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**INTEGRATING PHYSIOLOGY, PHENOLOGY AND DEMOGRAPHY IN
BIOGEOGRAPHICAL ANALYSIS**

A dissertation submitted in partial satisfaction

of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Gabriel Henrique de Oliveira Caetano

March 2019

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Abstract

Integrating Physiology, Phenology and Demography in Biogeographical Analysis

Gabriel Henrique de Oliveira Caetano

Biological processes underlying species responses to climate, such as physiology, phenology and demography, can add important information to the prediction of climate change effects on organisms, yet most studies do not consider those processes. On this thesis, I present and evaluate different venues of incorporating such processes on biogeographical analysis. On the first chapter, I show activity time can be a better predictor than environmental temperatures for the distribution a tropical lizard, *Tropidurus torquatus*. I also determine the best practices for obtaining those estimates. *Tropidurus torquatus* seems to be restricted in its distributions by colder temperatures and precipitation, thus climate warming could lead to potential range expansion. On the second chapter, I examine the drivers of reproductive seasonality in two tropical lizards, *Tropidurus torquatus* and *Ameiva ameiva*. Solar radiation and day length were the main factors determining the reproductive seasonality of *T. torquatus*, while *A. ameiva* was more sensitive to precipitation. Solar radiation could be driving *T. torquatus* breeding phenology through the parietal eye mechanism, while *A. ameiva*, which lacks such structure, could be more sensitive to immediate weather conditions. This might have important consequences for these *T. torquatus* adaptation to climate change, since the rapid shift in weather might cause a mismatch between the photoperiodic cue and optimal environmental conditions for reproduction. On the third chapter, I use the estimates of time of activity and breeding phenology o from the previous chapters to spatially extrapolate demographic rates obtained from a 12-year mark and recapture study on a *T. torquatus* population. Survival was correlated with time of activity and precipitation, both interacting with breeding phenology, while recruitment was correlated with temperature and precipitation, with no breeding season interaction. Population growth projections were not correlated with occurrence records, indicating that spatial predictions were unreliable. Physiology

and phenology add important information to the estimation of demographic rates at local scales but proved unreliable predictors for spatial extrapolation of those rates. This could be due to environmental variation, adaptation, plasticity or species interactions. We suggest possible venues for incorporating those processes and improving similar analysis. I provide an R package, *Mapinguari*, with tools to generate spatial predictors based on the processes described here.

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General Introduction

Climate change has severe effects on biodiversity (Pearson et al., 2004), such as changing species distribution, phenology, composition of communities, and ecosystem dynamics (Walther et al., 2002). It is not a question of if, but when and how those effects will occur, which brings the importance of understanding them to unprecedented levels. This understanding also improves our ability to predict biodiversity responses to future climate changes and use those predictions to inform appropriate conservation efforts.

A popular tool to predict effects of climate change on individual species is species distribution modeling (SDM). Also known as ecological niche modeling or climate envelope modeling, this method relates spatially explicit predictors (such as climate, soil composition, topography, geological features) to diagnostics of a species distribution or to a process that might limit a species distribution [i.e., occurrence records themselves, or climate-driven extirpation records (Sinervo et al., 2010), constraints on species physiology (Elith, Kearney, & Phillips, 2010; Buckley, Waaser, MacLean, & Fox, 2011)]. They allow us to better understand a species distribution and associated ecological and evolutionary patterns and processes, as well as to extrapolate the species distribution in space and time (Elith & Leathwick, 2009), and to study the dynamics of biological invasion (Urban, Phillips, Skelly, & Shine, 2007; Elith et al., 2010). The extrapolation in time can be projected both to the future and to the past. Forecasting SDMs can help us make decisions on conservation efforts (Thuiller et al., 2005; Araújo & New, 2007; Petchey et al., 2015a), while hindcasting SDMs can help us understand the effects of climate on a species evolutionary history (Kitchener, A. C., and Dugmore, 2000; Kristen, Robert, & Craig, 2006; Kozak, Graham, & Wiens, 2008).

There are two basic kinds of SDMs: correlative models relate occurrence records to environmental predictors on those locations and extend this relation to other areas; and mechanistic models try to elucidate the processes limiting a species range, then predict inhabitable locations from this information. This dichotomy has been extensively reviewed in two papers (Kearney & Porter, 2009; Buckley et al., 2010).

Most predictions currently don't consider processes underlying species responses to climate

change. In a recent review, it was found that 77% of prediction models published didn't incorporate any biological mechanism at all (Petchey et al., 2015b). Urban et al. (2016) identified six biological mechanisms crucial for more realistic predictions and called for an organized effort on the collection of this data and improvement of methods). Those mechanisms are: physiology, dispersal, species interaction, evolution, responses to environmental variation and demography, and they are fundamental to understand biological response to climate change (Zarnetske, Phoebe, Skelly, David, & Urban, Mark, 2012; Rissler, Wake, Hijmans, Moritz, & Graham, 2017a).

Correlative models require easily accessible data but have fragile assumptions when used predictively. They assume the species is in equilibrium with their environment, that occurrence records are unbiased in their distribution, the species range reflects its climate niche and there is no influence of species interactions, dispersal, genotypic and phenotypic variation (Pulliam, 2000; Midgley, Hughes, Thuiller, & Rebelo, 2006; Carsten F., 2007; De Marco, Diniz-Filho, & Bini, 2008; Elith & Leathwick, 2009; Pagel & Schurr, 2012; Schiffrers et al., 2016; Rissler et al., 2017a). This is the most widespread type of SDM and has been applied in many different contexts (Elith et al., 2006). They are still very useful for estimating current distributions, and identifying climate variables limiting them (Buckley et al., 2010), but don't do very well when extrapolated beyond the range of the variables they were fitted to (Klausmeier, Loeuille, Norberg, Urban, & Vellend, 2012; Zarnetske, Phoebe et al., 2012; Atkins et al., 2013; Schiffrers et al., 2016). Nevertheless, they will continue to be used due to easiness of implementation and demand for map products for conservation, especially in data deficient taxa (Guisan & Thuiller, 2005).

