

# Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients

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## Summary

1. Seasonal migration has evolved in many taxa as a response to predictable spatial and temporal variation in the environment. Individual traits, physiology and social state interact with environmental factors to increase the complexity of migratory systems. Despite a huge body of research, the ultimate causes of migration remain unclear.
2. A relatively simple, tractable system – giant tortoises on Santa Cruz Island, Galapagos, was studied to elucidate the roles of environmental variation and individual traits in a partial migratory system. Specifically, we asked: (i) do Galapagos tortoises undergo long-distance seasonal migrations? (ii) is tortoise migration ultimately driven by gradients in forage quality or temperature; and (iii) how do sex and body size influence migration patterns?
3. We recorded the daily locations of 17 GPS-tagged tortoises and walked a monthly survey along the altitudinal gradient to characterize the movements and distribution of tortoises of different sizes and sexes. Monthly temperature and rainfall data were obtained from weather stations deployed at various altitudes, and the Normalized Difference Vegetation Index was used as a proxy for forage quality.
4. Analyses using net displacement or daily movement characteristics did not agree on assigning individuals as either migratory or non-migratory; however, both methods suggested that some individuals were migratory. Adult tortoises of both sexes move up and down an altitudinal gradient in response to changes in vegetation dynamics, not temperature. The largest tagged individuals all moved, whereas only some mid-sized individuals moved, and the smallest individuals never left lowland areas. The timing of movements varied with body size: large individuals moved upward (as lowland forage quality declined) earlier in the year than did mid-sized individuals, while the timing of downward movements was unrelated to body size and occurred as lowland vegetation productivity peaked.
5. Giant tortoises are unlikely candidates for forage-driven migration as they are well buffered against environmental fluctuations by large body size and a slow metabolism. Notably the largest, and presumably most dominant, individuals were most likely to migrate. This characteristic and the lack of sex-based differences in movement behaviour distinguish Galapagos tortoise movement from previously described partial migratory systems.

**Key-words:** allometry, megavertebrate, NDVI, oceanic islands, partial migration

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## Introduction

Return migration in mobile animals is a behavioural response to predictable spatial and temporal variation in the availability and quality of food resources, predation risk, parasites and disease, temperature and other environmental conditions (Fryxell & Sinclair 1988; Alerstam, Hedenstrom & Akesson 2003; Holdo, Holt & Fryxell 2009). To evolve, the benefits to lifetime reproductive success of migrating must outweigh the costs of moving over long distances or of remaining sedentary (Lack 1968; Griswold, Taylor & Norris 2010).

Despite rapid growth in animal tracking research, the ultimate causes of migration remain unclear because environmental factors rarely act independently (Fryxell & Sinclair 1988; Bowlin *et al.* 2010; Holt & Fryxell 2011). For example, over several decades researchers in the Serengeti plains, arguably the most studied migratory system, have suggested numerous mechanisms that explain the movements of wildebeest in terms of responses to spatio-temporal pattern in precipitation, vegetation quantity and quality, and predation (Bell 1970; Maddock 1979; McNaughton 1985; Murray 1995; Fryxell, Wilmshurst & Sinclair 2004; Boone, Thirgood & Hopcraft 2006). The most recent model indicates that wildebeest migrate to maximize their intake of high-quality grass forage (Holdo, Holt & Fryxell 2009), which presumably enhances physiological condition and reproductive success.

While food acquisition is often a primary determinant of vertebrate migration (Alerstam, Hedenstrom & Akesson 2003), predation cannot be ignored as a major evolutionary force even when off-take levels are very low (McNamara & Houston 2008). Gradients in risk of predation also drive migrations among some ungulates (Hebblewhite & Merrill 2011), birds (McKinnon *et al.* 2010) and other taxa (Gliwicz 1986; Connor & Corkeron 2001; Bronmark *et al.* 2008).

In oviparous species, selection of suitable nesting conditions also contributes to migratory behaviour either through maximizing embryo and/or maternal fitness, modifying offspring phenotypes or selection of suitable habitat for offspring (Refsnider & Janzen 2010; Southwood & Avens 2010). Risk of infection from parasites and pathogens may also drive long-distance migrations in many species including birds (Buehler, Tieleman & Piersma 2010), ungulates (Folstad *et al.* 1991) and monarch butterflies (Altizer 2001). Ectothermic sea turtles may migrate in response to the seasonal distribution of food, preferred thermal conditions and the availability of suitable nesting sites (Hawkes *et al.* 2007; Sherrill-Mix, James & Myers 2008).

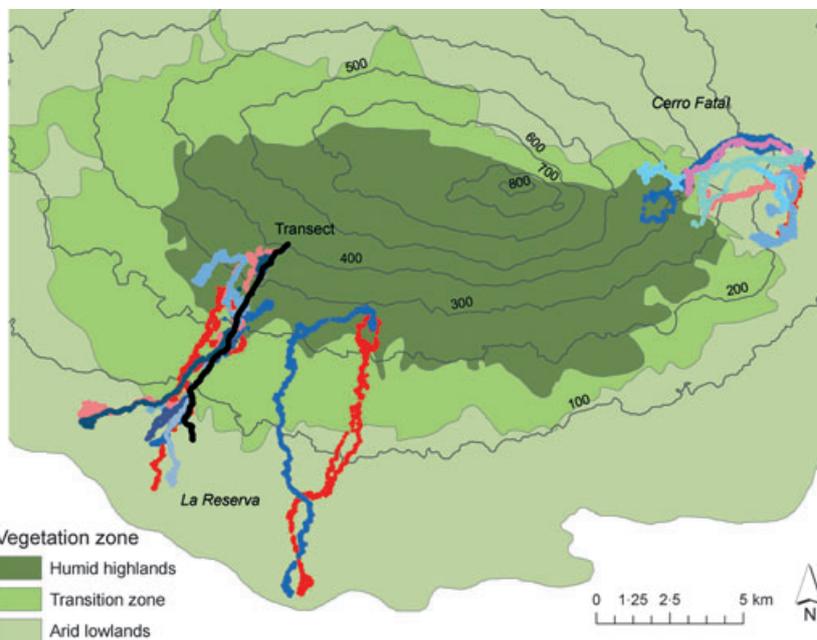
The interaction among environment and life-history traits, physiology and social state further increase the complexity of migratory mechanisms and may promote partial migration in which only a fraction of the population migrates (Chapman *et al.* 2011). Several non-mutually exclusive mechanisms to explain partial

migration have received support including the influence of body size, social dominance and competition (Lack 1968; Lundberg 1988; Boyle 2008; Bai, Severinghaus & Philippart 2012). The plethora of influencing factors and the logistical difficulty of studying migration mean that researchers are still answering fundamental questions such as who, when, where, how and why animals migrate (Bowlin *et al.* 2010).

