

# Allometric and temporal scaling of movement characteristics in Galapagos tortoises

Guillaume Bastille-Rousseau<sup>1,2\*</sup>, Charles B. Yackulic<sup>3</sup>, Jacqueline L. Frair<sup>1,2</sup>, Freddy Cabrera<sup>4</sup> and Stephen Blake<sup>1,4,5,6,7</sup>

<sup>1</sup>Department of Environmental and Forest Biology, College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA; <sup>2</sup>Roosevelt Wild Life Station, College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA; <sup>3</sup>U.S. Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and Research Center, Flagstaff, AZ 86001, USA; <sup>4</sup>Charles Darwin Foundation, Puerto Ayora, Isla Santa Cruz, Galápagos, Ecuador; <sup>5</sup>Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, D-78315, Radolfzell, Germany; <sup>6</sup>Whitney Harris World Ecology Center, University of Missouri-St. Louis, St. Louis, MO 63121, USA; and <sup>7</sup>Department of Biology, Washington University, St. Louis, MO 63130, USA

## Summary

1. Understanding how individual movement scales with body size is of fundamental importance in predicting ecological relationships for diverse species. One-dimensional movement metrics scale consistently with body size yet vary over different temporal scales. Knowing how temporal scale influences the relationship between animal body size and movement would better inform hypotheses about the efficiency of foraging behaviour, the ontogeny of energy budgets, and numerous life-history trade-offs.

2. We investigated how the temporal scaling of allometric patterns in movement varies over the course of a year, specifically during periods of motivated (directional and fast movement) and unmotivated (stationary and tortuous movement) behaviour. We focused on a recently diverged group of species that displays wide variation in movement behaviour – giant Galapagos tortoises (*Chelonoidis* spp.) – to test how movement metrics estimated on a monthly basis scaled with body size.

3. We used state-space modelling to estimate seven different movement metrics of Galapagos tortoises. We used log-log regression of the power law to evaluate allometric scaling for these movement metrics and contrasted relationships by species and sex.

4. Allometric scaling of movement was more apparent during motivated periods of movement. During this period, allometry was revealed at multiple temporal intervals (hourly, daily and monthly), with values observed at daily and monthly intervals corresponding most closely to the expected one-fourth scaling coefficient, albeit with wide credible intervals. We further detected differences in the magnitude of scaling among taxa uncoupled from observed differences in the temporal structuring of their movement rates.

5. Our results indicate that the definition of temporal scales is fundamental to the detection of allometry of movement and should be given more attention in movement studies. Our approach not only provides new conceptual insights into temporal attributes in one-dimensional scaling of movement, but also generates valuable insights into the movement ecology of iconic yet poorly understood Galapagos giant tortoises.

**Key-words:** *Chelonoidis* spp., correlated random walk, directional persistence, displacement, ectotherm, giant tortoise, interval, movement, temporal scale

## Introduction

Ecologists have long been interested in how biological processes, especially metabolic rates, vary with organism

size (Schmidt-Nielsen 1984; Brown & West 2000). Many life-history traits correlate closely with adult body size, scaling allometrically as:  $Y = cM^z$  where  $Y$  is the trait of interest,  $c$  is a taxon- and mass-specific normalization constant,  $M$  is adult body size, and  $z$  is a scaling exponent (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; McNab

\*Correspondence author. E-mail: gbastill@esf.edu

2002; Brown *et al.* 2004). Scaling estimates vary from approximately  $z \approx 3/4$  for whole-organism metabolic rates,  $z \approx 1/4$  for biological times including duration of pregnancy and life span and  $z \approx -1/4$  for biological rates such as rate of offspring production and population growth (Hamilton *et al.* 2011). Given that metabolic rates and consequently energy needs increase with body size, larger animals must generally move over larger areas in search of the resources necessary to meet their higher energetic requirements (Jetz *et al.* 2004). Allometric scaling of home-range size, in terms of the habitat volume or area used by an individual, has been much studied and generally leads to predictable interspecific comparisons (Lindstedt, Miller & Buskirk 1986; Kelt & Van Vuren 2001; Haskell, Ritchie & Olf 2002; Pearce *et al.* 2013; Tamburello, Côté & Dulvy 2015; Slavenko *et al.* 2016), but one-dimensional movement metrics such as movement rate seem to more consistently scale with body size (e.g. Garland 1983; Carbone *et al.* 2005). For terrestrial mammals, both average daily movement rates (Carbone *et al.* 2005) and maximum migration distances (Hein, Hou & Gillooly 2012; Teitelbaum *et al.* 2015) scale predictably with body mass, with the latter having a similar albeit slightly higher power exponent.

Understanding how ecological processes, such as the net displacement of an individual over time, scales with body size is of increasing interest to ecologists (Morales & Ellner 2002; Yackulic *et al.* 2011); yet, to our knowledge few studies have explicitly considered how temporal scale (being the temporal extent or the period over which movement is measured) influences allometric relationships (but see Schaefer & Mahoney 2003). Quantifying how temporal scale influences the relationship between animal body size and behaviour is central in animal ecology because it informs hypotheses on the efficiency of foraging behaviour, relationships between food distribution and food acquisition behaviour, the ontogeny of energy budgets and numerous life-history trade-offs (e.g. Fortin *et al.* 2003; Woodward *et al.* 2005; Eckert *et al.* 2008). Moreover, there is reason to believe that allometric relationships could either strengthen or weaken as larger temporal intervals are considered. For example, allometric relationships might weaken with increasing temporal interval if smaller individuals are able to compensate for their slower speeds by remaining active for longer periods. In contrast, larger individuals not only move more quickly than smaller animals over short time periods but also are capable of sustaining movement over longer time periods and may be able to move in less tortuous paths both because of their increased perceptual range (Mech & Zollner 2002), and their ability to navigate through obstacles that smaller individuals might be forced to move around. Thus, scaling in activity duration and directional persistence of animals are important links in one-dimensional scaling of movement behaviour across different temporal intervals (Turchin 1996).

