Environmental and Ecological Factors Affecting the Presence of Giant Land Turtles in the Late Cenozoic

COLLEGE OF
COMPUTER, MATHMATICAL, & NATURAL SCIENCES
DEPARTMENT OF GEOLOGY

Orion Jenkins-Houk
Instructor: Phil Piccoli, GEOL 394

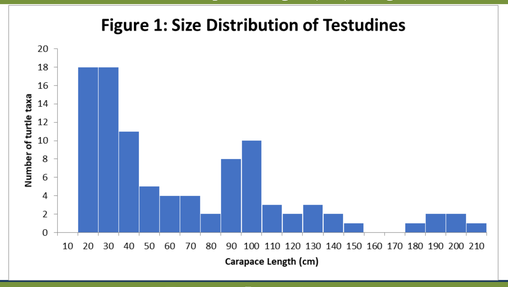
Advisor: Dr. Thomas Holtz

Introduction

Five factors were interrogated for statistically significant relationships with giant land turtle (GLT) occurrences throughout the Late Cenozoic Era (Miocene to Holocene Epochs): temperature, aridity, insularity, durophagous predation, and generalist terrestrial herbivore competition.

Figure 1: Size Distribution of Testudines

Based on the results of a size distribution analysis of the Rhodin *et al.* (2015) list of Cenozoic turtle taxa, the minimum carapace length (CL) for giant taxa was 80 cm.



Hypothesis

Temperature, aridity, landmass size, the presence of durophagous predators, and/or the presence of competing herbivores were related to giant land turtle occurrences.

Methods

Hypotheses were tested by performing Fisher exact tests on the distributions of turtle-bearing formations for each factor, epoch by epoch. Alpha value for significance was set at $\alpha = 0.05$.

Distributions were informed by the Paleobiology Database (PBDB; Czaplewski) and epoch climate estimate/paleogeography sources.

Epoch distributions were input to a Paleontological Statistics (PAST; Hammerer (2019)) spreadsheet as 2x2 boxes for each factor (GLTs present vs absent for all factors against humid vs arid for aridity, hot vs temperate for temperature, insular vs continental for landmass size, durophagous predators present vs absent, and herbivorous competition present vs absent).

Each 2x2 box was selected and run with the univariate statistics tool to determine Fisher exact values.

Holocene temperature bins: > 20 °C hot, 5-20 °C temperate

Holocene aridity bins: AI > 0.5 humid, < 0.5 arid

Results

Figure 2: Cases of Late Cenozoic Turtle Taxa, with Emphasis on Giantism

This map was modified from one found in Rhodin *et al.* (2015) to include several Miocene taxa and rough sketches of the distribution of giant land turtles throughout the Late Cenozoic.

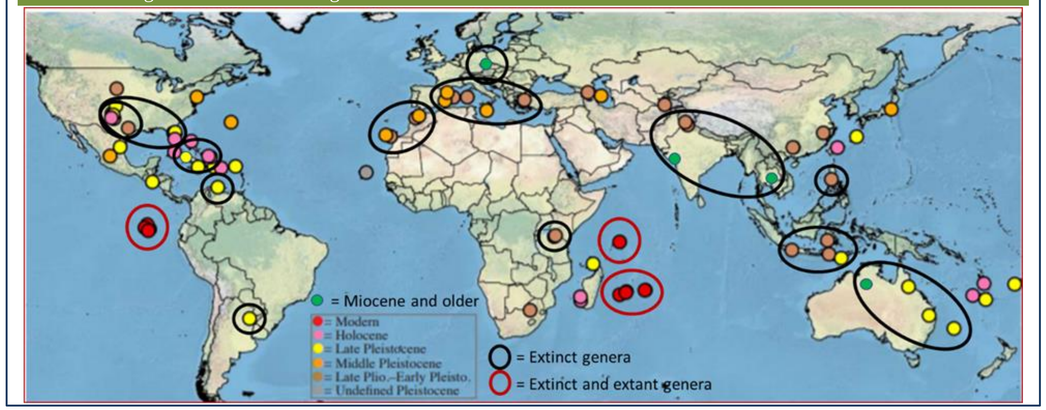


Figure 3: Summary of Statistical Analyses By Epoch and in Larger Groupings

This table shows the results of the Fisher exact tests run for each epoch, as well as various groupings of the individual epochs (all epochs combined, all epochs excluding the Holocene, Neogene Period, and Quaternary Period).

Statistically significant factors by Time Slice are as follows:

Holocene – Insularity and competing herbivores
Pleistocene – Temperature and competing herbivores
Pliocene – Temperature
Miocene – None
All Epochs – Temperature, aridity, competing herbivores
Pre-Holocene Epochs – Temperature and competing herbivores
Neogene (Miocene plus Pliocene) – None
Quaternary (Pleistocene plus Holocene) – Temperature, insularity, and competing herbivores

These results suggest an interesting trend from mostly ubiquitous giant land turtle occurrences in the Neogene Period, uncontrolled by any of the five factors interrogated here, to highly controlled GLT occurrences in the Pleistocene and especially Holocene Epochs, during which giant land turtles were largely restricted to hotter areas where competition from large-bodied mammalian herbivores was scarce. In the Holocene competition drove most GLTs to isolated oceanic islands.