Following a strong scientific tradition (Darwin 1859; MacArthur & Wilson 1967), we took advantage of a simplified ecosystem – an oceanic island in the Galapagos archipelago, and an iconic taxon – herbivorous giant tortoises (*Chelonoidis nigra* Quoy & Gaimard, 1824), to shed light on the mechanisms underlying a complex ecological problem. Giant tortoises (Testudinidae) are known to migrate seasonally over large distances, with evidence for partial migration; yet, the mechanisms are poorly understood (Rodhouse *et al.* 1975; Swingland & Lessells 1979; Gibson & Hamilton 1983). Unusual among migratory species, Galapagos tortoises are free from predation, except during the brief hatchling stage when they are vulnerable to Galapagos hawks (*Buteo galapagoensis* Gould, 1837) (Darwin 1839). The volcanic slopes of Galapagos present spatiotemporal variation in at least two variables, rainfall and temperature, that are likely candidates to promote migratory behaviour in large herbivorous ectotherms (Southwood & Avens 2010). Temperature decreases with elevation and could limit foraging and growth opportunities for tortoises in the highlands during the coldest parts of the year. In contrast, rainfall increases with altitude and varies predictably throughout the year (Trueman & d'Ozouville 2010).

Using a combination of data from GPS-tagged individuals in two separate populations of Galapagos tortoises on Santa Cruz Island (Fig. 1), and monthly surveys of tortoises made along an altitudinal gradient in one of these populations, the following three questions on movements and distribution at both individual- and population levels were addressed:

- 1 Is anecdotal evidence for long-distance seasonal altitudinal migration supported by on the daily movements of individual tortoises or by their net displacements over the course of a year? Both daily movement and overall net displacement have been the topic of separate analyses of migration in past studies (e.g. Morales *et al.* 2004; Bunnefeld *et al.* 2011); however, as far as we know they have not been applied to the same data sets and thus not compared for consistency.
- 2 Why do tortoises move up and down the elevation gradient? Answering this question involved testing two competing hypotheses: (i) forage-driven movement, in which tortoises time their movements during peak rainfall to exploit a seasonal flush of vegetation in the lowlands and move into the highlands when vegetation quality in the lowlands declines as rainfall diminishes; or (ii) thermoregulation-driven movement, in



**Fig. 1.** Migration routes of individual Galapagos tortoises on Santa Cruz Island.

which tortoises move to escape unfavourable minimum temperatures in highlands during the coldest months by moving into the warmer lowlands.

- 3 How do individual traits influence migration? Specifically: (i) is the timing of movements between the lowland and highlands dependent on body size; and (ii) are males and females equally likely to migrate? Question 3a is based on reports from unpublished literature (Guerra 2005), which suggest that only large adult tortoises occur in the highlands. This is counter-intuitive to current partial migration theory, which predicts that small-bodied tortoises should be more likely to migrate than larger ones under both the body size and dominance hypotheses (Cagnacci *et al.* 2011; Chapman *et al.* 2011). If thermoregulation were driving movements, we expect smaller individuals to migrate into more favourable thermal environments due to their lower thermal inertia compared with larger tortoises (Stevenson 1985). Question 3b is based on anecdotes that adults of both sexes prefer the highlands and females alone migrate into the lowlands and previous hypotheses that sex may play a key role in migration (e.g. Kaitala, Kaitala & Lundberg 1993; Kokko 2011).

Beyond its relevance to the development of migration theory, answering these questions is an important step towards protecting these threatened species, and the ecosystems in which they have key functions as seed dispersers, disturbance agents and herbivores (Gibbs, Marquez & Sterling 2008). The Galapagos Islands are under increasing threat from human population growth, infrastructure development such as roads and urbanisation, the spread of invasive species and climate change (Trueman & d'Ozouville 2010; Watson *et al.* 2010), all of which may impact tortoise movements and the spatial patterns of

their effects as ecosystem engineers (Blake *et al.* 2012). Improving our understanding of the ecology of the Galapagos tortoises will also inform policy for restoration programmes proposing to use extant giant tortoises as taxon substitutes to replace extirpated forms (Hansen *et al.* 2010; Griffiths *et al.* 2011).

## Materials and methods

### GPS TELEMETRY, TRANSECT AND ENVIRONMENTAL DATA COLLECTION

All animal handling procedures for this study adhered to the policies of the Galapagos National Park and the Max Planck Institute of Ornithology. In 2009–2010, custom-made GPS tags (e-obs, Munich, Germany) were fitted to the carapaces of 17 wild-adult Galapagos tortoises from two distinct taxa on Santa Cruz Island (Fig. 1). After examining potential study animals to tag in both highlands and lowlands, healthy adults with no obvious deformities or apparent signs of illness were chosen for the study. The GPS units recorded geographical position every hour as well as ambient temperature. Data were downloaded opportunistically every 1–3 months via a UHF radio modem.

The GPS data were supplemented with data from monthly tortoise population surveys carried out on foot on a pre-determined transect from 400 to 50 m a.s.l. to monitor the altitudinal distribution of tortoises by sex and body size at the population level (Fig. 1). The size (curved carapace length), sex and location of every tortoise encountered were recorded. Tortoise encounter rate in the Cerro Fatal site was insufficient to provide a quantitatively meaningful data set, and only data from La Reserva were included in the analysis. The survey route did not sample habitats at different altitudes in proportion to their availability; consequently, it is difficult to make direct inferences about the proportion of the adult population at different altitudes during different months or to make inferences concerning the average altitude occupied by tortoises of a given size. However, inferences can be

made about the average size of tortoises at a given altitude in different months and test hypotheses about the population based on variation in the slope of a regression between altitude and body size in different months.