The temporal scaling of displacement and the allometry of movement may be strongly influenced by individual behavioural states. Some species can display temporally heterogeneous movement strategies driven by environmental variability or life-history trade-offs (Ovaskainen *et al.* 2008; Mueller *et al.* 2011), shifting between 'motivated' periods (e.g. higher movement rate and activity level) and more sedentary states (Benhamou 2013). Animals that display migratory behaviour are prime examples, where periods of rapid and directed movement towards a targeted area are punctuated by longer periods of more stationary, more tortuous movements associated with some other behaviour (e.g. foraging and reproduction; Morales *et al.* 2004; Bunnefeld *et al.* 2011; Singh *et al.* 2012; Beyer *et al.* 2013). Investigating the relationships between body size and animal use of space across taxa requires integration of body size, movement heterogeneity, behaviour and the temporal resolution of movement sampling.

Here, we investigate how the temporal scaling of allometric patterns in movement varies over the course of a year and during periods of motivated (directional and fast speed) and unmotivated (tortuous and low speed) behaviour (Benhamou 2013). We focus on a recently diverged group of species, giant Galapagos tortoises (*Chelonoidis* spp.), that display wide variation in movement behaviour and which are well suited to this line of enquiry for several reasons. First, as ectotherms, the activity patterns of giant tortoises are more susceptible to environmental variation than endotherms, which has direct consequences on the variability of movement patterns. Secondly, radiation of genetically and morphologically distinct tortoise species on different islands (Caccone *et al.* 2002), each having unique environmental and biophysical properties (Snell, Stone & Howard 1996), has led to the presence of different movement strategies. These strategies range from sedentary individuals having stable range of limited size to typical migratory individuals travelling over 10 km of linear displacement on an annual basis (Blake *et al.* 2013). Thirdly, giant tortoise body mass can range by up to four orders of magnitude within a species and earlier work has shown that bigger tortoises within the same species were more likely to migrate and have more extensive movement relative to smaller individuals (Blake *et al.* 2013). As a result, giant tortoises provide a model system for exploring allometric relationships both within and among species while controlling for large differences in geography and life-history strategies. Finally, allometric relationships are different between endotherms and ectotherms (Gillooly *et al.* 2001; White, Cassey & Blackburn 2007); yet previous studies of movement allometry have been heavily biased towards mammals (e.g. Carbone *et al.* 2005; Vieira & De Almeida Cunha 2008; but see Tamburello, Côté & Dulvy 2015; Slavenko *et al.* 2016); therefore, elucidating allometric scaling relationships among Galapagos tortoises could potentially have important implications for a broader taxonomic range.

We focus on three basic questions. First, can allometric scaling be detected in Galapagos tortoise movements and, if so, how consistent is the scaling across sexes and taxa? Secondly, what temporal interval (hourly, daily and monthly) and period (motivated vs. not-motivated) best reveals allometric scaling in tortoise movements? Finally, can detected differences be attributed to the temporal structuring of movement metrics? To answer these questions, we fit state-space models to hourly and daily displacement of giant tortoises to examine how monthly movement rates vary by taxa, sex and body size. We predicted that allometric scaling for displacement would be most obvious (higher scaling coefficient) during periods when individuals were motivated to move. We also predicted similar scaling parameters among taxa, but expected to observe temporal variation among taxa in allometric scaling due to regional variation in environmental conditions and migratory behaviour. Our approach and system not only provide new conceptual insights into temporal influences on one-dimensional scaling of movement, but also generate valuable new information on the movement ecology of iconic yet poorly understood giant Galapagos tortoises.

## Materials and methods

Galapagos tortoises occur across the archipelago in 11 recognized species, each of which can be associated to one of two main morphotypes (Caccone *et al.* 2002; Poulakakis *et al.* 2015). Our design sampled tortoise movements over the range of environmental conditions they occupy, from arid lowlands to humid upland habitats, and included both tortoise morphotypes: 'saddlebacks' (with elevated frontal portions of the carapace which occur on arid low-lying islands) and 'domes' (the carapaces of which extend low over the head, and which occur on islands with humid highlands; Fritts 1983). Given the nature of the environment where they are found, saddleback tortoises are generally smaller than the domed morphotype, displaying limited movement during most of the year combined with a few exploratory trips (Gibbs *et al.* 2014; Bastille-Rousseau *et al.* 2016a). Domed tortoises, on the other hand, display larger movement, including migration (Blake *et al.* 2013). Earlier work has shown that vegetation quality is a key determinant of migration, although future work is required to test whether this is consistent across taxa (Blake *et al.* 2013). We attached custom-made GPS tags (e-obs, Munich, Germany) to 50 adult tortoises (four species on three different islands) and monitored them from 2009 to 2012 (Fig. 1). This sample comprised 11 saddleback individuals (five females, six males, 104 194 locations) on the relatively flat and arid Espanola Island (*Chelonoidis hoodensis*), 11 domed individuals (six females, five males, 143 129 locations) on Alcedo volcano on Isabela Island (*Chelonoidis vandenburghi*) and 28 domed individuals on Santa Cruz Island: 13 (seven females, six males, 128 462 locations) from eastern Santa Cruz (*Chelonoidis donfaustoi*) locally called 'Cerro Fatal' and 15 (eight females, seven males, 135 836 locations) from western Santa Cruz (*Chelonoidis porteri*) in 'La Reserva' (Russello *et al.* 2005; Poulakakis *et al.* 2015). Tortoises on Santa Cruz and Isabela islands were exposed to greater temporal differences in vegetation abundance along altitudinal and longitudinal gradients than tortoises on the

topographically less variable Espanola Island (Trueman & D'Ozouville 2010).

