12-1-2010

The spatial ecology of Galapagos tortoises and New Mexico's reptiles

Jacek Tomasz Giermakowski

Recommended Citation

Giermakowski, Jacek Tomasz. "The spatial ecology of Galapagos tortoises and New Mexico's reptiles." (2010). https://digitalrepository.unm.edu/biol_etds/41

Jacek Tomasz Giermakowski

Candidate

Biology

Department

This dissertation is approved, and it is acceptable in quality and form for publication:

Approved by the Dissertation Committee:

, Chairperson

C. R. Peterson

THE SPATIAL ECOLOGY OF GALAPAGOS TORTOISES AND NEW MEXICO'S REPTILES

by

JACEK TOMASZ GIERMAKOWSKI

B.Sc., Wildlife Biology, The University of Montana 1999

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

The University of New Mexico
Albuquerque, New Mexico

December, 2010

ACKNOWLEDGMENTS

I thank my advisor, Howard Snell, for an immeasurable amount of guidance and patience during my graduate studies and his invaluable support in dissertation research and writing. I also thank immensely the members of my graduate committee: Tom Turner, Chuck Peterson, and especially Blair Wolf, who has taught me about a whole new (physiological) way to look at ecology.

I extend my gratitude to the staff, students and volunteers at the Charles Darwin Research Station and the Galápagos National Park Service, both located in Puerto Ayora on Isla Santa Cruz, in the Galápagos Islands of Ecuador. Special thanks go to Cruz Márquez, Wacho Llerena, Hernán Vargas, Sixto Naranjo, Fausto Llerena, Wacho Tapia, Marco Altamirano, Sandra Landázuri, María Lourdes de Torres and Javier Álvaro Morán Guerra. I also thank Heidi Snell for much needed guidance and support before, during and after visiting the islands.

In New Mexico, I'd like to thank Bruce and Michelle Christman, Charlie Painter, Bill Degenhardt, and Lee Pierce. Among many other things, all have helped me to realize how much we can still learn about the amphibians and reptiles living in the Land of Enchantment.

Research for this dissertation would have not been possible without funding from several sources, including The University of New Mexico's Student Research Allocation Committee and the Latin American and Iberian Institute. TAME airlines provided discounted airfares and the Galápagos National Park Service and the Charles Darwin Research Station provided much needed funds and logistical support, including transportation and equipment. The Share with Wildlife Program of the New Mexico's Department of Game and Fish has provided funds for work in New Mexico.

I thank the many friends that have helped during this process, both scientifically and otherwise. Thanks to Hilary Lease, Tim and Ruth Meehan, Paul Cryan, Chris Frazier, Kate Thibault, Ian Latella, Heather Bateman, Andrés García, Anne Schultz, Robin Warne, Mason Ryan, Brittany Barker, Brand Phillips, Gerardo Suzán, Érika Marcé, Fernando Esponda, Horacio Samaniego, Dominique Alò, Laura González Bosc y Diego Grant. Thanks to my coworkers at the Museum of Southwestern Biology, with particular appreciation to Lex Snyder, Teri and Paul Neville, Jane Mygatt, and Tim Lowrey.

Finally, and most of all, I thank my family. Thank you to my parents, Jerzy and Wieslawa, for taking me on trips that involved nature ever since I can remember, for encouraging my experiences with tritons, frogs and lizards, and for supporting the pursuit of biology as my career. Special thanks to my wife, Valeria Rios, for her love and encouragement, and my children, Kamila and Maks, whose wander at the natural world makes being a biologist so much more worthwhile.

THE SPATIAL ECOLOGY OF GALAPAGOS TORTOISES AND NEW MEXICO'S REPTILES

by

JACEK TOMASZ GIERMAKOWSKI

ABSTRACT OF DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

The University of New Mexico
Albuquerque, New Mexico

December, 2010

THE SPATIAL ECOLOGY OF GALAPAGOS TORTOISES AND NEW MEXICO'S REPTILES

by

Jacek Tomasz Giermakowski

B.Sc., Wildlife Biology, The University of Montana, 1999

Ph.D., Biology, University of New Mexico, 2010

ABSTRACT

The analysis of spatial processes and spatial heterogeneity is an important part of ecology because distribution of organisms in space partly defines ecology as a discipline. In addition, advances in analysis of DNA, geographical computing and the availability of vast amounts of environmental data obtained by satellites provide new opportunities for studying ecology at different spatial and phylogenetic scales. My research takes advantage of information gathered by satellites and adds modeling and data collected on the distribution of different reptiles to examine processes at various spatial and temporal scales. In Chapter 1 I describe how juvenile Galapagos tortoises change their patterns of distribution as they grow. These patterns relate to different levels of productivity of vegetation, but that relationship is only evident for older juveniles. In Chapter 2, I examine body sizes in different taxa of Galapagos tortoises from an evolutionary and ecological perspective. While body sizes of adults of different taxa of tortoises covary with primary productivity, I did not find any association between body size and phylogeny of these tortoise taxa. In Chapter 3 I develop and field-test a method for modeling the potential distribution of species. I focus on reptiles in New Mexico and describe a multivariate technique that allows comparison of the suitability of landscape for different species between different areas. Maps produced with this method can be used for planning inventory and monitoring of species at coarse spatial scales and can help in identifying conservation opportunities.

Table of Contents

List of Figures

List of Tables

Introduction

Consideration of space is implicit in ecology because distribution and abundance of organisms in space are two topics that define ecology as a discipline (Andrewartha & Birch 1954; Krebs 1978; Caughley & Gunn 1996). Furthermore, linking ecological processes that influence distribution of species to spatial heterogeneity of the environment at coarse spatial scales is important to the advancement of both basic and applied ecology (Shaver 2005). Studies of spatial variation in abundance of individual species have been limited by emphases on particular taxa or mechanisms and this, in turn, has limited the advancement and generality of our understanding (Gaston 2003). For example, many studies do not consider the potential variation of individual responses to the environment that could occur from ontogeny. This is unfortunate for conservation, where management actions often occur at fine spatial scales. On the other hand, conservation efforts also rely on information about the distribution of organisms that is useful when presented at regional scales and for many species at once. In this dissertation I combine modeling, field-collected data, and remotely sensed information to examine the variation in responses to spatial heterogeneity in the environment by individuals and by species. I do that across phylogenetic and spatial scales that are useful in conservation biology.

The Galapagos Islands and their tortoises provide an excellent system for studies of variation of ecological processes across spatial and phylogenetic scales. On one hand, because tortoises have a large ontogenetic change in body size (150g to 200kg+), variation in response to the environment is expected based on the effects of size alone

(Peters 1983; Calder 1984; Schmidt-Nielsen 1984). On the other hand, many other factors that could play a significant role in distribution of other species are minimized, thus reducing confusion. For example, Galapagos tortoises lack ontogenetic trophic shifts in diet (they are herbivorous throughout their lifetime) and there appears to be no complex social structure. Populations of Galapagos tortoises are found in relatively natural environments, have few natural predators or direct competitors, and are wide-ranging throughout the islands. Finally, different taxa of tortoises present on different islands represent an important component of the fauna of Galapagos and are of great interest to conservation. For example, the Galapagos National Park Service is specifically interested in distribution of juvenile tortoises and whether information obtained from spatial analyses of abundance could be used to enhance its restoration programs.

The first chapter focuses on the formation of ontogenic patterns of distribution of juveniles of one taxon of Galapagos tortoises on Isla Santa Cruz. Knowing whether the variation in environmental factors affects distribution of tortoises of different ages is important to the design, implementation, and success of conservation programs. In the second chapter, I examine adult body sizes of different taxa of tortoises from different islands. Because of the complex geological history of the islands, I first evaluate whether phylogeny relates to body size and subsequently test several hypotheses with regards to the influence of primary productivity on body size in areas where different taxa of tortoises occur.

In chapter three, I consider much coarser spatial and phylogenetic scales by shifting focus to New Mexico and the distribution of its reptiles. Effective conservation at regional scales relies on a thorough knowledge of the distribution of different species.

Because the distribution of reptiles is not well understood in many areas of the state, I develop a multivariate technique that quantifies the suitability of landscape for different species of reptiles. This method differs from other modeling algorithms in that it focuses on the landscape rather than a particular species. I show that the methodology compares well with other established methods and that it is well-suited for the development of maps that can be used for planning inventory and monitoring efforts throughout the state.

Literature Cited

Andrewartha, H. G., and L. C. Birch 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, IL, USA.

Calder, W. A. 1984. Size, function, and life history. Harvard University Press, Cambridge, MA, USA.

Caughley, G., and A. Gunn 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, MA, USA.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, New York, NY, USA.

Krebs, C. J. 1978. Ecology: The experimental analysis of distribution and abundance. Benjamin-Cummings Publishing Company, San Francisco, CA, USA.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, New York, NY, USA.

Schmidt-Nielsen, K. 1984. Scaling: why is animal size so important? Cambridge University Press, Cambridge, UK.

Shaver, G. R. 2005. Spatial heterogeneity: past, present, and future. Pages 443-449 in G. M. Lovett, M. G. Turner, C. G. Jones, and K. C. Weathers, editors. Ecosystem function in heterogeneous landscapes. Springer, New York, NY, USA.

Chapter 1 : Ontogenetic differences in the spatial distribution of juvenile Galapagos tortoises

Abstract

Individuals of animal species are rarely distributed continuously in space. Knowledge of ontogenetic differences in distribution is particularly important for conservation efforts that involve repatriation of individuals to natural habitats. We examined the pattern of distribution of juvenile Galapagos tortoises and its relationship to the limited availability of nesting sites and variation in productivity of vegetation. Using individual-based modeling, we estimated a null distribution of tortoises in space and compared this null distribution to observed frequencies of tortoises. We then used significant deviations from the null model to study whether abundance of differently-sized juveniles is related to different environments. Juvenile tortoises that are small remain close to nesting areas and their frequencies do not differ from those calculated in a null model. Larger juvenile tortoises occur near nests at higher frequencies than predicted by the null model. Areas where larger juveniles dominate have a wider range of productivity of vegetation than those where smaller individuals are more frequent, suggesting that habitat choices might be different for juvenile tortoises of different sizes. Repatriation and monitoring efforts of Galapagos tortoises should take into account the importance of nesting areas for survival of small juveniles and the differential ability to detect tortoises of different sizes within the larger landscape.

Introduction

Species of animals are rarely distributed continuously in space and the identification of patterns and mechanisms of this variation form fundamental questions in ecology (Caughley 1978; Krebs 1978). In addition, detailed knowledge of the spatial arrangement of individuals and populations is particularly important for conservation and management (Caughley & Gunn 1996; Soulé & Orians 2001; Sinclair et al. 2006). Mechanisms involved in forming spatial variation in abundance of a species have been described by several theoretical models at broad spatial scales (Brown 1984; Hengeveld 1990; Brown et al. 1995; Holt et al. 1997; Ives & Klopfer 1997). Studies of mechanisms of distribution at finer scales are fewer but especially important for conservation efforts that involve repatriation. One such example is the captive breeding – repatriation program for the Galapagos tortoises, which has been established in response to a variety of threats (Fritts et al. 2000). To aid the effort involved in the repatriation of captive-bred tortoises to natural habitats, in this study we investigate the pattern of distribution of juvenile Galapagos tortoises.

Although Galapagos tortoises are broadly distributed among islands of the Galapagos archipelago, the areas they inhabit on an individual island are often restricted (Márquez et al. 2004). Furthermore, within the range of particular populations, sexual and ontogenetic patterns of distribution have been known and described a number of times (Van Denburgh 1914; MacFarland et al. 1974; Morán Guerra 2003). Even early explorers noted that smaller (thus young) tortoises, as well as females, were often encountered close to the coast and in areas that were more open and at lower elevations than large males. To reach the latter usually required long trips from the coast to more vegetated uplands (Slevin et al. 1982). Subsequent investigations confirmed these early observations, yet despite a long history of research on tortoises in the islands, hypotheses which try to describe the mechanisms of these intra-island patterns remain untested. For example, sexually dimorphic patterns of spatial distribution could be an artifact of human predation because it was physically difficult to remove large males of some populations (de Vries 1984). Herein we investigate ontogenetic patterns in spatial distribution of juvenile Galapagos tortoises on Isla Santa Cruz. We focus on two ecological factors that potentially influence patterns of the distribution of juveniles: the limited availability of nesting sites and ontogenetic variation in habitat requirements.

Areas where tortoises successfully nest are often very limited. The hydric environment where turtle eggs develop affects the hatching success and condition of the hatchlings (Packard et al. 1982; Tracy & Snell 1985; Earsom 2000) while the temperature determines gender (Sancho 1988). In the rocky lava habitats of the Galapagos, suitable combinations of soil, thermal and hydric conditions are rare (Earsom 2000) and most nesting sites are constrained to relatively small areas of the landscape. Because all hatchling tortoises start from nests, the youngest and smallest tortoises initially only occur in nesting regions, and then move away from these areas as they age. If juvenile tortoises move randomly as they grow, then the pattern of their distribution would be dependent on the spatial distribution of nests. Whether their movement differs from random or not forms the null hypothesis that we address first.

On the other hand, spatial patterns in abundance can also result from different environmental requirements of individuals as they change in size during ontogeny.

Factors such as risk of predation, nutritional necessities, and physiological challenges, often change with age or size (Werner & Gilliam 1984; McNamara & Houston 1986). This could be particularly important for ectothermic herbivores, which need to satisfy their nutritional requirements while at the same time behaviorally regulating body temperature. Unusually among terrestrial ectothermic vertebrates, juveniles of Galapagos tortoises vary in mass over two orders of magnitude (150g–40kg). Considering that physiological effects of size alone can create patterns of covariation between environment and size (Peters 1983; Schmidt-Nielsen 1984), juvenile tortoises of different sizes can be expected to select different environments. This is likely because different places provide differing foraging or thermoregulating opportunities. Here we do not examine any mechanisms but instead focus on the existence of such pattern by testing whether the abundance of differently-sized juveniles is related to different environments.

Methods

We first compare frequencies of differently sized tortoises within an imaginary grid that covers the study area to a null model of their distribution. We produce this null spatial distribution by modeling movement of hatchlings from nests as random. This null hypothesis is supported if the frequencies of observed tortoises within grid cells do not deviate from frequencies predicted by the null model. Because we are interested in ontogenetic variation, for further analyses we group grid cells based on the mean size of tortoises that occur there. We compare environments where tortoises of different sizes are prevalent to test whether tortoises select different environments as they grow.

Study area and tortoise distribution data

We observed juveniles from the population of tortoises that ranges in the southwestern part of Isla Santa Cruz (Figure 1.1). The island supports a diverse flora and a population of tortoises estimated at 3,400 individuals (Márquez et al. 2004). Although the island reaches 864m a.s.l., adult and juvenile tortoises are mostly found from sea level to 350m a.s.l. Precipitation varies with elevation and is very variable year-to-year, particularly in the coastal zone (Snell & Rea 1999). Mean annual temperature is 27°C on the coast and is usually 3°C lower at 194m a.s.l. (Snell & Rea 1999). Common plants in the arid zone, which extends to approximately 100m a.s.l., include *Bursera graveolens*, *Croton*, *Opuntia*, *Cordia*, and *Clerodendrum*. Higher elevations (100-300m a.s.l.) include both deciduous and non-deciduous trees (such as *Pisonia*, *Piscidia*, and *Psidium*) as well as many of the plants found in the arid zone (McMullen 1999).

The taxon of Galapagos tortoises we studied (*Chelonoidis nigra nigrita*) ranges throughout approximately 150 square kilometers. Our sampling focused on three areas, locally known as ‘Cerro Gallina’, ‘La Fe’ and ‘La Torta’ and consisted of five to 12 days in each one of the study areas. Our sampling spanned three years (2001 to 2003) and included three periods during the dry season and two periods during the wet season. Tortoises were found while walking on and off trails between 6:00 and 18:00 (approximately sunrise to sunset) within the boundaries of the Galapagos National Park. Trails within the park are only used by park rangers and, with special permission, by hunters and scientists; therefore tortoise-human contact is not frequent and unlikely to bias our observations. Galapagos tortoises are active year round, although during the colder dry months, most activity is concentrated around the middle part of the day, while during the hot wet season, tortoises are active in the morning, rest during the hottest part of the day, and some become active again in the afternoon (Cayot 1987, pers. obs.).

For each encounter with a tortoise, we recorded its geographic position (latitude and longitude) initially with a Garmin 12 and since 2002, with a Garmin eTrex Vista GPS receiver (Garmin International Inc., Olathe, KS, USA). For each observed juvenile we recorded its curved carapace length (CCL) to the nearest millimeter by using a flexible measuring tape. We classified tortoises as juveniles based on body size and lack of secondary sexual characteristics. We only considered individuals whose curved carapace length was less than 70cm. Because we needed data on unique individuals, during the entire study we marked a total of 297 juvenile tortoises with a hot steel brand on their 4th left costal scute. In addition, each tortoise was implanted subcutaneously at the base of the left rear leg with a passive integrated transponder (PIT) tag (AVID Microchip ID Systems Inc., Folsom, LA, USA). Previous marking programs by the Charles Darwin Foundation and Galapagos National Park (using the same protocol) allowed us to identify and incorporate more individuals in our analyses (Torres Corral 2001; Morán Guerra 2003; Márquez et al. 2004).

A null model of juvenile distribution within a population

We developed an individual-based model to estimate a null distribution in space of tortoises of different sizes. This model is based on movement of juvenile tortoises after hatching from nests. The model assumes that tortoises move randomly but are limited by their morphology and physiology and it accounts for changes in survival and size with time. It is a correlated random walk movement model (Kareiva & Shigesada 1983) where step length and direction of movement are independent but the direction is chosen relative to that of the preceding step (Model I(b), Marsh & Jones 1988). Each individual simulation of a tortoise consists of the following parameters: stride length (the distance between points where one of the legs leaves the substrate to where it touches again), angle at a given step (for each step, angle of deviation from the previous direction), and frequency of steps per unit time. We used MATLAB 7.1 (The MathWorks Inc., Natick, MA, USA; see appendix for source code) for all calculations.

We used data from unpublished theses, published literature, video footage and our own observations on different aspects of turtle morphology, physiology, and behavior to provide values for parameters in the model. Because turtles have a very conservative morphology that does not differ drastically between terrestrial species, we considered published data on similar species to be representative of Galapagos tortoises. To derive values of stride length for different sizes, we fit a power function with a scaling exponent of 0.33 to data on stride length from adult Galapagos tortoises (Zani et al. 2005), and two species of box turtles: *Terrapene ornata* (Wren et al. 1998) and *Terrapene carolina* (Muegel & Claussen 1994), whose high-domed shells closely resemble those of tortoises. We used a fixed value of 0.33 for the scaling exponent because in measurements of scaling of stride length in other species of turtles the exponent did not statistically differ from the expected value of 0.33 (Wren et al. 1998). We assumed that the angle of the movement in relation to the main body axis of a tortoise can only change between steps, not during a step, due to the inflexible shell. In the model, tortoises at each step had a uniform probability of turning at any angle between 0° and 45° to either side of their main body axis. This value was based on observation of tortoises in the wild, in video footage, as well as measurements of hip angles during locomotion of other turtles

(Earhart & Stein 2000). In order to estimate the total distance a tortoise travels each day, we fit a linear regression to data on different species and sizes of tortoises within the family Testudinidae, including Galapagos tortoises, which were trailed daily with a thread (Aguirre et al. 1984; Hailey 1989; Díaz-Paniagua et al. 1995; Hailey & Coulson 1996; Ortiz 2003). However, there is a positive and significant relationship between size of a tortoise and the distance it covers during a day and we used this relationship to calculate the number of steps per day (Rodhouse et al. 1975; Hailey 1989). Though no data exists for juveniles, the amount of time adult Galapagos tortoises spend moving does not appear to vary between seasons (Cayot 1987) and we assumed no variation in distances moved throughout the year. Finally, we used an exponential growth curve to account for change in sizes of tortoises in time. We derived this growth curve from our own data on changes in sizes of 219 tortoises found at a yearly interval between year 2000 and 2003.

