

The evolution of island gigantism and body size variation in tortoises and turtles

Alexander L. Jaffe^{1,2}, Graham J. Slater^{2,*} and Michael E. Alfaro^{2,*}

¹Harvard-Westlake School, North Hollywood, CA 91604, USA

²Department of Ecology and Evolutionary Biology, University of California Los Angeles, 610 Charles E. Young Drive East, Los Angeles, CA 90095, USA

*Authors for correspondence (gslater@ucla.edu; michaelalfaro@ucla.edu).

Extant chelonians (turtles and tortoises) span almost four orders of magnitude of body size, including the startling examples of gigantism seen in the tortoises of the Galapagos and Seychelles islands. However, the evolutionary determinants of size diversity in chelonians are poorly understood. We present a comparative analysis of body size evolution in turtles and tortoises within a phylogenetic framework. Our results reveal a pronounced relationship between habitat and optimal body size in chelonians. We found strong evidence for separate, larger optimal body sizes for sea turtles and island tortoises, the latter showing support for the rule of island gigantism in non-mammalian amniotes. Optimal sizes for freshwater and mainland terrestrial turtles are similar and smaller, although the range of body size variation in these forms is qualitatively greater. The greater number of potential niches in freshwater and terrestrial environments may mean that body size relationships are more complicated in these habitats.

Keywords: adaptation; body size evolution; chelonia comparative methods; island gigantism; Ornstein–Uhlenbeck; turtles

1. INTRODUCTION

The giant tortoises of the Galapagos, Seychelles and Mascarene islands represent some of the most conspicuous examples of island gigantism. These species, which fall at the upper end of the size scale for extant chelonians (turtles and tortoises), are thought to have achieved their large size as a consequence of relaxed predation pressure, competitive release, or as an adaptation to increased environmental fluctuations on islands [1]. Remarkable as these island giants are, size diversity in the approximately 330 extant chelonian species is equally impressive. Chelonians span almost four orders of magnitude of body mass, from tiny terrestrial species, such as the 80 g speckled padloper tortoise (*Homopus signatus*), to giant marine turtles, such as the 500 kg leatherback (*Dermochelys coriacea*) [2]. Surprisingly, the potential correlation between habitat

and size in chelonians has never, to our knowledge, been tested in a quantitative evolutionary framework. Here, we compare the fit of a series of models of body size evolution to a comparative dataset and time calibrated phylogeny of approximately 70 per cent of extant species of turtle and tortoise. Our results suggest that body size variation in chelonians can be explained by broad habitat differences.

2. MATERIAL AND METHODS

(a) Phylogenetic reconstruction

We used BEAST v. 1.5.4 [3] to simultaneously infer phylogeny and branch lengths of chelonians under a relaxed molecular clock. Our data comprised 1140 bp of cytochrome *b* for 233 species obtained from GenBank and 14 fossils, spanning a range of clades and ages from approximately 200 to 4.9 Myr ago, which represented the minimum age for the most recent common ancestor for extant crown clades. We enforced monophyly constraints on all clades represented by calibration points, meaning that our higher level topology was consistent with previous studies of chelonian phylogeny (e.g. [4,5]). Full details of phylogenetic analyses are provided in the electronic supplementary material.

(b) Modelling body size evolution

We collected maximum straight-line carapace length (centimetre) from the literature for 226 chelonian species represented in our phylogenetic tree (figure 1). Each species was classified into one of four, broad habitat categories, freshwater, marine, mainland or oceanic island.

We compared the fit of a Brownian motion (BM) model of body size evolution in chelonians with Ornstein–Uhlenbeck (OU) models that allow for different optimal body sizes according to habitat. BM has only two parameters: the evolutionary rate, σ^2 , and root state of the trait, θ . OU adds additional parameters, $\theta_1, \dots, \theta_n$ representing the optimal state for each of the n habitat regimes modelled, as well as a parameter representing the strength of selection, α . Also referred to as a ‘rubber-band’ parameter, larger values of α indicate stronger levels of selection, resulting in trait distributions that are more tightly distributed around their optima. As $\alpha \rightarrow 0$, OU degenerates to BM. We compared the fit of models with a single optimal size for all turtles (OU1), and separate optima for each habitat type (mainland, island, freshwater and marine—OU2). If habitat influences body size, then we would expect OU2 to best fit our data. Conversely, if habitat has no influence on body size BM or OU1 should fit better.