Holocene Factors	Fisher p-value	Significance
Temperature	0.245	Not significant
Aridity	0.603	Not significant
Insularity	0.002	Significant
Durophagous predators	1.00	Not significant
Competing herbivores	0.002	Significant
Pleistocene Factors	**Fisher p-value**	**Significance**
Temperature	0.001	Significant
Aridity	0.615	Not significant
Insularity	0.063	Not significant
Durophagous predators	0.060	Not significant
Competing herbivores	0.005	Significant
Pliocene Factors	**Fisher p-value**	**Significance**
Temperature	0.025	Significant
Aridity	0.183	Not significant
Insularity	1.00	Not significant
Durophagous predators	0.342	Not significant
Competing herbivores	0.444	Not significant
Miocene Factors	**Fisher p-value**	**Significance**
Temperature	0.491	Not significant
Aridity	1.00	Not significant
Insularity	1.00	Not significant
Durophagous predators	1.00	Not significant
Competing herbivores	0.491	Not significant
All Formations Factors	**Fisher p-value**	**Significance**
Temperature	0.002	Significant
Aridity	0.778	Not significant
Insularity	0.002	Significant
Durophagous predators	0.207	Not significant
Competing herbivores	1.58×10^{-5}	Significant
Pre-Holocene Fms. Factors	**Fisher p-value**	**Significance**
Temperature	0.005	Significant
Aridity	1.00	Not significant
Insularity	0.199	Not significant
Durophagous predators	0.130	Not significant
Competing herbivores	0.004	Significant
Neogene Period Factors	**Fisher p-value**	**Significance**
Temperature	0.264	Not significant
Aridity	0.539	Not significant
Insularity	1.00	Not significant
Durophagous predators	0.466	Not significant
Competing herbivores	0.539	Not significant
Quaternary Period Factors	**Fisher p-value**	**Significance**
Temperature	0.001	Significant
Aridity	0.311	Not significant
Insularity	1.26×10^{-4}	Significant
Durophagous predators	0.461	Not significant
Competing herbivores	5.45×10^{-6}	Significant

Conclusions

The trend of increasing controls on GLT occurrences from these analyses suggests that as large-bodied mammal generalist herbivores became widespread in the Pleistocene, giant land turtles were rapidly outcompeted on the continents and thus either took refuge or evolved from smaller turtle forms on isolated oceanic islands.

The combined analyses reinforced the individual epoch results by showing a similar progression from largely uncontrolled GLT occurrences in the Neogene to greatly restricted distributions in the Quaternary.

It is interesting to note that aridity and durophagous predation were insignificant in all the analyses. The most likely explanation is that bone-crushing predators preyed equally on both large and small land turtles, so their presence would not be a differentiating factor between areas with and without giant land turtles.

Further research should focus on more specific analyses of a single factor to determine more exact relationships. These analyses could also be applied to other Cenozoic nanoid and giant organisms.

Acknowledgements and References

Acknowledgements: Dr. Laurent Montessi for assistance with minimum CL determination and Dr. Michael Evans for insightful advice on the statistical analyses and the idea of binning the continuous environmental variables.

Behl, R. J. (2011). Glacial demise and methanes rise. *Proceedings of the National Academy of Sciences*, 108(15), 5925–5926. doi: 10.1073/pnas.1101146108

Boucot, A. J., Xu, C., & Scotese, C. R. (2013). *Phanerozoic paleoclimate an atlas of lithologic indicators of climate* (Concepts in Sedimentology and Paleontology, no. 11, 478 pp.). Tulsa: Society of Economic Paleontologists and Mineralogists.

Czaplewski, J. J. PBDB Navigator. Retrieved from https://paleobiodb.org/navigator/

FAO (Food and Agriculture Organization of the United Nations). (2015). FAO GEONETWORK. Global map of aridity - 10 arc minutes (GeoLayer). Accessed November 6, 2019. URI: http://data.fao.org/ref/221072ae-2090-48a1-be6f-5a88f061431a.html?version=1.0. FAO, Rome, Italy.

Hammer, Ø. (2019). PAST: Paleontological Statistics Software Package for Eduction and Data Analysis. Version 3.25. http://folk.uio.no/ohammer/past

Matsuura, K. and National Center for Atmospheric Research Staff. (2017). "The Climate Data Guide: Global (land) precipitation and temperature: Willmott & Matsuura, University of Delaware." Accessed 11/22/2019. URI: https://climatedataguide.ucar.edu/climate-data/global-land-precipitation-and-temperature-willmott-matsuura-university-delaware.

Rhodin, A., Thomson, S., Georgalis, G., Karl, H.-V., Danilov, I., Takahashi, A., de la Fuente, M. S., Bourque, J. R., Delfino, M., Bour, R., Iverson, J. B., Shaffer, H. B., and van Dijk, P. P. (2015). "Turtles and Tortoises of the World During the Rise and Global Spread of Humanity: First Checklist and Review of Extinct Pleistocene and Holocene Chelonians." *Chelonian Research Monographs Conservation Biology of Freshwater Turtles and Tortoises*. doi: 10.3854/crm.5.000e.fossil.checklist.v1.2015

Salzmann, U., Williams, M., Haywood, A. M., Johnson, A. L. A., Kender, S., & Zalasiewicz, J. (2011). Climate and environment of a Pliocene warm world. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 309(1-2), 1–8. doi: 10.1016/j.palaeo.2011.05.044