Detailed paths were recorded for each tortoise from each simulation, which visually resembled paths of tortoises from field studies (Figure 1.2, Hailey 1989). To stabilize the age distribution of tortoises, we let the simulation run for 14 years and only used the positions of tortoises for the last year of the simulation for the analyses. We assumed that nine hatchling tortoises left each known nest (n=211) yearly. Because we do not know of any published estimates of survival rates for populations of Galapagos tortoises, the survival rate was estimated by fitting a least-squares regression line to data on other species of tortoises. For species of tortoises of which survival has been studied in natural populations, approximately 50% of hatchlings survive first year and adult survival is much higher, often exceeding 90% (Turner et al. 1987; Iverson 1991;

Germano 1994; Pike & Seigel 2006). Sensitivity of the model to changes in survival rate was tested by repeating all analyses with a survival curve based on only 10% of hatchlings surviving during first year. The results did not differ qualitatively. We placed the simulated tortoises within the same geographic space as our study area by treating the origin coordinate from the simulation (0, 0) as the nest and randomly assigning tortoises to known nests. Coordinates for locations of nests were obtained during field observations and from the monitoring efforts of the Galapagos National Park. In order to account for all possible nests in the area, we supplemented data on nests that we found with data from a monitoring database compiled by the Galapagos National Park Service (2000-2003, Figure 1.1b). Thus we used the largest set of nest localities available, even if not all of the nests at those localities were successful every year.

Statistical analyses of distributional data

We determined the relation between modeled and observed frequencies of differently sized tortoises by nonlinear least squares regression and analysis of residuals. We predicted that if the spatial distribution of observed juvenile tortoises matched the null model, the distances to the nearest nest would not be significantly different between areas where the mean size of observed tortoises is similar to the mean size of simulated tortoises. We used ArcGIS software (ver. 9.2, Environmental Systems Resource Institute Inc., Redlands, CA, USA) to produce a grid that encompassed all study areas and whose cells measure 250m on the side. This coarse spatial scale lessens the impact of imperfect detection of nests and matches environmental data (see below). From this grid, we only selected cells that we visited in the field and for each one of these cells, calculated the mean size of simulated and observed tortoises. Using the Spatial Analyst extension of

ArcGIS software, we calculated Euclidean distances from the center of each cell to the center of the nearest known cell with a nest. For cells that contained a nest, we used the mean distance from any point within that cell to that cell's center (88.39m). No individual was counted twice in a cell but some were used more than once in the analyses if found in different cells. We used the mean size of simulated tortoises within a cell as a predictor variable in a non-linear regression, where the dependent variable was the distance to nearest known nest. Using the coefficients from the regression equation (derived with function 'nls' within the R statistical framework, R Development Core Team 2010), we then calculated standard residuals for each cells with values for observed tortoises. We considered a cell with observed values significantly different from the regression of simulation data if the absolute value of the standard residual was more than two.

Comparison of environmental characteristics

We tested whether abundance of differently-sized juveniles is related to different environments by first noting which cells were significantly different from simulated data and establishing groups of cells based on the mean sizes of tortoises within them. We used one-way ANOVA in SPSS software (SPSS for Windows, Rel. 17. 2009. SPSS Inc., Chicago, IL, USA) to compare environments between these groups of cells. Parametric assumptions were met and where homogeneity of variance was suspect, nonparametric tests confirmed that results from the general linear models were robust.

To quantify differences in the environment, we used a satellite-based measure of vegetative productivity. Data were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensors mounted on two different satellites launched in

2000 and 2002 by the US National Aeronautical and Space Administration (NASA). We used data from the Terra satellite for 2000 and 2001, and an average of the values obtained by Terra and Aqua satellites for 2002 through 2006. These data have the highest spatial (250m) and temporal (16d) resolution available globally (Justice et al. 2002). We used ERDAS Imagine software ver. 9.3 (ERDAS Inc., Altanta, GA, USA) to prepare a time series of 155 images of the MODIS 16-day vegetation index (MOD13Q1). The data were downloaded from the United States Geological Survey's Land Processes Distributed Active Archive Center (http://lpdaac.usgs.gov). For each 250m x 250m cell, this product provides an enhanced vegetation index (EVI) value, which is directly related to the amount of photosynthetic activity in the observed vegetation (Wilkie & Finn 1996). EVI has been especially developed to improve vegetation monitoring in areas of high biomass while at the same time reducing atmospheric influences (Huete et al. 2002). High values of EVI (maximum of 10,000) indicate high densities of green vegetation, while values near or below zero characterize land with no vegetation, including lava fields, water or bare soil. In order to increase the quality of data, we excluded any cells that received a quality rating lower than "good" by the NASA processing center. Because this resulted in missing data, we used the program TIMESAT (Jönsson & Eklundh 2004) to produce a seasonally smoothed time-series for each cell. We calculated EVI values using the Savitzky-Golay filter (window size set at 10) for a seven year period spanned by the data (23 data points per year). We obtained a yearly measure of EVI by summing all of the smoothed EVI values and dividing the total by seven (for the seven years of data). We used the yearly sum of raw EVI values as a statistic that best describes yearly productivity (Pettorelli et al. 2005) because EVI correlates strongly with vegetation biomass, leaf area and gross primary productivity (Xiao et al. 2004; Rahman et al. 2005).

Results

We observed 681 juvenile tortoises in 72 of the 192 cells (n=1 to 49 per cell) we visited. On the other hand, our simulation rendered 3,985 individual tortoises in 166 of all cells that we visited (n=1 to 912 per cell). The non-linear regression equation that best described the distances to nearest nests from cells with simulated tortoises was a power function (Figure 1.3). Because of heterogeneity of variances, we weighted the predictor variable by the power-of-the-mean model (Ritz & Streibig 2008). Based on which cells with observed data were significantly different from the simulation model, we divided cells into two groups: those where the mean sizes of juvenile tortoises were either smaller or larger than 51.5cm CCL (dashed vertical line of Figure 1.3). Of the 31 cells in the latter group, 14 cells (>45%) were significantly closer to nearest nests than predicted, two cells (<7%) were significantly further than predicted, and nearly half (n=15) were not significantly different from the null model. Thus cells where the mean size of juvenile tortoises was small did not differ from the null model, while those where the mean size of juvenile tortoises was large were at a wide range of distances from nearest nests; however, nearly half of those cells were closer to nests than predicted.

In areas where large juvenile tortoises are prevalent, annual productivity of vegetation, as a derivate from satellite measurements, was higher than in areas where the mean size of tortoises is small (Table 1.1, Figure 1.4). However, finer comparisons of the variation in the productivity of vegetation between groups of cells based on their deviation from the null distribution model reveal subtle relationships between productivity of vegetation in different areas and different groups of cells (Table 1.1). Productivity of vegetation was similar in cells close to nests, regardless of the mean size of juvenile tortoises within those cells. However, productivity of vegetation also did not differ between areas of where tortoises were large, regardless whether the grid cells were significantly different from the null distribution model or not. Therefore, areas where large juveniles are abundant vary with respect to annual productivity of vegetation, but include areas of productivity similar to those where nests and small juveniles are present.

Discussion

Frequencies of tortoises observed in the wild do not differ significantly from frequencies calculated in a null model based on random movements and indicate that juvenile tortoises that are small remain close to nesting areas. However, some areas near nests are occupied by larger tortoises at higher frequencies than predicted by the null model. It appears that after hatching, young tortoises do not disperse selectively but that some older, and therefore larger, tortoises remain close to nests in areas not frequented by small juveniles. In addition, larger juvenile tortoises occur in areas with a wider range of productivity of vegetation than smaller individuals. This indicates that habitat choices might be different for juvenile tortoises of different sizes.

Comparisons of observed and simulated data can often have differing results if variation in the parameters of the model has large effects on its output. However, in our null model of the distribution of tortoises based on their random movements we used parameters conservatively. For instance, we assumed that for each step a tortoise chooses an angle to either side of its body axis from a uniform probability function. Most animals have a tendency to move forward, and models that incorporate random movement often assume that probability distribution to be Gaussian (Turchin 1998). Using a Gaussian probability distribution would result in higher frequencies of tortoises further from nests, however we observed larger juveniles in cells closer to nesting areas which would still be significantly different when compared to the modeled data. It is unlikely that the results would be altered qualitatively. Similarly, different survival rates for hatchlings used in the model did not result in qualitative changes to results. We speculate that this is the result of the coarse scale of analysis, that is, the size of grid cells used in the analyses. Because small tortoises move only hundreds of meters at monthly time scales (MacFarland et al. 1974; Ortiz 2003), their movements are likely to be contained within a 250m x 250m cell or directly neighboring cells.

We concede that robustness of results from this observational study depends on how rates of detection affect the estimation of real rates or proportions and the spatial scales of analyses. If we consistently failed to detect juveniles of small sizes near nests, there would be a higher proportion of grid cells that are close to nesting sites with high frequencies of large juvenile tortoises in those cells. However, in many areas we found juveniles as small as 9.6 cm CCL likely because nesting areas are limited to low elevations where vegetation is open (Reeder & Riechert 1975; Itow 1992). Likewise, we did not find small juveniles far from known nesting areas, suggesting that imperfect detection of nests is unlikely to influence the results. Another potential limitation in the interpretation of results is the size of cell used in our analysis. The size of cell for analyses (250m x 250m) was determined by the scale of productivity data and the amount of tortoises encountered in each cell. Finer scale (smaller cells) would allow more resolution, but our concern was with sampling as much terrain as possible where juveniles were present. In addition, daily movements of tortoises were usually contained within one cell whereas finer scales of analysis would have to account for finer scale temporal movements of tortoises.

The hypothesis that the distribution of juveniles is dependent on the spatial pattern of nest sites is well supported for juveniles of small sizes (less than 50cm CCL). We only found small juveniles near nesting areas and their distribution did not vary from a random movement model. The limited distribution of nesting areas in the archipelago has also been proposed to result in higher numbers of females at low altitudes (where the nesting conditions are good) and higher number of males at higher elevations (MacFarland et al. 1974). Our results indicate that juvenile tortoises rely on nesting areas during early development and that some larger juveniles continue to use these habitats heavily. Limited data on a population of Galapagos tortoises from a different island suggest that movements of juveniles are not selective, at least on short time scales (Ortiz 2003). Our observations are also consistent with patterns of distribution from movements of juveniles of other species of tortoises, including gopher and desert tortoises (Freilich et al. 2000; Pike 2006).

Many larger juveniles can be found near nests, where productivity of vegetation is not as high as further away from nests and we propose that this pattern is likely related to a trade-off strategy that maximizes growth. Generally, animals distribute themselves between habitats based on decisions that relate to demands of foraging and avoidance of predators (Sutherland 1996) and ultimately, increase fitness (Fretwell & Lucas 1969). For non-reproducing juveniles, increased fitness means increased probability of survival to next size or age class, thus individuals should select habitats to maximize energy gains and consequently growth (Morris 2003; Morris et al. 2004). In case of Galapagos tortoises, which are herbivorous and ectothermic, this might translate into a trade-off between areas of open vegetation where body temperatures can be maintained higher, such as those close to nesting areas, and areas where it is harder to maintain high body temperatures because of more vegetation, but where there are more foraging opportunities because productivity of vegetation is higher. This assumes that juveniles of all sizes are generalist herbivores, which is likely because there is no evidence for major ontogenetic shifts in diet for adults (Cayot 1987). For very small tortoises such trade-offs either might not be present or exist at different scales (not measured here). This is because the microhabitats necessary for temperature regulation are likely to be present at very fine scales, e.g. it is very easy for a tortoise 15cm CCL to hide behind a lava outcrop. A similar trade-off, but at different scales, has been described for the Aldabra tortoise, where costs of movements to highly desirable habitats are balanced with the risk of overheating (Swingland & Lessells 1979).

Our findings that small juveniles are limited to nesting areas and that larger juveniles range near and away from nests have important consequences for management of repatriated and natural tortoise populations. Galapagos tortoises face multiple threats, primarily because of human activities and introduced mammals and ants (Fritts et al. 2000). While some populations are supplemented with captive-bred individuals, others are still in need of a thorough conservation assessment (Fritts et al. 2000; Márquez et al. 2004). The results from this study raise at least two important points. First, small juveniles concentrate within approximately 700m of nests, thus those areas are critical not only because of their importance for nest success but also for survival of juveniles. These areas should be given special emphasis in any management strategies. This could be especially important in regards to introduced species of mammals, such as burros that destroy nests (Fowler de Neira & Roe 1984). Second, population estimates must take into account the habitat specific frequencies of different tortoise sizes. Thus monitoring programs should account for differential ability to detect tortoises of different sizes not only because of their visibility, but location within the larger landscape.

The approach of using satellite-based measures of the environment within a coarse spatial scale can provide insights into ontogenetic patterns of distribution and directly inform landscape-level management strategies. However, detailed investigations on several topics would help to explain the mechanisms behind the observed distribution of juvenile tortoises within the landscape. Most important future needs include a finer scale examination of distribution patterns of juveniles and an empirical determination of the relationship between the index of productivity of vegetation and forage quantity and digestibility.

Literature Cited

Aguirre, G., G. A. Adest, and D. J. Morafka. 1984. Home range and movement patterns of the Bolson Tortoise, *Gopherus flavomarginatus*. Acta Zoologica Mexicana, nueva serie. Instituto de Ecología, Mexico, D.F., Mexico.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist **124**:255-279.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology **76**:2028-2043.

Caughley, G. 1978. The analysis of vertebrate populations. John Wiley and Sons, London, United Kingdom.

Caughley, G., and A. Gunn 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, MA, USA.

Cayot, L. J. 1987. Ecology of giant tortoises (*Geochelone elephantopus*) in the Galapagos Islands. Ph.D. dissertation. Syracuse University, Syracuse, NY, USA.

de Vries, T. J. 1984. The giant tortoises: A natural history disturbed by Man. Pages 145-156 in R. Perry, editor. Key Environments. Galápagos. Pergamon Press, New York, NY, USA.

Díaz-Paniagua, C., C. Keller, and A. C. Andreu. 1995. Annual variation of activity and daily distances moved in adult spur-thighed tortoises, *Testudo graeca*, in southwestern Spain. Herpetologica **51**:225-233.

Earhart, G. M., and P. S. G. Stein. 2000. Step, swim, and scratch motor patterns in the turtle. Journal of Neurophysiology **84**:2181-2190.

Earsom, S. 2000. Nesting ecology of the Galápagos giant tortoise (*Geochelone vicina*) during an episode of El Niño. M.S. Thesis. Department of Biology. University of New Mexico, Albuquerque, NM, USA.

Fowler de Neira, L. E., and J. H. Roe. 1984. Emergence Success of Tortoise Nests and the Effect of Feral Burros on Nest Success on Volcan Alcedo, Galapagos. Copeia **1984**:702-707.

Freilich, J. E., K. P. Burnham, C. M. Collins, and C. A. Garry. 2000. Factors affecting population assessments of Desert Tortoises. Conservation Biology **14**:1479-1489.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica **19**:16-36.

Fritts, T. H., H. L. Snell, L. Cayot, C. MacFarland, S. Earsom, C. Marquez, W. Llerena, and F. Llerena. 2000. Progress and priorities in research for the conservation of reptiles. Bullletin de l'Institut Royal des Sciences Naturelles de Belgique **SUPPLEMENT: 70**:39–45.

Germano, D. J. 1994. Biology of North American Tortoises: Comparative life histories of North American Tortoises. National Biological Survey, Fish and Wildlife Research **13**:175-185.

Hailey, A. 1989. How far do animals move? Routine movements in a tortoise. Canadian Journal of Zoology **67**:208-215.

Hailey, A., and I. M. Coulson. 1996. Temperature and the tropical tortoise *Kinixys spekii*: Constraints on activity level and body temperature. Journal of Zoology **240**:523-536.

Hengeveld, R. 1990. Dynamic biogeography. Cambridge University Press, New York, NY, USA.

Holt, R. D., J. H. Lawton, and K. J. Gaston. 1997. On the relationship between range size and local abundance: back to basics. Oikos **78**:183-190.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment **83**:195-213.

Itow, S. 1992. Altitudinal change in plant endemism, species turnover, and diversity on Isla Santa Cruz, the Galapagos Islands. Pacific Science **46**:251-268.

Iverson, J. B. 1991. Patterns of survivorship in turtles (order Testudines). Canadian Journal of Zoology **69**:385-391.

Ives, A. R., and E. D. Klopfer. 1997. Spatial variation in abundance created by stochastic temporal variation. Ecology **78**:1907-1913.

Jönsson, P., and L. Eklundh. 2004. TIMESAT - a program for analyzing time-series of satellite sensor data. Computers & Geosciences **30**:833-845.

Justice, C. O., J. R. G. Townshend, E. F. Vermote, E. Masuoka, R. E. Wolfe, N. Saleous, D. P. Roy, and J. T. Morisette. 2002. An overview of MODIS land data processing and product status. Remote Sensing of Environment **83**:3-15.

Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia **56**:234-238.

Krebs, C. J. 1978. Ecology: The experimental analysis of distribution and abundance. Benjamin-Cummings Publishing Company, San Francisco, CA, USA.

MacFarland, C. G., J. Villa, and B. Toro. 1974. The Galapagos giant tortoises (*Geochelone elephantopus*) Part I: Status of the surviving populations. Biological Conservation **6**:118-133.

Márquez, C., D. Wiedenfeld, H. Snell, T. Fritts, C. MacFarland, W. Tapia, and S. Naranjo. 2004. Estado actual de las poblaciones de tortugas terrestres gigantes (*Geochelone* spp., Chelonia: Testudinae) en las Islas Galápagos. Ecología Aplicada **3**:98-111.

Marsh, L. M., and R. E. Jones. 1988. The form and consequences of random walk movement models. Journal of Theoretical Biology **133**:113-131.

McMullen, C. K. 1999. Flowering plants of the Galapagos. Cornell University Press, Ithaca, NY, USA.

McNamara, J. M., and A. I. Houston. 1986. The common currency for behavioral decisions. The American Naturalist **127**:358-378.

Morán Guerra, Á. J. 2003. Biogeografía y distribución estacional de la tortuga terrestre gigante (*Geochelone nigrita*) de la Isla Santa Cruz, Galápagos, Ecuador. Tesis de Licenciatura. Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia **136**:1-13.

Morris, D. W., J. E. Diffendorfer, and P. Lundberg. 2004. Dispersal among habitats varying in fitness: reciprocating migration through ideal habitat selection. Oikos **107**:559-575.

Muegel, L. A., and D. L. Claussen. 1994. Effects of slope on voluntary locomotor performance in the turtle, *Terrapene carolina carolina*. Journal of Herpetology **28**:6-11.

Ortiz, A. G. 2003. Improving efficiency of restoration ecology programs - dispersal patterns of repatriated Galápagos tortoises. M.S. Thesis. Department of Biology. University of New Mexico, Albuquerque, NM, USA.

Packard, M. J., G. C. Packard, and T. J. Boardman. 1982. Structure of eggshells and water relations of reptilian eggs. Herpetologica **38**:136-155.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, New York, NY, USA.

Pettorelli, N., J. Vik, A. Mysterud, J. Gaillard, C. Tucker, and N. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution **20**:503-510.

Pike, D. A. 2006. Movement patterns, habitat use, and growth of hatchling tortoises, *Gopherus polyphemus*. Copeia **2006**:68-76.

Pike, D. A., and R. A. Seigel. 2006. Variation in hatchling tortoise survivorship at three geographic localities. Herpetologica **62**:125-131.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahman, A. F., D. A. Sims, V. D. Cordova, and B. Z. El-Masri. 2005. Potential of MODIS EVI and surface temperature for directly estimating per-pixel ecosystem C fluxes. Geophysical Research Letters **32**.

Reeder, W. G., and S. E. Riechert. 1975. Vegetation Change Along an Altitudinal Gradient, Santa Cruz Island, Galapagos. Biotropica **7**:162-175.

Ritz, C., and J. Streibig 2008. Nonlinear regression with R. Springer, New York, NY, USA.

Rodhouse, P., R. W. A. Barling, W. I. C. Clark, A. L. Kinmonth, E. M. Mark, D. Roberts, L. E. Armitage, P. R. Austin, S. P. Baldwin, A. d. A. Bellairs, and P. J. Nightingale. 1975. The feeding and ranging behaviour of Galapagos giant tortoises (*Geochehne elephantopus*) The Cambridge and London University Galapagos Expeditions, 1972 and 1973. Journal of Zoology **176**:297-310.

Sancho, A. C. 1988. Influencia de la temperatura de incubación en el sexo y parámetros para el reconocimiento del sexo de la Tortuga gigante de Galápagos (*Geochelone elephantopus*) e histología de la gónada iguana terrestre (*Conolophus subcristatus*). Tesis de Biología. Pontificia Universidad Católica, Quito, Ecuador.

Schmidt-Nielsen, K. 1984. Scaling: why is animal size so important? Cambridge University Press, Cambridge, UK.

Sinclair, A. R. E., J. M. Fryxell, and G. Caughley 2006. Wildlife ecology, conservation, and management. Blackwell Publishing, Malden, MA, USA.

