) and adjusted by the associated activity multiplier for that day. For a tortoise, leaving on day x , we calculated the travel time between the highlands and lowlands, χ_x (assumed to be the same in either direction) by determining the minimum days required to cover 7 km, the approximate average distance between highland and lowland habitats on Santa Cruz (Blake *et al.* 2013). In other words,

$$\chi_x = \min(\Delta x) s.t. \sum_x^{x+\Delta x} D_x > 7 \quad \text{eqn 12}$$

We also test versions of the model where D_x was increased to 70 km and results are reported in Appendix S3.

Dynamic programming

For a tortoise of a given mass, we determine the optimal movement behaviour using deterministic dynamic programming. This approach is based on working backwards, determining at each

time step whether the cumulative energetic balance, $\eta_{x,y}$, would be higher if a tortoise remained in the current habitat or migrated to the other habitat. So for example, the cumulative energetic balance for a tortoise in the lowlands on day x , would be calculated as:

$$\eta_{x,1} = \max(\eta_{x+1,1} + \omega_{x,1}, \eta_{x+\chi_x,3}) \quad \text{eqn 13}$$

So as to avoid any effect of choice of starting or ending date on our results, we ran our dynamic program on 3 years of data (in which each year was exactly the same) and based inference on the middle year.

PARAMETERIZING AND TESTING THE MODEL

Environmental data

Collection and processing of environmental data (NDVI and temperature) associated with the two migratory species (*C. porteri* and *C. donfaustoi*) is described in Blake *et al.* (2013). For resident species, *C. hoodensis*, we used temperature data from the lowland range of *C. porteri* combined with NDVI measurements from the portion of Espanola inhabited by tortoises. All data are from February 1, 2010 through January 31, 2011.

Estimating search rate

We estimate the search rate, s , that leads to the lowest sum of squares when comparing observed vs. predicted growth of three sub-adult tortoises from the *C. donfaustoi*. These growth predictions rely on lowland temperature and NDVI data from the February 2010 – February 2011 interval. We annually update weights under the assumption that all surplus energy is converted to mass at a rate of 13 000 kJ kg⁻¹ (Peters 1983) and ran the growth model for the 3-3 years interval between initial capture and subsequent recapture of the three individuals. The search time, s , was estimated at 27 000 kJ·NDVI⁻¹·day⁻¹.

Predicting annual energy surplus and migration timing

We ran the model for tortoises at 10-kg intervals between 10 and 400 kg and calculated annual energetic surplus for seven hypothetical groups: (i) *C. donfaustoi* confined to their lowland range; (ii) *C. donfaustoi* confined to their highland range; (iii) *C. donfaustoi* given the option of migrating between ranges; (iv) *C. porteri* confined to their lowland range; (v) *C. porteri* confined to their highland range; (vi) *C. porteri* given the option of migrating between ranges; (vii) sedentary *C. hoodensis*. To ease interpretation, annual energetic surplus are reported in units of mass using a conversion factor of 13 000 kJ kg⁻¹ (Peters 1983), however, we recognize that adult tortoises, particularly females likely invest most surplus into production of eggs. Predictions for the *C. donfaustoi* and *C. porteri* species were very similar and predictions presented in figures are all based on the *C. donfaustoi* conditions.

Comparison of predictions and observations

We compared the predicted size at which migration should occur to observations of the smallest sized tortoise found in the highlands during the latter 3 months of the dry season in 2010. To

evaluate energy surplus predictions we focused on the maximum body sizes for males and females within *C. hoodensis*, and across the two species on Santa Cruz (data were sparse and required pooling). Specifically we were interested in: (i) whether maximum observed adult males size was close to the point when energetic surplus approached zero under the assumption that males maximize body size in order to outcompete other males for females, and (ii) whether maximum adult female sizes were close to peak predicted annual surplus under the assumption that female body size evolved to maximize fecundity. Tortoise measurements in the field are based on curved carapace length, CC , so we converted these measurements to masses using $M = (CC/\nu)^3$, where $\nu = 23.9$ for the pair of migratory, domed Santa Cruz species and $\nu = 22.4$ for the single sedentary, saddle-backed Espanola species. At those masses where migration was an optimal behaviour, we also calculated the day on which individuals were predicted to cross the mid-point of their upward and downward altitudinal migrations. Migration timing predictions were compared to results from tagged individuals previously reported in Blake *et al.* (2013).