Mechanistic models, on the other hand, have the disadvantage of being more data intensive and species specific, (i. e. the same parameterization will have very different accuracies, depending on the species) (Kearney & Porter, 2009; Buckley et al., 2010). They are also very sensitive to errors, such as mischaracterization of the process modeled or choice of processes that do not limit the species range (Buckley et al., 2010; but see Sinervo et al. 2018 for a decomposition of the two basic types of errors in the context of observed extirpations). They are especially useful for species known to be constrained by specific mechanisms (Elith et al., 2010). Mechanistic models might perform very similarly or

weaker than correlative models for predicting current distributions (Buckley et al., 2010) but outperform correlative models in hindcasting (Araújo, Pearson, & Thuiller, 2005; Randin et al., 2006; Wethey & Woodin, 2008; Jones, Mieszkowska, & Wethey, 2009) and forecasting (Pagel & Schurr, 2012; Schiffers et al., 2016). Researchers might be discouraged to gather the amount of data necessary to fit mechanistic models and incur in the risk of getting poor predictions. However, that should be an incentive to further improve mechanistic models, instead of abandoning them, since they allow us to overcome severe limitations of correlative models. With mechanistic models, we can realistically incorporate important factors for a species distribution such as demography, evolution, plasticity, dispersal and biotic interactions (Urban et al., 2016), unlike correlative models [but see (Peterson & Holt, 2003; Rissler, Wake, Hijmans, Moritz, & Graham, 2017b)]. Mechanistic models also allow us to account for multiple interacting processes, non-linear dynamics and uncertainty (Pulliam, 2000; Kearney & Porter, 2009; Pearson et al., 2014; Mouquet, Lagadeuc, & Devictor, 2015; Pe'er et al., 2015; Urban et al., 2016).

Global climate models were once very poor and climate was considered a very complicated thing to be predicted, but through an organized effort and a lot of data collection, climate scientists are now able to accurately model climatic patterns (Urban et al., 2016). If a similar effort is to be made on the biodiversity front, it will require scientist to continue collecting data on processes and updating mechanistic modeling (Urban et al., 2016).

Hybrid approaches that take advantage of both model types' strengths might be applied. The convenience of correlative models makes them useful for identifying common variables that limit the current range of a taxon, and then scientists can focus on collecting data and modeling the processes underlying the influence of those variables. The output of mechanistic models can be used as predictors for correlative models (Kearney & Porter, 2009; Buckley et al., 2010, 2011), so the model considers both factors with well described underlying mechanism and those without. An example would be a correlative model using as predictors a geographical projection of daily hours of activity, a species specific mechanistic variable detailing the response of organisms to temperature (Sinervo et al., 2010), along with total rainfall (Vicenzi et al. 2017), a simple climatic variable without detailed

account of how it affects organisms. Example of hybrid models can be found on the literature (Midgley et al., 2006; Kearney & Porter, 2009; Morin & Thuiller, 2009; Buckley et al., 2010; Elith et al., 2010).

In an effort to facilitate the incorporation of biological processes in biogeographical analysis, we developed Mappinguari, an add-on package for the statistical environment R (R Development Core Team, 2018) that offers tools for process based SDMs. I hope this package stimulate scientists and conservationists to use processes in species distribution modeling, as well as provides convenience and stimulates good practices in species distribution modeling. Using package Mappinguari, here I evaluate venues of incorporating thermal physiology, breeding phenology and demography in biogeographical analysis. On the first chapter of this thesis, I test if estimates of time of activity determined by thermal tolerances are better predictors of the distribution a tropical lizard, *Tropidurus torquatus*, than environmental temperatures. I also determine which are the best practices for obtaining those estimates. On the second chapter, I examine the drivers of reproductive seasonality in two tropical lizards, *Tropidurus torquatus* and *Ameiva ameiva*. I then predict the geographical variation in breeding season duration for both species across the Brazilian Cerrado. On the third chapter, I use the estimates of time of activity and breeding physiology obtained from the previous chapters to spatially extrapolate demographic rates obtained from a 12-year mark and recapture study in central Brazil.

Chapter 1 - Time of activity is a better predictor than environmental temperature for the distribution of a tropical lizard and a R package for estimating ecophysiological spatial predictors

Abstract

Environmental temperatures influence ectotherms' physiology and their capacity to perform activities necessary for survival and reproduction. Thermal tolerance allows us to estimate the time available to perform those activities under different temperature regimes. Estimates of activity time might enhance our ability to predict the suitability of areas for the persistence of a species, compared to using exclusively abiotic parameters, such as environmental temperature. We compare the ability of

environmental temperature and estimates of activity time to predicting the distribution of a tropical lizard, *Tropidurus torquatus*. We compare 105 estimates of activity time, generated by the combination of four methodological decisions: a) how to estimate daily environmental temperature variation (*sinusoid*: modeling a sinusoid wave ranging from monthly minimum to maximum temperature, *operative*: extrapolating from operative environmental temperatures measured in field or *microclim*: using geographical projections of microclimate), b) within which temperature range an animal should be considered to be active, c) should body temperatures obtained in laboratory or in the field be used to determine those temperature ranges, d) should thermoregulation simulations be included in the estimations? We show activity time estimates made with the sinusoid and microclim methods of temperature variation had higher predictive power than environmental temperatures, with sinusoid being the best for this species. Lower thresholds of wide temperature ranges measured in laboratory generated the best predictors. Thermoregulation simulations did not improve model predictions. Precipitation ranked high in both algorithms. Activity time adds important information to distribution modeling at low cost and should be considered as a predictor in studies of ectotherms. *Tropidurus torquatus* seems to be restricted in its distributions by colder temperatures and precipitation, thus climate warming could lead to potential range expansion. We provide an R package, Mapinguari, with tools to generate spatial predictors based on the processes described here.

Introduction

Ectotherms' metabolism depends on environmental temperatures at any range. Temperature changes influence their foraging, digestion and escape from predators, activities critical for survival, growth and reproduction (Porter et al., 1973; Adolph, 1990; Adolph & Porter, 1993). Ectotherms are vulnerable to global climate change, especially in tropical areas (Deutsch et al., 2008; Huey et al., 2009; Sinervo et al., 2010). Several extirpations of lizard populations due to climate change have been documented and more are predicted to happen in 30 years (Sinervo et al., 2010; Foufopoulos, et al., 2011).

Physiology modulates the effect of abiotic conditions on behavior, phenology and dispersal, which influence population dynamics and persistence (Huey, 1991; Walther et al., 2002; Kearney & Porter, 2009). Climate change interacts with thermal tolerance, changing the time available for critical activities each day (Grant & Dunham, 1988; Adolph & Porter, 1993; Sinervo & Adolph, 1994). Activity time constrains the energy an individual can allocate to growth, maintenance and reproduction (Porter et al., 1973; Sinervo & Adolph, 1994; Kearney & Porter, 2009). Time in which activity is restricted by extreme temperatures has been correlated with persistence of lizards' populations (Sinervo et al., 2010).

Estimating time of activity depends on two important decisions: 1) the choice of temperature ranges in which to consider animals active and 2) the choice of a method to estimate the temperature variation animals experience. Numerous combinations of methodologies can result from those decisions, generating considerable variation in estimates of activity time, which influences prediction accuracy. It is crucial to make informed decisions before applying those methodologies.