Slevin, J., T. Fritts, and P. Fritts. 1982. Race with Extinction: Herpetological Notes of JR Slevin's Journey to the Galapagos 1905-1906. Herpetological Monographs **1**.

Snell, H., and S. Rea. 1999. The 1997–98 El Niño in Galápagos: can 34 years of data estimate 120 years of pattern? Noticias de Galápagos **60**:11-20.

Soulé, M. E., and G. H. Orians, editors. 2001. Conservation biology: research priorities for the next decade. Island Press, Washington, DC, USA.

Sutherland, W. 1996. From individual behaviour to population ecology. Oxford University Press, New York, NY, USA.

Swingland, I., and C. Lessells. 1979. The natural regulation of giant tortoise populations on Aldabra Atoll. Movement polymorphism, reproductive success and mortality. Journal of Animal Ecology **48**:639-654.

Torres Corral, M. d. L. 2001. Distribución, estructura poblacional y demografía de la tortuga gigante *Geochelone nigrita* (Reptilia: Testudines) en la Isla Santa Cruz, Galápagos. Tesis de Licenciatura. Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Tracy, C. R., and H. L. Snell. 1985. Interrelations Among Water and Energy Relations of Reptilian Eggs, Embryos, and Hatchlings. American Zoologist **25**:999-1008.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in plants and animals. Sinauer Associates, Sunderland, MA, USA.

Turner, F. B., P. A. Medica, and R. B. Bury. 1987. Age-size relationships of Desert Tortoises (*Gopherus agassizi*) in southern Nevada. Copeia **1987**:974-979.

Van Denburgh, J. 1914. John Van Denburgh's The Gigantic Land Tortoises of the Galapagos Archipelago. Society for the Study of Amphibians and Reptiles, USA.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**:393-425.

Wilkie, D. S., and J. T. Finn 1996. Remote sensing imagery for natural resources monitoring: a guide for first-time users. Columbia University Press, New York, NY, USA.

Wren, K., D. L. Claussen, and M. Kurz. 1998. The effects of body size and extrinsic mass on the locomotion of the ornate box turtle, *Terrapene ornata*. Journal of Herpetology **32**:144-150.

Xiao, X., Q. Zhang, B. Braswell, S. Urbanski, S. Boles, S. Wofsy, B. Moore Iii, and D. Ojima. 2004. Modeling gross primary production of temperate deciduous broadleaf forest using satellite images and climate data. Remote Sensing of Environment **91**:256-270.

Zani, P. A., J. S. Gottschall, and R. Kram. 2005. Giant Galapagos tortoises walk without inverted pendulum mechanical-energy exchange. Journal of Experimental Biology **208**:1489-1494.

Table 1.1. Results from one-way ANOVA tests that compare groups of grid cells where mean sizes of tortoises and their deviation from a null model of distribution differ. See Fig. 3 for correspondence.

Comparison	df	F	*p*
Small juveniles X Large Juveniles	1,69	7.378	0.008
Small juveniles X Large Juveniles, excluding grid cells that are significantly different from the null model and far from nearest nests	1,67	5.409	0.023
Small juveniles X Large Juveniles, only grid cells that are significantly different from null distribution model and close to nearest nests	1,52	2.161	0.148

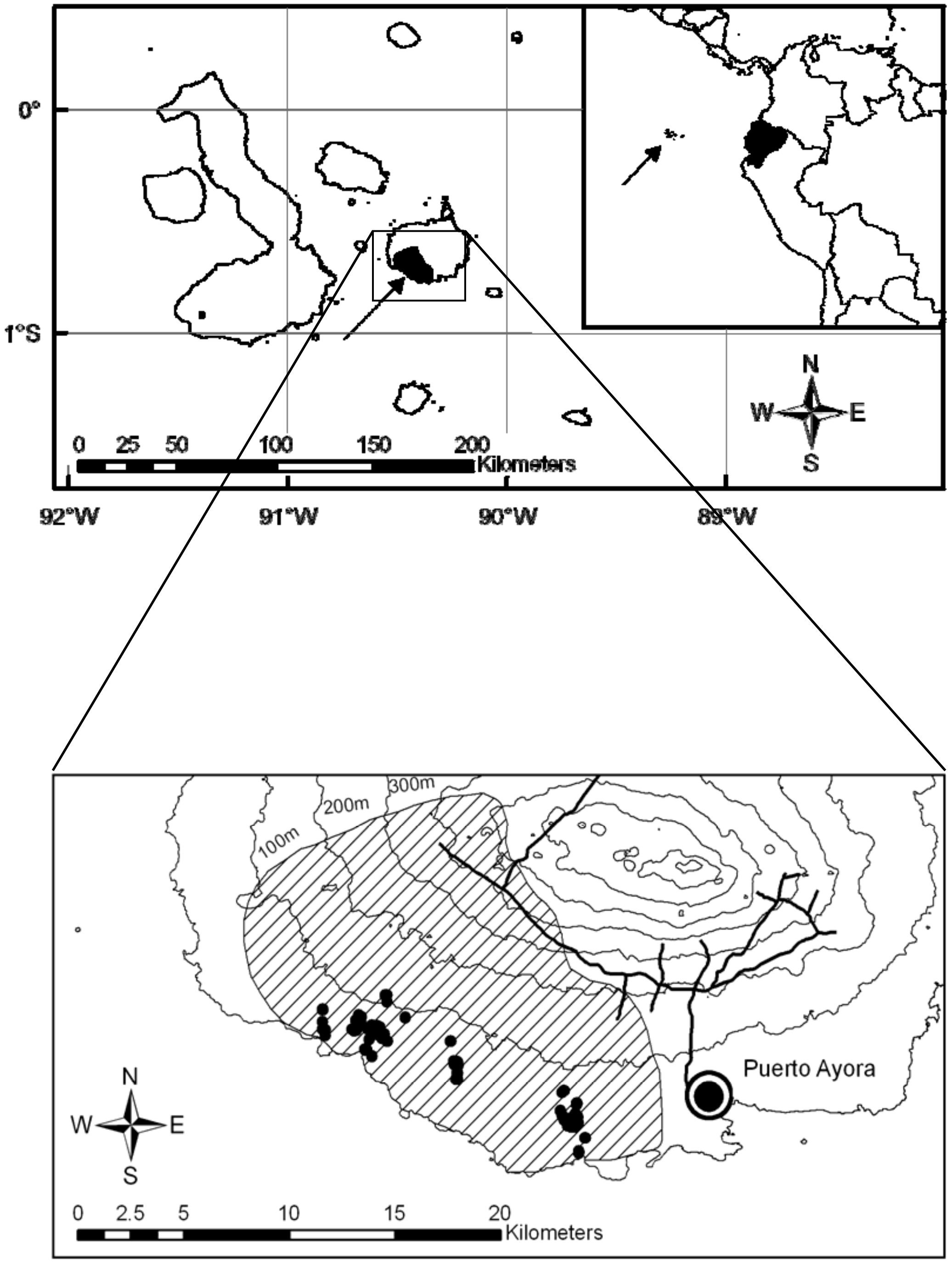

Figure 1.1. The location of the studied population of tortoises (*Chelonoidis nigra nigrita*) is the southwestern part of Isla Santa Cruz, in the Galapagos Archipelago, approximately 1000km west of the coast of Ecuador. The detailed map shows the distribution of known tortoise nests in years 2000–2003 (black dots) in relation to the approximate area where tortoises are known to occur (hatched). Thick lines indicate paved roads from the coastal town of Puerto Ayora and contour lines are at 100m intervals.

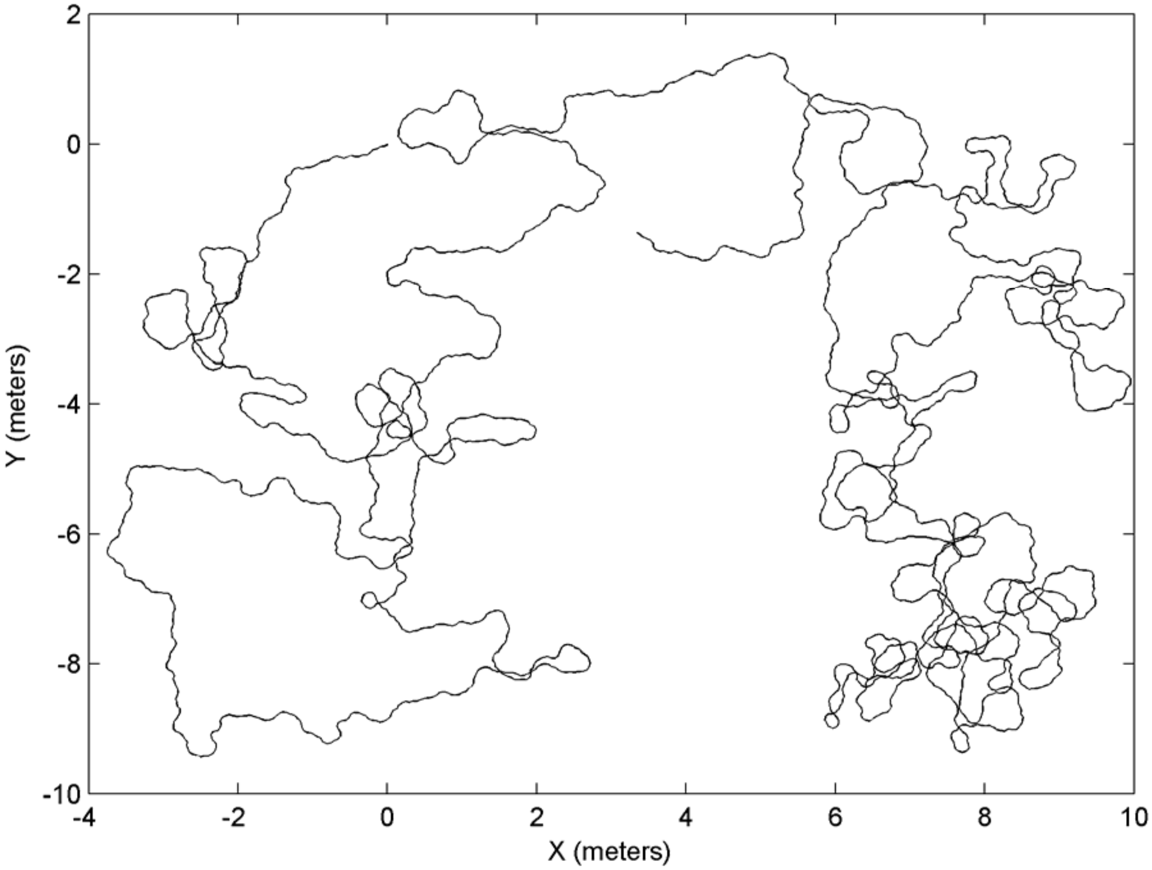

Figure 1.2. An example of a simulation used for the null model of distribution of juvenile tortoises. The line shows the path of one tortoise for five days and is plotted in an arbitrary Cartesian coordinate system. Note that despite a correlated random walk (directional angle is always chosen relative to the previous directional angle), the simulated tortoise frequently maintains direction but also turns around.

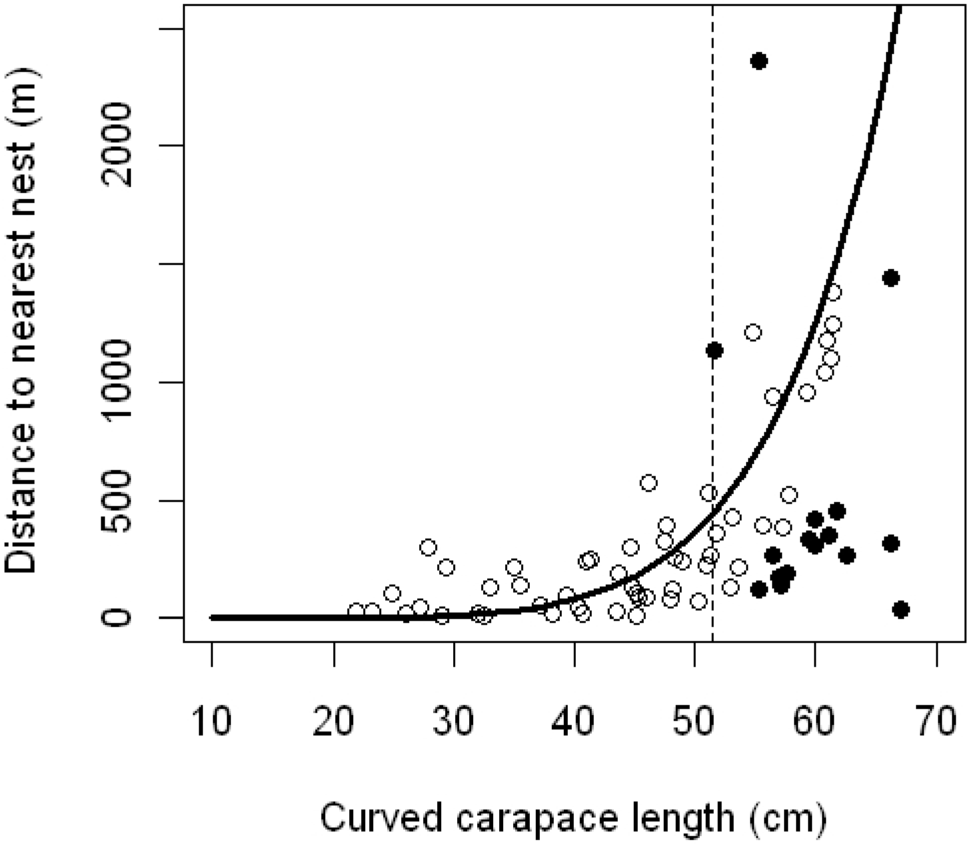

Figure 1.3. Observed relationship between mean sizes of tortoises within a 250m x 250m cell and distance to nearest known nest. Power function line indicates best fit of a simulation model based on random movement of tortoises. Filled circles are cells whose residuals are two standard deviations away from that function. Hatched line at 51.5cm curved carapace length separates the group of cells where no cells significantly different from the line occur.

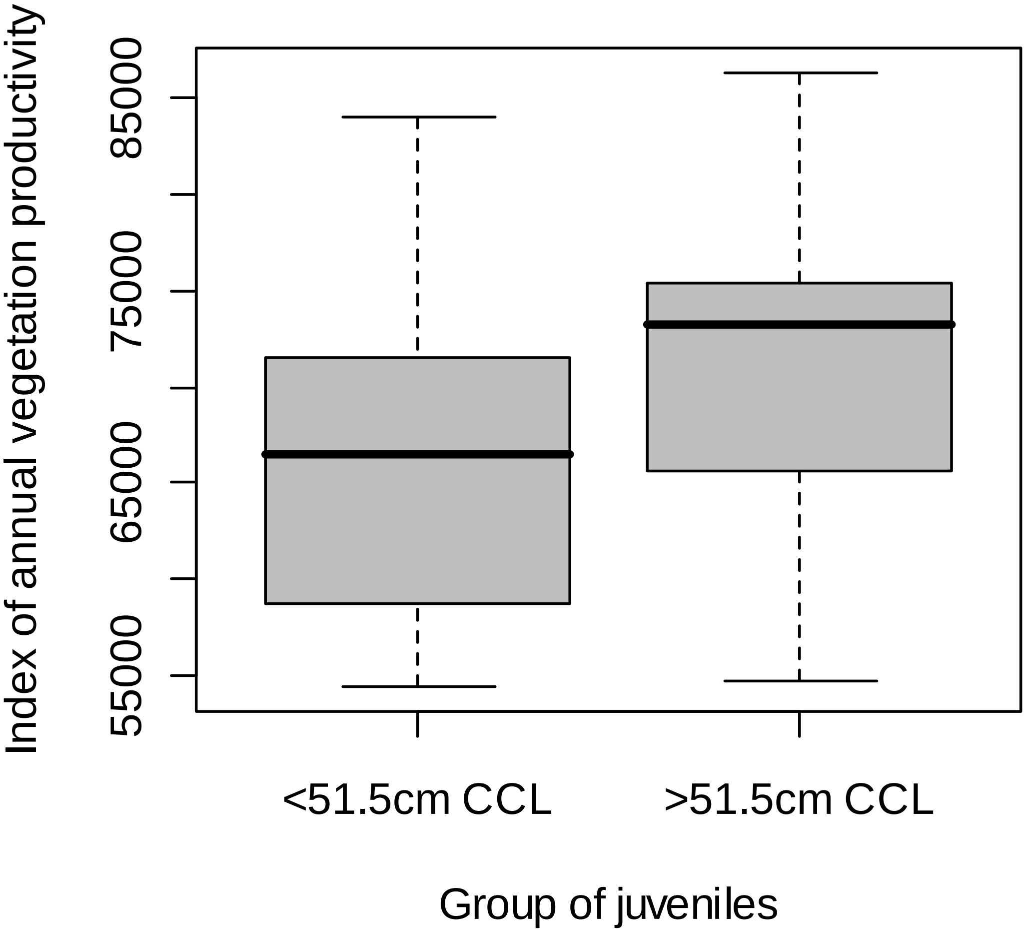

Figure 1.4.Difference in a seven-year average of an index of annual vegetation productivity between areas where the mean curved carapace lengths (CCL) of tortoises are small (<51.5cm) and large (>51.5cm).

Appendix

Functions used in Matlab to generate the simulated distribution of tortoises.

```
function rwm(angle, runtimes, days)
%---------------------------------------------------------------
% Simulates a correlated random walk movement by a tortoise
% Input parameters are [angle] [runtimes] [number of days]
% angle = max angle for either left/right turn, chosen at random
% runtimes = number of simulations
% number of days = number of days since leaving nest
%---------------------------------------------------------------
% default settings are angle=45deg, runtimes=2 and days=30
if (nargin < 3)
    angle = 45;
    runtimes = 1;
    days = 365;
end
numdays = int32(days);
tspan=linspace(0,days-1,days);
[t,f]=ode113('turtlegrowth',tspan,10);
sizeofstep = 0.0115*(((f/21.263).^2.8433)*1000).^0.33; % depends on tort size
stepsperday = int32(((4.42.*f)-7.43).*(sizeofstep.^-1)); % depends on step and tort size
numsteps = int32(sum(stepsperday));
rand('state', sum(100*clock));

for i = 1:runtimes
    position = zeros(4, numsteps+1);
    position(1,1) = 0;
    position(2,1) = 0;
    position(3,1:2) = 1;
    position(4,1:2) = i;
    initangle = 360*rand(1);
    [polx, poly] = pol2cart(initangle*pi/180,sizeofstep(1));
    position(1,2) = (position(1,1)+polx);
    position(2,2) =(position(2,1)+poly);
    previousangle = initangle;
    stepstaken = 2;
    for d = 1:numdays
        for s = 1:stepsperday(d)
            stepsize = sizeofstep(d);
            angleatstep = previousangle-angle+2*angle*rand(1);
            [polx, poly] = pol2cart(angleatstep*pi/180,stepsize);
            position(1, stepstaken+1) = (position(1, stepstaken)+ polx);
            position(2, stepstaken+1) = (position(2, stepstaken)+ poly);
            position(3, stepstaken+1) = d;
            position(4, stepstaken+1) = i;
            previousangle = angleatstep;
            stepstaken = stepstaken + 1;
    end;
end;

%Write data to output file named after the parameters chosen
outputfile = strcat(sprintf('%04.0f',i),strcat('_1000step_',int2str(numdays),'days.tab'));
fid=fopen(outputfile,'wt');
fprintf(fid,'%10.2f\t %10.2f\t %10.0f\t %10.0f\n',position(:,1:1000:end));
fclose(fid);
end;

%define function of tortoise growth
function df=turtlegrowth(t,f)

% using percent growth per month divided by initial CCL from all tortoises
% period between growth measurements was 237d to 494d (one year's growth)
df=(3.217/30.4375)*f.*exp(-0.029*f)/100;
```

Chapter 2 : Body size of Galapagos tortoises covaries with environmental primary productivity but not phylogeny

Abstract

Phylogenetic history and ecological selection pressures can influence maximal body sizes in many species of animals. Galapagos tortoises are particularly suitable for examination of variation in body size because of the diversity of adult sizes between taxa, differences between areas they inhabit, and the complex relationships between their populations. We investigated how variation in body size of different populations of Galapagos tortoises relates to phylogeny and primary productivity of the environment. We tested predictions drawn from previous work and in light of recent indications that the geological history of the islands is not entirely consistent with the diversification of tortoise populations. Data on tortoises and their phylogeny was gathered from observations and published studies, whereas productivity of the environment was estimated with remotely sensed imagery. Maximal body size measured, as curved width of carapace, ranged twofold (767-1532mm) in 11 taxa while measures of primary productivity, where tortoises occur, ranged two- to threefold. We did not find an association between relationships of tortoise populations and their body size. However, patterns of increased body size covary with increased primary productivity within areas where individual populations occur. This suggests that body sizes in different populations of Galapagos tortoises are a consequence of rapid diversification and adaptation to local conditions.