Monthly rainfall in the lowlands and highlands of each population (100 and 400 m a.s.l. respectively) was estimated from rainfall accumulators. Ambient-shade temperature was measured every 4 h with iButton thermochrons (Maxim Integrated Products, Inc., Sunnyville, CA, USA) placed at 1m above-ground level at 50 m altitude intervals from 50 to 400 m a.s.l. For the analyses of the impact of environmental variables on tortoise movement and distribution, the average monthly temperature derived from the thermochron at 350 m within each population was used. The Normalized Difference Vegetation Index (NDVI) of the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument (Huete *et al.* 2002) (specifically Global MOD13Q1 data, which are provided every 16 days at 250-m spatial resolution) was used as an index of vegetation quality. The NDVI was used because of its proven strong correlation to vegetation productivity and quality (Pettorelli *et al.* 2005; Singh *et al.* 2010). Monthly average NDVI values within the range of each tortoise population were derived based on grid sampling within the convex hull created by non-migratory upland and lowland relocations. For some months NDVI data were missing because of cloud cover, so values were interpolated from the surrounding months using a simple model:

$$NDVI_t = \min(\max NDVI, NDVI_{t-1} * e^{\beta * ppt_{t-1} - \epsilon}) \quad \text{eqn 1}$$

Where  $\epsilon$  is the rate of decay in NDVI without rain,  $\beta$  is the positive effect of rain on NDVI, and  $\max NDVI$  is the value of NDVI when the vegetation is saturated with rain.

## STATISTICAL ANALYSES

### Comparison of methods for identifying migration based on movement patterns

Two methods to identify migration were compared; one based on daily altitudinal change and turning angles of tortoises and the other based on net altitudinal change. Altitude values of tortoises were obtained using ArcGIS 9.3.1 (ESRI, Redlands, CA, USA) by projecting the tortoise GPS data onto the Shuttle Radar Topography Mission (SRTM) (Rabus *et al.* 2003) elevation data, because GPS-based estimates of altitude were relatively imprecise. Evidence for migration in the daily movement statistics of the 17 tagged tortoises was sought by comparing the fit of two models: (i) a simple model in which turning angles and daily altitudinal change are drawn from the same distributions at all times; and (ii) a more complex 'switch' model in which animals switch between two unobserved or latent states, each of which has its own distribution of altitudinal change and turning angles (Morales *et al.* 2004; Yackulic *et al.* 2011). Latent state models allow users to objectively distinguish groups of movements (i.e. migratory and non-migratory movements) without defining the characteristics that define these groups *a priori* (Morales *et al.* 2004; Fryxell *et al.* 2008; Yackulic *et al.* 2011). Elevation change ( $x$ ) was modelled using the Weibull distribution:

$$W(x|v, \lambda) = v\lambda x^{v-1} \exp(-\lambda x^v); x > 0, \quad \text{eqn 2}$$

where  $v$  and  $\lambda$  were estimated parameters that varied between states [i.e. a single  $v$  and a single  $\lambda$  were estimated in the simple model and two sets of  $v$  and  $\lambda$  in the switch model – e.g.  $v$ , for migratory ( $v_M$ ) and non-migratory states ( $v_{NM}$ )]. Observed turning angles ( $\phi$ ) were modelled using the compound wrapped Cauchy distribution (Yackulic *et al.* 2011):

$$CC(\phi|\varphi_N, \rho_N) = \frac{\sum_{i=1}^N C(\phi|\varphi_i, \rho_i)}{N}, \quad \text{eqn 3}$$

which is the average of multiple wrapped Cauchy distributions ( $C$ ) each with a bearing,  $\varphi$ , and scaling parameter,  $\rho$ . Although the compound wrapped Cauchy distribution can accommodate many modes, two principal movement types were investigated: (i) reversals, because they are associated with foraging and home ranging behavior; and (ii) persistence, because it provides evidence of a more migratory state. Therefore, turning angles were modelled as a mixture of distributions centred around 0 (persistence –  $\rho_1$ ) and  $\pi$  (reversals –  $\rho_2$ ) where larger values of each  $\rho$  indicate that movement is more biased in that direction. In the switch model, the values of  $\rho$ 's varied between states (i.e.  $\rho_{1,M}$  and  $\rho_{2,M}$  were estimated in addition to a  $\rho_{1,NM}$  and  $\rho_{2,NM}$ ). Models were fitted using WinBugs (Lunn *et al.* 2000) (Code, including priors, is listed in Supplementary Materials). Models ran for 25,000 iterations using 3 chains and had converged ( $\hat{R}$ ). Single and switch models were compared using deviance information criterion (DIC) (Spiegelhalter *et al.* 2002). Odds ratios of turning angles were based on estimates of  $\rho_{1,M}$ ,  $\rho_{1,NM}$ ,  $\rho_{2,M}$  and  $\rho_{2,NM}$ ; all other summary statistics were based directly on the data.

Two additional models were also considered based on net (as opposed to daily) movement. These models were introduced by Bunnefeld *et al.* (2011) and were referred to as the migratory and home range models. Net displacement (NSD) under the home range model is described by the following equation:

$$NSD = c \quad \text{eqn 4}$$

Where  $c$  is a constant. Net square displacement under the migration model over the course of a year is described by a double logistic equation of the following form:

$$ND(t) = \frac{\alpha}{1 + e^{\frac{\mu_a - t}{\sigma_a}}} - \frac{\alpha}{1 + e^{\frac{\mu_b - t}{\sigma_b}}} \quad \text{eqn 5}$$

where  $\alpha$  is the maximum displacement (altitudinal displacement in this case),  $\mu_a$  and  $\mu_b$  are the points at which net displacement is half the maximum on the ascending ( $\mu_a$ ) and descending ( $\mu_b$ ) limbs and  $\sigma_a$  and  $\sigma_b$  are the slopes of the respective limbs. These models were fitted to 10 of the 17 individuals (the other tortoises were not analysed because their GPS records were less than a year in length or because the migratory model did not converge) using the nlme package in R, version 2.15.0 (R Development Core Team 2008), and the fit of the home range and

migratory models were compared based on Bayesian Information Criterion (BIC) (Spiegelhalter *et al.* 2002).