Giant tortoises are largely immobile at night (S. Blake, unpublished data), so GPS units were programmed to record locations every hour during the day (6 am–7 pm) to maximize battery life. Since tortoises move slowly, hourly locations should be sufficient to obtain unbiased movement estimates (Marcus Rowcliffe *et al.* 2012). Locations acquired at a finer temporal resolution would not have been beneficial given the precision of the GPS tags deployed relative to movement of tortoises [13 m in closed habitat (>50% canopy closure,  $n = 709$  locations, three tags), 7 m in open habitat (<50% canopy closure,  $n = 1221$  locations, three tags), G. Bastille-Rousseau, unpublished]. All tagged tortoises were monitored for at least one year. When tags were attached, the size (curved carapace length) and sex of the individual was recorded. All animal handling procedures followed guidelines of the Galapagos National Park Service, the Max Planck Institute for Ornithology and IACUC protocol #121202 of the State University of New York, College of Environmental Science and Forestry.

## MASS CALCULATION

Mass is the general proxy of animal body size used for investigating allometric scaling of movement (e.g. Garland 1983; Carbone *et al.* 2005). However, mass was not recorded for our tagged tortoises. Therefore, we first developed a predictive relationship for tortoise mass from curved carapace length using a data set of tortoise observations collected from each island during routine population surveys by the Galapagos National Park Service and Charles Darwin Foundation between 1962 and 2006 that yielded for this analysis 7420 observations across our three islands.

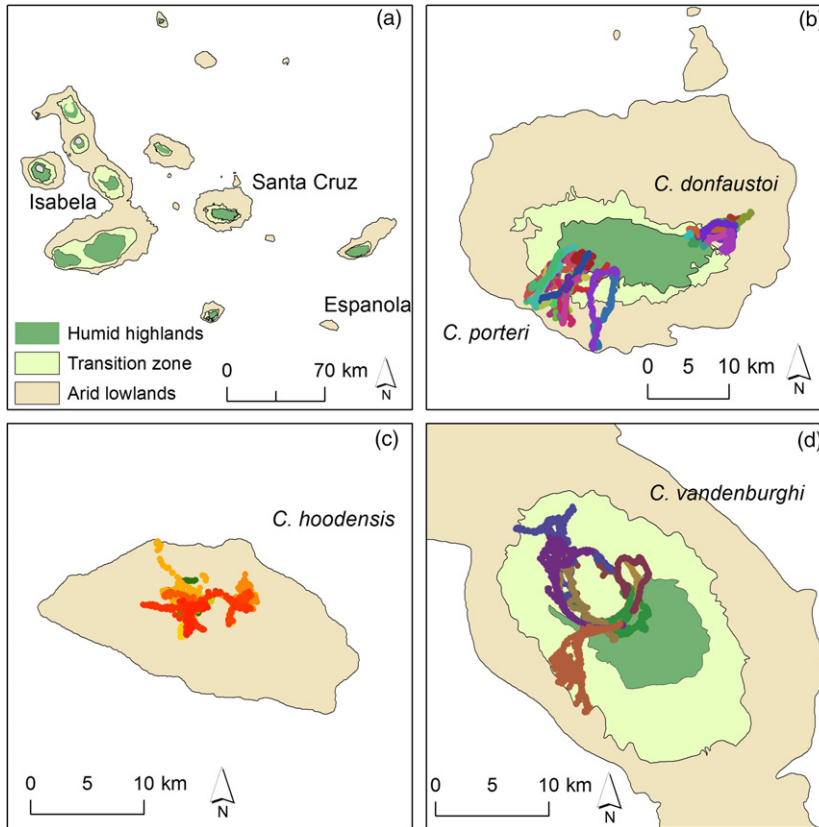
We used log-log regression of the power formula,  $Y = cM^z$ , to evaluate the relationship between curved carapace length  $Y$  and mass  $M$ . We first tested if the relationship was similar among islands (each island has a specific tortoise morphotype), and then between males and females, by creating different linear models by adding categorical interactions (i.e. ANCOVA) for island and sex with tortoise mass. We used the second-order Akaike Information Criteria (AIC<sub>c</sub>; Burnham & Anderson 2002) to test which model provided the most parsimonious fit and used the best model to predict the mass of GPS tagged tortoises.