Introduction

Phylogenetic history and ecological factors can result in strikingly different body sizes, even within closely related taxa (e.g. Case 1978, Boback 2003). Body size is an important characteristic because it influences many physiological and ecological parameters (Peters 1983; Calder 1984; Brown & Maurer 1986) and often covaries with life history variables (Stearns 1992; Blanckenhorn 2000). Ecological hypotheses proposed to explain differing body sizes include competition, predation and changes in resource availability (e.g.: Foster 1964; Case 1978; Heaney 1978; Lomolino 1985; Madsen & Shine 1993; Adler & Levins 1994; Hasegawa 1994). However, phylogenetic effects, that is, the influence of ancestral form on the phenotypes of descendants (Blomberg & Garland 2002), potentially restrict the evolution of body size. Phylogeny influences body size for closely related mammal taxa (Smith et al. 2004) and shapes many life-history characters among lizards (Dunham & Miles 1985; Dunham et al. 1988; Miles & Dunham 1992). Although on short time scales a genetic component to body size has been documented for several reptiles (Tracy 1999; Wikelski & Romero 2003), it is not clear whether phylogenetic patterns of body size occur within turtles (Lomolino 2005; but see Price & Phillimore 2007). In this study, we analyze variation in body size among taxa of Galapagos tortoises and its relationship to their phylogeny and ecology.

Galapagos tortoises are particularly suitable for questions about body size because of the diversity of their sizes, habitats and geographical relationships between their populations. First, both the size and shape of their bodies vary greatly between populations (Van Denburgh 1914; Fritts 1983) and the islands and volcanoes they inhabit offer a wide range of ecological conditions (Perry 1984; McMullen 1999). The pattern of variation in body size is notable because the mean size of adults within populations correlates with a subjective index of moisture availability, suggesting ecological selection pressures on body size (Fritts 1983). Second, Galapagos tortoises have few native predators and are the larger of the two native reptilian herbivores on the islands. Thus variation in body size is unlikely to have evolved in response to other ecological factors, such as predation or interspecific competition. Finally, taxa of Galapagos tortoises represent distinct lineages that diversified approximately in parallel to the geological formation of the islands (Caccone et al. 1999; Caccone et al. 2002; Ciofi et al. 2002). Thus despite some genetically identifiable populations having diverged less that 0.5 mya (Caccone et al. 2002), current variation in body-size between taxa could be strongly related to their evolutionary history. Moreover, early descriptions of evolutionary relationships between Galapagos tortoises relied exclusively on size and shape of their carapace (Van Denburgh 1914).

We test several hypotheses with regards to the ecological and phylogenetic influences on patterns of body size. We first evaluate influence of phylogeny on variation in body size and then focus on ecological resources. Body size is expected to covary with availability of resources because maintenance of large bodies, despite lower metabolic requirements per gram of body weight, ultimately requires more energy. To quantify ecological resources for these herbivorous tortoises, we calculate direct metrics of vegetative productivity for areas where different populations of tortoises occur. Specifically, we consider differences in (1) yearly productivity of vegetation, (2) its availability in space (within area where tortoises occur), and (3) seasonal differences in its availability. If vegetation available to primary consumers relates to body size, we expect body sizes to increase in areas that are more productive both temporally (yearly productivity) and spatially (high vegetative productivity in at least part of an area occupied). Large body sizes are also expected in areas where seasonal differences are greatest because selection could work to allow for greater storage of energy during times of food shortage. We contrast the productivity within an area with its spatial availability because seasonal movements of Galapagos tortoises to areas of high productivity are well known and have been quantified for some populations (Morán Guerra 2003). Analyses of the evolutionary ecology of Galapagos tortoises allow for separating ecological and phylogenetic factors involved in determining body size in their populations while at the same time, provide insight into the capacity of tortoises to adapt to changing environments.

Methods

Study area

This study included most taxa of Galapagos tortoises that occur in the Galapagos archipelago, which is located approximately 1000km west of continental Ecuador. The Galapagos Islands are volcanic in origin, with the oldest and most eroded islands in the east (Isla Española and Isla San Cristóbal), and the youngest islands containing active volcanoes (Isla Isabela and Isla Fernandina) in the west (McBirney & Williams 1969; Geist 1996). The highest elevation reaches 1707m on Volcán Wolf on Isla Isabela. Because of seasonality associated with ocean currents, the climate on some islands, especially those low in elevation, is very dry when compared to other tropical archipelagos. In addition, the amount of precipitation varies with elevation and aspect and is highly variable year-to-year, particularly near the coast. For example, during dry years the arid coastal region of Isla Santa Cruz receives only about 13.5% of the average 1110mm of rain that falls at 194m a.s.l. but up to 71% of it in the wettest years (Snell & Rea 1999). The warm season (January to May) is caused by warm ocean currents from the north and it is during this period where heavy rainfall occurs and the productivity of lowland vegetation reaches its peak. During the cool season (June to December), cold waters from the south result in cooler air temperatures and, while the lowlands are dry, higher elevations are almost constantly wet due to a mix of rain and fog. Vegetation communities vary with aspect and elevation and can be broadly generalized into a littoral zone, arid lowlands, and moist uplands (Johnson & Raven 1973). Tortoises occur in both the arid and moist zones.

Tortoise populations and body sizes

We use data from 11 taxa of Galapagos tortoises occurring on seven islands in the Galapagos archipelago (Figure 2.1). Taxonomic status of Galapagos tortoises has long been debated (Zug 1997) and different authors have treated different taxa as species or subspecies (Pritchard 1967; Ernst & Barbour 1989; Bonin et al. 2006). In our analysis, we did not include populations of tortoises from the southern volcanoes of Isla Isabela (Cerro Azul and Sierra Negra), with the exception of a population from the western flank of Cerro Azul, at Caleta Iguana. Although relationships between different populations found near those two volcanoes have been made clearer by recent genetic analyses (Ciofi et al. 2006), data on their distribution and sizes are scarce and complicated by many taxonomic revisions. In addition, the southern coast of Isla Isabela was colonized by humans in the late 1800’s and since then, the accompanying introduction of animals and hunting of tortoises has severely fragmented tortoise populations (Fritts et al. 2000). In order to delineate the spatial extent of each population of tortoises, we combined previously published maps (MacFarland et al. 1974) with our own data. Because in Galapagos some areas are dominated by inland water or lava of various ages and are not inhabitable by tortoises, we further limited the extent of occurrence of tortoises to those areas that are vegetated. We derived this vegetation mask from remotely sensed imagery of fine spatial resolution (30m pixels). We used a series of SPOT images (Satellite Pour l'Observation de la Terre; SPOT Image SA, Toulouse, France) collected in 1999 and processed in ArcView 3.2 (ESRI Inc., Redlands, CA, USA). The mask excluded all areas with a vegetation index of less than 0, which we calculated as a sensor-specific Normalized Difference Vegetation Index (Wilkie & Finn 1996).

Sizes of tortoises were gathered from published literature (Van Denburgh 1914; Fritts 1983), unpublished theses (Torres Corral 2001; Morán Guerra 2003), and our own observations recorded between 2001 and 2003 during other studies. We focused on the measurements of the carapace as indicative of body size and did not include body mass because of lack of its availability for some populations and its large seasonal variability in individual tortoises (unpublished data). For each population, we calculated a measure that is based on the curved width of the carapace of males. We limited our analysis to males because females tend to be much smaller and could be confused with sub adult males in the field. Curved width of carapace is a particularly appropriate for Galapagos tortoises because variability in the height of the frontal opening (the saddleback morphology unique to some populations) limits the usefulness of carapace length. The measure of size is an average of the maximum and mean measurements of curved carapace width for males from each data source, weighted by the number of sampled tortoises in that data source (Figure 2.1, Table 2.1). This measure simultaneously minimizes the effects of sub adults on the average adult size and the effect of extreme values for the maximum. Although the combined data for each population could be skewed by differences in size structure between populations, we did not have access to individual measurements in each case. Given the variety of data sources, it is unlikely that sub adults were disproportionately recorded in each population.

Phylogeny and measures of primary productivity

To test whether body size among different taxa of tortoises relates to their phylogeny, we constructed a phylogenetic correlogram following Gittleman and Kot (1990). We produced two matrices of genetic distances from the analysis of mitochondrial DNA (mtDNA) by Caccone et al. (2002). That analysis was based on 161 individuals and included sequences for six regions of mtDNA that total approximately 4,500 base pairs. We used branch lengths from a maximum-parsimony consensus tree as presented in figure four and, as a more conservative test, the number of nodes only between each pair of populations. To test the null hypothesis of no overall correlation between body size and phylogeny, we calculated the Moran's *I* coefficient with the APE package written for the R statistical framework (Paradis et al. 2004).

To quantify the availability of primary productivity for these large herbivorous tortoises, we used an integrative measure based on satellite imagery. Data were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensors mounted on two different satellites launched in 2000 and 2002 by the US National Aeronautical and Space Administration (NASA). We used data from the Terra satellite for 2000 and 2001, and an average of the values obtained by both Terra and Aqua satellites for 2002 through 2006. Although the data span only seven years, they have the highest spatial (250 m) and temporal (16 d) resolution available globally (Justice et al. 2002). We used a time series of 155 images of the product referred to as MODIS 16-day vegetation index (MOD13Q1), which were obtained from the United States Geological Survey's Land Processes Distributed Active Archive Center (http://lpdaac.usgs.gov). For each 250m x 250m pixel, this product provides an enhanced vegetation index (EVI) value. This index represents the difference in reflection between the near infrared and red parts of the electromagnetic spectrum, which in turn is directly related to the amount of photosynthetic activity in the observed vegetation (Wilkie & Finn 1996). High values of EVI (maximum of 10000) indicate high densities of green vegetation, while values near or below zero characterize land with no vegetation, including lava fields, water or bare soil. We use raw EVI values (data range -850 to 9855) because they correlate strongly with vegetation biomass, leaf area and gross primary productivity (Huete et al. 2002; Xiao et al. 2004; Rahman et al. 2005) and other ecologically meaningful factors, such as availability of shade (Justice et al. 2002; Huete et al. 2006). In order to increase the quality of data used in this study, we excluded any pixels that received a quality rating lower than "good" by the NASA processing center. We also excluded images from analysis when good quality pixels covered less than 50% of the area of interest. This resulted in statistics for each area being based on between 68 and 151 images out of the complete time series of images available (n=155). There was no association between the number of images for a season (hot or cold) and the area of interest (X^2 test, X^2=14.33, p > .23), thus despite a variable number of images used, both wet and dry seasons were represented adequately for each area. We applied a 5x5 low-pass smoothing kernel to reduce any effect of outliers or rogue pixels when calculating EVI values across space. All processing of satellite imagery was done with LDOPE Tools (Earth Resources Observation and Science Center, United States Geological Survey, Sioux Falls, SD, USA) and ERDAS Imagine software (ver 9.1, Erdas Inc., Atlanta, GA, USA).

For each spatially distinct taxa of tortoises, we expressed data on primary productivity in that area in three ways: (1) total energy available, (2) maximum energy available spatially, and (3) seasonal amplitude of energy availability. The total energy available was calculated as the yearly mean of mean EVI values for an area, whereas the maximum amount of primary productivity available spatially was calculated as a yearly average of maximum EVI values in each area. Seasonal amplitude in primary productivity was derived by calculating a seven year EVI time-series within the program TIMESAT (Jönsson & Eklundh 2004).

We used ANOVA and linear regression techniques to analyze the relationships between primary productivity and body size. To test the appropriateness of including different primary productivity measures, we first compared productivity measures for each area populated by tortoises with a one-way ANOVA. The overall primary productivity available to tortoises (yearly mean) was transformed to its natural logarithm to better satisfy the assumption of equality of variances (Quinn & Keough 2002). We then regressed body size on primary productivity measures to describe the relationship and assess the importance of each variable. All statistical analyses were done within the R statistical framework version 2.8 (R Development Core Team 2010).

Results

Analyses of the correlation between phylogeny and body size did not find a significant relationship regardless of the method of comparison. The null hypothesis of no overall correlation was not rejected in a test based on branch lengths (Moran's I = -0.06, p > 0.76). Similarly, a test with the number of nodes was also statistically non significant (Moran's I = -0.08, p > 0.80).

There were significant differences between areas inhabited by tortoises with respect to measures of primary productivity. Islands low in elevation (Isla San Cristóbal, Isla Pinzón and Isla Española) and the two northernmost volcanoes on Isla Isabela (Volcán Wolf and Darwin) were the least productive on a yearly basis, while southwestern Isla Santa Cruz and Isla Santiago were the most productive (Figure 2.2a). Yearly means of productivity, after transformation to their natural logarithm, varied significantly among all areas of interest (one way ANOVA: $F_{10,1293}$=120.74, p<.001). Likewise, maximum primary productivity available spatially was significantly different between different islands and volcanoes (one way ANOVA: $F_{10,1293}$=252.84, p<.001; Figure 2.2b). On the other hand, seasonal amplitude in productivity was different between only a few areas. Although overall it varied significantly at the α=0.05 level (one way ANOVA: $F_{10,52}$=2.694, 0.01<p<0.05), only 8 of the 55 possible pairwise post hoc comparisons were statistically significant.

The relationship between body size and total primary productivity could be described by a statistically significant linear regression model (R^2=0.4818, $F_{1,9}$=8.367, p<.05). A linear model based on maximum productivity available in an area explained a much higher percentage of variation in body size (R^2=0.7608, $F_{1,9}$=28.62, p<.001; Figure

2.3). A measure of seasonal differences in productivity was not significantly related to body size (R^2=0.0863, $F_{1,9}$=0.85, p>0.38). Comparisons based on adjusted R^2 did not find any significant multiple regression models (with or without interactions) that were better than a linear model based on maximum productivity alone.

Discussion

Although we did not find that variation of body sizes of tortoises related to their phylogeny, the maximum amount of primary productivity available throughout a year explained over 75% of variation in body size for adult males of Galapagos tortoises. Seasonal amplitude in primary productivity did not relate to body size and a yearly mean of primary productivity covaried weakly, likely because of differences in types and availability of vegetation within each area.

Measures of primary productivity obtained remotely by satellites have inherent limitations that relate to the lack of verified correspondence to ‘on the ground’ conditions. However, when sensors fly frequently across large areas, satellite images are the only consistent source of data for remote and logistically expensive places such as Galapagos. Additionally, the correlation of ecologically meaningful factors, such as availability of shade, with values obtained from the satellite is well supported for the MODIS sensor, which we used as our data source (Huete et al. 2002; Justice et al. 2002; Xiao et al. 2004; Huete et al. 2006). Tree cover could potentially confuse the interpretation of satellite imagery as it relates to availability of vegetation for tortoises. However, tree canopy appears to be relatively constant at different altitudes and rarely exceeds 50% (Reeder and Riechert 1975). Comparisons of primary productivity characteristics between areas highlight the spatial heterogeneity of vegetation within these areas. This and movements of male tortoises between seasons within an area further limit interpretation of the results. It is likely that primary productivity relates even more strongly to body size in males if foraging requirements and seasonal migration patterns for each population were to be examined in detail. This is expected because adults appear to be selective in their diets with respect to changes in water availability between seasons (Cayot 1987).

Despite our coarse-scaled approach, the results are consistent with selection acting on body size due to direct effects of resource availability (Case 1978; Heaney 1978; Lomolino 1985). In particular, our findings confirm the analyses by Fritts (1983, 1984), who found strong correlations between size and a moisture index based on sun exposure and terrain elevation. In at least two other taxa of herbivorous tortoises body size increases with latitude or cooler environments (Willemsen & Hailey 1999; Sacchi et al. 2007), suggesting effects of the environment at coarse scales. In other reptiles, density of prey or some measure of primary productivity also covaries with body size. For example, in herbivorous *Sauromalus* lizards, body size of adults is positively correlated with amount of local winter precipitation, which in turn affects the availability of forage (Case 1976). In marine iguanas, unique herbivores dependent on algal growth for forage, energy also limits body size (Wikelski et al. 1997); however, akin to Galapagos tortoises, phylogeny does not relate to their body sizes (Wikelski 2005). Boback (2003) found a similar pattern among four families of snakes, where phylogeny was not relevant but species of snakes were either small or big depending on availability of prey. In snakes, a response to resources on short evolutionary scales seems to be present at finer taxonomic scales as well (Keogh et al. 2005; Meik et al. 2010). However, the covariation between availability of resources and sizes of tortoises does not help to explain the lack of the effect of phylogeny.

We did not find that phylogenetic relationships between populations of Galapagos tortoises had any association to their body sizes. There are several factors that could account for lack of correlation. First, reptiles have been shown to adapt quickly to new environments, including rapid changes in body size (Losos et al. 1997; Losos et al. 1998) or morphology and social structure (Herrel et al. 2008). In addition, despite their long generation times, Galapagos tortoises have among the highest recorded rates of mtDNA evolution for ectotherms (Caccone et al. 2004). Finally, evolutionary response to environmental conditions is probably enhanced by low rates of gene flow between populations. In the Galapagos Archipelago, oceanic currents that are undoubtedly involved in interisland dispersal probably prevent frequent two-way exchange of individuals between populations. Thus if populations of Galapagos tortoises are evolving independently in response to environmental conditions and at rates similar (or higher) to other reptiles, then phylogenetic relationships would not affect changes in body size among populations and our analyses support this hypothesis.

Specific mechanisms involved in determining body sizes of Galapagos tortoises most likely relate to individual growth rates. Growth rate in other tortoises co varies with amount of energy available and temperatures adequate to process it (Jackson et al. 1976; Willemsen & Hailey 1999). In Galapagos, areas of continually high primary productivity provide not only more opportunities for foraging, but also a variety of microenvironments for thermoregulation. Moreover, the tropical climate of Galapagos Islands has relatively small seasonal changes in temperature when compared to extreme northern or southern latitudes and therefore allows for tortoises to grow continually. When species of tortoises are compared worldwide, despite different types of relationships between geography and body size at the species level, large-bodied tortoises occur only in environments with high average annual temperatures (Hailey & Coulson 1999).

Models of the evolution of life history traits are consistent with the observed pattern of variation of body sizes in Galapagos tortoises. Palkovacs (2003) calculated that increased body sizes were expected in case of reduced extrinsic mortality (predator release) while reduced resource availability would result in decreased body size. These predictions are well supported in populations of Galapagos tortoises. The tortoises are the largest native vertebrate herbivores on Galapagos Islands thus direct competition is only likely from conspecifics and there’s no evidence of a major role of any predators. Consequently, their body size is unlikely to relate to pressure from predators or interspecific competition. Furthermore, on most productive islands, tortoises are large, but on least productive islands, there is likely intense competition and higher relative densities of conspecifics. This pattern has led to proposition of several hypothesis explaining the evolution of different morphotypes (dome versus saddle-backed carapaces, Fritts 1983, 1984). Testing these hypotheses by examining diet and directly measuring intraspecific competition could provide for fruitful future work on the evolution of body size in Galapagos tortoises.

Literature Cited

Adler, G. H., and R. Levins. 1994. The island syndrome in rodent populations. Quarterly Review of Biology **69**:473-490.

Blanckenhorn, W. U. 2000. The evolution of body size: what keeps organisms small? Quarterly Review of Biology **75**:385-407.

Blomberg, S. P., and T. Garland. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology **15**:899-910.

Boback, S. M. 2003. Body size evolution in snakes: evidence from island populations. Copeia **2003**:81-94.

Bonin, F., B. Devaux, and A. Dupré 2006. Turtles of the World. The Johns Hopkins University Press, Baltimore, MD, USA.

Brown, J. H., and B. A. Maurer. 1986. Body size, ecological dominance and Cope's rule. Nature **324**:248-250.

Caccone, A., G. Gentile, C. E. Burns, E. Sezzi, W. Bergman, M. Ruelle, K. Saltonstall, and J. R. Powell. 2004. Extreme difference in rate of mitochondrial and nuclear DNA evolution in a large ectotherm, Galapagos tortoises. Molecular Phylogenetics and Evolution **31**:794-798.

Caccone, A., G. Gentile, J. P. Gibbs, T. H. Fritts, H. L. Snell, J. Betts, and J. R. Powell. 2002. Phylogeography and history of giant Galapagos Tortoises. Evolution **56**:2052-2066.

Caccone, A., J. P. Gibbs, V. Ketmaier, E. Suatoni, and J. R. Powell. 1999. Origin and evolutionary relationships of giant Galapagos tortoises. Proceedings of the National Academy of Sciences **96**:13223-13228.