We subsequently compared the fit of three additional models that account for more generalized evolutionary hypotheses. OU3 condensed mainland and freshwater chelonians into one category, accounting for the possibility that only oceanic islands and marine adaptation required different optimal sizes. OU4 condensed mainland and oceanic island chelonians into one terrestrial category, accounting for the possibility that there is only one optimal size for terrestrial taxa. OU5 condensed all species to one of two categories: marine or terrestrial. We fit all models using OUCH 2.6-1 [6] in R v. 2.11.1 [7].

An advantage of model-fitting approaches over phylogenetically informed analogues of conventional statistics (e.g. phylogenetic ANOVA [8]) is that uncertainty and error in phylogenetic reconstruction and branch length estimation easily be incorporated by averaging model fits over a sample of trees. We fitted each model of body size evolution to 500 trees drawn at random from the post burn-in sample retained in our BEAST analysis. For each tree, we assigned habitat states to internal branches using maximum-likelihood estimates of ancestral states computed using functions in the APE package [9] for R. The state with the highest marginal likelihood was assigned in each case (e.g. figure 2). Where two or more states had equal marginal likelihoods, we selected a state at random. We averaged parameter estimates over the 500 models and assessed model fit using average Akaike’s Information Criterion scores with small sample correction (AICc).

3. RESULTS

The model allowing each habitat to take a separate optimal body size (OU2) was best supported (table 1). Taking $\Delta\text{AICc} > 4$ as indicating strong support for the best model over other candidate models [10], all other models performed poorly with respect to this model

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.1084> or via <http://rsbl.royalsocietypublishing.org>.

Received 16 November 2010
 Accepted 4 January 2011



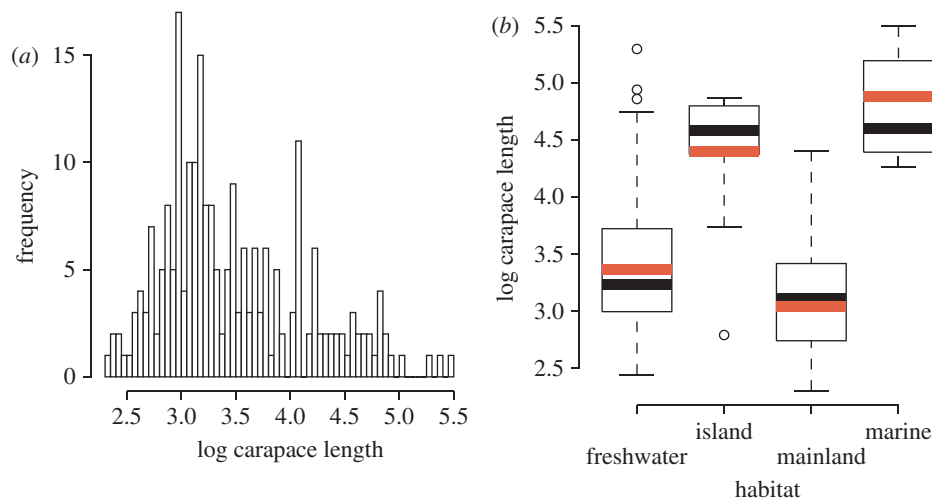


Figure 1. Natural log (\ln) transformed carapace lengths for (a) all turtles and (b) by habitat type. Red bars indicate OU optima from the best-fitting model of body size evolution.