### Calculating monthly positions of individuals and crossing days

For each of the two populations, the midway points between the highland and lowland range extremes were determined based on the means of the maximum and minimum altitudes of each individual in the population, then identifying when individuals crossed this point on either downward or upward migrations (crossing day) and classifying the average monthly position of each individual relative to this mid-point (above = 1, below = 0; hereafter referred to as monthly individual position data). For upward migration, crossing days were expressed in terms of how many days after 1 May they occurred, and for downward migrations, how many days after 1 January (no migrations in the respective directions occurred before these dates). The crossing day and the monthly positions relative to the mid-point were used in further analyses described below.

### Environmental analyses

A monthly resolution was chosen for the analysis of environmental data because tortoises are capable of responding to differences between lowlands and highlands at this temporal scale, and because rainfall and NDVI data were only available at this resolution. The monthly individual position data were analysed with Generalized Linear Mixed Models (GLMMs) with a binomial error distribution, a logit link and individual as a random effect. BIC was used to compare models in which either upland temperature or lowland vegetation predicted the monthly position of each tortoise. It was hypothesised that the beta in the lowland vegetation model should be negative (i.e. tortoises would be more likely to be found in the lowlands when lowland vegetation was abundant) and that the beta associated with temperature should be positive (i.e. tortoises would be more likely to be found in the highlands when upland temperatures were warmest).

### Test of forage and thermoregulation migration hypotheses based on tortoise distribution patterns

The monthly tortoise population survey data were analysed with respect to the thermoregulation and foraging hypotheses of migration to determine whether the patterns in the size of adult tortoises found at different elevations were consistent with the monthly analysis of tortoise GPS data. GLMMs were used to determine how average tortoise size varied as a function of altitude over time. In these analyses, the response variable was the carapace length ( $Z$ ) of each individual encountered, and the predictors include altitude by itself and in interaction with either lowland NDVI or upland temperature. NDVI and temperature were z-transformed to ease interpretation of coefficients. Initially, models were run without transforming altitude; however, this led to high covariance between the coefficients associated with the intercept and the effect of altitude. Therefore, altitude values were transformed by subtracting 310 m from all altitudes. A value of 310 m was chosen because at least a few tortoises were found at the altitude or greater in each month. This transformation had no effect on BIC values and did not affect estimates of

the betas associated with altitude. It only changed the interpretation of the intercept from the expected size at an altitude of 0 m, to the expected size at an altitude of 310 m. This value was stable across months because only large individuals are found at this elevation. The beta associated with the effect of altitude was treated as a random effect to control for the multiple observations within each month. In other words, we fit the following regressions:

$$Z = \beta^{310m} + (\beta_t^A + \beta^{A,T} * T) * A + \epsilon \quad \text{eqn 6}$$

$$Z = \beta^{310m} + (\beta_t^A + \beta^{A,F} * N) * A + \epsilon \quad \text{eqn 7}$$

Where  $\beta^{310m}$  is the expected size at an altitude of 310 m,  $\beta^{A,T}$  or  $\beta^{A,F}$  is the effect of either thermoregulation or forage on the relationship between altitude and size, is a random variable that varies by month,  $t$ , (i.e.  $\beta_t^A \sim N(\mu^A, \sigma^A)$ ), and the residuals, are normally distributed. It was hypothesised that the mean value of the random variable relating altitude to expected size ( $\mu^A$ ) would be positive under both the forage and thermoregulation hypotheses because some large individuals are always found in the highlands, and no smaller adults are ever found there. It was further hypothesised that the beta associated with vegetation ( $\beta^{A,F}$ ) would be negative, and the beta associated with temperature ( $\beta^{A,T}$ ) would be positive for the same reasons as listed in the previous section.

### Influence of sex and body size on the presence and timing of migration

The tortoise population survey data were used to determine whether the responses of individuals to variation in lowland vegetation varied by sex. Adult female tortoises are smaller than males, so the null model stated that a female will have a lower intercept than a male ( $\beta^{310m,\text{f}} < \beta^{310m,\text{m}}$ ) but that the coefficients associated with altitude and lowland NDVI will not vary between the sexes. This null model was compared with the following three hypotheses: (i) males are larger ( $\beta^{310m,\text{m}} > \beta^{310m,\text{f}}$ ) and are always found at higher elevations than females of the same size, but both sexes respond to vegetation changes in the same way (i.e.  $\beta^{A,\text{f}} \neq \beta^{A,\text{m}}$  and  $\beta^{A,N,\text{f}} = \beta^{A,N,\text{m}}$ ); (ii) males and females respond the same to altitude under average vegetation conditions, but one sex responds more strongly to changes in vegetation (i.e.  $\beta^{A,\text{f}} = \beta^{A,\text{m}}$  and  $\beta^{A,N,\text{f}} \neq \beta^{A,N,\text{m}}$ ); and (iii) there are sex based differences in the altitude of a given sized tortoise, and that the different sexes respond to vegetation in different ways (i.e.  $\beta^{A,\text{f}} \neq \beta^{A,\text{m}}$  and  $\beta^{A,N,\text{f}} \neq \beta^{A,N,\text{m}}$ ).

### Timing of migration

Initially, the impacts of body size on the timing of migration were analysed using a version of equation 4, with random effects for each individual where  $\mu_a$  or  $\mu_b$  was made a function of body size. However, these models did not converge using either the nlme function in R or a WinBugs version of the analysis. Therefore, a simpler analysis was carried out on crossing days calculated above using linear mixed models with individuals as a random effect.

## Results

### DO INDIVIDUAL GALAPAGOS TORTOISES MIGRATE SEASONALLY AS DEFINED BY EITHER DAILY MOVEMENTS OR NET DISPLACEMENT OVER THE COURSE OF A YEAR?

The movements of the 17 GPS-tagged tortoises were tracked for a minimum of 329 days and an average of 548 days per tortoise, from which strong qualitative evidence for seasonal altitudinal migration was found. The tortoises occurred at elevations between 6 and 423 m a.s.l. and covered linear distances of >10 km (Fig. 1). Fourteen of the tortoises ranged over more than 100 m in elevation and these individuals moved annually between highlands and lowlands characterized by relatively rapid long-distance movements up or down slope followed by extended sedentary periods in small upland or lowland ranges (Fig. 2).