A direct way to obtain temperature ranges for activity is to measure animals body temperatures in natural habitats. However, temperatures sampled may not capture the range of activity, since activity may be restricted by predation risk, social interactions, or lack of thermal opportunity (Hertz, et al., 1983; Autumn & Denardo, 1995; Iburgüengoytia, 2005). An alternative is to measure the temperature ranges of activity animals in laboratory, using thermal gradient experiments. Animal would not be subject to costs of thermoregulation, but artificial conditions subject individuals to stresses that might affect their activity patterns. Another advantage of those experiments is that they provide a greater volume of data, compared to field sampling.

We can derive important thermal traits, such as preferred temperatures (T_{pref}), or ranges of preferred temperatures (T_{set}) using field or laboratory data (Hertz et al., 1993), but it is important to test which method produces most informative estimates. T_{pref} is calculated as the mean or median temperature selected by individuals at thermal gradients, while T_{set} can be estimated as the whole range of temperatures observed or a quantile range around the median (Hertz et al., 1993; Huey et al., 2009; Gutiérrez et al., 2010). Choosing T_{pref} or T_{set} to determine temperature ranges of activity, and which

quantile to use for T_{set} , will influence results of subsequent analysis, thus it is important to determine what produces better estimates. Neurophysiological evidence suggests ectotherms regulate body temperatures between two set points (Firth & Turner, 1982), but single set-points are widely used and available in the literature (Sinervo et al., 2010). Further complexity can be added to models of activity time by including microclimatic variation or thermoregulatory behavior. However, adding complexity requires additional data, and the benefit is not always clear.

Our goal is to verify if activity time is a better predictor of species distributions than temperature measurements used to calculate it. We assess the accuracy of different estimates of activity time in predicting the distribution of a tropical lizard, *Tropidurus torquatus* Wied, 1820 (Squamata, Tropiduridae), generated under different methodological decisions. *Tropidurus torquatus* occurs throughout the Cerrado savanna and Atlantic rainforest in South America (Rodrigues, 1987). It is a locally abundant and conspicuous lizard, making it convenient to collect thermal ecology data. Finally, we provide tools to facilitate the described estimations in a statistical package for programming environment R, named Mappinguari.

Methods

Distribution data:

We used 359 distribution records from the literature and scientific collections spanning the range of *T. torquatus*. To minimize the effects of spatial autocorrelation and sampling bias, we used function `clean_points` from Mappinguari eliminate records within 40 km from each other, leaving us with 144 records. This large buffer area was determined by fitting Random Forest models under different buffers (1, 5, 10, 20, 30, 40 and 50 kilometers) and comparing Moran's I index (Gittleman & Kot, 1990) calculated from the models' residuals and choosing the smaller buffer with no spatial autocorrelation, using R package `ape` (Paradis et al., 2004). Thirty percent of the distribution data, 44 records, was set aside for model cross-validation.

Physiological data:

From 2013 to 2017, we obtained laboratory physiological data from five populations of *T. torquatus* sampled during monitoring studies and field expeditions. Monitoring took place in Brasília, Distrito Federal (15.7998°S, 47.8645°W, 24 individuals) and Nova Xavantina, Mato Grosso (14.6644°S, 52.3585°W, 4 individuals). Short-term field sampling occurred at Gaúcha do Norte (12.9656°S, 53.5636°W, 13 individuals) and Alta Floresta, Mato Grosso (9.8765°S, 56.0855°W, 3 individuals); and Lagoa da Confusão, Tocantins (10.9201°S, 50.1833°W, 8 individuals). We captured animals using pitfall traps, nooses and by hand.

We placed captured lizards on thermal gradients, which were created by a 60-watt incandescent lamp on one end and an ice pack on the other (Paranjpe, Bastiaans, Patten, Cooper, & Sinervo, 2013). Lizards could stay in the gradient for one hour while their body temperature was recorded every minute by a thermocouple attached to their abdomen and connected to a data logger (Eltek® 1000 Series Squirrel Meter Data Logger 64K, 10 Channel 1001WD), excluding temperatures during the first ten minutes (Paranjpe et al., 2013), in which individuals were acclimating to the gradient. We calculated for each individual and for the whole sample: (1) the range between the 5th and 95th temperature percentile registered in the gradient (T_{90}), (2) range between the 25th and 75th temperature percentile registered (T_{50}) and (3) average temperature (T_{pref}). T_{pref} and T_{50} have been used in previous studies (Sinervo et al., 2010; Kubisch et al., 2016; Piantoni, et al., 2016), and the broader range, T_{90} , was chosen under the hypothesis that lizards spend almost all of their time in the gradient at comfortable temperatures.

We obtained field body temperatures from lizards in Brasília, Distrito Federal, from natural populations occurring within the city's Zoo (15.8512°S, 47.9379°W, details in Wiederhecker, et al., 2002), and Santa Terezinha, Mato Grosso (10.3705°S, 50.5145°W). Animals observed in activity were noosed and had their cloacal temperature measured with a Miller & Weber T-6000 quick reading cloacal thermometer (0.02 °C precision). We then calculated T_{90} , T_{50} and T_{pref} from the aggregated body temperatures.

The different methods of collecting body temperatures result in very different data structures. While the laboratory experiments allow extensive sampling of fewer individuals, field sampling allows

the collection of many individuals, but few samples from each. In laboratory, we sampled 52 individuals with median 65 measures per individual and 9.48 standard deviation, while in field we sampled 649 individuals with median 1 measure per individual and 1.58 standard deviation. This presents a challenge when comparing the data from the two sources, since we could calculate the temperature ranges individually for the laboratory data but not for most individuals sampled in the field. For the field data, we pooled the data across all individuals and assumed thermal tolerances of the entire sample are equivalent to that of individuals. For laboratory data, we estimated temperature ranges as both averages of individual values or from the data aggregated from the whole sample, and then assessed which choice generated better results. We performed an analysis of variance to verify if body temperatures measured in gradients differed between populations and between individuals inside the same population.

Operative Environmental Temperatures:

We recorded operative temperatures using dataloggers (HOBO® U23 Pro v2 2x External Temperature Data Logger-U23-003) with sensors attached to PVC models of equivalent size and color as *T. torquatus*. This methodology has been validated by previous studies with small ectotherms (Adolph, 1990; Lara-Reséndiz et al., 2015; Kirchof et al., 2017). We placed models adjacent to pitfall trap arrays, in the locations where lizards were captured for the physiological trials, in microhabitats where they were observed in activity –shaded and open spots on the ground, on termite mounds, and at the base of trees. Data loggers recorded temperatures every 10 minutes during the trapping period at each location. Variation in air temperature was also measured at the same time and locations, using another data logger without a PVC model (HOBO® U23 Pro v2 Temperature/Relative Humidity Data Logger).