Scenarios to test hypotheses

To understand the relative importance of the forage and movement hypotheses in determining model behaviour, we ran scenarios where the model components calculating annual energetic surpluses at migratory destinations and travel time between destinations were calculated independently for all combinations of masses between 10 kg and 400 kg at 10 kg intervals.

Results

The model makes predictions of adult body sizes of males and females in both migratory and resident taxa, as well as the size at which individuals should adopt a migratory tactic, that generally agree with observations (Fig. 4a–c). The model also does a reasonable job of predicting the timing of migration (Fig. 4d). Specifically, the timing of downslope migration coincides with rapid greening in the lowlands at the onset of the rainy season and is size-independent. Upslope migration, in contrast, is accurately predicted to be size-dependent with larger tortoises migrating first and the smallest tortoises migrating c. 3 months later. In the model, this size-dependency in timing is driven by body size-specific responses to slowly declining food densities in the lowlands.

To test the relative importance of the movement vs. the forage hypothesis in determining the size at which individuals begin to migrate, we ran a range of scenarios where the body masses used to calculate migration speed and energetic balances at the migratory destinations were varied independently between 10 and 400 kg. Migration is always predicted to be optimal if the energetic balances at the migratory destinations are calculated based on a mass greater than 70 kg, regardless of the mass used to calculate migration speed (Fig. 5a). A lowland-only sedentary tactic is always predicted to be optimal if the energetic balances at the migratory destinations are calculated based on a mass less than 50 kg. Model results are insensitive to variation in the mass used to

calculate migratory speed when the mass used to calculate energetic balances at destinations is fixed (Fig. 5b). In contrast, fixing migratory speed leads to negligible changes in model behaviour relative to when all model components are calculated based on the same mass (Fig. 5c and d). Although the size at which migration

becomes optimal increases when the migration distance is increased by a factor of 10, the same pattern of model results being driven primarily by foraging and metabolism persists (Appendix S3). Thus, our modelling demonstrates that energetic balances at the destinations drive migratory patterns.