The switch model was better supported by the daily movements of 10 of the 17 individuals than the single model (Table 1); yet for net displacement data, the migratory model was better supported than the home range model for all ten individuals analysed. Movements of five of the 10 individuals analysed using both methods supported the switch model over the single model, indicat-

ing little agreement between the two methods. Neither method of identifying migration seemed to be consistent with the results that might have been expected from a simpler definition of migration, such as a change in elevation of > 100 m within a year (Fig. 2).

### IS THE TIMING OF STAYS IN THE HIGHLANDS OR LOWLANDS CONSISTENT WITH THERMOREGULATORY-DRIVEN OR FORAGE-DRIVEN MIGRATION?

Weather station data confirmed strong opposing gradients in temperature and rainfall with altitude (Fig. 3a,b). Rainfall and vegetation cover in the lowlands were highly correlated – a peak NDVI occurs during heavy rains that recedes over subsequent months (Fig. 3b,c); however, in the highlands NDVI remains stable throughout the year (Fig. 3b) likely due to the persistent damp conditions. Maximum temperatures occur during the high-rainfall months of January to March, although highland temperatures throughout the year are consistently 2–2.5°C lower than lowland temperatures (Fig. 3a).

Comparison using BIC of models based on the monthly locations of the individually tagged tortoises strongly supported the hypothesis that lowland vegetation dynamics, and not upland temperatures, drive migration (Table 2). Moreover, while the sign of the beta in the vegetation

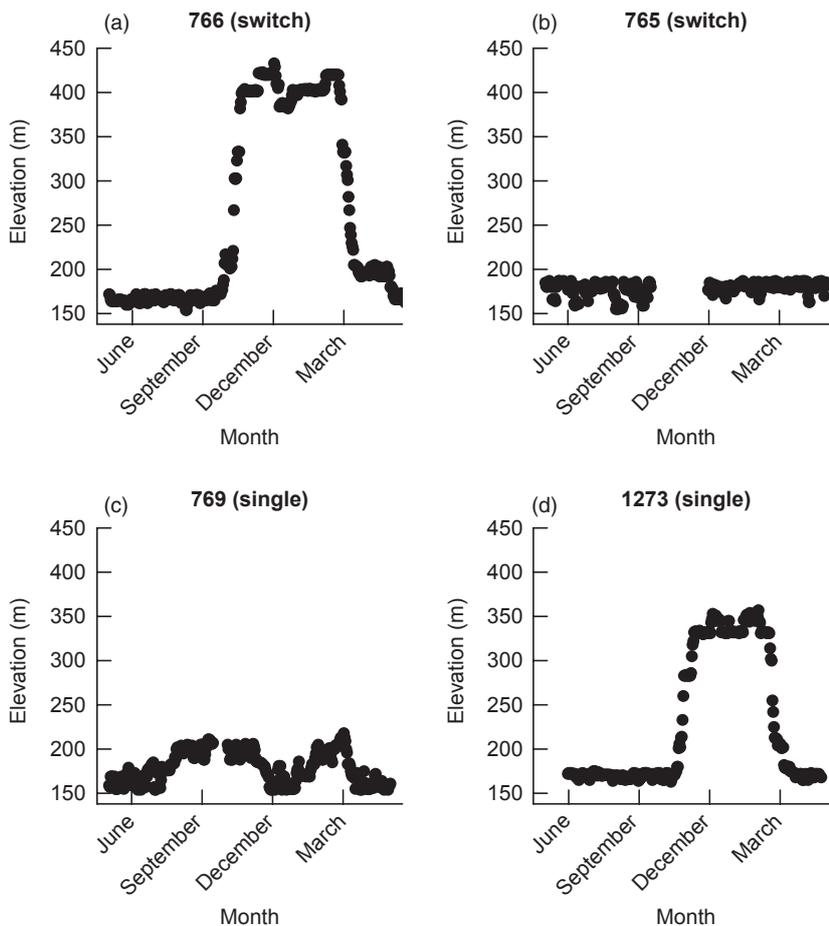


Fig. 2. Paths of four individuals all classified as migratory based on net altitudinal displacement. Titles indicate tag numbers of individuals (see Table 1), and whether the data better fit the switch or the single model based on daily displacement.

**Table 1.** Comparisons of models of Galapagos tortoise migration based on daily movements and net displacement. Delta Akaike Information Criterion (AIC) values are based on the two models in each set. Zeroes signify the model that is better supported by the data

Tag no.	Size (cm)	Sex	Date of tagging	Range in altitudes	Delta AIC			
					Models based on daily movement		Models based on net displacement	
					Single	Switch	Home range	Migratory
765	90.3	Female	27 April 2009	36	179	0	30	0
766	118.5	Male	29 April 2009	279	49	0	1518	0
767	89.5	Female	29 April 2009	144	5	0	–	–
769	109.5	Male	30 April 2009	66	0	104	152	0
770	100	Female	4 May 2009	196	0	18	–	–
771	151	Male	4 May 2009	197	39	0	–	–
774	105	Female	14 May 2009	315	147	0	947	0
775	142	Male	14 May 2009	267	34	0	992	0
1021	93	Female	9 December 2009	272	0	151	685	0
1022	150.2	Male	11 December 2009	279	0	35	799	0
1190	96.1	Female	24 February 2010	22	0	900	–	–
1191	129.6	Male	24 March 2010	265	0	343	1630	0
1273	113.8	Female	28 May 2010	194	0	15	1472	0
1274	126.8	Male	8 June 2010	171	73	0	1715	0
1396	139.2	Male	14 September 2010	303	73	0	–	–
1397	149.4	Male	15 September 2010	305	122	0	–	–
1403	145	Male	20 September 2010	277	56	0	–	–

dynamics model agreed with the *a priori* hypothesis that it would be negative, the sign of the beta in the temperature model did not agree with the prediction if that hypothesis were true. In other words, the temperature model showed that individuals are more common in the highlands during the coldest, not the warmest, time of year. Results from the analysis based on survey data were entirely consistent with the results from the individual analysis. The model based on lowland vegetation was supported by BIC comparison over the model based on temperature (Table 3). As in the individual analysis, the beta of interest ( $\beta^{A,N}$ ) was negative as expected under the forage-driven movement hypothesis, while ( $\beta^{A,T}$ ) was negative in contradiction of the expectation under the thermoregulatory-driven movement hypothesis.