Data analysis:

All analyses were performed in the R programming environment, version 3.5.0 (R Development Core Team, 2018). To perform time of activity estimates, we developed a custom library

for R, named Mappinguari, which provides tools for incorporating diverse biological processes in species distribution modeling. Mappinguari is an open source program and available on a GitHub repository github.com/gabrielhoc/Mappinguari with a tutorial on gabrielhoc.github.io/Mappinguari.

Pseudoabsences:

We used two different algorithms to infer the accuracy of estimates in predicting distribution: Random Forest (RF), using R package randomForest (Breiman & Cutler, 2012) and Gradient Boosting (GB), using R package gbm (Ridgeway, 2007). We generated 100 different sets of pseudoabsences, each with 100 pseudoabsences, the same number of presences (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012) . We used environmental profiling with One-Classification Support Vector Machine (OCSVM), using the R package mopa, (Senay, Worner, & Ikeda, 2013). This methodology restricts the background sampled for pseudoabsences to a distance from presence points determined by the variation in environmental conditions and selects points representing that variation. We obtained climate variables (maximum daily temperature, minimum daily temperature, average daily temperature, precipitation and altitude) from the WorldClim 2.0 database at 2.5 arc minutes resolution for present-day (1970-2000) (Fick & Hijmans, 2017). Every subsequent analysis was repeated for each pseudoabsence set and the results were averaged between sets.

Temperature variation estimation:

We used three different methods to estimate daily temperature variation to which animals are subject to, and from which we determine how much time they spent within or without temperature ranges for activity:

a) Sinusoid method:

We used the approach of Sinervo and collaborators (Sinervo et al., 2010) implemented in the Mappinguari function `sin_h`. This approach requires the least amount of data and assumes lizard body temperature tracks environmental temperature. It models daily air temperature

variation as a sinusoidal curve ranging between the maximum and minimum daily air temperatures at a location. Then we recorded how much time the environmental temperature is within T_{90} , within T_{50} , above T_{pref} , for both field and lab temperature ranges at each occurrence and pseudoabsence point. We also did the same calculations for the lower and upper temperatures thresholds of T_{90} and T_{50} to verify if colder or hotter thresholds are more relevant than the whole range of activity. We used a time resolution of 1 hour to make estimates comparable with the microclim method, which is derived from hourly data. Hours above T_{pref} is a measure of hours of restriction to activity, so it should be interpreted on the opposite ways as the other metrics. These estimates of activity time, as well as all subsequent ones, were capped by day length at each location, calculated using Corripio's method (Corripio, 2003).

b) Operative temperature method:

We used daily temperature variation collected with operative temperatures models (T_e) (Bakken, 1992) to estimate time of activity for each day, location and microhabitat sampled, using the same temperature ranges mentioned above. These data were regressed against maximum daily air temperatures for the same period, using a Richards growth model (Richards, 1959). These models were applied to present-day maximum daily air temperature data from the WorldClim 2.0 database at 2.5 minutes resolution, for each occurrence and pseudoabsence point.

c) Microclim method:

We used the microclim database (Kearney, et al., 2014), which simulates environmental temperatures for each hour of the day in six levels of shade and different kinds of substrate for the whole world. We used the soil substrate, which we regarded as the most common for *T. torquatus* based on field observations. We used function `summary_microclim` from `Mapinguari` to estimate time of activity, for the same temperature ranges mentioned above, at

each shade level, for each occurrence or pseudoabsence point (Sinervo et al., 2018).

Microclim data are available at 10 arc minute resolution, so they were rescaled to 2.5 arc minutes raster using bilinear interpolation in package raster (Hijmans et al., 2016).

Thermoregulation simulation:

Operative temperature and microclim methods provide information on microclimatic variation at each site, so we simulated thermoregulation, assuming lizards would choose any microhabitat with temperatures inside the activity range when available. For comparison, we generated estimates of time of activity under no thermoregulation by averaging the time of activity between all microhabitats. Names used to represent each estimate are summarized in the appendix table A1, hereafter the estimates will be designated by these names.

Predictor evaluation:

Estimates of activity time were used as predictors of species distribution in models constructed with different algorithms, and their quality as predictors was assessed using the protocol describe below. Each model also included maximum air temperature as a comparison, since estimates were derived from maximum air temperature and should outperform it if they add any relevant information. We also include average air temperature, a commonly used climate variable, and precipitation, to control for variation not associated with thermal physiology.

Considering the problem at hand, all estimates are expected to be highly correlated. So we used algorithms robust to multicollinearity, Random Forest and Gradient Boosting (James et al., 2013), to assess predictor importance. We evaluated the performance of each algorithm by the area under the receiver operating characteristic curve (AUC), constructed with the set of presence records set aside for cross-validation and 100 sets of pseudoabsences. The agreement between algorithms' variable importance indexes was used to determine predictor importance. The importance index used for Random Forest was mean decrease in accuracy (Archer & Kimes, 2008) and for Gradient Boosting, relative influence (Friedman, 2001). Importance measures of variables obtained from each algorithm

were grouped by each methodological decision, weighted by the AUC of each algorithm and averaged to obtain a consensus of importance of each decision. Finally, activity time estimates and climate variables with greater support were used to predict the potential distribution of the animal.

Results

Body temperatures measured in laboratory differed significantly between populations ($F=124.17$, $df=4$, $p<0.0001$) and between individuals in each population (Brasília: $F=186.32$, $df=23$, $p<0.0001$; Alta Floresta: $F=1502.4$, $df=2$, $p<0.0001$; Gaúcha do Norte: $F=180.82$, $df=12$, $p<0.0001$; Lagoa da Confusão: $F=88.849$, $df=7$, $p<0.0001$; Nova Xavantina: $F=9.5095$, $df=3$, $p<0.0001$;). We can observe a lot of variation in the distribution of body temperatures (Figure 1.1). This indicates lizards are comfortable in wide temperature ranges and each lizard is not exploring its whole thermal tolerance range in the gradient. This suggests it is better to pool all body temperatures in order to characterize thermal tolerance ranges.