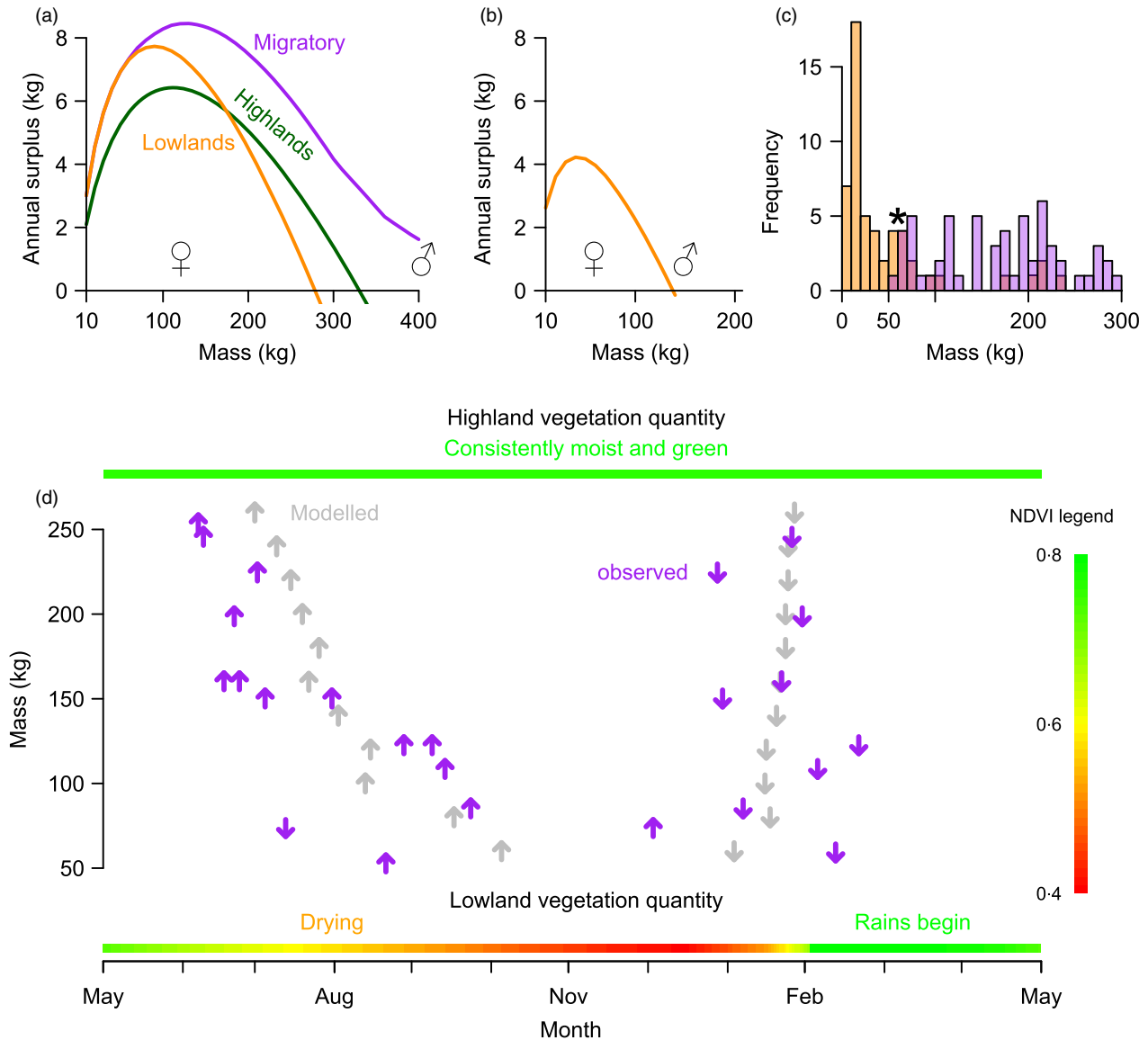


Fig. 4. Predictions from the model generally agree with data not included in model fitting. (a) For migratory species, the model predicts annual energetic surplus as a function of body size for three potential strategies: a sedentary lowland-only tactic (orange), a sedentary highland-only tactic (green), and a migratory tactic (purple). The body size of the largest adult female (♀) observed during long-term monitoring aligns with model predictions of maximum annual surplus – a sensible pattern if female maximum body size has evolved to maximize energy available for reproduction. In contrast, the body size of the largest observed adult male (♂) is much larger (males compete over mates and larger body size likely confers an advantage). Predictions and data were pooled between the two migratory species because predictions were very similar and data were sparse. (b) For the non-migratory species found on Espanola Island, predicted growth also aligns well with observations of maximum male and female body size derived from long-term monitoring. (c) Migrants (purple; individuals found above 300 m during Oct-Dec 2010) are generally larger than non-migrants (orange; individuals found below 150 meters during Oct-Dec 2010) based on previously published population survey data (Blake *et al.* 2013) and the size of the smallest migrants corresponds to the predicted size at which migration becomes profitable (indicated with asterisk). (d) Timing of modelled (grey) migrations upslope (upward pointing arrows) and downslope (downward pointing arrows) are consistent with observations of gps-tagged individuals (purple), with the exception of a 70 kg female that migrated downslope in July and upslope in December. Colour ramps at top and bottom of panel illustrates seasonal changes in vegetation quantity in the highlands and lowlands respectively, with green and red representing high (0.8) and low (0.4) NDVI (see NDVI legend in figure).