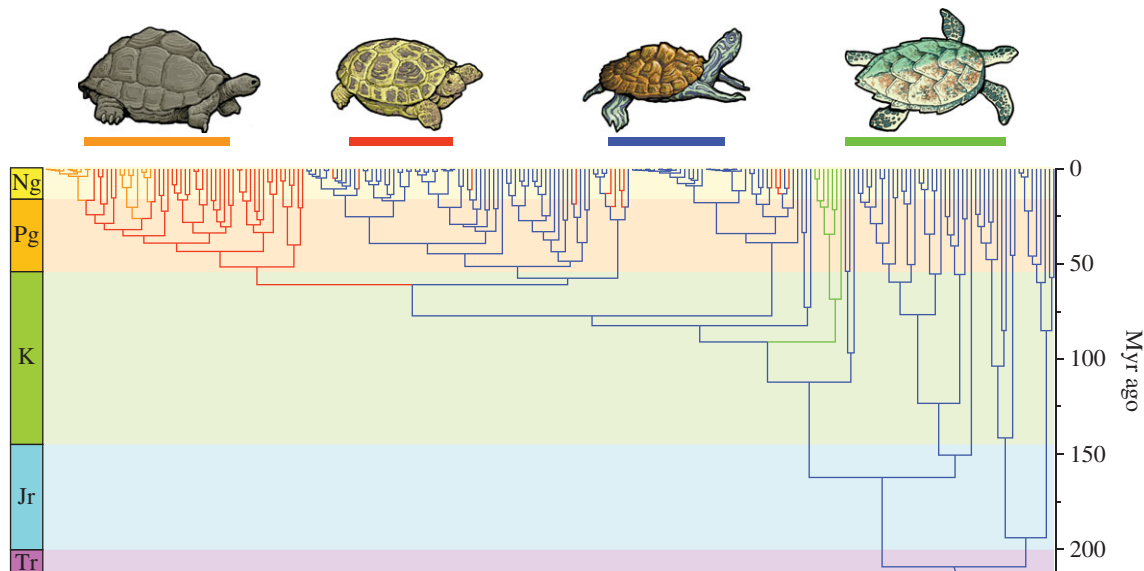


Figure 2. Maximum clade credibility chronogram of 226 turtle species. Branch colours indicate reconstructed habitat states: freshwater (blue), marine (green), mainland (red) and island (orange). Exemplar species from each habitat are illustrated. Colour bar lengths indicate log optimal size.

(table 1). This result supports our hypothesis that habitat differences can explain body size diversity in chelonians.

Average parameter estimates for the strength of selection and Brownian rate parameters proved sensitive to a few outlying values. We therefore present median rather than mean values for those parameters here. Selection and Brownian rate parameters were greatest for OU2, the best-fitting model (table 2). Focusing on the best model, OU2, we found evidence for large optimal sizes in oceanic island and marine chelonians (island optimum = 82.6 cm, marine optimum = 132.6 cm). Optimal size in freshwater and mainland chelonians were smaller and more similar to one another (freshwater optimum = 33.7 cm, mainland optimum = 24.18 cm).

4. DISCUSSION

We found strong support for different optimal sizes in turtles and tortoises that occupy different habitats.

Notably, we recovered similar, large optimal body sizes for both oceanic island tortoises and sea turtles. Despite these similarities, the reasons why these lineages evolved large body size are probably quite different.

Although several studies have examined the relationship between body size and island endemism, particularly in birds and mammals (e.g. [11] and references therein), ours is the first that we are aware of to demonstrate strong evolutionary signal for gigantism as an optimal condition in oceanic island tortoises. It has been suggested that large optimal size was a preadaptation for increased dispersal abilities that allowed the ancestors of these populations to initially colonize islands [1]. However, the retention of large size, combined with convergent loss of anti-predator behavioural and morphological characteristics [12,13], suggests that this condition was at least selectively maintained in the descendants of these initial immigrants. Oceanic Islands are susceptible to unpredictable periods of adverse conditions, while larger size is associated with increased

Table 1. Mean scores for body size models fit to 500 trees randomly sampled from the post-burn in output of BEAST. (Refer to text for model descriptions.)

model	AICc	Δ AICc	weights
OU2	297.34	—	0.89
OU3	301.65	4.30	0.10
OU4	310.91	13.57	1×10^{-3}
OU5	328.97	31.62	1×10^{-7}
OU1	330.42	33.08	5.88×10^{-8}
BM	426.74	129.39	7.15×10^{-29}

Table 2. Summary parameter values for models of body evolution for turtles. (Models were fit to 500 random phylogenies from the post burn-in posterior sample. θ values are ln-transformed and averaged over the 500 model fits while σ^2 and α values are medians. Refer to text for model descriptions.)