Median body temperature collected at the gradients was very similar to the one collected on field (laboratory= 33.6°C , field= 33°C), but with higher standard deviation (laboratory= 6.02 , field= 2.62). This lead to broader temperature ranges for activity when compared to field estimates. Physiological temperature thresholds and ranges for *T. torquatus*, calculated from the gradient experiments, had the following values: $T_{pref}=31.5^{\circ}\text{C}$ (standard deviation: 6.02), $T_{50_lwr}=26.7^{\circ}\text{C}$, $T_{50_upr}=36.6^{\circ}\text{C}$, $T_{90_lwr}=12.4^{\circ}\text{C}$, $T_{90_upr}=47.2^{\circ}\text{C}$, whereas estimates calculated from field temperatures had the following values $T_{pref}=32.6^{\circ}\text{C}$ (standard deviation: 2.62), $T_{50_lwr}=30.9^{\circ}\text{C}$, $T_{50_upr}=34.6^{\circ}\text{C}$, $T_{90_lwr}=25.2^{\circ}\text{C}$, $T_{90_upr}=40.2^{\circ}\text{C}$. Figure 1.2 shows the distribution of activity time estimates grouped under each methodological decision.

Random Forest had similar AUC (0.783 ± 0.047) to Gradient Boosting (0.762 ± 0.053). Predictor importances are summarized in Table 1.1. Precipitation ranked highest for RF and second highest for GB. Across both algorithms, activity time estimates ranked higher than environmental temperature. Estimate *sin_t90_lwr_lab* (Table A1) ranked on both algorithms (Table 1.1). The consensus between algorithms averaged for methodological decisions is summarized in Table 1.2. The

distribution predicted by the most supported variables, *sin_t90_lab_lwr* and precipitation, is displayed on Figure 1.3.

Discussion

All decisions made for the estimation of time of activity generated significantly different estimates, demonstrating each of them can severely influence activity time estimates and should be carefully considered before making them. Estimates under many permutations of methodological decisions ranked above environmental temperatures, as much as 6 times more importance on the RF algorithm and 27 times more on the GB algorithm (Table 1.2). This indicates activity time is a useful to model mechanisms by which temperature restricts the distribution of species. Our results are further evidence that incorporating mechanisms improve the accuracy of species distribution models (Buckley et al., 2010; Urban et al., 2016).

The simplest temperature variation method, sinusoid, ranked highest in both algorithms (Table 1.1), and when averaged across all variables using this decision (Table 1.2). This shows this method is the most reliable for our study species. The microclim method also generated better predictors than environmental temperatures, so it is a viable alternative. Estimates made with the operative method ranked below environmental temperature indicating this method needs refinement, perhaps by modeling how microclimates interact with microhabitat structure and macroclimate. Lizards' access to microhabitats might be limited by species interactions and dispersal capacity. Modeling such processes is complex and data is scarce, complicating the prospects of realizing such a detailed model. Using simpler and general methods could yield more accurate predictors at lower costs.

The lower threshold of T_{90} measured in laboratory had the most predictive power. This shows lower temperatures are limiting this species distribution, unlike other species studied previously (Sinervo et al., 2010; Andrango et al., 2016; Medina et al., 2016). Estimates made with interquartile ranges also ranked higher than environmental temperatures on average, so this range could also be informative and used in future studies, though our results favor the use of the 90th quantile ranges. The

upper threshold of T_{90} was rarely crossed (Table 1.1), showing this lizard is rarely experiencing temperatures above its tolerance in its current range. The species is tolerant to heat and could benefit from climate warming, expanding its distribution to areas previously too cold for it to inhabit, where it could potentially displace native species less adapted to hotter conditions. Future studies should be done to verify if the same methodological choices apply to more thermally restricted species.

Laboratory body temperatures yielded better results in general field ones, reinforcing the importance of experiments for characterizing thermal physiology. Animals might explore wider temperature ranges in thermal gradients than the field, avoiding constraints present in their natural habitats. We recommend future studies thermal gradients for estimating thermal tolerances. Aggregating temperatures from all individuals then calculating thermal tolerances yielded better results than calculating thermal tolerances individually. Individuals might not be exploring their full thermal tolerance in the thermal gradient, so observing all individuals together could give us a better picture of the species' thermal tolerance.

We and could not generate informative estimates of activity time with the model of thermoregulation employed. This may be due to the assumption that animals would have immediate access to all microhabitats available for thermoregulation. Laboratory experiments to elucidate how efficient animals are in choosing appropriate microclimates and projections of microhabitat structure might help add realism to those models.

Precipitation ranked high in both algorithms, in agreement with studies that show it is a reliable predictor of lizard distribution (Araújo, et al., 2006; Barrows, 2011; Nasrabadi et al., 2018). *Tropidurus torquatus* contract its range at more arid regions, such as the interface of the Cerrado with the semi-arid Caatinga the northeast of the species distribution. Modeling the processes by which rainfall affects ectotherm distribution is more complex than with thermal physiology, since it might involve species interactions, prey availability and egg survival, which would require data not commonly available.

We found *T. torquatus* rarely experiences temperatures above its upper thermal tolerance, suggesting high levels of warming would be required for distribution contraction. Previous work has

found H_{ipref} to be a good predictor for the persistence of desert lizard populations in Mexico (Sinervo et al., 2010), while the same estimate ranked very low for *T. torquatus*. This could be due to the extreme differences in the environments inhabited by those animals: desert lizards experienced much higher temperatures along their evolutionary history than *T. torquatus* and thus have evolved preferred temperatures closer to their upper thermal tolerance limits, so smaller levels of warming may be required to endanger those species.

Most studies report negative effects of climate warming on Lepidosauria (Diele-Viegas & Rocha, 2018), unlike what was found for *T. torquatus*. Thermal tolerant species might dominate reptile communities in the near future, given other species are expected to decline (Diele-Viegas & Rocha, 2018). Other studies found lower thermal tolerance to evolve quickly in tropical lizards (Leal & Gunderson, 2012), reinforcing the hypothesis that thermal tolerant lizards could expand their distributions after climate change.

Activity time alone is not the sole factor determining the presence of a species (Kearney, 2013), but it is a better predictor than environmental temperature alone. It is possible to model mechanisms by which the environment affects physiological with limited information adding important information to distribution modelling. Package Mappinguari is an effort to increase accessibility to the techniques used here and facilitate their further development. We hope users of the package can generate biologically relevant information to provide policy makers with tools to mitigate the effects of climate warming on vulnerable species.

Tables and Figures

Table 1.1. Median, standard deviation (SD) and importance indexes of each estimate of time of activity to predict distribution of *Tropidurus torquatus*, under Random Forest (RF) and Gradient Boosting (GB) algorithms. The importance index used for RF was mean decrease in accuracy and for GB was relative influence. Variables ranked above environmental temperatures, are in bold and include their ranks on parenthesis. Precipitation was included as a covariate. Detailed description of variables can be found on Table A1.