## MOVEMENT MODELLING AND ASSOCIATED METRICS

We used a state-space approach to account for position uncertainty from GPS tags and discriminate whether a tortoise has moved or not, and modelled movement as a correlated random walk (Patterson *et al.* 2008). Correlated random walk models include statistical distributions that describe turn angles (the angle created by three successive hourly locations) and step lengths (the Euclidean distance between two consecutive hourly locations). We modelled turn angles using the wrapped Cauchy distribution, which takes the form:

$$C(\theta|\psi, \rho) = \frac{1 - \rho^2}{2\pi(1 + \rho^2 - 2\rho \cos(\theta - \psi))},$$

where  $\theta$  is the step orientation in the previous step,  $\psi$  is the predicted step orientation in the current step, the difference between  $\theta$  and  $\psi$  is the turning angle centred on zero, and  $\rho$  is a measure



**Fig. 1.** Population ranges of 50 giant tortoises of four different taxa inhabiting the Galapagos islands, 2009–2012. (a) The Galapagos Archipelago, illustrating vegetation zones; (b) Santa Cruz Island, including tortoise tracks and the Cerro Fatal (*Chelonoidis donfaustoi*) and La Reserva (*Chelonoidis porteri*) regions; (c) Tortoise tracks on Espanola Island (*Chelonoidis hoodensis*); (d) Tortoise tracks on Alcedo Volcano (*Chelonoidis vandenburghi*).

of the movement concentration around the expectation and is a measure of directional persistence. The mean turning angle is zero, and  $\rho$  is bounded between zero (indicating no correlation in the direction moved between two successive turn angles) and one (Morales *et al.* 2004). Because Galapagos tortoises sometimes spend many hours in the same location, we modelled hourly step lengths using a zero-inflated log-normal distribution where the probability of a nonzero value was defined as the probability of movement ( $P$ ):

$$L(x|\mu, \tau) = \sqrt{\frac{\tau}{2\pi}} \frac{1}{x} e^{(-\frac{1}{2\tau}(\log x - \mu)^2)} * A,$$

where  $\mu$  and  $\tau$  represent the mean and precision, respectively,  $x$  represents the step length, and  $A$  is an indicator function taking values of zero or one.  $A$  follows a Bernoulli distribution of the form:

$$A(k|P) = P^k (1 - P)^{1-k}$$

where  $P$  is the probability of movement, and  $k$  is a variable taking values of one or zero. We used the dilution of precision (DOP) metric provided by the GPS tags to derive a prior for location precision (correlation between DOP and estimated precision of tags from stationary test:  $R = 0.53$ , G. Bastille-Rousseau, unpublished). We modelled movement from 7 am to 6 pm hours only, as locations were only acquired during the day. Data were subset for each month and individual (we explain later how we handled repeated measures) and analysed independently both for computational reasons and because it allowed us to address a number of different questions through meta-regression.

We calculated seven different movement metrics to test for the presence of allometric scaling in tortoise movement. Metrics included directional persistence (mean turning angle), probability of movement (bA) and mean hourly displacement (estimated directly from the state-space model) as well as maximum hourly displacement, mean and maximum daily displacement, and total monthly displacement (quantities derived from the observed displacement). Monthly value estimates and their associated standard errors were used to test for the presence of allometric relationships in movement (see next section). Models ran for 8000 iterations using three chains. Movement metrics estimations and meta-regression models (see below) were fitted using Winbugs 1.4 (Lunn *et al.* 2000). The codes, including priors, are presented in Appendix S2 (Supporting information).

#### ALLOMETRIC RELATIONSHIPS

We tested for the relevance of allometric scaling to tortoise movement using the seven movement metrics estimated previously. Power-law regression has a long tradition in allometric scaling studies (Brown & West 2000), and we used a weighted power-law meta-regression of the form  $Y = cX^z$  in a Bayesian framework. We regressed the natural logarithm of the estimated mass of a tortoise with the natural logarithm of the monthly value of each estimated movement metric for each tortoise:

$$\log(Y_i) = \alpha + \beta \log(M_i) + \varepsilon + \tau,$$

where  $Y_i$  and  $M_i$  are the movement metric and mass, respectively, for individual  $i$ ,  $\alpha$  is the intercept,  $\beta$  is the slope (and equivalent to the scaling coefficient  $z$ ),  $\varepsilon$  represents a normally distributed



error term for interindividual variation, and  $\tau$  is a second normally distributed error term associated with the precision of the movement metric. It would have been possible to add a prior characterizing the precision of the estimated mass, but we decided not to do so to facilitate convergence given all predicted masses had small and constant uncertainties. To facilitate convergence, we centred  $\log(M_i)$  around zero. This did not change the scaling  $\beta$ , only the interpretation of the intercept  $\alpha$  to the expectation for an average tortoise size. To account for repeated measures, we retained one monthly value only per individual for a given movement metric  $Y$ . We used the median or maximum value of the overall range of the movement metric across all months in the study for each individual and therefore ran two series of regressions.

The maximum value should reflect when individuals are 'motivated', exhibiting movement rates close to their upper capabilities within a given temporal interval. These motivated periods could be associated to exploratory trips for sedentary individuals or the migratory journey for individuals displaying this behaviour. This means that the maximum and median values could come from a different month for different individuals. We weighted each monthly movement value using its associated standard error, which downweighted values having high variability within that month. This yielded 14 different models – seven each based on median vs. maximum values – enabling a robust comparison of how allometric relationships vary based on the temporal interval and period under investigation.

To evaluate differences between sexes or among taxa, we expanded the previous model to integrate the calculation of multiple intercepts and slopes:

$$\log(Y_{ip}) = \alpha_p + \beta_p \log(M_i) + \varepsilon + \tau,$$

where  $p$  represents sex, taxa or a combination of both. This resulted in a total of four different model structures that we ran for each series of values (median or max. values) and for each of our seven movement metrics, giving a total of 56 individual models. Models ran for 3 000 000 iterations using three chains, with convergence achieved at  $\hat{R} < 1.1$ . We used the Deviance information criteria (DIC; Spiegelhalter *et al.* 2002) to test whether covariates for sex or taxon improved model fit.