Calder, W. A. 1984. Size, function, and life history. Harvard University Press, Cambridge, MA, USA.

Case, T. J. 1976. Body size differences between populations of the Chuckwalla, *Sauromalus obesus*. Ecology **57**:313-323.

Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology **59**:1-18.

Cayot, L. J. 1987. Ecology of giant tortoises (*Geochelone elephantopus*) in the Galapagos Islands. Ph.D. dissertation. Syracuse University, Syracuse, NY, USA.

Ciofi, C., M. C. Milinkovitch, J. P. Gibbs, A. Caccone, and J. R. Powell. 2002. Microsatellite analysis of genetic divergence among populations of giant Galápagos tortoises. Molecular Ecology **11**:2265-2283.

Ciofi, C., G. A. Wilson, L. B. Beheregaray, C. Marquez, J. P. Gibbs, W. Tapia, H. L. Snell, A. Caccone, and J. R. Powell. 2006. Phylogeographic history and gene flow among giant Galapagos Tortoises on southern Isabela Island. Genetics **172**:1727-1744.

Dunham, A. E., and D. B. Miles. 1985. Patterns of covariation in life history traits of squamate reptiles: The effects of size and phylogeny reconsidered. The American Naturalist **126**:231-257.

Dunham, A. E., D. B. Miles, and D. N. Reznick. 1988. Life history patterns in squamate reptiles. Pages 441–522 in C. Gans, and R. Huey, editors. Biology of the Reptilia. Academic Press, San Diego, CA, USA.

Ernst, C. H., and R. W. Barbour 1989. Turtles of the World. Smithsonian Institution Press, Washington, D.C., USA.

Foster, J. B. 1964. Evolution of mammals on islands. Nature **202**:234-235.

Fritts, T. H. 1983. Morphometrics of Galápagos tortoises: Evolutionary implications. Pages 107–122 in R. I. Bowman, M. Berson, and A. E. Leviton, editors. Patterns of Evolution in Galápagos Organisms. Pacific Division of the American Association for the Advancement of Science, San Francisco, CA, USA.

Fritts, T. H. 1984. Evolutionary divergence of giant tortoises in Galapagos. Biological Journal of the Linnean Society **21**:165-176.

Fritts, T. H., H. L. Snell, L. Cayot, C. MacFarland, S. Earsom, C. Marquez, W. Llerena, and F. Llerena. 2000. Progress and priorities in research for the conservation of reptiles. Bullletin de l'Institut Royal des Sciences Naturelles de Belgique **SUPPLEMENT 70**:39–45.

Geist, D. 1996. On the emergence and submergence of the Galápagos Islands. Noticias de Galápagos **56**:5-9.

Gittleman, J. L., and M. Kot. 1990. Adaptation: Statistics and a null model for estimating phylogenetic effects. Systematic Biology **39**:227-241.

Hailey, A., and I. M. Coulson. 1999. The growth pattern of the African tortoise *Geochelone pardalis* and other chelonians. Canadian Journal of Zoology **77**:181.

Hasegawa, M. 1994. Insular radiation in life history of the lizard Eumeces okadae in the Izu Islands, Japan. Copeia **1994**:732-747.

Heaney, L. R. 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. Evolution **32**:29-44.

Herrel, A., K. Huyghe, B. Vanhooydonck, T. Backeljau, K. Breugelmans, I. Grbac, R. Van Damme, and D. J. Irschick. 2008. Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. Proceedings of the National Academy of Sciences **105**:4792-4795.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment **83**:195-213.

Huete, A., K. Didan, Y. Shimabukuro, P. Ratana, S. Saleska, L. Hutyra, W. Yang, R. Nemani, and R. Myneni. 2006. Amazon rainforests green-up with sunlight in dry season. Geophysical Research Letters **33**:L06405.

Jackson, C. G., J. A. Trotter, T. H. Trotter, and M. W. Trotter. 1976. Accelerated growth rate and early maturity in *Gopherus agassizi* (Reptilia: Testudines). Herpetologica **32**:139-145.

Johnson, M. P., and P. H. Raven. 1973. Species number and endemism: the Galapagos Archipelago revisited. Science **179**:893-895.

Jönsson, P., and L. Eklundh. 2004. TIMESAT - a program for analyzing time-series of satellite sensor data. Computers & Geosciences **30**:833-845.

Justice, C. O., J. R. G. Townshend, E. F. Vermote, E. Masuoka, R. E. Wolfe, N. Saleous, D. P. Roy, and J. T. Morisette. 2002. An overview of MODIS land data processing and product status. Remote Sensing of Environment **83**:3-15.

Keogh, J. S., I. A. Scott, and C. Hayes. 2005. Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes. Evolution **59**:226-233.

Lomolino, M. V. 1985. Body size of mammals on Islands: the island rule reexamined. The American Naturalist **125**:310-316.

Lomolino, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography **32**:1683-1699.

Losos, J. B., T. R. Jackman, A. Larson, K. Queiroz, and L. Rodriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science **279**:2115-2118.

Losos, J. B., K. I. Warhelt, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature **387**:70-73.

MacFarland, C. G., J. Villa, and B. Toro. 1974. The Galapagos giant tortoises (*Geochelone elephantopus*) Part I: Status of the surviving populations. Biological Conservation **6**:118-133.

Madsen, T., and R. Shine. 1993. Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. Evolution **47**:321-325.

McBirney, A. R., and H. Williams 1969. Geology and petrology of the Galápagos Islands. Geological Society of America, Boulder, CO, USA.

McMullen, C. K. 1999. Flowering plants of the Galapagos. Cornell University Press, Ithaca, NY, USA.

Meik, J. M., A. M. Lawing, and A. Pires-daSilva. 2010. Body size evolution in insular Speckled Rattlesnakes (Viperidae: *Crotalus mitchellii*). PLoS ONE **5**:e9524.

Miles, D. B., and A. E. Dunham. 1992. Comparative analyses of phylogenetic effects in the life-history patterns of Iguanid reptiles. The American Naturalist **139**:848-869.

Morán Guerra, Á. J. 2003. Biogeografía y distribución estacional de la tortuga terrestre gigante (*Geochelone nigrita*) de la Isla Santa Cruz, Galápagos, Ecuador. Tesis de Licenciatura. Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Palkovacs, E. P. 2003. Explaining adaptive shifts in body size on islands: a life history approach. Oikos **103**:37-44.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of Phylogenetics and Evolution in R language. Bioinformatics **20**:289-290.

Perry, R. 1984. Galapagos - Key Environments. Pergamon Press, New York, NY, USA.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, New York, NY, USA.

Price, T. D., and A. B. Phillimore. 2007. Reduced major axis regression and the island rule. Journal of Biogeography **34**:1998-1999.

Pritchard, P. C. H. 1967. Living turtles of the world. TFH Publications, Neptune, NJ, USA.

Quinn, G. P., and M. J. Keough 2002. Experimental design and data analysis for biologists. Cambridge University Press, New York, NY, USA.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahman, A. F., D. A. Sims, V. D. Cordova, and B. Z. El-Masri. 2005. Potential of MODIS EVI and surface temperature for directly estimating per-pixel ecosystem C fluxes. Geophysical Research Letters **32:** L19404.

Sacchi, R., F. Pupin, D. Rosa, and M. Fasola. 2007. Bergmann's rule and the Italian Hermann's tortoises (*Testudo hermanni*): latitudinal variations of size and shape. Amphibia-Reptilia **28**:43-50.

Smith, F. A., J. H. Brown, J. P. Haskell, S. K. Lyons, J. Alroy, E. L. Charnov, T. Dayan, B. J. Enquist, S. K. M. Ernest, and E. A. Hadly. 2004. Similarity of mammalian body size across the taxonomic hierarchy and across space and time. The American Naturalist **163**:673-691.

Snell, H., and S. Rea. 1999. The 1997–98 El Niño in Galápagos: can 34 years of data estimate 120 years of pattern? Noticias de Galápagos **60**:11-20.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, NY, USA.

Torres Corral, M. d. L. 2001. Distribución, estructura poblacional y demografía de la tortuga gigante *Geochelone nigrita* (Reptilia: Testudines) en la Isla Santa Cruz, Galápagos. Tesis de Licenciatura. Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Tracy, C. 1999. Differences in body size among chuckwalla (*Sauromalus obesus*) populations. Ecology **80**:259-271.

Van Denburgh, J. 1914. John Van Denburgh's The Gigantic Land Tortoises of the Galapagos Archipelago. Society for the Study of Amphibians and Reptiles, USA.

Wikelski, M. 2005. Evolution of body size in Galapagos marine iguanas. Proceedings of the Royal Society B: Biological Sciences **272**:1985.

Wikelski, M., V. Carrillo, and F. Trillmich. 1997. Energy limits to body size in a grazing reptile, the Galapagos Marine Iguana. Ecology **78**:2204-2217.

Wikelski, M., and L. M. Romero. 2003. Body size, performance and fitness in galapagos marine iguanas. Integrative and Comparative Biology **43**:376-386.

Wilkie, D. S., and J. T. Finn 1996. Remote sensing imagery for natural resources monitoring: a guide for first-time users. Columbia University Press, New York, NY, USA.

Willemsen, R. E., and A. Hailey. 1999. Variation of adult body size of the tortoise *Testudo hermanni* in Greece: proximate and ultimate causes. Journal of Zoology **248**:379-396.

Xiao, X., Q. Zhang, B. Braswell, S. Urbanski, S. Boles, S. Wofsy, B. Moore Iii, and D. Ojima. 2004. Modeling gross primary production of temperate deciduous broadleaf forest using satellite images and climate data. Remote Sensing of Environment **91**:256-270.

Zug, G. R. 1997. Galápagos tortoise nomenclature: still unresolved. Chelonian Conservation and Biology **2**:618-619.

Table 2.1. Body sizes and ecological characteristics of areas inhabited by different populations of Galápagos tortoises. All curved carapace widths (CCW) are in millimeters and were calculated as an average (weighted by *n* in data source) of the maximum and mean sizes for each data source.

		Measures of Primary Productivity		
Tortoise Population	**CCW**	**Yearly Mean**	**Yearly Mean of Maximum Available**	**Seasonal Amplitude**
Isla Española	767	1674	2311	2118
Isla San Cristóbal	1057	1984	2742	2206
Isla Santa Cruz – Southwest	1528	4073	7065	2323
Isla Santa Cruz – El Fatal	1420	3197	5918	2164
Isla Pinzón	833	2054	2852	1537
Isla Santiago	1381	3454	5708	2353
Isla Isabela – Volcán Wolf	1107	2113	4907	1544
Isla Isabela – Volcán Darwin	1166	1601	2953	933
Isla Isabela – Volcán Alcedo	1532	2660	5364	2185
Isla Isabela – Caleta Iguana	1149	2765	4624	2620
Isla Pinta	986	3077	3887	2165

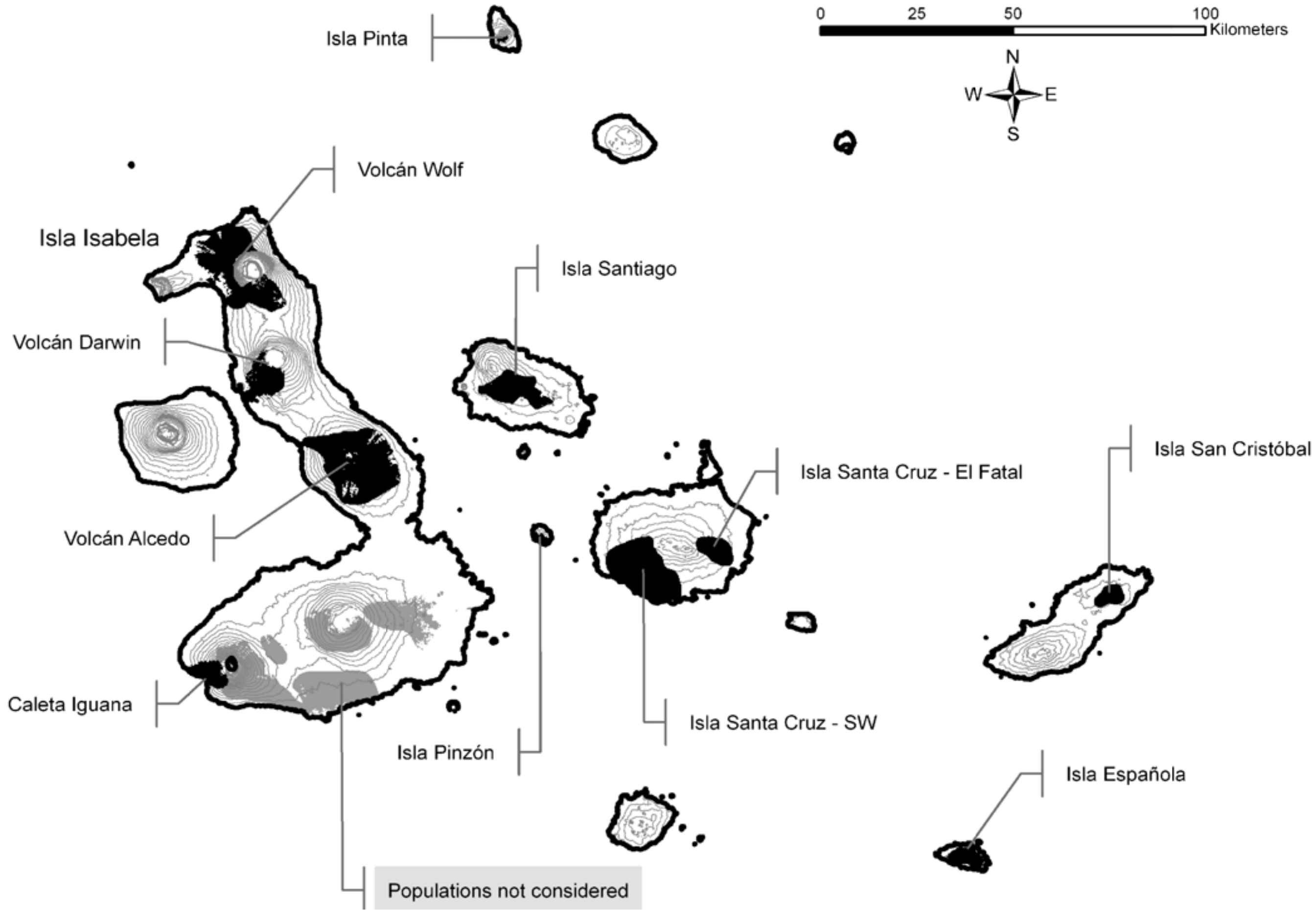

Figure 2.1. The extent of occurrence of Galápagos tortoise populations. Distribution information combines previously published maps with our own data. Contour lines are 100m apart. There is no current record of tortoises on Isla Pinta, although one surviving male is held in captivity at the Charles Darwin Research Station on Isla Santa Cruz.

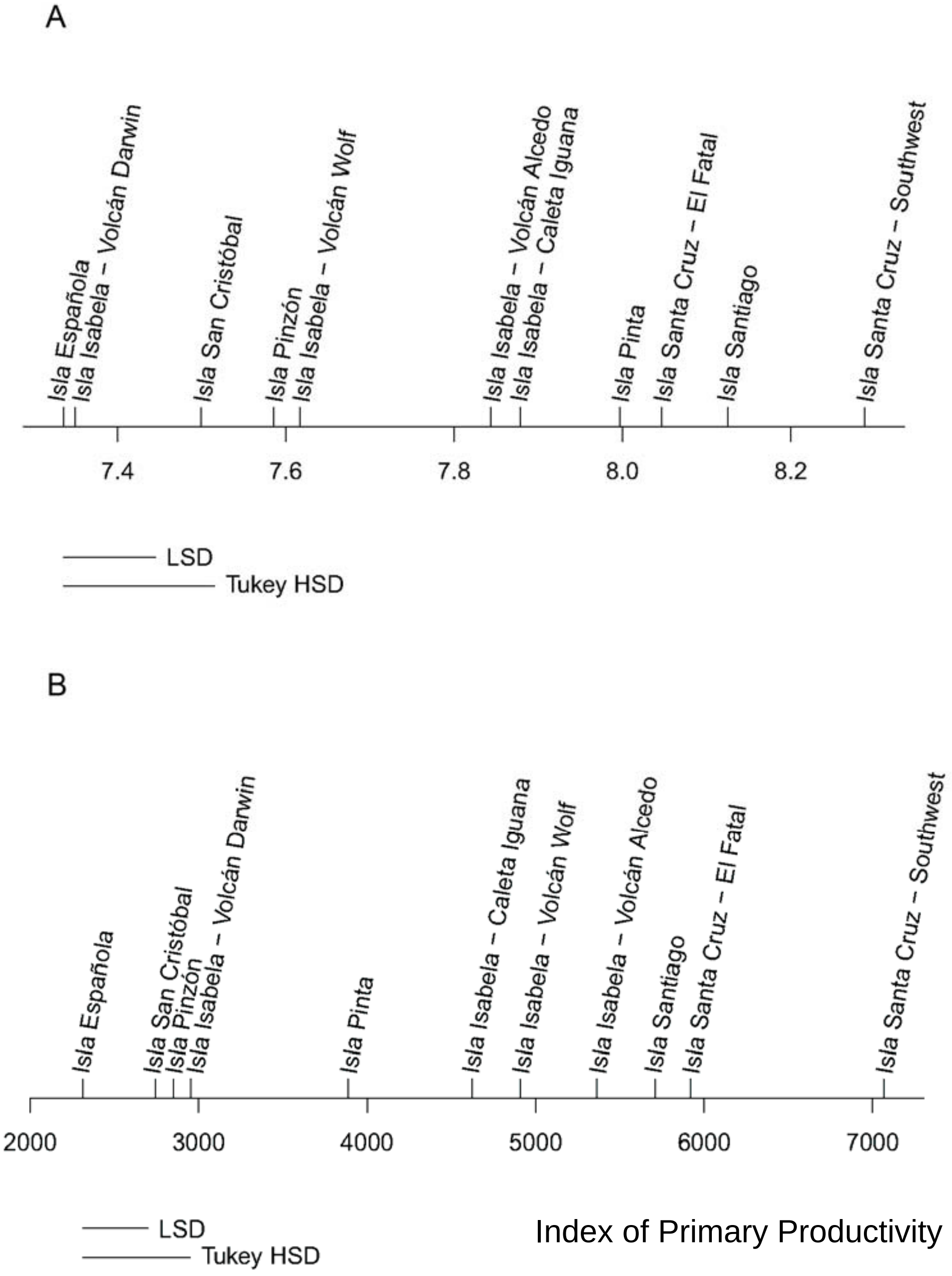

Figure 2.2. Results from a one-way analysis of indices of primary productivity for each area inhabited by tortoises. Yearly mean of primary productivity (A) was transformed to its natural logarithm while analysis of the yearly mean of maximum productivity in an area is based on raw index values (B). Means that differ by more than the LSD (least significant difference) are different, at the 5% level, in a *t*-test that compares the two means. Tukey's Honest Significant Difference (HSD) takes into account the number of means that are compared.