Variable	Median	SD	RF (rank)	GB (rank)
prec	121.275	21.744	0.044 (1)	0.083 (3)
sin_tabs_lwr_lab	11.676	1.103	0.033 (2)	0.374 (1)
sin_tabs_lab	11.676	1.103	0.032 (3)	0.000
mc_tiq_lab_avg	4.954	0.742	0.022 (4)	0.157 (2)
mc_tiq_lab_ind_avg	1.695	0.347	0.021 (5)	0.000
mc_tabs_field_avg	4.053	0.733	0.020 (6)	0.010 (8)
mc_tabs_lab_ind_avg	3.626	0.641	0.018 (7)	0.021 (6)
mc_tp_lab_min	0.281	0.477	0.015 (8)	0.000
mc_tiq_upr_lab_avg	1.810	1.002	0.015 (9)	0.000
mc_tp_lab_ind_min	0.237	0.410	0.014 (10)	0.000
mc_tabs_lab_avg	9.067	0.901	0.014 (11)	0.000
mc_tiq_field_avg	1.661	0.351	0.013 (12)	0.030 (5)
mc_tabs_upr_field_avg	1.870	1.013	0.013 (13)	0.000
mc_tabs_lwr_lab_max	10.557	0.792	0.013 (14)	0.000
mc_tabs_lab_max	10.557	0.792	0.013 (15)	0.000
mc_tabs_lwr_lab_avg	10.036	1.140	0.011 (16)	0.000
mc_tiq_upr_field_avg	2.560	1.166	0.011 (17)	0.000
mc_tabs_upr_lab_avg	1.245	0.846	0.010 (18)	0.000

mc_tp_lab_avg	3.829	1.392	0.010 (19)	0.008 (9)
mc_tp_field_min	0.091	0.184	0.009 (20)	0.000
mc_tiq_upr_lab_ind_avg	2.989	1.247	0.009 (21)	0.047 (4)
mc_tp_lab_ind_avg	3.747	1.375	0.009 (22)	0.006 (10)
op_tabs_lab_ind_max	3.784	1.300	0.009 (23)	0.000
mc_tabs_upr_lab_ind_avg	2.274	1.105	0.009 (24)	0.000
mc_tiq_lwr_field_avg	4.221	1.461	0.009 (25)	0.013 (7)
mc_tp_field_avg	3.327	1.294	0.008 (26)	0.000
mc_tabs_lwr_field_avg	5.924	1.614	0.008 (27)	0.000
mc_tiq_lwr_lab_max	8.689	0.982	0.008 (28)	0.000
mc_tabs_lwr_lab_ind_avg	5.900	1.612	0.008 (29)	0.000
mc_tiq_lab_ind_max	7.435	1.239	0.008 (30)	0.000
mc_tiq_lab_max	8.689	0.982	0.008 (31)	0.000
mc_tabs_field_max	8.244	1.120	0.008 (32)	0.000
mc_tiq_lwr_lab_avg	6.764	1.549	0.007 (33)	0.000
mc_tabs_lwr_field_max	8.244	1.120	0.007 (34)	0.000
mc_tiq_field_max	7.119	1.313	0.007 (35)	0.000
sin_tiq_lwr_lab	6.463	3.129	0.007 (36)	0.001
mc_tiq_lwr_field_max	7.121	1.314	0.007 (37)	0.000

mc_tiq_lwr_lab_ind_avg	4.684	1.530	0.007 (38)	0.000
sin_tabs_lwr_field	4.587	3.033	0.007 (39)	0.000
tavg	23.108	2.152	0.007	0.003
op_tabs_field_max	3.848	1.322	0.007	0.000
sin_tiq_lab	6.463	3.129	0.007	0.000
op_tabs_lwr_lab_ind_max	3.818	1.362	0.007	0.000
mc_tabs_lwr_lab_ind_max	8.229	1.126	0.007	0.000
op_tiq_upr_lab_avg	0.441	0.459	0.007	0.000
op_tabs_upr_field_avg	0.444	0.466	0.007	0.000
mc_tiq_lwr_lab_ind_max	7.463	1.272	0.006	0.000
mc_tabs_lab_ind_max	8.229	1.126	0.006	0.000
sin_tabs_field	4.587	3.033	0.006	0.000
sin_tabs_lwr_lab_ind	4.544	3.030	0.006	0.000
op_tabs_lwr_field_max	3.862	1.350	0.006	0.000
op_tiq_field_max	1.788	1.372	0.006	0.000
op_tabs_lab_max	9.520	0.369	0.006	0.000
op_tp_lab_ind_avg	0.939	1.049	0.006	0.000
sin_tabs_lab_ind	4.544	3.030	0.006	0.000
op_tabs_lwr_lab_ind_avg	2.009	1.495	0.006	0.000

op_tabs_lwr_lab_avg	8.259	0.917	0.006	0.000
sin_tiq_lab_ind	2.141	2.187	0.006	0.000
sin_tiq_lwr_field	1.520	1.965	0.006	0.000
sin_tiq_lwr_lab_ind	2.275	2.430	0.006	0.000
op_tiq_lab_ind_avg	0.461	0.470	0.006	0.000
sin_tiq_field	1.501	1.918	0.006	0.000
op_tiq_lwr_field_avg	1.028	1.159	0.006	0.000
tmax	28.945	2.413	0.005	0.004
op_tiq_lwr_lab_ind_avg	1.207	1.271	0.005	0.000
op_tabs_upr_lab_ind_avg	0.503	0.597	0.005	0.000
sin_tp_lab_ind	0.887	1.434	0.005	0.001
op_tabs_lwr_field_avg	2.070	1.478	0.005	0.000
op_tp_field_avg	0.813	0.907	0.005	0.000
op_tabs_lab_avg	8.016	0.688	0.005	0.000
op_tp_lab_avg	0.957	1.065	0.005	0.000
op_tiq_lwr_field_max	1.855	1.487	0.005	0.000
op_tiq_lab_max	4.629	1.222	0.005	0.000
op_tiq_lwr_lab_ind_max	2.580	1.383	0.005	0.000
op_tiq_upr_lab_ind_avg	0.747	0.813	0.005	0.000