#### TAXON-SPECIFIC MOVEMENT METRICS

We estimated monthly variation in each movement metric among the four taxa of tortoises by fitting a power-law meta-regression of the natural logarithm of the estimated mass of a tortoise with the natural logarithm of the monthly value of each movement metric, but with different intercepts for each month and taxon. Following previous notation, the model took the form:

$$\log(Y_{ipm}) = \alpha_{pm} + \beta_p \log(M_i) + \varepsilon + \tau,$$

where  $p$  represented one of the taxa and  $m$  represented a given month. The normally distributed error term  $\varepsilon$  accounts for interindividual variation while the multiple intercepts account for the repeated structure of the analysis akin to the addition of a random intercept in a multilevel/mixed model (Gelman & Hill 2006). The structure of this model required us to keep all monthly data rather than focusing on the median and maximum individual values. Comparing the monthly intercept  $\alpha$  estimates

among the different taxa enabled us to analyse differences in movement rates at the taxon level, independent of the specific set of tortoise masses tracked in each taxon. Models ran for 10 000 000 iterations using three chains and achieved convergence.

## Results

Curved carapace length was a strong predictor of tortoise mass. The most parsimonious model indicated a slightly different relationship between curved carapace length and tortoise mass by island, as well as between males and females on each island (AICc weight >0.99). Fitting the models by island revealed strong predictive relationships ( $R^2 = 0.86\text{--}0.96$ ) with increasing values of the scaling exponent from Santa Cruz to Espanola to Alcedo (Fig. S1, Supporting information). For a male tortoise having a curved carapace length of 80 cm, our models predicted mass at 42.72 kg for *C. vandenburghi*, 46.72 kg for *C. hoodensis* and 43.58 kg for *C. donfaustoi* and *C. porteri*. An 80 cm female was predicted to weigh 42.93, 45.34 and 48.71 kg for *C. vandenburghi*, *C. hoodensis*, and *C. donfaustoi* and *C. porteri*, respectively. Masses predicted for tagged tortoises ranged from 70 to 218 kg for *C. vandenburghi*, 26–75 kg for *C. hoodensis*, 67–200 kg for *C. porteri* and 66–281 kg for *C. donfaustoi*.

#### ALLOMETRIC SCALING

The single model (no taxon or sex effects) performed as well or better than models including taxon, sex or both for the majority of movement metrics, whether based on the median or maximum movement values (Table 1). We therefore focus the interpretation of the results based on this model. However, notable differences were observed among taxa for directional persistence (based on median and maximum movement values), maximum hourly displacement (based on median values), probability of movement (based on maximum values) and mean hourly displacement (based on maximum values; Table 1). In these instances, the taxon-specific model offered a better fit providing some evidence that allometric relationships differ among taxa.

Important allometric relationships were identified for the majority of models (five of seven) based on maximum values of movement metrics, but only for a minority (three of seven) when based on median values (Fig. 2). For models based on maximum movement metrics, only probability of movement and hourly directional persistence failed to show a relationship with tortoise mass. With the exception of these variables, models based on maximum values consistently produced equivalent or larger scaling parameters relative to the median values, indicating that scaling is more pronounced when animals are motivated to move (Figs 2 and 3). Whether using median or maximum movement values, scaling parameters for mean daily movement rates and total monthly

**Table 1.** Deviance information criteria (DIC) for alternative allometric scaling models for giant Galapagos tortoises, 2009–2012. For each of seven movement metrics (described in the methods), models included either a single intercept and slope (single), different intercepts and slopes by either taxon or sex, or different intercepts and slopes for both taxon and sex. Models were fit separately using individual median or maximum values for each movement metric

	Prob. Movement	Direct. Persist.	Mean hourly	Max. hourly	Mean daily	Max. daily	Total monthly
Median values							
Single	–40.715	–7.213	–19.595	–77.050	–209.558	–188.342	–209.461
Taxon	–39.102	<b>–18.035</b>	–19.006	<b>–80.934</b>	–209.420	–189.269	–209.369
Sex	–39.689	–7.830	–19.806	<b>–78.572</b>	–208.877	–189.014	–209.516
Taxon, sex	–38.178	<b>–12.643</b>	–18.121	<b>–79.209</b>	–209.117	–189.735	–209.474
Maximum values							
Single	–64.105	–58.143	–35.264	–64.122	–254.144	–251.406	–251.295
Taxon	<b>–70.306</b>	<b>–76.636</b>	<b>–38.293</b>	–65.409	–254.126	–251.060	–251.579
Sex	–65.582	<b>–66.501</b>	–34.234	–63.929	–252.559	–250.602	–252.577
Taxon, sex	–64.328	<b>–69.000</b>	–37.993	–66.317	–253.174	–250.922	–250.896

Bolded values indicate where a more complex model fit considerably better than the null model. Lower DIC values indicate better fit.

displacement were higher than for mean hourly displacement, indicating these two parameters to be the most reliable metrics for allometric scaling.

Allometric models fitted to each of the four taxa, based on the maximum movement values only, showed that *C. donfaustoi* and *C. hoodensis* have scaling parameters different from zero for four movement metrics (mean hourly, mean daily, max. daily and total monthly displacement; Fig. 2). In contrast, *C. porteri* tortoises demonstrated positive scaling parameters for only two metrics (mean and max. hourly displacement), while *C. vandenburghi* displayed none at all (Figs 2 and 3). Models based on the median movement values yielded no clear positive scaling parameters for either *C. porteri* or *C. vandenburghi* (Figs 2 and 3). Results for models based on sex or combination of sex and taxon revealed few allometric relationships (Table S1, Appendix S1).