Energetic balances at the destinations differ as a function of body size, because body size determines the sensitivity of tortoises to variation in forage quantity over time. Forage quantity in the lowlands is seasonally variable, but generally of high quality, while the highlands offer a steady supply of low quality forage. For a small tortoise, forage acquisition is relatively insensitive to forage quantity over the range of NDVI values experienced in either the lowlands or highlands (Fig. 6a). As a result, a small tortoise is predicted to have higher greater energetic surpluses (i.e. fitness *sensu* Brown, Marquet & Taper 1993) in the lowlands relative to the highlands for 97% of the year (Fig. 6b). In contrast, forage acquisition in a large tortoise is highly sensitive to forage quantity (Fig. 6a) and the lowlands only provide greater energetic surpluses for 45% of the year (Fig. 6c). For both small

and large tortoises the ‘better habitat’ changes throughout the year, however this condition is not sufficient to promote migration among all tortoises. High sensitivity to changing forage quantity in larger tortoises leads to large absolute difference between the daily energetic balances in the highlands and the lowlands over the course of the year (Fig. 6c).

Discussion

Body size, like many biological traits, frequently affects multiple interrelated physiological, behavioural and ecological processes. Past analyses of the effects of body size on migration propensity have focused primarily on the relationship between body size and movement speed during the migratory phases of the annual migratory cycle