op_tiq_field_avg	0.516	0.528	0.005	0.000
op_tiq_lwr_lab_max	4.645	1.252	0.005	0.000
op_tabs_lwr_lab_max	9.524	0.374	0.005	0.000
op_tp_lab_ind_min	0.373	0.570	0.005	0.000
op_tabs_lab_ind_avg	1.505	0.922	0.005	0.000
sin_tp_lab	0.990	1.513	0.005	0.002
op_tp_field_min	0.208	0.364	0.005	0.000
op_tiq_lab_ind_max	2.458	1.193	0.005	0.000
op_tabs_field_avg	1.627	1.029	0.005	0.000
op_tiq_upr_field_avg	0.512	0.643	0.004	0.000
op_tp_lab_min	0.380	0.582	0.004	0.000
op_tiq_lwr_lab_avg	3.102	1.429	0.004	0.000
op_tiq_lab_avg	2.661	0.996	0.004	0.000
op_tabs_upr_lab_avg	0.243	0.308	0.003	0.000
sin_tp_field	0.389	0.845	0.003	0.001
mc_tiq_upr_lab_ind_min	0.028	0.074	0.003	0.000
op_tiq_upr_lab_ind_min	0.122	0.249	0.003	0.000
op_tiq_upr_field_min	0.067	0.165	0.002	0.000
sin_tiq_upr_lab_ind	0.134	0.439	0.001	0.000

mc_tabs_upr_lab_ind_min	0.000	0.000	0.000	0.000
sin_tabs_upr_lab_ind	0.000	0.000	0.000	0.000
sin_tiq_upr_lab	0.000	0.000	0.000	0.000
sin_tabs_upr_lab	0.000	0.000	0.000	0.000
sin_tabs_upr_field	0.000	0.000	0.000	0.000
mc_tiq_upr_lab_min	0.000	0.000	0.000	0.000
mc_tabs_upr_lab_min	0.000	0.000	0.000	0.000
mc_tabs_upr_field_min	0.000	0.000	0.000	0.000
op_tabs_upr_lab_ind_min	0.035	0.115	0.000	0.000
mc_tiq_upr_field_min	0.001	0.011	0.000	0.000
sin_tiq_upr_field	0.019	0.121	0.000	0.000
op_tabs_upr_lab_min	0.005	0.033	-0.001	0.000
op_tabs_upr_field_min	0.014	0.063	-0.001	0.000
op_tiq_upr_lab_min	0.016	0.069	-0.001	0.000

Table 1.2. Median, standard deviation (SD) and weighted average of variable importance for activity time estimates for the distribution of the tropical lizard *Tropidurus torquatus*, grouped under different methodological decisions. (1) method of estimation of temperature variation to which animals experienced. Sinusoid simulates temperature variation as a sine wave spanning from daily maximum to minimum air temperatures. Operative used operative temperature models to measure daily temperature variations *in situ* and them extrapolated time of activity measures by

correlating it to air temperatures. Microclim used microclimatic surfaces (Kearney et al., 2014) containing estimates of daily temperature variation in different microhabitats. (2) range of temperatures in which animals were regarded as active. T_{pref} : above average body temperature, T_{50_lwr} : above 25th quantile, T_{50_upr} : above 75th quantile, T_{90_lwr} above 5th quantile, T_{90_upr} above 95th quantile. T_{50} : between T_{50_lwr} and T_{50_upr} and T_{90} : between T_{90_lwr} and T_{90_upr} (3) origin of body temperatures used for range estimation: field or laboratory. Laboratory ranges were obtained by aggregating data from all individuals then calculating range or calculating range for each individual and averaging between them. (4) use of thermoregulation simulations on operative and microclim methods of temperature variation. The average between microhabitats for each temperature range is also included for comparison. Also included are (5) climate variables: average air temperature (T_{avg}), maximum air temperature (T_{max}) and precipitation. Importance indexes were obtained from Random Forest (mean decrease in accuracy) and Gradient Boosting (relative influence) regressions of distribution against hours of activity and climate.

Methodological decisions	Median	SD	Importance
<u>(1) temperature variation</u>			
sinusoid	0.917	4.024	0.012
operative	0.917	2.385	0.002
microclim	3.639	2.590	0.008
<u>(2) range</u>			
T_{pref}	1.250	1.816	0.004
T_{50}	1.736	2.420	0.010
T_{90}	4.250	3.638	0.006

T_{50_lwr}	3.167	2.779	0.004
T_{90_lwr}	6.042	3.655	0.017
T_{50_upr}	0.333	1.323	0.003
T_{90_upr}	0.208	1.029	0.002
<u>(3) origin</u>			
laboratory-pooled	3.750	4.114	0.012
laboratory-individual	1.583	2.249	0.004
field	1.361	2.210	0.004
<u>(4) thermoregulation</u>			
average-T₅₀, T₉₀	2.382	2.782	0.015
maximum-T₅₀, T₉₀	7.000	3.022	0.004
average-T_{50_lwr}, T_{90_lwr}	4.333	3.087	0.004
maximum-T_{50_lwr}, T_{90_lwr}	7.000	3.014	0.003
average – T_{pref}, T_{50_lwr}, T_{90_lwr}	1.188	1.536	0.006
minimum – T_{pref}, T_{50_lwr}, T_{90_lwr}	0.000	0.301	0.002
<u>(5) climate</u>			
precipitation	124.000	21.744	0.064
T_{avg}	23.175	2.152	0.005
T_{max}	28.630	2.413	0.005