	BM	OU1	OU2 ^a	OU3	OU4	OU5
σ^2	4.28	6.82	7.91	7.42	7.52	7.01
α	—	7.34	11.63	10.16	10.11	7.95
θ_0	—	3.59	—	—	—	—
$\theta_{\text{freshwater}}$	—	—	3.52	—	3.54	—
θ_{marine}	—	—	4.89	4.91	4.91	—
θ_{mainland}	—	—	3.19	—	—	—
θ_{island}	—	—	4.41	4.52	—	—
$\theta_{\text{freshwater/mainland}}$	—	—	—	3.45	—	—
$\theta_{\text{terrestrial}}$	—	—	—	—	3.31	3.31
θ_{aquatic}	—	—	—	—	—	3.65

^aBest-fitting model.

fasting ability. Gigantism may have been selectively maintained to allow island tortoises to survive prolonged periods of reduced resource availability and drought, or to facilitate long distance travelling between watering holes and feeding sites [1,11,12,14].

Sea turtles exhibited the largest optimal size in our analysis. As has been suggested for ancestors of island tortoise lineages, large size in sea turtles may reflect adaptation for increased dispersal abilities as many sea turtles seasonally migrate vast distances. For example, green turtles (*Chelonia mydas*) have been recorded to trek 2300 km on their journey from the remote Atlantic Ascension Island to the Brazilian coast [15]. Some species such as green (*C. mydas*) and loggerhead (*Caretta caretta*) turtles range from equatorial regions to colder areas of the northern or southern oceans [16], and larger body size also becomes advantageous in cold waters because lower surface area to volume ratios reduce heat lost to the environment. Arguing against large size purely as a thermoregulatory adaptation is the observation that the leatherback turtle can use changes in blood flow to maintain body temperatures above ambient in colder waters [16,17]. Furthermore, the largest turtles to have ever lived, such as the 4.6 m *Archelon ischyros* [18], inhabited Mesozoic seas that would have been much warmer than today's oceans [19–21].

Predation risk presents an additional explanation for large optimal sizes in sea turtles. The largest sea turtle species evolved during the Late Mesozoic, and

co-occurred with massive reptilian predators, such as mosasaurs and pliosaurs [19,20]. During the Cenozoic, smaller sharks and toothed whales have become the dominant predators of marine turtles [22], relaxing selection for extreme body size in more recent species. However, extant marine predators remain larger than most of their terrestrial counterparts, and this may be sufficient to maintain an optimal size difference between marine turtles and terrestrial or freshwater species.

Despite our striking results for oceanic island and marine chelonians, optimal size estimates for freshwater and mainland terrestrial chelonians were similar. Based on our raw data, members of these two groups also span qualitatively similar large body size ranges (figure 1b). A more complicated set of ecological factors may be responsible for determining body size in these species. Terrestrial and freshwater chelonians occur in diverse environments, from arid deserts to temperate forests, and often coexist with several other turtle species. Body size also appears to be correlated with diet in chelonians, possibly owing to size-related increases in bite force [23,24]. Given that many freshwater and terrestrial chelonian clades exhibit considerable ecological diversity (e.g. [25]), their similar, broad distributions of body size variation are perhaps to be expected.

We thank Chris Muller for illustrating figure 2, and two anonymous reviewers, Shauna Price, and the Alfaro and Harmon laboratories for comments on the manuscript. This work was supported by NSF grant DEB 0918748 to M.E.A.