#### HOW IS MIGRATION AFFECTED BY INDIVIDUAL TRAITS?

Migration was strongly size dependent, but not in the directions predicted based on prevailing migration theory. Of the 17 tagged individuals, the 10 largest individuals (carapace length >110 cm) all migrated, while smaller individuals did not. Monthly survey data also strongly supported the hypothesis that migration was size dependent (Fig. 4). Throughout the year, the minimum size of detected individuals gradually increased as elevation increased up to *c.* 200 m. Furthermore, juveniles were never found above 170 m and over 80% of juveniles were detected below 100 m (Fig. 4). The number of individuals detected above 300 m declined dramatically after March, the end of the rainy season and time of peak lowland

NDVI; however, a few large individuals were always found in the highlands throughout the year.

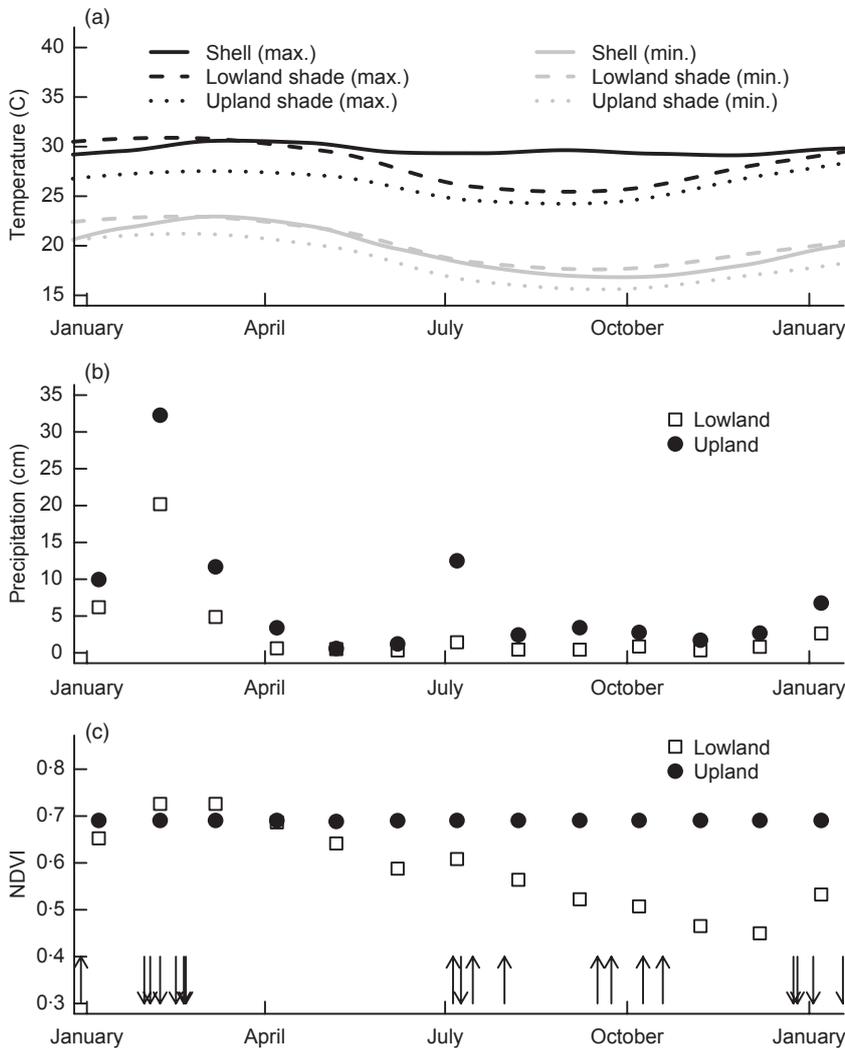
Trends in the average length of adult tortoises detected in the lowlands were consistent with those observed amongst the tagged individuals. From October to December the average length of an individual detected in the lowlands was *c.* 30 cm less than the average length from February to August (Fig. 5). Females detected during surveys were generally smaller and found at lower altitudes than males; however, the relationship between size and altitude was consistent for both males and females (Table 3). Furthermore, no evidence of sex-specific timing of migration was found in response to vegetation dynamics (Table 3).

The timing of migrations varied with tortoise body size; large individuals began their upward migration earlier than smaller individuals ( $P < 0.05$ ). The largest individuals began migrating upwards in July, three to four months after the peak in lowland NDVI and as temperatures were approaching their lowest values (Fig. 3), while many smaller adults waited until October to migrate upslope as lowland NDVI neared minimum values. The timing of downward migration, however, was not influenced by body size (NS; Table 4).

## Discussion

#### DO GALAPAGOS TORTOISES UNDERGO SEASONAL ALTITUDINAL MIGRATION?

Visual examination of movements by individual tortoises (Figs 1 and 2) suggests that at least some individuals (e.g.



**Fig. 3.** Temporal pattern of potential environmental drivers of tortoise migration in highlands and lowlands: (a) tortoises modulated their maximum daytime temperature (values obtained from temperature sensors in the GPS tags) by selecting sun vs. shade conditions (values obtained from iButtons located in the field), but were unable to modulate minimum night time temperatures, (b) patterns of precipitation in upland and lowland areas, (c) monthly change in Normalized Difference Vegetation Index in highlands and lowlands (arrows facing upwards indicate upward migrations of tagged individuals, while arrows facing down indicate downward migrations).

766 and 1273 in Fig. 2) are moving in a way that most observers would classify as migratory, for example, long linear displacements that started abruptly and were persistent and directed (Dingle & Drake 2007).