#### TEMPORAL VARIATION IN MOVEMENT METRICS

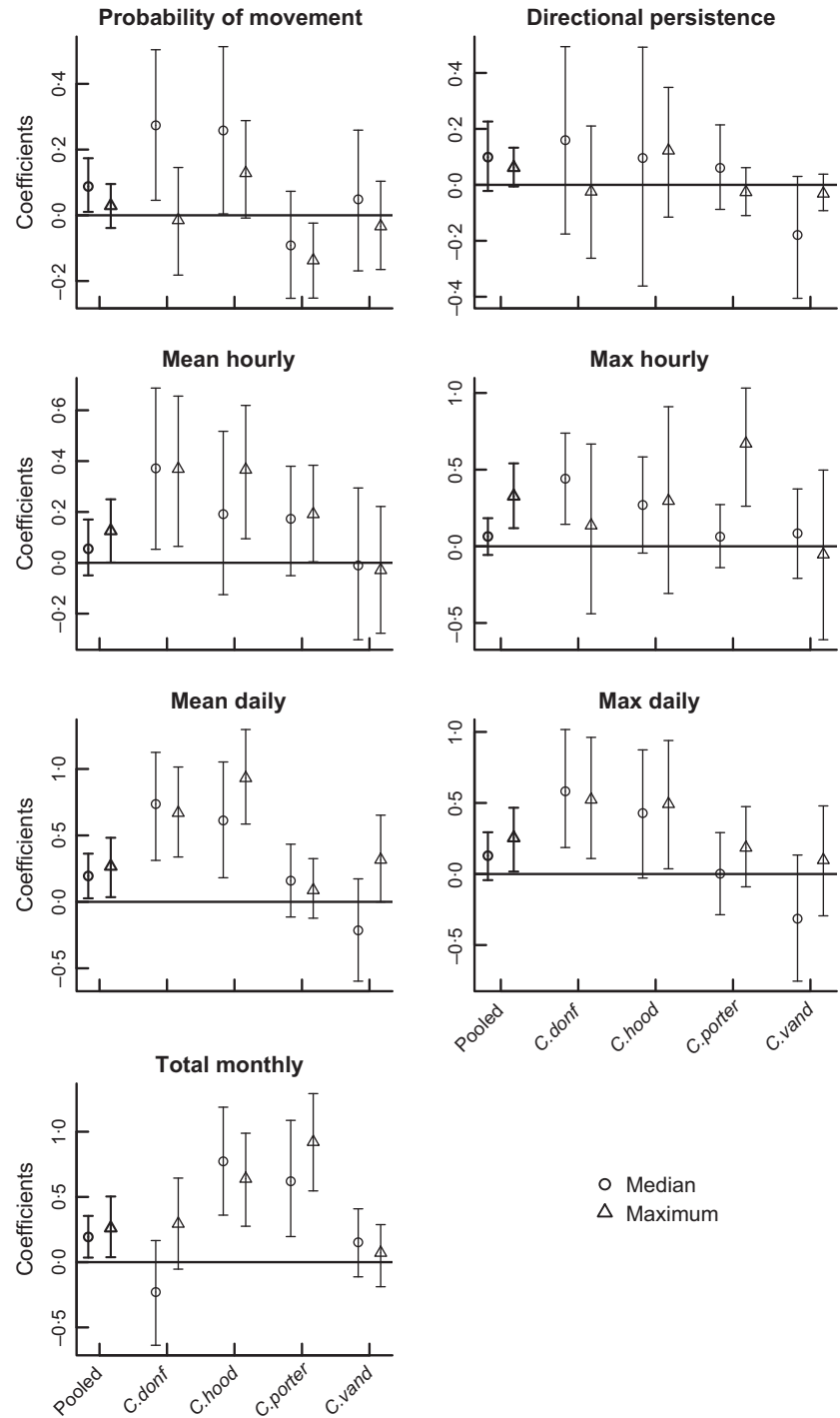
Periodicity was apparent in movement patterns across the annual period, but patterns differed among taxa (Fig. 4). *Chelonoidis vandenburghi* showed strong temporal patterns, with high values in January and June, depending upon the movement metric, and low values during the latter part of the year for all metrics. Striking differences were observed regarding probability of movement, which peaked in February for all but one taxon. *Chelonoidis porteri* exhibited no clear temporal variation for all movement metrics. *Chelonoidis donfaustoi* and *C. hoodensis* displayed smaller variation relative to *C. vandenburghi* tortoises in most movement metrics. All movement metrics other than probability of movement peaked in June and were lowest between October and December for *C. hoodensis*. Probability of movement peaked in April and then declined throughout the rest of the year for *C. hoodensis*. Most movement metrics for *C. donfaustoi* peaked in February and again between June and August. Like *C. vandenburghi*, the probability of movement of *C. porteri* was inconsistent with other metrics, displaying

highest values in January and December. Movement metrics with their confidence interval are presented in Fig. S2 in Appendix S1.

#### Discussion

We provide the first evidence of allometric scaling of movement for different species of a large terrestrial herbivorous ectothermic species – giant Galapagos tortoises. We found that scaling was more pronounced during periods of higher movement rates (i.e. when animals were motivated to move) and for movement metrics integrated over daily and monthly time-scales. We further observed differences in the magnitude of scaling among taxa that did not directly reflect differences in the temporal variation in their movement rates. Overall, our work provided insights into how subjectively defined temporal intervals or period, and pooling across different populations having potential different factors motivating their movements, can affect the evaluation of movement scaling.