- 1 Pritchard, P. C. H. 1996 *The Galapagos tortoises: nomenclatural and survival status*. Lunenburg, MA: Chelonian Research Foundation in association with Conservation International and Chelonia Institute.
- 2 Bonin, F., Devaux, B. & Dupré, A. 2006 *Turtles of the world* (transl. from the French by P. C. H. Pritchard). Baltimore, MD: The Johns Hopkins University Press.
- 3 Drummond, A. J. & Rambaut, A. 2007 BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **7**, 214. (doi:10.1186/1471-2148-7-214)
- 4 Near, T. J., Meylan, P. A. & Shaffer, H. B. 2005 Assessing concordance of fossil calibration points in molecular clock studies: an example using turtles. *Am. Nat.* **165**, 137–146. (doi:10.1086/427734)
- 5 Thomson, R. C. & Shaffer, H. B. 2010 Sparse supermatrices for phylogenetic inference: taxonomy, alignment, rogue taxa, and the phylogeny of living turtles. *Syst. Biol.* **59**, 42–58. (doi:10.1093/sysbio/syp075)
- 6 Butler, M. A. & King, A. A. 2004 Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* **164**, 683–695. (doi:10.1086/426002)
- 7 R Development Core Team 2010 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org>.
- 8 Garland Jr, T., Dickerman, A., Janis, C. & Jones, J. 1993 Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* **42**, 265–292.
- 9 Paradis, E., Claude, J. & Strimmer, K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
- 10 Burnham, K. P. & Anderson, D. R. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Berlin, Germany: Springer.

- 11 Lomolino, M. V. 2008 Body size evolution in insular vertebrates: generality of the island rule. *J. Biogeogr.* **35**, 191.
- 12 Arnold, E. N. 1979 Indian ocean giant tortoises: their systematics and island adaptations. *Phil. Trans. R. Soc. Lond. B* **286**, 127–145. (doi:10.1098/rstb.1979.0022)
- 13 Austin, J. J. & Arnold, E. N. 2001 Ancient mitochondrial DNA and morphology elucidate an extinct island radiation of Indian Ocean giant tortoises (*Cylindraspis*). *Proc. R. Soc. Lond. B* **268**, 2515–2523. (doi:10.1098/rspb.2001.1825)
- 14 Darwin, C. R. 1838 *The zoology of the voyage of H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836*. London, UK: Smith, Elder and Co.
- 15 Luschi, P., Hays, G. C., Del Seppia, C., Marsh, R. & Papi, F. 1998 The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc. R. Soc. Lond. B* **265**, 2279–2284. (doi:10.1098/rspb.1998.0571)
- 16 Mrosovsky, N. 1980 Thermal biology of sea turtles. *Am. Zool.* **20**, 531–547.
- 17 Standora, E. A., Spotila, J. R. & Foley, R. E. 1982 Regional endothermy in the sea turtle, *Chelonia mydas*. *J. Therm. Biol.* **7**, 159–165. (doi:10.1016/0306-4565(82)90006-7)
- 18 Derstler, K., Leitch, A., Larson, P. L., Finsley, C. & Hill, L. 1993 The world's largest turtles, the Vienna *Archelon* (4.6 m) and the Dallas *Protostega* (4.2 m), upper Cretaceous of South Dakota and Texas. *J. Vert. Paleont.* **13**, 33A.
- 19 Bernard, A. *et al.* 2010 Regulation of body temperature by some Mesozoic marine reptiles. *Science* **328**, 1379–1382. (doi:10.1126/science.1187443)
- 20 Motani, R. 2010 Warm-blooded 'sea dragons'? *Science* **328**, 1361–1362. (doi:10.1126/science.1191409)
- 21 Jacobs, D. K. & Lindberg, D. R. 1998 Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas. *Proc. Natl Acad. Sci. USA* **95**, 9396–9401. (doi:10.1073/pnas.95.16.9396)
- 22 Lutz, P. L. & Musick, J. A. (eds) 1997 *The biology of sea turtles*. Boca Raton, FL: CRC Press.
- 23 Claude, J., Paradis, E., Tong, H. & Auffray, J. C. 2003 A geometric morphometric assessment of the effects of environment and cladogenesis on the evolution of the turtle shell. *Biol. J. Linn. Soc.* **79**, 485–501. (doi:10.1046/j.1095-8312.2003.00198.x)
- 24 Herrel, A., O'Reilly, J. C. & Richmond, A. M. 2002 Evolution of bite performance in turtles. *J. Evol. Biol.* **15**, 1083–1094. (doi:10.1046/j.1420-9101.2002.00459.x)
- 25 Stephens, P. R. & Wiens, J. J. 2003 Ecological diversification and phylogeny of emydid turtles. *Biol. J. Linn. Soc.* **79**, 577–610. (doi:10.1046/j.1095-8312.2003.00211.x)