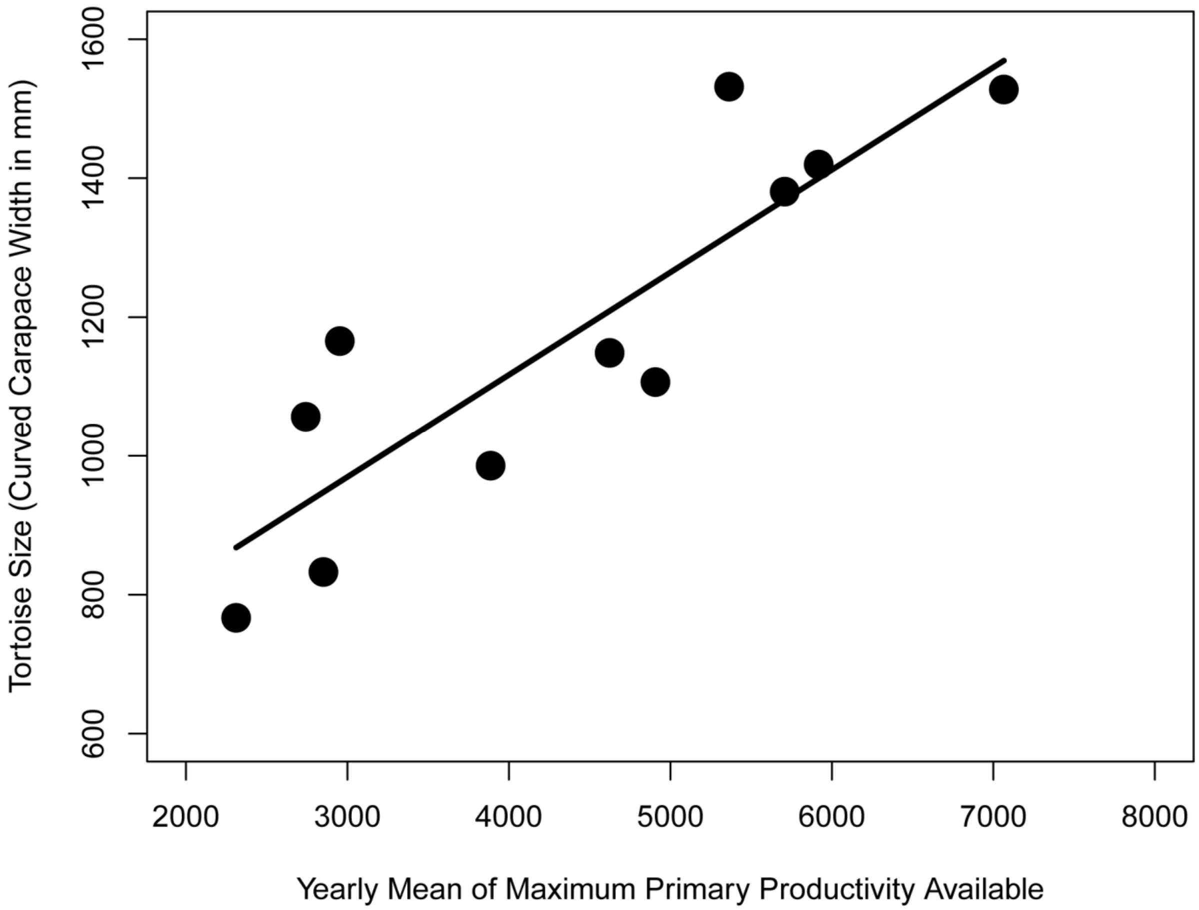

Figure 2.3. Relationship between body sizes of adult male tortoises in different taxa and maximum primary productivity available in an area (MODIS EVI). A linear regression model is statistically significant and explains over 76% of variation.

Chapter 3 : Improving models of distribution for reptiles of New Mexico, USA

Abstract

Increasing availability of remotely-sensed environmental data and advances in geographical computing have led to a variety of methods that predict habitat suitability and the distributional ranges of organisms. Because the state-wide distribution of reptiles in New Mexico is poorly known, the objective of this study was to create state-wide maps that indicate the likelihood of occurrence of different species. Specimen-based locality records and remotely measured climatic, hydrologic, geologic, and vegetational data were combined to calculate the suitability of landscape for species of reptiles. We initially proposed that the Maxent algorithm would produce reliable estimates of probable distributions because of its general acceptance as one of the most accurate methods. However, validation of Maxent-derived potential ranges with previously unknown occurrences identified inconsistent results. We developed a new methodology that is easier to interpret and that validates well. Using the same variables, we calculated a measure of landscape suitability based on principal component analyses (PCA). We then compared both methodologies with new observations gathered throughout New Mexico for 20 different species of reptiles. Due to its well-known statistical foundation, the PCA-based approach allowed for simpler descriptions of suitability and provided more consistent predictions between species. Predictions with Maxent were more variable between species and overall failed to correctly identify highly suitable habitats.

The PCA approach appears to represent suitability of the landscape for different species very well. Moreover, it is useful at scales appropriate for statewide conservation efforts and at scales where land ownership and policy change. Maps generated with this method will help increase overall knowledge of New Mexico's reptiles and prove useful to a variety of biologists and resource managers.

Introduction

Development and evaluation of multivariate techniques for modeling biological distributions, often known as species distribution modeling (SDM), has experienced an explosive growth (Elith & Leathwick 2009; Franklin 2009). Of the many methods reviewed, a maximum entropy approach, implemented in the program Maxent, has been proposed as one of the most accurate (Elith et al. 2006). Maxent has been used extensively for different purposes and with different taxa, including plants, birds, mammals, and reptiles and amphibians (Elith et al. 2006; Pawar et al. 2007; Brito et al. 2008; Buermann et al. 2008; Hernandez et al. 2008). However, ecological interpretation of its outputs is not easy because Maxent uses interactions between input variables via complex functions (Philips and Dudik 2008). In addition, our initial validation of potential ranges of species derived with Maxent resulted in inconsistent predictions. If outputs from efforts of modeling the distributions of species are to be useful for biodiversity conservation and management, the resulting predictions need to be consistently accurate for different species. Specifically, model predictions should be proportional to the probability of occurrence of a species, which is a characteristic of a good model.

Aside from accuracy of models for different species, another fundamental challenge for planning monitoring and conservation efforts over large spatial areas is deciding where to invest field effort. This is particularly the case of the state of New Mexico, a large administrative division (5th largest state in USA) that has limited resources for biological management. Knowledge of the state's amphibians and reptiles has been summarized by Degenhardt et al (1996) and statewide distribution maps have been produced since then, most notably by the GAP analysis project (Prior-Magee et al. 2007) and Painter and Pierce (2000). However, these recent maps provide only a binary estimation of presence or absence, without well-defined thresholds of occurrence. In addition, comprehensive knowledge of distribution of amphibians and reptiles in New Mexico is still lacking: in a ten year period 52 new county records of 43 species have been published (Herpetological Review 1999—2008). Thus distribution maps that provide relative suitability of landscape for different species would be useful for a variety of purposes. Such maps could allow the identification of areas where many species are likely to occur together (thus maximizing personnel efforts during inventory or monitoring), or where individual species are likely to occur but have not yet been recorded.

Considering the inconsistency of predictions derived with Maxent and the need for maps indicating relative suitability of landscape for reptiles in New Mexico, our goal became to develop and evaluate a general method for predicting distributions. This method should be easy to interpret and should correspond well with new observations. We focus on an approach that is based on characteristics of the landscape and its suitability for different species, rather than an approach that centers on individual species. The former should be well suited for a variety of species or, in other words, it should accommodate a range of individual species requirements (from generalist species to those highly specialized). Furthermore, unlike many modeling approaches that are focused on individual species, a consistent description of landscape that is species-independent fosters cross-species evaluation. Our specific objectives in this study were to 1) develop a method that in simple statistical terms summarizes suitability of landscape for different species of reptiles in New Mexico, 2) evaluate the accuracy of maps developed with this method, and 3) compare that method to Maxent, a well-known algorithm.

Methods

Study area

The area of analysis encompasses the entire state of New Mexico (315,194 km^2), the fifth largest US state, which spans 31°20′ to 37° North and 103° to 109°3′ West. Ecologically, New Mexico has a variety of biomes, ranging from hot and dry Chihuahuan desert to the cool and wet alpine areas, the latter being devoid of any herpetofauna. The majority of the state consists of grasslands (40%), of which half is desert grassland while other major biomes include woodland savanna (23%), desert scrublands (17%), and coniferous forests (Dick-Peddie et al. 1999). Despite variable topography and altitude (which ranges between 861m and 4,011m a.s.l.), most of New Mexico has a generally mild, arid or semiarid, continental climate characterized by light precipitation, infrequent cloud cover, low relative humidity, and a relatively large annual and diurnal temperature range (Sheppard et al. 1999). In part because temperatures are high and because its average yearly precipitation is only 380mm, New Mexico has very little surface water (610km^2).

Data on the distribution of species and the environment

Geographic coordinates for use in the distribution models were obtained from specimens at the Museum of Southwestern Biology, which holds the most comprehensive herpetological collections for the state of New Mexico (>43,000 specimens). We included only those specimens for which geographic coordinates could be assigned with precision better than 1,500m.

In order to describe the available environment, we compiled 31 variables: 19 variables that relate to climate, three topography variables, five variables related to soils and geology, and four related to water availability and landcover (Table 3.1). When necessary, we rescaled the data to fit a common spatial resolution, which matched that of the climate data (30 arcseconds or 30", equivalent to < 1km^2). All processing of spatial information was done with ERDAS Imagine version 9.1 (ERDAS Inc., Norcross, GA, USA) or with ArcGIS version 9.2 (ESRI, Redlands, CA, USA).

The 19 variables that characterize climate were extracted from the Worldclim dataset, which was developed by interpolation of weather station data (Hijmans et al. 2005). We used all of the 19 variables since including only simple gross means (e.g. mean annual temperature) across a varied terrain is unlikely to properly represent the spatial variability of the variable. Moreover, different species of reptiles likely respond differently to at least some key climate variables relating to temperature and/or precipitation. The three variables describing topography were calculated from a statewide digital elevation model distributed by New Mexico Resource Geographic Information

System Program (2006). Since the original horizontal resolution of the elevation data was 30m, elevation for each 30" cell was calculated as the average elevation within that cell. An index (0 to 1) of "northerness", or of how much a cell faces away from geographic South or 180°, was calculated from this re-sampled grid of elevation. The coefficient of variation of slope (as a representation of topographical variation) was based on the original elevation data. We expected that "northerness" would relate to the thermal opportunities for ectotherms, while the topographic variation would relate to structural habitat complexity (flat vs. broken-up landscapes).

Geology and soils not only influence the types of vegetation present or the degree of water accumulation, but also affect life history parameters of animals, such as their ability to burrow. To depict these ecological factors we used five variables from two data sets. We included a map of 183 different geological classes for New Mexico, developed by New Mexico Bureau of Geology and Mineral Resources. This layer represents the relative ages of formations and consequently the distribution of different types of rock and surficial deposits, as well as locations of geologic structures such as faults and folds. These, in turn, are likely to relate to different types of environments available to different species, such as areas of volcanic rock. We also used a soil map unit layer based on a nationwide database created by generalizing soil-survey maps, including published and unpublished detailed soil surveys, county general soil maps, state general soil maps, state major land resource area maps, and, where no soil survey information was available, Landsat imagery (Miller & White 1998). From these latter set of data we extracted: (1) available water content, (2) average soil porosity (3) percent of clay and (4) percent of sand in the first 10cm of soil.

Finally, we used two major sources of data that relate to water availability and different types of vegetation cover, both of which are likely to relate to physiological limits of animals. We used data from the MODIS satellite sensor that quantifies each square kilometer into percentage that is bare ground, covered by herbs and forbs or trees (Hansen et al. 2003), which collectively provide a measure of habitat structure. To address the dependence of some species on water, we used a measure of distance from permanent water sources. Using the National Hydrography Database of the United States Geological Survey (http://nhd.usgs.gov/), we created a grid where each cell is assigned a value that represents measured distance from that cell to nearest permanent body of water identified in the database.

Modeling of the distribution of species

We related the environmental variables to known localities for species with two different methods: a new general approach based on principal component analyses and Maxent version 3.2.1 (Phillips & Dudik 2008). We then produced maps representing the suitability of landscape for individual species with each method.

We developed a new method for deriving suitability of landscape for species that is based on principal component analyses and normal distributions. We characterized environmental variation for each grid cell and then related that to each species. In this way, what is known about the environment can be related to occurrences of different species and compared at coarse scales between species. This approach can thus be used for a number of species, without the need for recalculation for each species. To characterize the environment, we first subjected all variables to a principal component extraction, reducing the 31 environmental variables to significant (eigenvalues greater than 1) principal components (McGarigal et al. 2000). Principal component analysis reduces data dimensionality by performing a covariance analysis between variables. It reduces the number of variables but retains those characteristics of the data set that contribute most to its variance. Each extracted principal component (or factor) is still informative when compared with variables in the original data by examining component loadings (McGarigal et al. 2000). Spatially, each analysis cell was assigned all factor values for that cell – providing an estimate of environmental variation for that cell. On the other hand, we calculated the mean of each of the factor scores for all the cells where a particular species was observed, obtaining an estimate of the environmental requisites for that species. Since factor scores are computed such that their mean value in the data set is 0, identifying the factor with the values furthest from zero helps to distinguish the requirements of particular species. In addition, because these are calculated on the same scale, it is possible to compare their values between species.

To calculate the suitability of each cell throughout New Mexico for each species, we calculated the similarity between the factor scores for a cell to the mean of factor scores for that species. The difference between the mean value of a factor for a species and a particular analysis cell represents a 'distance' of how far the value for the analysis cell is from what is known about a species for that factor. We treated these distances as equivalent to *z-scores*, also known as 'standard normal deviates' (Sokal & Rohlf 1995), so that the resulting measures might be conceptually related to probabilities that the environment was suitable. For each species, we did this for each analysis cell and factor without regard to the direction of difference:

$$\text{Suitability} = (1-P(z)) * 2$$

where *P(z)* is the area to the left of *z* (or *z-score* value) under the standard normal curve. Thus, if values for all factors of a particular cell were close to values of means for that species, *z-scores* would be small and resulting calculated probabilities would be high (suitability for that cell would be high because the environment is similar to what is known about this species). Finally, to obtain a combined (and final) suitability value for each analysis cell, we calculated the mean of probabilities calculated from all the factors for that cell, weighted by the coefficient of variation for each factor. We did this so that factors for a species that had the smallest standard deviations would be treated as the most informative for that species. The resulting suitability values were rescaled between 0 and 100 for each species. Principal component analysis was done with SPSS ver 16 (SPSS Inc., Chicago, IL, USA) whereas all other data manipulation and calculations were done within the R statistical framework (R Development Core Team 2010).

For comparison of the newly developed method to a well-regarded method, we produced suitability maps with Maxent. Maxent is a statistical machine learning method for making predictions from incomplete information that has recently been brought into the domain of modeling distributions of species (Phillips et al. 2006; Phillips & Dudik 2008). The method consists of estimating a target probability distribution across an area by finding the probability distribution that is closest to uniform (spread-out) but subject to constraints. This probability distribution is based on a set of real-valued variables (or functions of them, including linear, quadratic, product, and hinge) and the constraints are that the value of the feature should match the average value for a set of sample points. In Maxent, pixels of known occurrences of species are the sample points, the predictive variables that have geographic representation (such as temperature or elevation) are the features and the cells of the study area are the space over which the probability distribution is calculated. For each analysis cell, Maxent calculates, as a percentage, the cumulative value of the probability value for the current analysis cell and all other cells with equal or lower probability. Thus cells with values of 100 are the most suitable whereas cells with values close to 0 are least suitable (Hernandez et al. 2006). We evaluated Maxent's deviation from random by using the built-in test (area under curve or AUC) that sets aside a proportion of the data (here, we used 10%). We used default values for regularization and selection of functions (linear, quadratic, product, threshold and hinge) of environmental variables.

Evaluation of model performance and comparison

We compare the accuracies of each modeling method in two ways: how frequently previously unknown occurrences of species correspond to calculated suitability values for each species (consistency between different suitability classes), and the degree to which each modeling method is consistent when multiple species are considered at once (consistency between species). Close agreement between predicted suitability and frequency of new observations, when summarized between species and corrected for area sampled, would indicate that the modeling method performs well.

To compare the two modeling methods, we obtained data that were completely independent from that used to calculate the suitability maps. Observations of species in new localities occurred between April 2007 and Jun 2008, when we travelled throughout New Mexico covering different climatic and ecological gradients. Sampling consisted of visual encounter surveys, including common techniques for reptiles such as road cruising, examination of rock piles, crevices and shelters, etc. The techniques we used were consistent with those used for traditional museum collections and thus are directly comparable to those used in collecting museum specimens that were used for developing the models. Once the animal was observed, we usually relied on hand capture or noosing for its capture and examination. We identified each animal to species. Using Garmin global positioning system (GPS) units (Garmin International Inc., Olathe, KS, USA) and their tracking feature, we recorded the geographic coordinates of the found animal as well as our own movements. The latter data allowed us to map areas where no observations were made. We converted all of the spatial data collected into the same grid as the modeled distributions and delimited the area for analysis by selecting only those cells which were visited either on foot or in a vehicle at a speed lower than 25mph, regardless of whether any animals were found.

After selecting species for comparison between models based on their prevalence (number of cells where new observations were made), we employed an evaluation technique based on resource selection (Boyce et al. 2002) to quantify how accurately the maps predict different suitability levels for each species. Commonly, evaluation and comparison of distribution models is based on presence/absence indices such as Kappa, MaxKappa, AUC, and adjusted D^2 (Segurado & Araújo 2004; Elith et al. 2006; Hernandez et al. 2006; Tsoar et al. 2007; Buermann et al. 2008; Hernandez et al. 2008). However, these testing methods either rely on absence data or depend on establishing presence thresholds (levels of suitability at which species is considered present). For some evaluation metrics such as Kappa (Cohen 1960), low prevalence may introduce bias to estimates of accuracy (McPherson et al. 2004). In addition, our data precluded the use of these comparative indices because we could not confirm the absences of species with our field methods. The index developed by Boyce et al. (2002) is a measure that is based on presence only data and has its roots in resource selection functions, that is, it relies on the concept of use/availability rather than presence/absence. Despite its simplicity, it correlates well with measures such as AUC and is insensitive to species prevalence (Hirzel et al 2006). More specifically, Boyce indices provide predicted-to-expected ratio curves that offer insights into model quality such as robustness, habitat suitability and deviation from randomness (Hirzel et al. 2006). The method consists of partitioning the calculated suitability into several classes and for each class, calculating two frequencies: 1) predicted frequency of evaluation points, where a ratio is calculated for each suitability class of the number of evaluation points to the total of points, and 2) the expected frequency of evaluation points, where, for each class, the ratio is that of expected frequency of evaluation points in that class to the overall area of all cells in the study area. Subsequently, for each class, a ratio of predicted-to-expected is calculated. If the model properly identifies suitable areas, the ratio of predicted-to-expected should be higher with each higher ranked class. In other words, a low suitability class should contain fewer evaluation points than expected by chance whereas higher suitability classes should have a higher proportion of evaluation points than expected by chance. Following Boyce et al (2002), we measured this monotonic increase between the predicted-to-expected ratio and suitability class rank with the Spearman rank correlation.

To test consistency in model accuracy between species, we first used a goodness of fit test to evaluate whether the two models produced different predictions. For each species and method, we separated all of the sampled cells into no more than 5 classes based on calculated suitability, where each class contained at least 5 previously unknown observations. If the observed proportions of cells were different between models (models made different predictions), the test would reject the null hypothesis of similar expected proportions of cells between models for that species. We then examined the consistency with which predictions are made with each model by calculating the Boyce index for each of the 20 species. We assessed the consistencies between the two modeling methods by examining the value of Spearman's *rho* for each species.

For an overall test of consistency between classes of suitability, we split data on the suitability of landscape for each species and modeling method into five classes based on quantiles derived from new observations. Our intent was to create as many classes as possible without any class for any of the species containing less than one field observation. We calculated Spearman's *rho* for Maxent and PCA-based modeling methods based on an average value of the predicted-to-expected ratio for each suitability class. We then compared these rank correlation coefficients following Fitz-Gibbon and Morris (1993), but modified Fisher's Z for rank correlation coefficients as described by Fieller et al (1957). The test establishes whether rank correlations from the two models have different strengths. A higher value of Spearman's *rho* indicates that the modeling method is more consistent between suitability classes. All calculations of the Boyce index were programmed within the R statistical framework (R Development Core Team 2010).

Results

Converting all of the environmental data into a common grid of approximately 1km^2 (30-arc seconds) resulted in 445,009 cells covering the state of New Mexico.

Against this grid, we used 8,176 records of museum specimens of 20 species of reptiles for the development of the models (Figure 3.1). However, many records were in close proximity consequently the number of cells represented by these records varied between 28 and 656, depending on the species. Therefore, despite high number of specimens that had been collected historically, prevalence was low within the entire state (<0.02%).

We extracted seven significant components from the PCA of environmental characteristics and those components accounted for >82% of the variance in the 31 variables (Table 3.2). The components were related to temperature, precipitation, topographical as well as geological and soil characteristics (Table 3.3). The first factor, accounting for 38% of variance, describes extremes and means of temperatures related to elevation, and also relates to tree cover and availability of water. The second PCA factor, accounting for 16% of variance, focuses on herbaceous landcover, high precipitation during summer, and low temperatures during dry periods. The remaining five significant factors, which combined account for 29% of variation, are more easily related to specific landscape features (Table 3.3). When summarized by species, the PCA factors reflected the known environmental correlates of individual species as expected. For instance, *Phrynosoma cornutum* and *Terrapene ornata,* both species that occur in areas of low altitude and high temperatures (Degenhardt et al. 1996), exhibited high values for the first principal component, while *Sceloporus undulatus*, a species found throughout the state, had values near the state's mean for four of the seven principal components (Table 3.4). For the models developed with the Maxent algorithm, individual values of AUC for all 20 species modeled were greater than 0.9 (mean=0.952, SD=0.028) and Wilcoxon rank tests of AUC were statistically significant (p<0.001) in all cases. Likewise, the same test of AUC values for test data for 20 species in Maxent (mean=0.881, SD=0.084) was statistically significant (p<0.001). Thus the performance of the Maxent model when developed and tested with 10% of the original data was better-than-random for all species.