However, our quantitative analyses of movement data indicated a more complex pattern of movement. The net displacement model universally classified individuals as migratory (Table 1), even although a visual examination clearly suggests some individuals did not migrate (e.g. 765 and 769, Fig. 2). This approach may have failed to distinguish some individuals as non-migratory because the alternative model (the home range model) is inappropriate. The analysis based on daily movements was more discriminating, but also did not always agree with visual assessments (Fig. 2). The switch model was preferred in some individuals that did not appear to migrate (e.g. 765) presumably because patterns in the daily movements did not scale up to affect net altitudinal displacement. The single model was preferred in individuals (e.g. 1273) that appeared to migrate suggesting that there was sufficient variation in their displacement and turning angles during non-migratory phases such that migratory movements can

be more parsimoniously explained as outliers within a single joint distribution, as opposed to requiring a separate joint distribution.

The above assessment suggests that there are still difficulties in making quantitative definitions of migration operational. In this study, a simple *a posteriori* rule, such as individuals are migratory if the ranges of elevation over a year are >100 m, agreed with visual assessments. While such ad hoc rules are neither general nor satisfying, this rule or visual assessments rather than sophisticated quantitative models strongly indicates that adult Galapagos tortoises of both sexes from two separate taxa exhibit altitudinal seasonal migration.

#### IS MIGRATION FORAGE-DRIVEN OR THERMOREGULATION-DRIVEN?

Temperature is often the primary determinant of migration among terrestrial ectotherms (Southwood & Avens 2010); however, our data strongly suggest that tortoise migration was driven by lowland vegetation dynamics. By timing their migration to track the altitudinal changes in

**Table 2.** A comparison of two model of Galapagos tortoise migration based on movement data from 10 GPS-tagged adult tortoises, including both model comparison statistics and coefficient estimates. The hypothesis that the location of each individual (up or down) is determined by lowland vegetation dynamics is much better supported by the GPS data than a model based on the minimum temperature in the highlands [lower Bayesian Information Criterion (BIC) values]. In addition, while the sign of the estimate of  $\beta$  for the lowland vegetation dynamic is consistent with the *a priori* hypothesis, the sign of the estimate of  $\beta$  for the upland temperature model is not consistent with our expectation. (Values in Parentheses are standard errors). Normalized Difference Vegetation Index (V) and Temperature (T) were standardized to have mean of 0 and standard deviation of 1 so as the ease comparisons of their coefficients)

Migration hypothesis	BIC	$\beta_0$	$\beta$
Migration in response to lowland vegetation dynamics	178	0 (0.3)	-1.7 (0.2)
Migration in response to upland minimum temperature	198	0 (0.3)	-1.4 (0.2)

NDVI, tortoises migrated into the coldest altitudes, the highlands, at the coldest time, the dry season and contrary to the hypothesis of thermoregulation-driven migration. Migration into the lowlands during vegetation flush is consistent with the timing of migration in mammalian herbivores in montane, tundra and savannah biomes (Berger, Cain & Berger 2006; Hebblewhite, Merrill & McDermid 2008). Ungulate herbivores feed in areas that are 'greening up' (Bauer *et al.* 2011) because new herbaceous growth is low in structural carbohydrates and secondary compounds and high in protein, thus is both easier to digest and has higher nutritional value than older plant material (Hebblewhite, Merrill & McDermid 2008). Galapagos tortoise migration is also consistent with those of giant tortoises (*Aldabrachelys gigantea* Schweigger 1812) on Aldabra Atoll that migrate early in the wet season from inland to coastal areas to exploit new

grass sward (Gibson & Hamilton 1983). Thus, giant tortoises may have more in common with Serengeti wildebeest and other large terrestrial ungulates than with other migratory terrestrial reptiles.

#### MIGRATION BY SEX AND BODY SIZE

Interestingly, the largest individuals, regardless of sex, are those most likely to migrate. Smaller individuals never migrate out of the lowlands. This contradicts the prevailing hypotheses of partial migration, which suggest that smaller and subdominant individuals should be more prone to migrate than larger animals (Cagnacci *et al.* 2011; Chapman *et al.* 2011). Several *a posteriori* hypotheses may explain this observation. Larger tortoises may be more likely to migrate because, in general, both speed and efficiency increase with body mass (Peters 1983). Thus, the direct energetic cost (efficiency) and indirect cost (amount of time – speed) of migration may be prohibitively high for smaller-bodied tortoises. However, this hypothesis does not explain why larger individuals leave for the highlands earlier in the dry season or why all individuals return to the lowlands at approximately the same time. We can think of two possible explanations. First, cool temperatures, prolonged fine drizzle and overcast conditions may restrict small individuals from taking advantage of upland vegetation during the dry season (when large tortoises migrate into the highlands). Larger-bodied tortoises should be better able to maintain acceptable internal temperature under these conditions than small ones as thermal inertia increases with body mass (Spotila *et al.* 1973), and core temperature in large reptiles is higher than in small-bodied individuals (Seebacher, Grigg & Beard 1999).

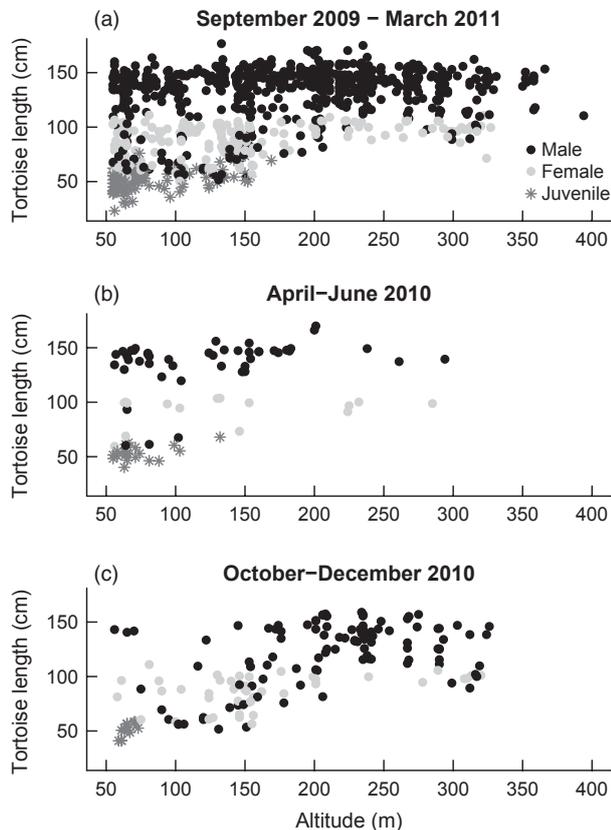
Secondly, larger individuals may be more sensitive to declining forage quality and quantity in the lowlands because of their higher absolute food requirements. Following peak NDVI values, declining size and quality of