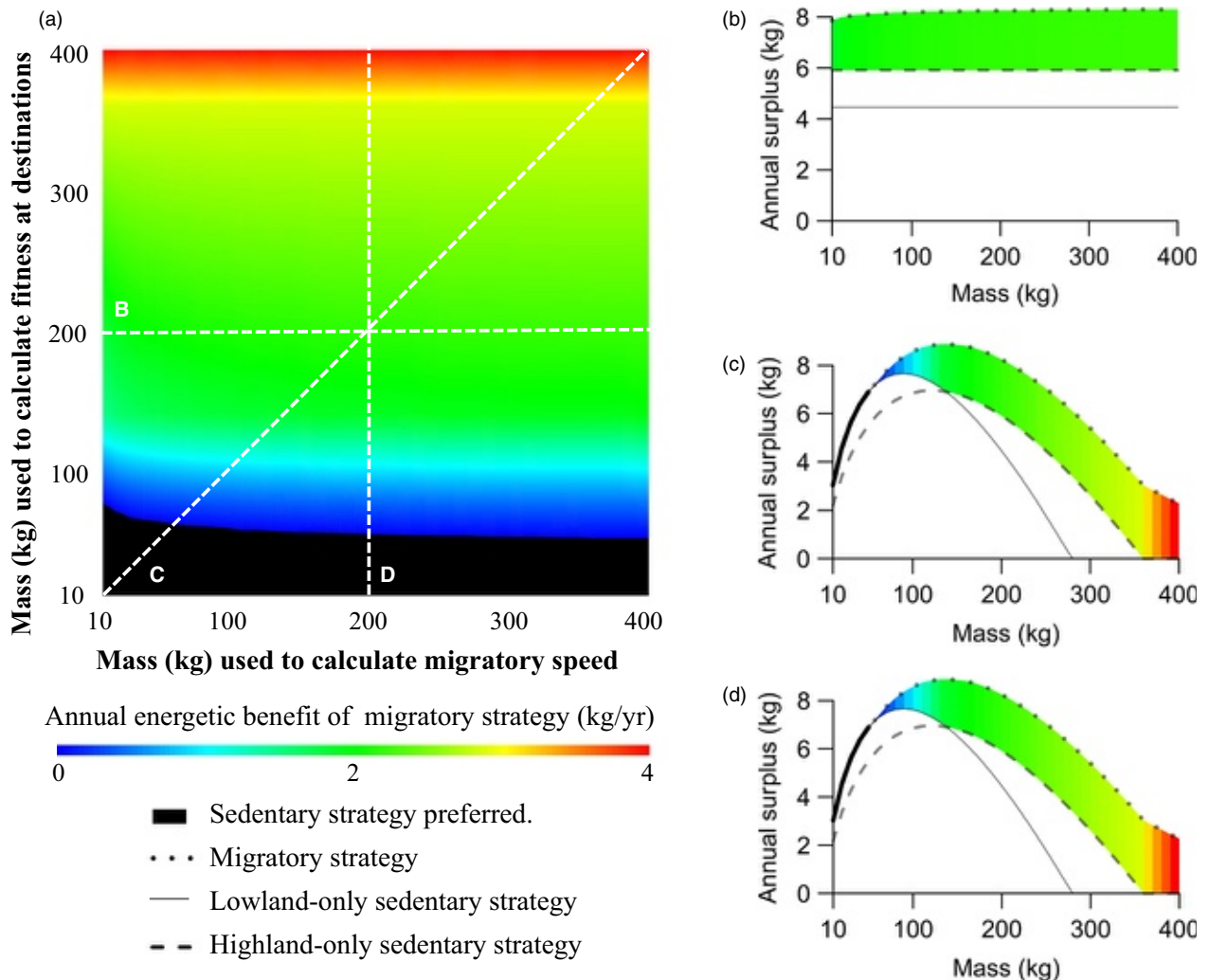


Fig. 5. Migratory behaviour is primarily driven by energetic balances at the migratory destinations. (a) Migration speed and energetic balances at destinations were calculated using separate masses to explore their relative importance. Colours in all panels correspond to the annual energetic benefit associated with a migratory tactic over the best sedentary tactic, with black representing no migratory advantage. White letters and adjacent lines correspond to specific scenarios highlighted in other panels. (b) Model behaviour is insensitive to changes in the mass used to calculate migratory speed while holding mass used to calculate energetic balances at the destinations constant at 200 kg. (c) Speed and energetic balances calculated using same mass. (d) Responses of varying mass used to calculate energetic balances at the destinations while holding mass used to calculate migration speed constant at 200 kg.

(Peters 1983; Alerstam, Hedenstrom & Akesson 2003). We posed an alternative hypothesis; that larger animals are more sensitive to spatial and temporal variation in food densities during the sedentary phases and thus have a greater incentive to track resources. Given the legendary ability of Galapagos tortoises to survive for many months without food and water (Van Denburgh 1914), and the