During collection of data on previously unknown occurrences, we found 74 species in 802 different cells out of the 2616 cells that we visited. Twenty species were detected in more than 10 cells (range 11—46 cells) and those were used for the comparison of modeling methods. For each of the 20 species of interest, there was a lack of association between modeling methods (all p< 0.001). Thus both modeling methods produced different results for all 20 species and we included all 20 species in the subsequent comparison. When species were considered individually, of the 20 species examined, nearly twice as many (12 species with the PCA-based method vs. 7 for Maxent) had a rank correlation value higher than 0.7 (Table 3.5). In the overall comparison between modeling methods, the Spearman's rank correlation between the class rank and area-adjusted frequency for Maxent was 0.48 whereas the value of *rho* for the PCA-based method was 1. Variation in class ranks two through four was much higher for Maxent than for the PCA-based method while the highest class rank was low for Maxent (Figure 3.2). The difference between overall rank correlation coefficients for the two modeling methods was statistically significant (Fisher's Z=3.11, p<0.01).

Discussion

We developed a general method for modeling distributions of species that is based on principal component analysis of the characteristics of the environment. This method relates environmental characteristics to the suitability of landscape for species or reptiles throughout New Mexico. An evaluation of this PCA-method with new observations of different species compares this method favorably to a well-known algorithm. Although the Maxent algorithm performed better than random in this study, overall, the maps generated by Maxent failed to identify the most suitable landscapes. In addition, the predictions from a PCA-based method were more consistent for different suitability levels when summarized for all 20 species. When models were compared for individual species, suitability for almost two thirds of species was calculated with a higher degree of correspondence between model and validation data using the PCA-based method. Visual inspection of maps confirms that Maxent did not identify areas where species were encountered (Figures 3.3 and 3.4). In summary, suitability was better described by the PCA method because more animals of a particular species were found in progressively more suitable areas (as modeled) for that species.

The measures of suitability of landscape, either calculated by PCA or Maxent, should not be confused with probabilities of species occurrence. The suitability value for each cell in New Mexico ranges between 0 and 100 in order to compare the suitability of a cell for a species relative to other cells, not to indicate the likelihood of detection. In addition, because individual species models were derived from the same set of principal components, cells in PCA-based maps can be compared between species. However, while some areas can appear highly suitable, some species might not be present there because some factors were not built into the models. Those include biotic interactions with other species, such as competition and predation and others, such as limited dispersal opportunity. In other studies when community interactions or distance constraints are incorporated, accuracy of models improves (Elith et al. 2006; Allouche et al. 2008). However, dispersal capabilities for majority of species in New Mexico are not known, especially on coarse time scales. Thus artificially weighing the suitability (for example, based on distances to nearest known occurrence) would likely bias the representation of suitability for a species in an unknown direction. The PCA-based method only identifies how similar a cell is to what is known about environmental correlates for a species.

The PCA-based method of turning a suite of environmental variables into a reduced set is very similar to Ecological Niche Factor Analysis (Hirzel et al. 2002); however, unlike ENFA, PCA-based calculation of suitability is not species-specific. In ENFA, PCA is used to summarize predictors into a few uncorrelated factors so that the first factor is based on variables for which the niche of a species mostly differs from the conditions in the study area (termed marginality). Subsequent factors represent how restricted is the species' niche as compared to all available variables, termed specialization (Hirzel et al. 2001; Hirzel et al. 2002). Rather than creating principal components to summarize specialization and marginality of a particular species, the PCA in this study characterizes the environment in an analysis cell in relation to the whole area and then compares a cell to cells where a species occurs. Thus while ENFA is species-centric and can be used for analyses of the ecological niche of a species (Reutter et al. 2003), the PCA-based approach developed here focuses on the landscape and can be used to compare the suitability of landscape for various species. On the other hand, a modeling approach that treats a variety of species equally might not be better than an approach in which a composite model is built from models of distribution of individual species. The use of multiple approaches and development of consensus areas with several methods has been advocated even for models of individual species (Burgman et al. 2005; Araújo et al. 2006). However, developing distribution models using multiple methods and algorithms might not be practical or could be cost-prohibitive. It could also result in unintentional error if models differ widely in output or are not directly comparable.

In this study we compared two modeling methods by using a modified index based on resource selection function theory (Boyce et al. 2002), which differs strikingly from comparative statistics such as Cohen's Kappa (Cohen 1960) or the threshold-independent AUC (Hanley & McNeil 1982). The appropriateness of presence/absence indices, such as Kappa, has been questioned because many recent modeling techniques (including Maxent) are not developed with, nor do they calculate, true absences (Pearce & Boyce 2006; Lobo et al. 2008). Output from Maxent and PCA-based method in this study relies on presence-only data and the evaluation data used represents presence/availability, thus a comparison based on resource selection is more suitable (Boyce et al. 2002). Despite using a threshold independent and robust comparison method, bias could have been introduced into the models. Sources of bias include proximity to roads when sampling or binning the calculated suitability into too few or too many classes. However, the 20 species that were sampled represent a variety of ecological traits and it is unlikely that any model (particularly Maxent) would change drastically if species were sampled differently. Binning the suitability was also selected to capitalize on the sampled species for evaluation (see Methods).

It is possible that Maxent did not compare well with a presence-only approach that used PCA because Maxent is constrained by the amount of information available

(Phillips et al. 2006) and the data used for training the model might not represent completely the range of environments that are suitable for a species. In other words, because reptiles in New Mexico have not been sampled thoroughly, there's too little variation captured and available for effective model development. Furthermore, Maxent relies on pseudo-absences, which when taken from throughout New Mexico, might in reality be highly suitable areas for a particular species (or be false absences). Recent analyses that evaluate the development of pseudo-absences by other means greatly improve the accuracy measures of model outputs (Chefaoui & Lobo 2008). It is possible that an alternative selection of pseudo-absences would result in a Maxent output more similar to that of the PCA-based method.

On the other hand, there was more environmental data available to Maxent than used in the PCA-based method. While Maxent used all 31 variables in a variety of functions, the PCA method relied on converting all variables that describe the environment into only seven principal components, which represented less than 84% of variance in all data. However, although interpretation of principal components requires a systematic approach (McGarigal et al. 2000), individual principal components can be related easily to models of individual species. Although Maxent allows for some examination of the importance, or contribution, of individual variables to predictions, interactions of variables remain unavailable for examination by the modeler (Phillips & Dudik 2008). Thus despite using more data, Maxent outputs and the interpretation of variable contributions to its outputs are not easy.

We developed and tested an approach that identifies highly suitable areas for species and that is useful at scales appropriate for statewide conservation efforts. Scales coarser than the one used here would not be productive. For example, land ownership changes too frequently at scales much coarser than 100 km^2. In other words, maps of habitat suitability for a 10km x 10km piece of land would not be useful since in many cases several land managers share those 100 km^2. This translates to models that are at geographical scales where land ownership and policy can be influenced.

Maps of species distributions have one of their greatest utilities in planning for conservation and monitoring; however, the maps produced in this project are probabilistic and therefore should be treated as such. Predictions developed with the PCA-based approach can used by a wide range of people that are involved in natural resource management. The most effective use of maps produced with this method is for comparison of habitat suitability for different species between different areas. This can help identify conservation opportunities for certain areas within the state. The maps can also useful in planning monitoring effort because some areas will have highly suitable habitats for many different species of interest. We do not recommend the use of these maps as a substitute for thorough surveys of species presence. While the maps can guide monitoring efforts, they should be treated as probabilistic expressions of suitability of landscape.

Literature Cited

Allouche, O., O. Steinitz, D. Rotem, A. Rosenfeld, and R. Kadmon. 2008. Incorporating distance constraints into species distribution models. Journal of Applied Ecology **45**:599-609.

Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography **33**:1712-1728.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157**:281-300.

Brito, J. C., M. A. Carretero, S. Larbes, D. J. Harris, and A. Kaliontzopoulou. 2008. Modelling the partially unknown distribution of wall lizards (*Podacris*) in North Africa: ecological affinities, potential areas of occurrence, and methodological constraints. Canadian Journal of Zoology **86**:992-1001.

Buermann, W., S. Saatchi, T. B. Smith, B. R. Zutta, J. A. Chaves, Mil, Borja, and C. H. Graham. 2008. Predicting species distributions across the Amazonian and Andean regions using remote sensing data. Journal of Biogeography **35**:1160-1176.

Burgman, M. A., D. B. Lindenmayer, and J. Elith. 2005. Managing landscapes for conservation under uncertainty. Ecology **86**:2007-2017.

Chefaoui, R. M., and J. M. Lobo. 2008. Assessing the effects of pseudo-absences on predictive distribution model performance. Ecological Modelling **210**:478-486.

Cohen, J. 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement **20**:37.

Degenhardt, W. G., C. W. Painter, and A. H. Price 1996. Amphibians and Reptiles of New Mexico. University of New Mexico Press, Albuquerque, NM, USA.

Dick-Peddie, W. A., W. H. Moir, and R. Spellenberg 1999. New Mexico vegetation: past, present, and future. University of New Mexico Press, Albuquerque, NM, USA.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A.

Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**:129-151.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics **40**:677-697.

Fieller, E. C., H. O. Hartley, and E. S. Pearson. 1957. Test for rank correlation coefficient I. Biometrika **44**:470-481.

Fitz-Gibbon, C. T., and L. L. Morris 1993. How to analyze data. SAGE Publications, Thousand Oaks, CA, USA.

Franklin, J. 2009. Mapping species distributions: spatial inference and prediction. Cambridge University Press, New York, NY, USA.

Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology **143**:29.

Hansen, M. C., R. S. DeFries, J. R. G. Townshend, M. Carroll, C. Dimiceli, and R. A. Sohlberg. 2003. Global percent tree cover at a spatial resolution of 500 meters: First results of the MODIS vegetation continuous fields algorithm. Earth Interactions **7**:1-15.

Hernandez, P. A., I. Franke, S. K. Herzog, V. Pacheco, L. Paniagua, H. L. Quintana, A. Soto, J. J. Swenson, C. Tovar, and T. H. Valqui. 2008. Predicting species distributions in poorly-studied landscapes. Biodiversity and Conservation **17**:1353-1366.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography **29**:773-785.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology **25**:1965-1978.

Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology **83**:2027-2036.

Hirzel, A. H., V. Helfer, and F. Metral. 2001. Assessing habitat-suitability models with a virtual species. Ecological Modelling **145**:111-121.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling **199**:142-152.

Lobo, J. M., A. Jimenez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology & Biogeography **17**:145-151.

McGarigal, K., S. Cushman, S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York, NY, USA.

McPherson, J. M., W. Jetz, and D. J. Rogers. 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? Journal of Applied Ecology **41**:811-823.

Miller, D. A., and R. A. White. 1998. A conterminous United States multilayer soil characteristics dataset for regional climate and hydrology modeling. Earth Interactions **2**:1-26.

Painter, C. W., and L. J. S. Pierce. 2000. Distribution of New Mexico Amphibians and Reptiles. A Report to the New Mexico State Land Office.

Pawar, S., M. S. Koo, C. Kelley, M. F. Ahmed, S. Chaudhuri, and S. Sarkar. 2007. Conservation assessment and prioritization of areas in Northeast India: priorities for amphibians and reptiles. Biological Conservation **136**:346-361.

Pearce, J. L., and M. S. Boyce. 2006. Modelling distribution and abundance with presence-only data. Ecology **43**:405-412.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling **190**:231-259.

Phillips, S. J., and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography **31**:161-175.

Prior-Magee, J. S., K. G. Boykin, D. F. Bradford, W. G. Kepner, J. H. Lowry, D. L. Schrupp, K. A. Thomas, and B. C. Thompson. 2007. Southwest Regional Gap Analysis Project Final Report. U.S. Geological Survey, Gap Analysis Program, Moscow, ID, USA.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reutter, B. A., V. Helfer, A. H. Hirzel, and P. Vogel. 2003. Modelling habitat-suitability using museum collections: an example with three sympatric *Apodemus* species from the Alps. Journal of Biogeography **30**:581-590.

Segurado, P., and M. B. Araújo. 2004. An evaluation of methods for modelling species distributions. Journal of Biogeography **31**:1555-1568.

Sheppard, P. R., A. C. Comrie, G. D. Packin, K. Angersbach, and M. K. Hughes 1999. The climate of the Southwest. Institute for the Study of Planet Earth, The University of Arizona, Tucson, AZ, USA.

Sokal, R. R., and F. J. Rohlf 1995. Biometry: the principles and practice of statistics in biological research. WH Freeman & Company, New York, NY, USA.

Tsoar, A., O. Allouche, O. Steinitz, D. Rotem, and R. Kadmon. 2007. A comparative evaluation of presence-only methods for modelling species distribution. Diversity & Distributions **13**:397-405.

Table 3.1. Summary of environmental data used for models of species distributions.

Data category	Data type	Brief description	Source
Climate	Climatic variables	Climatic variables describing variation in temperature and precipitation at a resolution of 30 arc-seconds	Worldclim (Hijmans et al 2005) http://www.worldclim.org
Topography	Elevation	Average elevation derived from 30m resolution digital elevation model (DEM)	New Mexico Resource Geographic Information System http://rgis.unm.edu
	Northerness	A 0 to 1 index of how much a cell faces away from geographic south (or 180°) derived using above DEM	
	Topographic roughness	Coefficient of variation of slope derived using above DEM	
Geology and soils	Geology	183 different geological classes representing a distinct formation. The variable is ordinal: smaller numbers represent a younger formation.	New Mexico Resource Geographic Information System http://rgis.unm.edu
	Available water content	The volume of water that should be available to plants if the soil, inclusive of rock fragments, were at field capacity in the root-zone depth of 100cm.	Miller and White (1998) http://www.soilinfo.psu.edu/index.cgi?soil_data&conus
	Average soil porosity	Measure of the volume of air and water-filled pores in the soil in the first 10cm of soil	
	Percent of clay	Measure of clay quantity in the first 10cm of soil.	
	Percent of sand	Measure of sand quantity in the first 10cm of soil.	
Vegetation and water availability	Structure of habitat	Percent of ground that is bare, herbaceous, or tree-covered derived from satellite measurements at a 500m resolution.	Hansen et al (2003) http://glcf.umiacs.umd.edu/data/vcf/
	Distance from permanent water source	Calculated distance to nearest permanent water source for each cell.	United States Geological Survey, National Hydrography Dataset http://nhd.usgs.gov

Table 3.2. Matrix of seven principal components that were significant (Eigenvalues > 1). Variables are listed by their rank of importance for the PC; values used in interpretation of each PC are in bold.

Variable	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Annual Mean Temperature	**0.95**	-0.21	0.10	-0.05	0.00	0.08	0.12
Mean Temperature of Wettest Quarter	**0.95**	-0.16	-0.06	-0.06	0.04	0.10	0.07
Mean Temperature of Warmest Quarter	**0.94**	-0.26	-0.07	-0.08	0.01	0.09	0.10
Elevation	**-0.94**	0.14	0.11	0.06	-0.05	-0.10	-0.15
Mean Temperature of Coldest Quarter	**0.92**	-0.15	0.30	0.00	-0.02	0.06	0.13
Max Temperature of Warmest Month	**0.89**	-0.34	-0.19	0.03	0.01	0.07	0.11
Min Temperature of Coldest Month	**0.89**	-0.18	0.35	-0.12	-0.05	0.06	0.11
Precipitation of Driest Quarter	**-0.86**	0.18	0.12	-0.34	0.01	0.00	0.15
Precipitation of Driest Month	**-0.84**	0.18	0.04	-0.32	0.03	0.03	0.11
Precipitation of Coldest Quarter	**-0.78**	0.00	0.33	-0.05	-0.12	-0.16	**0.38**
Precipitation Seasonality (Coefficient of Variation)	**0.65**	0.25	0.46	0.42	0.04	0.03	-0.23
Percent tree cover	**-0.65**	0.21	0.41	-0.18	0.02	0.05	0.10
Precipitation of Warmest Quarter	-0.20	**0.84**	0.43	-0.09	0.09	0.04	-0.05
Percent herbaceous cover	-0.13	**0.84**	-0.09	0.05	-0.07	-0.15	0.20
Percent bare ground	0.42	**-0.78**	-0.13	0.05	0.01	0.10	-0.21
Precipitation of Wettest Quarter	-0.28	**0.76**	0.55	0.04	0.03	0.00	0.03
Precipitation of Wettest Month	-0.36	**0.73**	0.54	0.05	0.04	-0.02	-0.01
Annual Precipitation	-0.55	**0.66**	0.34	-0.20	0.04	0.00	0.16
Mean Temperature of Driest Quarter	0.18	**-0.62**	0.21	0.20	-0.24	-0.21	**0.42**
Temperature Seasonality (standard deviation)	0.13	-0.29	**-0.89**	-0.22	0.09	0.07	-0.06
Temperature Annual Range[1]	-0.06	-0.24	**-0.89**	0.25	0.11	0.01	0.00
Distance from permanent water source	**0.30**	-0.22	**0.30**	0.16	0.00	0.08	0.04
Mean Diurnal Range[2]	0.05	-0.13	-0.11	**0.93**	0.04	-0.05	0.15
Isothermality[3]	0.09	0.06	0.62	**0.72**	-0.06	-0.07	0.16
Soil porosity	0.05	0.03	0.02	0.00	**0.91**	-0.05	0.10
Available water capacity	0.00	0.04	-0.13	0.02	**0.88**	-0.10	0.05
Percent clay in soil	-0.11	0.07	0.00	0.07	0.06	**-0.88**	-0.01
Percent sand in soil	0.13	-0.03	-0.03	0.00	-0.09	**0.87**	0.14
Geological class	-0.08	0.04	0.18	0.11	0.06	0.03	**0.59**
Topographic roughness (CV of slope)	0.44	0.05	-0.20	0.00	0.23	0.13	**0.45**
Northerness	-0.10	-0.12	0.07	-0.02	-0.04	-0.10	**-0.22**

[1] (Max Temp of Warmest Month - Min Temp of Coldest Month); [2] (Mean of monthly (Max temp-Min temp)); [3] (Temp Mean Diurnal Range/Temp Annual Range)

Table 3.3. Narrative descriptions of significant principal components derived from PCA.

Principal component	**Variance explained**	**Interpretation**
PC1	38%	Extremes and means of temperature related to elevation; also relates to tree cover and water availability.
PC2	16%	Herbaceous, but not barren, landcover, with high summer precipitation and low temperatures during dry periods.
PC3	8%	Seasonality of temperature
PC4	7%	Range of temperatures
PC5	5%	Availability of water in soil
PC6	5%	Structure of soil (sand vs clay)
PC7	4%	Geological age and relation to topography and dryness

Table 3.4. Values of seven principal components of environmental data for the 20 species whose models were compared to Maxent. Data show means and standard deviations from cells where specimens of the species were collected. For each principal component the overall mean for the entire state of New Mexico was 0±1SD.