In general, models pooled across taxa offered a similar fit, explaining a similar amount of information, as taxon-specific models. This is consistent with an abundance of studies showing allometric relationships to be generalizable among species (Kelt & Van Vuren 2001; Carbone *et al.* 2005), but also that *Chelonoidis* radiation in Galapagos is relatively recent. For most movement metrics (e.g. hourly distance, daily distance, monthly distance), we detected scaling using monthly maximum values. However, scaling between body mass and the probability of movement was only present using the median values. This indicates that heavier individuals generally moved more, but that all individuals had the potential to reach similar movement levels over a month when motivated to do so. Nevertheless, despite not showing scaling on their own, probability of movement and directional persistence played an important role during the motivated period as they contributed to higher coefficients for daily scale metrics relative to hourly metrics. In contrast, scaling coefficients for daily and monthly values were very similar.

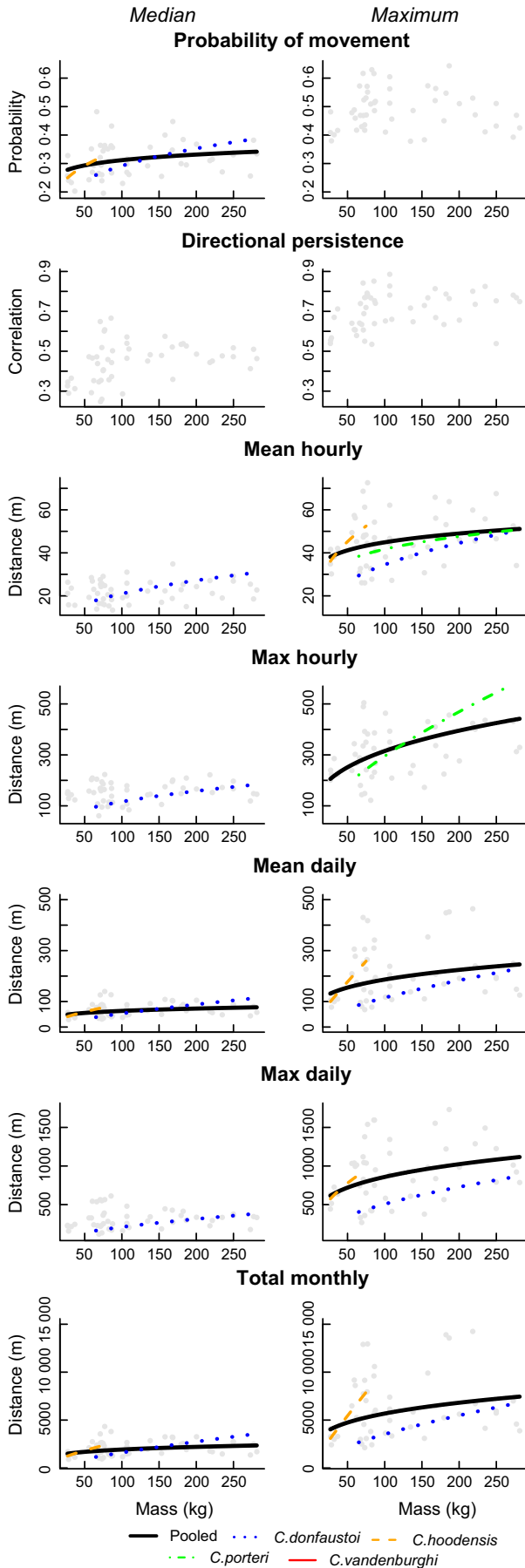


**Fig. 2.** Scaling coefficients for seven movement metrics of 50 individuals of four taxa of giant tortoises inhabiting the Galapagos islands, 2009–2012. Coefficients were estimated using a weighted log-log regression analysis of the form:  $\log(Y_i) = \alpha_p + \beta_p \log(M_i)$  where  $Y$  was one of the seven movement metrics, and  $\alpha$  and  $\beta$  were estimated with all individuals pooled and separately for each taxon (*Chelonoidis donfaustoi*, *Chelonoidis hoodensis*, *Chelonoidis porteri* and *Chelonoidis vandenburghi*). Scaling coefficients ( $\beta$ ) are presented with their 95% credible intervals. Full results of the models are given in the Supporting Information.

This suggests that autocorrelation in movement involving probability of movement and directional persistence was strong at the daily scale with its magnitude decreasing at higher temporal resolutions.

Not unexpectedly, our analysis also revealed that scaling of movement relationships may be different among different taxa for some movement metrics, most especially regarding directional persistence which may be influenced by landscape configuration. Evidence of taxon-level scaling was not as strong for other movement metrics. Scaling was most consistently detected in two taxa, *C. donfaustoi*

and *C. hoodensis*, which are exposed to markedly different environments (Trueman & D'Ozouville 2010). For *C. porteri* and *C. vandenburghi*, most variables qualitatively showed scaling, but not to the same magnitude as for other taxa. This is difficult to explain because stronger scaling could have been expected for taxa displaying longer migratory movements. One potential explanation is that *C. donfaustoi* and *C. hoodensis* are overall experiencing lower resource densities and are required to search farther to collect enough food, particularly for bigger individuals having higher energetic needs (Haskell, Ritchie



**Fig. 3.** Allometric scaling in seven movement metrics of 50 giant tortoises of four different taxa inhabiting the Galapagos islands, 2009–2012. Relationships were estimated using median (left panels) individual values and maximum (right panels) individual values for each metric. Best fit lines were added where a relationship (95% credible intervals excluding zero) was detected. Lines are drawn within the range of a taxon estimated tortoise masses.

& Olf 2002). Following Carbone *et al.* (2005) who observed that variation in diet and habitat types explained most of the variation in the magnitude of day range scaling in mammals, our results are likely an indication of small variation in the energetic budget of each taxon of tortoises emerging from environmental variation.