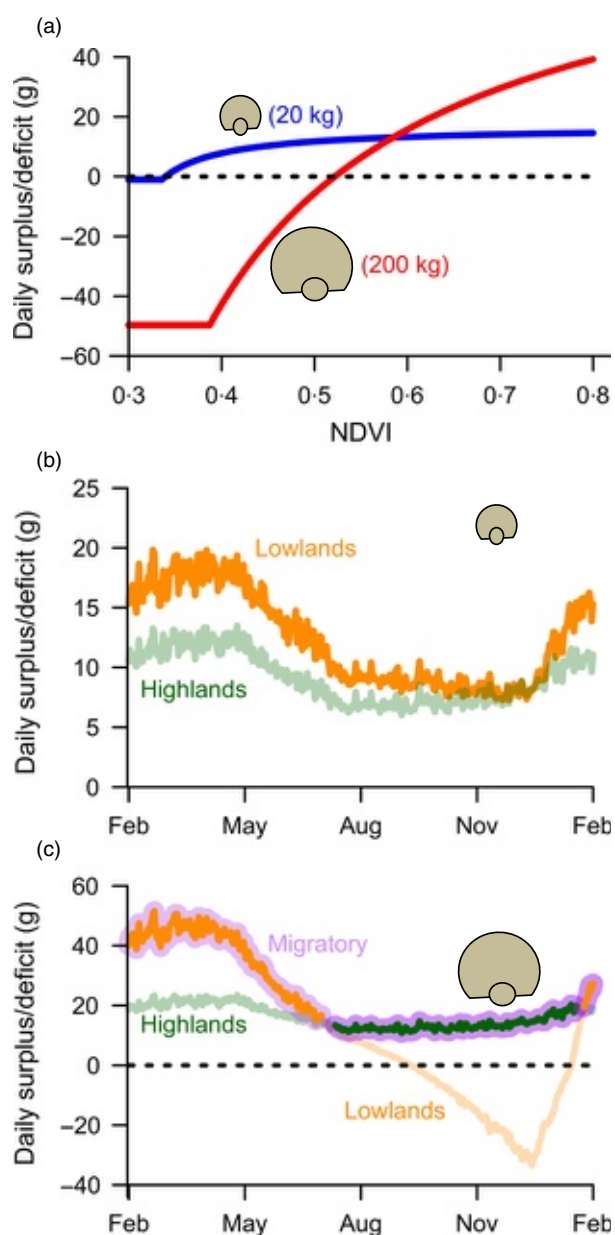


Fig. 6. The energetic balances of small (20 kg) and large (200 kg) tortoises respond differently to seasonal changes in food availability, explaining migratory patterns. (a) Energetic balances of small, as opposed to large, tortoises are less sensitive to seasonal changes in NDVI. (b) For most of the year, the energetic surpluses of small tortoises is higher in the lowlands, which are characterized by higher vegetation quality and temperatures. (c) Daily energetic balances for large tortoises in the lowlands are high during the wet season, but decline rapidly during the dry season. A 200-kg individual is predicted to migrate upslope in July.

general observation across species that larger individuals have greater energy reserves (Lindstedt & Boyce 1985), this hypothesis may at first seem counterintuitive. However, even if tortoises are well-equipped to survive periods of shortage, it is not surprising that they would migrate if better options are available. Moreover, since predictable seasonal variation in the distribution of food resources is associated with many migratory systems (e.g. Holdo, Holt & Fryxell 2009; Blake *et al.* 2013), it is logical to suspect the balance of foraging gains and metabolic costs may link body size to migratory patterns.

To determine the relative importance of speed during the migratory phases and sensitivity during the sedentary phases, we developed a full migratory cycle bioenergetics model. The model predicts patterns including the body size at which migration begins and the timing of seasonal migration that generally agree with data (Fig. 4). Scenarios clearly illustrate that body size effects on foraging and metabolism are far more important than body size effects on movement speed (Fig. 5). Large tortoises in the lowlands run large energetic surpluses during the wettest period of the year, but would also run large energetic deficits during the driest period of the year if they were unable to migrate to the highlands (Fig. 6). In contrast, changes in forage quantity in the lowlands have relatively small impacts on the energetic balances of smaller tortoises.

Forage quality also plays an important role in shaping the tortoise migratory patterns, in agreement with past studies of habitat selection in mammalian herbivores of the Serengeti (Wilmshurst *et al.* 1999; Wilmshurst, Fryxell & Bergman 2000). We calculated difference in forage quality between highlands and lowlands based on the frequency with which grasses and forbs were eaten during foraging observations, but we assumed forage quality within these habitats did not vary over time. If variation in forage quality between the highland and lowland habitats is ignored, the model predicts tortoises should prefer a highland-only sedentary tactic until a mass of 190-kg, and at larger masses a migratory tactic is only marginally better than a highland-only sedentary tactic (predictions in disagreement with observed patterns). We are unable to test our assumption that forage quality within habitats is constant over time, but hope to address this assumption through future empirical work. Studies in other systems have found that forage quality often varies with forage biomass, so we expect that some variation within habitats over time is likely. Nonetheless, our model did a reasonable job of prediction (Fig. 4) while ignoring temporal variation in forage quality and this suggests that the effects of temporal variation in forage quality in our system are not as important as the spatial variation in forage quality. In other systems, the relatively simple relationship between forage quantity, forage quality and energetic intake that we have used here may not sufficiently describe spatio-temporal variation. However, even in more complex systems, we suspect that our main conclusion – that energetic balances at destinations, and not

movement costs, drive migratory patterns – will still be supported.