**Table 3.** We used survey data to compare multiple models based on different hypotheses about the role of environmental drivers and sex in altitudinal migration patterns. Results are consistent with the hypothesis that lowland vegetation, and not upland temperature, is the driver of migration. While there is a systematic difference in size between males and females, both sexes respond similarly to altitude and Normalized Difference Vegetation Index (NDVI)

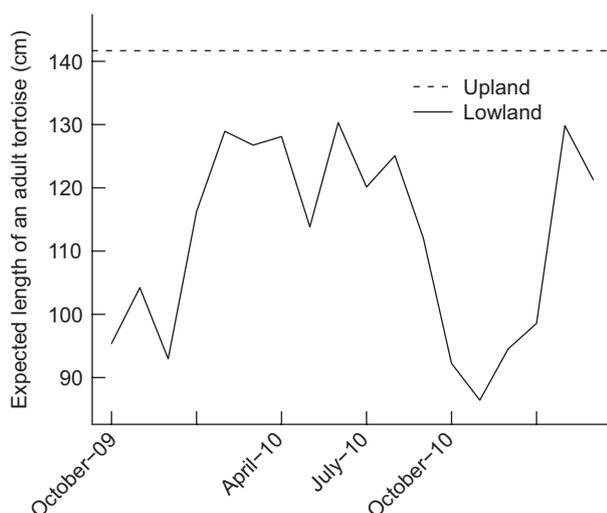
Environmental drivers	BIC	$\beta^{310m}$	$\mu^A$	$\beta^{A,N}$	$\beta^{A,T}$	$\sigma^A$
Migration driven by lowland vegetation dynamics	7259	141 (2)	0.24 (0.02)	-0.19 (0.03)	–	0.04
Migration driven by thermoregulation	7276	141 (2)	0.20 (0.04)	–	-0.11 (0.06)	0.08

Role of sex	BIC	$\beta^{310m}$		$\mu^A$		$\beta^{A,N}$		$\sigma^A$
		♀	♂	♀	♂	♀	♂	
Null model: no sex-specific relationship with altitude or response to vegetation	6882	103 (2)	144 (1)	0.13 (0.02)		-0.09 (0.03)		0.04
Sex-specific relationship with altitude	6895	102 (3)	144 (2)	0.13 (0.03)	0.14 (0.02)	-0.09 (0.03)		0.04
Sex-specific response to NDVI	6891	105 (3)	144 (2)	0.14 (0.02)		-0.05 (0.04)	-0.10 (0.03)	0.04
Both sex-specific relationship with altitude and response to vegetation	6900	102 (3)	145 (2)	0.10 (0.03)	0.16 (0.03)	-0.03 (0.04)	-0.12 (0.03)	0.04



**Fig. 4.** Summary of results of tortoise surveys along an elevation gradient over (a) 18 months, (b) three months at the end of rainy season and beginning of dry season and (c) three months at the end of the dry season.



**Fig. 5.** Change in the expected length of adult tortoises highlands at the upper and lower ends of the altitudinal gradient based on tortoise survey data.

lowland forage patches may limit food intake rates earlier in the dry season for large individuals than small ones, provoking migration to the more persistent vegetation cover of the highlands. If food quality declined while

**Table 4.** A model that used body size to predict the timing of migration was better than a null model in predicting upward migration, but performed worse than the null in predicting downward migration (For parameter estimates, values in parentheses are standard errors)

Upward migration	BIC	$\beta_0$	$\beta_{\text{size}}$
Null model	163.9	127 (15)	
Body size dependent	160.7	330 (90)	-1.7 (0.7)
Downward migration			
Null model	225.9	80 (20)	
Body size dependent	226.1	180 (80)	-0.9 (0.7)

BIC, Bayesian Information Criterion.

quantity remained high, large tortoises might be expected to remain in the lowlands as they have low metabolic costs per unit mass and can tolerate lower quality foods better than smaller individuals (Schmidt-Nielsen 1997). While we have no quantitative data on food availability, our qualitative observations indicate that lowland forage abundance declines to very low levels in the dry season likely rendering it intolerable for the largest tortoises to remain there. Moreover, the negative consequences of declining forage quantity and quality will be exacerbated by the energetic cost of high-metabolic rate imposed in the relatively warm lowlands and that cost will increase with body size. Larger tortoises should escape this cost by migrating to the cooler highlands sooner than small ones. We are currently exploring mathematical models to test these ideas.

#### MAINTAINING MIGRATION IN GALAPAGOS TORTOISES

Animal migrations are in global decline due to a suite of anthropogenic factors, including habitat loss and fragmentation, overexploitation, barrier creation and climate change (Wilcove 2008), the consequences of which can be catastrophic to migratory populations and ecosystem function (Berger 2004; Wilcove & Wikelski 2008; Harris *et al.* 2009; Holdo *et al.* 2011). Several Galapagos tortoise taxa have become extinct in recent centuries, and remaining taxa are at varying states of conservation concern (IUCN 2011). Disruption of tortoise migrations may have a serious negative impact on remaining populations and their role as ecosystem engineers (Blake *et al.* 2012).

Threats to altitudinal migration for Santa Cruz tortoises include habitat conversion, fencing, road building, urbanization and the spread of invasive species. Maintaining migrations in the face of human development is notoriously difficult (Berger 2004) and with a dramatically expanding local population and economy in Galapagos the threats to tortoise migration are likely to increase. Conservation efforts should include the promotion of 'tortoise friendly' fencing, preventing further fragmentation of habitats by roads and maintenance of movement corridors in areas heavily invaded by aggressive plant species. Applied research is needed to better understand the

dynamics of tortoise migration including identifying the extent of movements at the population level, and the interactions of environmental and physiological drivers of migration with climate change and anthropogenic modification of habitats, and subsequent ecosystem-level effects caused by changes in abundance and distribution of giant tortoises.

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## Supporting Information

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

**Data S1.** Winbugs code for latent state model.