Species	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Arizona elegans	0.56±0.47	0.09±0.86	-0.71±0.82	0.01±0.98	0.43±2.31	0.6±1.39	0.5±0.8
Aspidoscelis exsanguis	0.46±0.6	0.17±0.6	0.36±1.09	0.28±1.06	-0.27±2.2	-0.51±0.77	0.64±1.04
Cophosaurus texanus	0.67±0.37	-0.47±0.84	0.27±0.77	0.25±1	0.81±4.09	-0.46±0.89	0.18±1.09
Crotalus atrox	0.61±0.58	-0.26±0.77	0.11±1.02	0.15±1.04	0.19±2.45	-0.3±1.01	0.28±0.9
Crotalus viridis	0.21±0.76	-0.32±0.83	-0.35±0.95	0.22±1.03	0.31±1.82	0.11±1.25	0.31±0.92
Crotaphytus collaris	0.26±0.76	-0.23±1	-0.13±1.02	-0.2±1.08	0.06±2.68	-0.19±0.97	0.16±1.12
Gambelia wislizenii	0.4±0.41	-0.8±0.59	-0.47±0.77	0.06±1.1	0.42±2.56	0.93±1.31	0.25±0.59
Masticophis flagellum	0.58±0.51	-0.13±0.81	-0.47±0.91	-0.12±0.95	0.53±2.52	0.19±1.31	0.45±0.92
Masticophis taeniatus	0.23±0.61	-0.13±0.68	0.19±0.96	0.11±1.28	-0.33±2.04	-0.3±0.8	0.39±1.05
Phrynosoma cornutum	0.87±0.38	-0.06±0.87	0.12±0.86	-0.03±0.97	0.44±2.53	-0.34±1.25	0.41±0.98
Phrynosoma modestum	0.51±0.59	-0.48±0.76	-0.08±0.92	-0.04±1.05	0.49±2.99	0.11±1.36	0.17±0.86
Pituophis catenifer	0.12±0.74	-0.2±0.86	-0.39±1.05	0.16±1.18	0.38±2.72	-0.18±0.96	0.42±1.09
Rhinocheilus lecontei	0.74±0.45	-0.17±0.74	-0.25±0.78	-0.2±0.94	0.34±2.05	0.07±1.22	0.5±0.88
Sceloporus magister	0.41±0.54	-0.67±0.78	-0.35±0.96	0.78±0.94	1.09±3.64	0.22±1.53	0.27±1.04
Sceloporus poinsettii	0.06±0.78	0.49±0.52	0.98±0.62	0.72±1.28	-0.74±0.76	-0.24±0.62	0.01±0.85
Sceloporus undulatus	0.01±0.86	0.09±0.96	-0.21±1.03	-0.19±1.07	0.07±2.35	-0.01±1.02	0.22±1.1
Sistrurus catenatus	0.5±0.54	-0.36±0.95	-0.35±0.48	0.02±0.8	0.18±0.48	1.77±1.2	0.72±0.65
Terrapene ornata	0.75±0.44	0.29±0.93	-0.27±0.82	-0.18±0.82	0.88±2.8	0.14±1.46	0.47±0.91
Urosaurus ornatus	0.15±0.68	0.07±0.61	0.58±0.96	0.65±1.14	-0.71±1.49	-0.39±0.84	0.76±1.07
Uta stansburiana	0.53±0.57	-0.35±0.93	-0.46±0.8	-0.15±0.92	0.2±2.56	0.8±1.41	0.46±0.86

Table 3.5. Summary of data used in comparisons: number of locality cells used in modeling (N_{model}), number of cells where new observations of species occurred (N_{obs}), and rank correlation coefficients for PCA-based and Maxent methods. The coefficients indicate the monotony of the relationship between modeled suitability of landscape and binned frequencies of new observations, corrected for area sampled (values greater than 0.7 are in bold).

Species	**Common name**	N_{model}	N_{obs}	**Spearman's *rho***	
				PCA	**Maxent**
Arizona elegans	Glossy Snake	106	17	-0.1	0.6
Aspidoscelis exsanguis	Chihuahuan Spotted Whiptail	271	11	-0.5	**0.9**
Cophosaurus texanus	Greater Earless Lizard	143	48	0.6	**0.7**
Crotalus atrox	Western Diamond-backed Rattlesnake	147	43	**0.9**	0.4
Crotalus viridis	Prairie Rattlesnake	190	48	**0.7**	**0.9**
Crotaphytus collaris	Eastern Collared Lizard	225	57	0.6	0.3
Gambelia wislizenii	Long-nosed Leopard Lizard	61	14	**0.9**	0.4
Masticophis flagellum	Coachwhip	170	22	**0.9**	**0.7**
Masticophis taeniatus	Striped Whipsnake	100	11	**0.8**	0.6
Phrynosoma cornutum	Texas Horned Lizard	133	28	**0.7**	0
Phrynosoma modestum	Round-tailed Horned Lizard	164	16	**0.7**	0.3
Pituophis catenifer	Gophersnake	321	45	**0.8**	0.3
Rhinocheilus lecontei	Long-nosed Snake	67	17	0.3	**1**
Sceloporus magister	Desert Spiny Lizard	57	22	**0.9**	0.4
Sceloporus poinsettii	Crevice Spiny Lizard	53	35	**0.8**	0.4
Sceloporus undulatus	Eastern Fence Lizard	651	66	**0.7**	0.3
Sistrurus catenatus	Massasauga	28	13	0	0.1
Terrapene ornata	Ornate Box turtle	78	18	0	0.1
Urosaurus ornatus	Ornate Tree Lizard	212	44	0.4	**0.9**
Uta stansburiana	Common Side-blotched Lizard	413	51	**0.7**	**0.7**

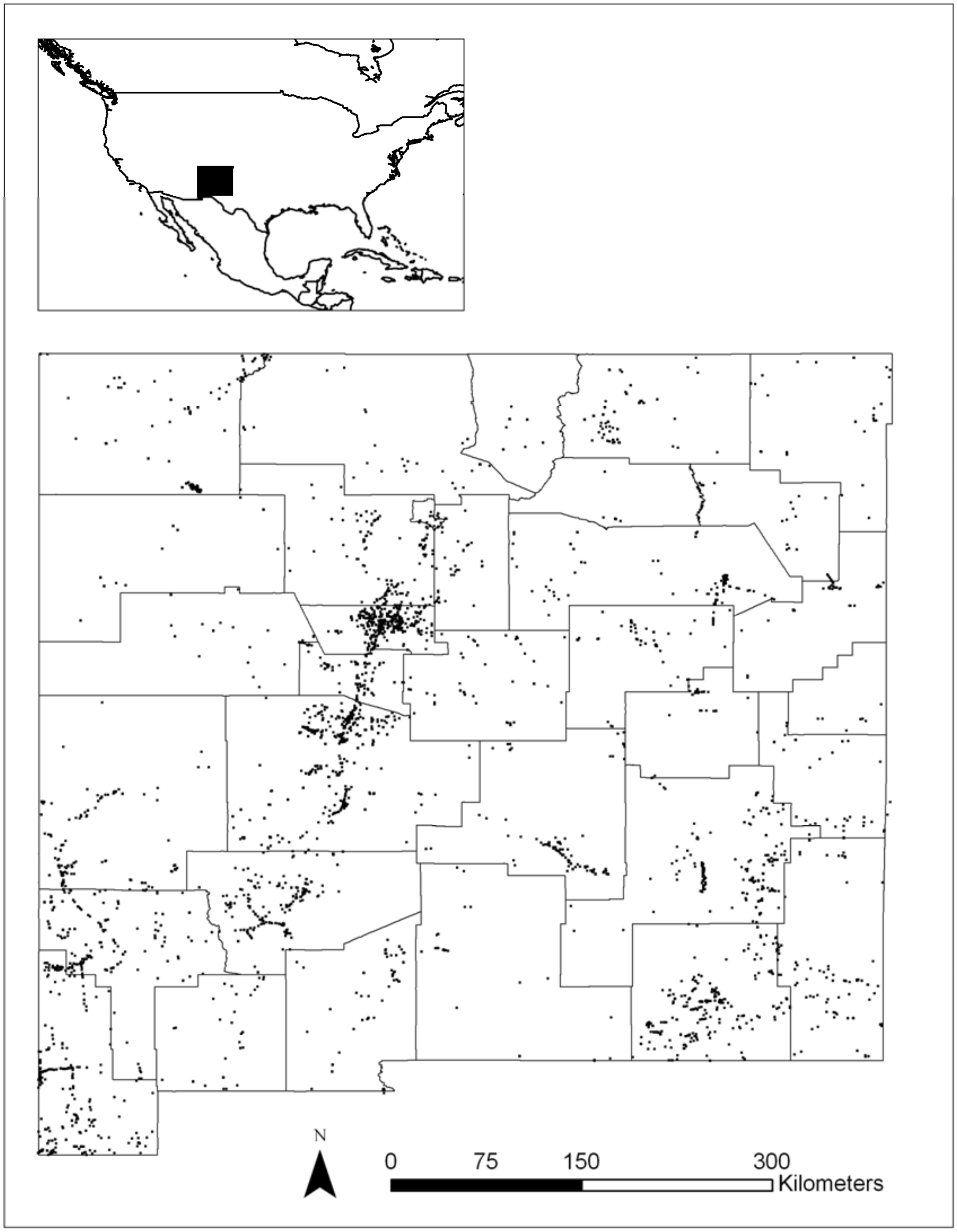

Figure 3.1. Distribution of localities for 20 species of reptiles in New Mexico, USA that were used in this study for development and comparison of models of distribution.

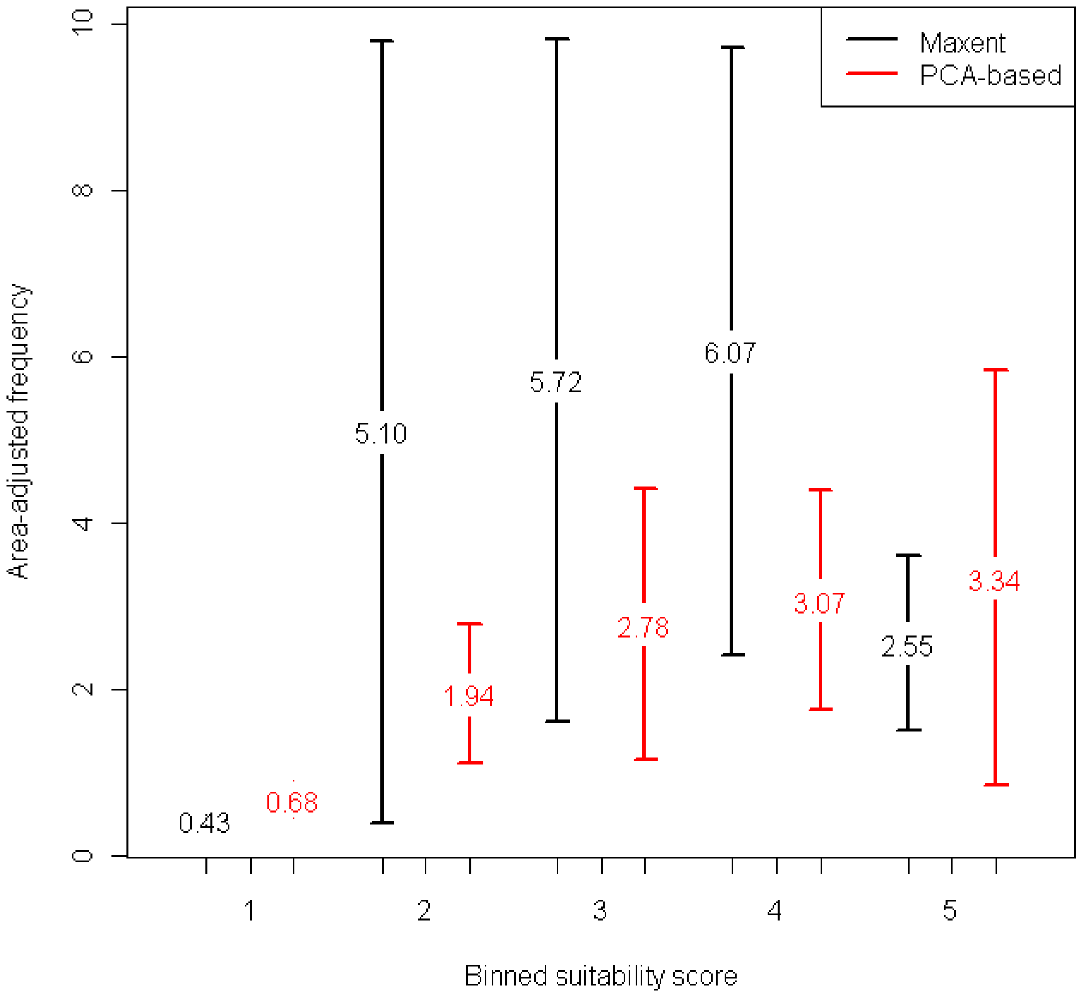

Figure 3.2. Differences in area-adjusted frequency of new observations among modeling methods (Maxent and PCA-based) when data for 20 species of reptiles are binned into five quantiles of suitability classes. In accurate models, observations of animals should be more frequent in areas of higher suitability scores. An overall rank correlation coefficient (Spearman's *rho*) for Maxent is 0.4 while that for PCA-based method is 1. Error bars represent ±1 standard error.

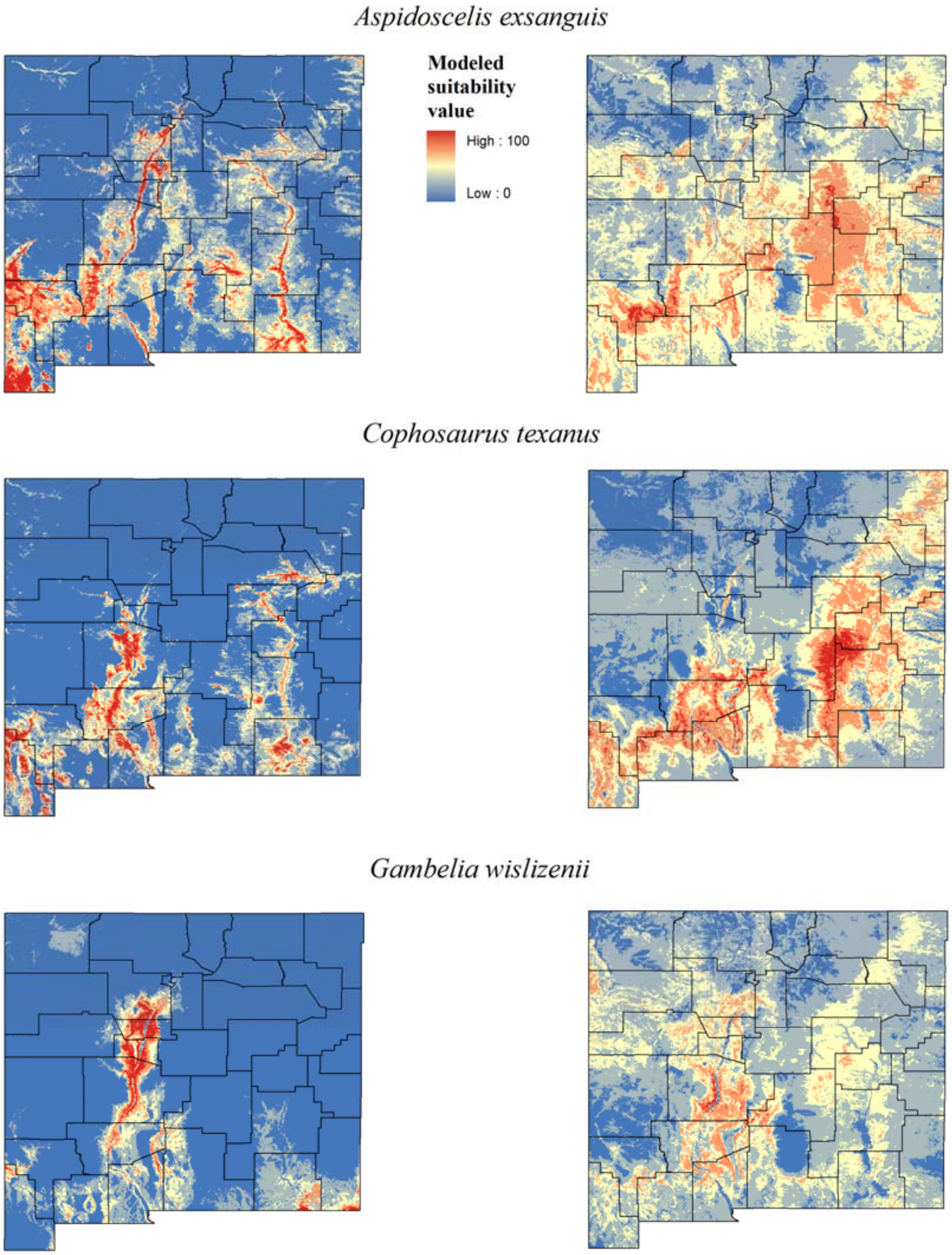

Figure 3.3. Examples of predicted suitability maps generated by Maxent (left column) and PCA-based (right column) approaches for three species of lizards. When tested with previously unknown observations, Maxent had higher accuracy for *Aspidoscelis exsanguis*, both methods had similar accuracy for *Cophosaurus texanus*, and PCA had higher accuracy for *Gambelia wislizenii*.

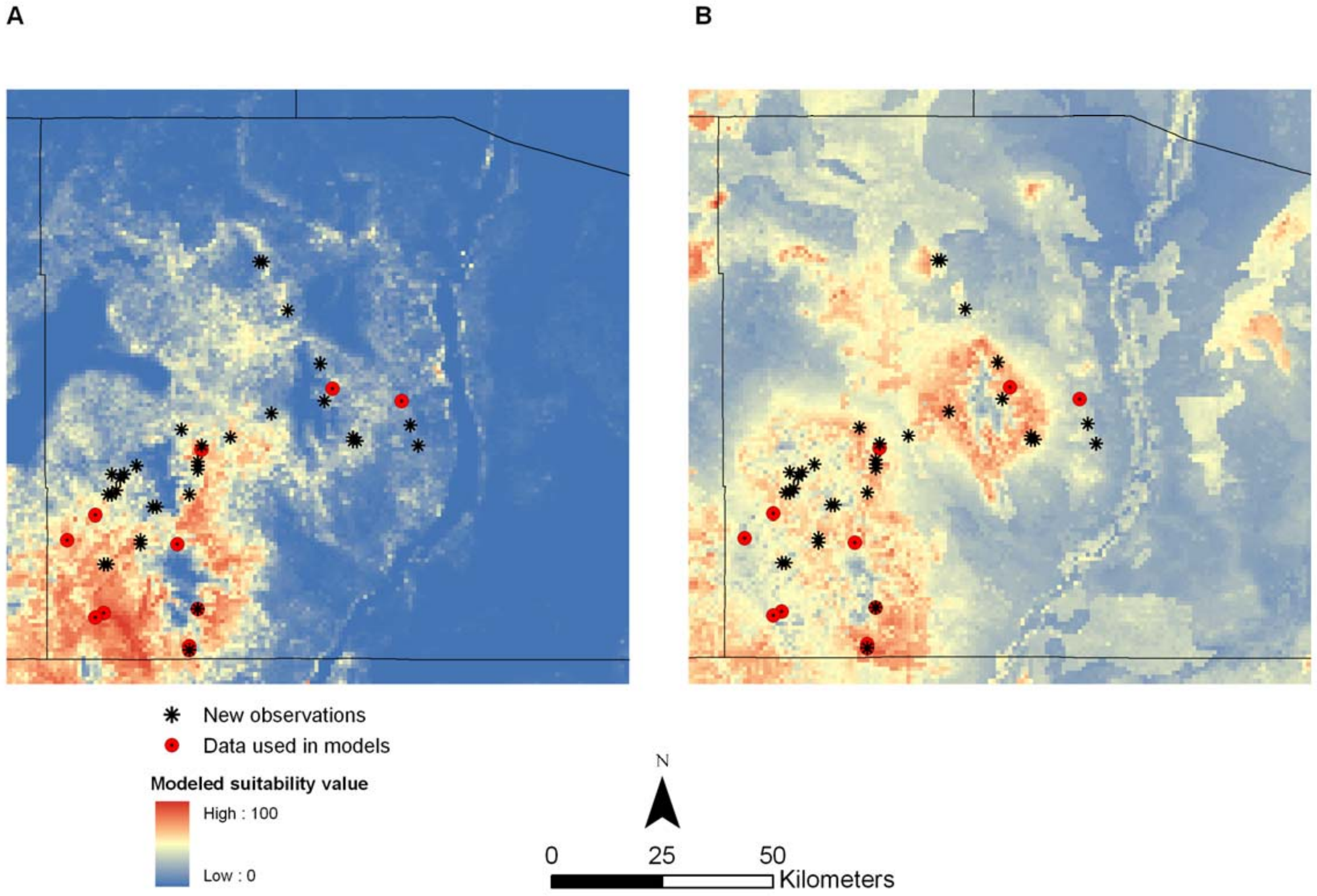

Figure 3.4. Detail of predicted suitability of landscape for *Sceloporus poinsettii* (Crevice Spiny Lizard) in western Socorro Co., New Mexico produced with (A) Maxent and (B) PCA-based methods.

Summary

This work demonstrates how the study of spatial processes in ecology at different spatial and phylogenetic scales can benefit conservation efforts by taking advantage of recent advances in geospatial technologies. By combining modeling and field-collected data, I investigated the formation of fine-scaled patterns of distribution within a species (Chapter 1). At a coarser spatial and phylogenetic scale, I studied the mechanisms involved in the creation of patterns of body sizes between taxa (Chapter 2). Finally, I used spatial data derived from satellites at regional scales to model the potential distribution of many species of reptiles in New Mexico. Using spatially-explicit environmental data, I showed how multivariate techniques can be used to successfully estimate the suitability of landscape for different species (Chapter 3).