Exposure to different environmental conditions may be structuring monthly temporal patterns of movement of giant tortoises. Notably, individuals on Alcedo volcano (*C. vanderburghi*) displayed strong peaks in their daily and monthly distance travelled in January and June. These periods correspond to changing seasonal weather conditions; January marks the beginning of the hot wet season, while June is often the transition from hot wet to cool dry (*garua*) season, characterized by low precipitation, damp misty conditions and cooler temperatures. These seasonal changes correlate with the main migratory phases of *C. vanderburghi* (G. Bastille-Rousseau, unpublished) during which many individuals migrate along the Alcedo volcano crater rim, a relatively easy environment along which to travel, consisting of open grassland and numerous permanent tortoise trails. These higher movement rates reflect a stronger persistence in movement combined with an increase in hourly displacement (Fig. 4). Interestingly, these periods of high linear displacement are not associated with an increase in the probability of movement relative to some other months (e.g. February and March), perhaps indicating an increase in foraging during this period. There is a similar tendency among *C. donfaustoi* and *C. hoodensis* tortoises to show peak displacement around June which are presumably in response to the same environmental cues.

Earlier studies using one-dimensional scaling of movement have focused on daily distance travelled without much attention to other temporal scales related to period and interval or regarding the sample of individuals (Garland 1983; Schradin 2006; Vieira & De Almeida Cunha 2008). Our results confirm that focusing on a daily scale without consideration of whether the animal was motivated or not would have been appropriate for tortoises, as this captured mechanisms related to probability of movement, directional persistence and distance travelled that finer (hourly) temporal scale would not detect. The appropriateness of the daily scale should hold for a range of organisms that are able to direct their movement on a daily to monthly basis, but longer temporal scales (weeks or months) may be better suited for organisms directing their movements at greater scales (e.g. long distance migratory birds and fish; Åkesson & Hedenström 2007). We suggest that future studies on the allometry of displacement should include analyses at





multiple temporal scales. Our study also shows the importance of considering temporal period as stronger allometry was detected when limited to the motivated period (i.e. using maximum rather than median movement values). It is unclear whether this finding is specific to ectothermic animals such as tortoises where energy budget and level of activity may be more strongly influenced by external factors (Dunham, Grant & Overall 1989), but we suggest that this requires investigation in other taxa under laboratory and field conditions. Nevertheless, to reduce potential bias, we recommend future work on uni-dimensional scaling of movement to be carried on a long time-scale so that observed movement encompasses potential motivated and non-motivated periods. While allometric relationships are expected to hold across taxa, our results also indicate that environmental variation can lead to variation in the magnitude of scaling among taxa.

In contrast to previous work, we did not develop an *a priori* model predicting scaling of movement with body mass (Garland 1983; Carbone *et al.* 2005). Previous models have been developed and tested using mammalian systems, but it was unclear how they would extend to an ectotherm species like giant tortoises given their very specific movement constraints including the absence of inverted pendulum mechanical energy exchange (Zani, Gottschall & Kram 2005; Slavenko *et al.* 2016). For example, applying a model for migration distance developed using terrestrial mammals and based on biomechanics would predict migration distances exceeding 100 km for an average tortoise (80 kg) in Galapagos, a distance that greatly exceeds island size in most cases (Hein, Hou & Gillooly 2012). Without the integration of the taxon-specific normalization constant, this theoretical approach is obviously limited since the motivation to migrate also depends on the spatial distribution of the resources that motivate migration, rather than simply an intrinsic characteristic of the species (Haskell, Ritchie & Olf 2002; Teitelbaum *et al.* 2015). Another model based on home-range allometry parameters for tortoises would predict a home-range size of *c.* 3.8 km<sup>2</sup> for a 45 kg tortoise (Tamburello, Côté & Dulvy 2015). Such prediction would be reasonable for sedentary tortoise such as those inhabiting Espanola, but not for migratory tortoises.

Given the uncertain predictive capabilities of these models for our system, we evaluated scaling of movement for tortoises empirically using different temporal intervals and period and compared model adequacy with previous models *a posteriori*. Previously documented scaling patterns, based on the energetic requirements of mammals, predict one-fourth scaling in daily movement range (Carbone *et al.* 2005). While most of the credible intervals for the scaling coefficients were extremely wide, some of the estimated slopes were close to the one-fourth value. It is therefore difficult to conclude whether drivers of scaling of movement in mammals (resource needs and resource distribution; Carbone *et al.* 2005; Teitelbaum *et al.* 2015) exert a similar influence on the movement of ectotherms.

Nevertheless, allometric models of movement based on resource acquisition and distribution or combining foraging with cost of locomotion in different habitats should better allow generalization than models derived from energetic constraints alone (Garland 1983; Haskell, Ritchie & Olf 2002; Hein, Hou & Gillooly 2012; Slavenko *et al.* 2016). Building generalizations that extend across taxa is a primary goal of ecology, thus exploring the predictive potential of a framework that integrates dimensions of resource availability and locomotion costs merits specific attention.

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## Data accessibility

Data from the Galapagos Tortoise Movement Ecology Programme are archived and freely available on Movebank ([www.movebank.org](http://www.movebank.org)). Data used in the analyses are available from the Movebank Data Repository: <http://dx.doi.org/10.5441/001/1.2cp86266> (Bastille-Rousseau *et al.* 2016b).

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## Supporting Information

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

**Appendix S1.** Additional results.

**Appendix S2.** Winbugs codes.