The model we developed is based on general ecological relationships with a few species-specific exceptions. Firstly, we modelled internal temperature in tortoises as a function of external temperatures and body size using a general model developed for poikilotherms (see Appendix S2 for details). Interestingly, removing this model component (i.e. assuming steady temperatures of 25.5 °C in both lowlands and highlands) leads to predictions that are qualitatively similar (but slightly poorer in terms of fit to observed growth and migratory timing). Secondly, because Galapagos tortoises forage as they migrate they both maintain approximately neutral energy budgets during this time and move at speeds substantially slower than would be expected based on relationships between body size and optimal movement speed in other terrestrial turtle species or based on peak movement rates observed for Galapagos tortoises (Bastille-Rousseau *et al.* 2016). Therefore, we predicted movement speed using a relationship developed from observations of migrating tortoises, which has a similar exponent, but significantly smaller constant than relationships based on all reptiles (Peters 1983; Bastille-Rousseau *et al.* 2016). Given the increasing use of GPS telemetry, we suspect that it will be possible to estimate travel times between breeding and non-breeding habitats for many species and rely less on estimates of velocities over shorter time scales. However, if questions about stop-over habitat are of interest, application of a full migratory cycle model like ours may require modelling energetic balances in stop-over habitat. Lastly, although the total amount of time spent migrating per year by Galapagos tortoises is modest (roughly 2–4 weeks) compared to some other migrations, our modelling suggests that sensitivity to vegetation dynamics is still more important than movement speeds in determining migratory patterns when the distance separating ranges is an order of magnitude greater (Appendix S3).

In parameterizing the model, we used relationships derived from evolutionary, ontogenetic and static allometries (Cock 1966; Gould 1966) to predict a behaviour, migration, that can itself vary between closely related species, according to life stage, and among individuals in the same life stage. Past work has generally found relationships at these three levels to be tightly interrelated, however there are exceptions (Klingenberg & Zimmermann 1992) and this could have important consequences for attempts to apply similar models in other systems. In particular, when modelling specific outcomes in a single species, we might expect evolutionary allometries to do a poorer job of prediction than ontogenetic or static allometries fit specifically to the species being studied. On the other hand, in instances where allometries were available from different levels, we found the powers to be very similar, suggesting that qualitative predictions may be similar even when imperfect relationships are used.

Full migratory cycle bioenergetics models can help in predicting the response of imperiled migratory systems to multiple forms of environmental change and aid development of relevant conservation strategies. Galapagos tortoises on Santa Cruz Island encounter many physical barriers during their migration and individuals can be trapped by fences in the highlands for up to a year (Blake *et al.* 2015b). Such disruptions to seasonal migration in Galapagos tortoises have the potential to deplete their energy reserves as the largest tortoises are predicted to run energetic deficits in both the highlands and lowlands if their movements are restricted (Fig. 4). Over the course of an annual cycle, these periods of energetic deficits will lead to diminished somatic growth rates and/or reproductive output. Landscape planning and management that maintains connectivity between and within migratory destinations will likely be necessary to minimize the impacts of increasing economic development on Santa Cruz Island to Galapagos tortoises.

More broadly, climate change is predicted to change precipitation patterns and vegetation dynamics, impacting the fitness of both migratory and non-migratory strategies across many species. Rainfall and lowland vegetation dynamics in the Galapagos Islands already vary dramatically in response to extreme El Niño and La Niña events (Restrepo *et al.* 2012), and the frequency and intensity of such events is expected to increase in the future (Wang *et al.* 2012). The condition of larger tortoises will likely be more sensitive to increased inter-annual variation in vegetation dynamics and decreased condition may ultimately lead to declines in maximum adult body size and reduced reproductive output. Impacts of altered resource dynamics on body size are likely in those systems in which food availability limits growth during part or all of the year. While researchers have focused on the role warming temperatures may play in decreasing body size globally (Gardner *et al.* 2011; Sheridan & Bickford 2011), our modelling suggests that energetic budgets, and ultimately adult body sizes, may respond to changing resource densities just as strongly.

Authors' contributions

C.B.Y. conceived the ideas and developed the model; S.B. and G.B.R. collected the data; C.B.Y. analyzed the data; C.B.Y. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Relevant code for the model is available in the Appendix and at <https://doi.org/10.5066/f78k777n> (Yackulic 2017). Data required to run the bioenergetics model for Galapagos tortoises are available at <https://doi.org/10.5066/f7154f7p> (Yackulic, Blake & Bastille-Rousseau 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. R Model code.

Appendix S2. Details of internal temperature modeling.

Appendix S3. Dependence of model output on migration distance.