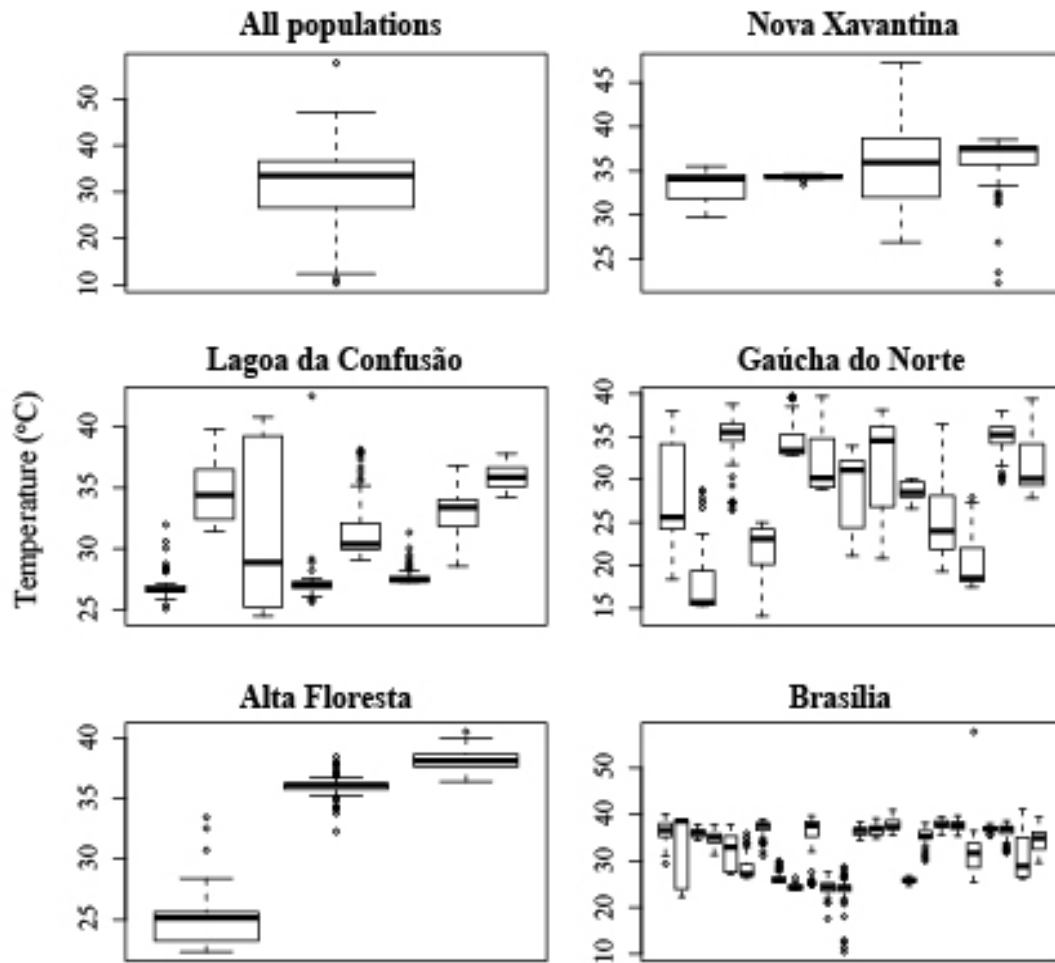


Figure 1.1. Distribution of body temperatures of *Tropidurus torquatus* lizards in 5 populations in Brazil. Body temperatures were collected every minute for one hour at a thermal gradient.

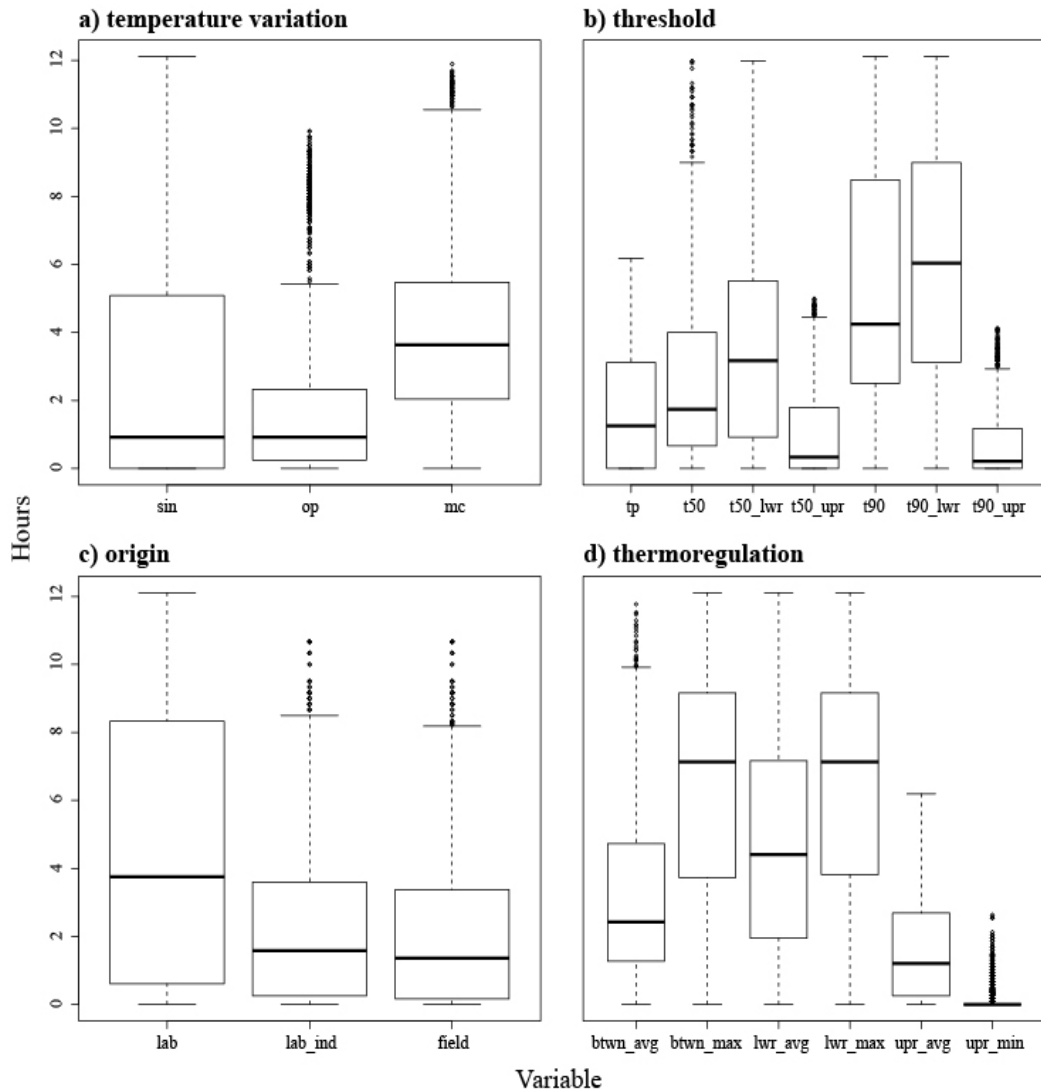


Figure 1.2. Distribution of activity time estimates at known occurrence sites of *Tropidurus torquatus*. a) grouped by temperature variation method. Sinusoid simulates temperature variation as a sine wave spanning from daily maximum to minimum air temperatures. Operative used operative temperature models to measure daily temperature variations *in situ* and them extrapolated time of activity measures by correlating it to air temperatures. Microclim used microclimatic surfaces (Kearney et al., 2014) containing estimates of daily temperature variation in different microhabitats. b) grouped by temperature range of activity. T_{pref} : above average body temperature, T_{50_lwr} : above 25th quantile, T_{50_upr} : above 75th quantile, T_{90_lwr} above 5th quantile, T_{90_upr} above 95th quantile. T_{50} : between

T_{50_lwr} and T_{50_upr} and T_{90} : between T_{90_lwr} and T_{90_upr} c) grouped by origin of body temperatures used to estimate temperature ranges of activity (laboratory or field) d) grouped by use of thermoregulation simulations.

Probability of Occurrence of the lizard *Tropidurus torquatus* across Brazil

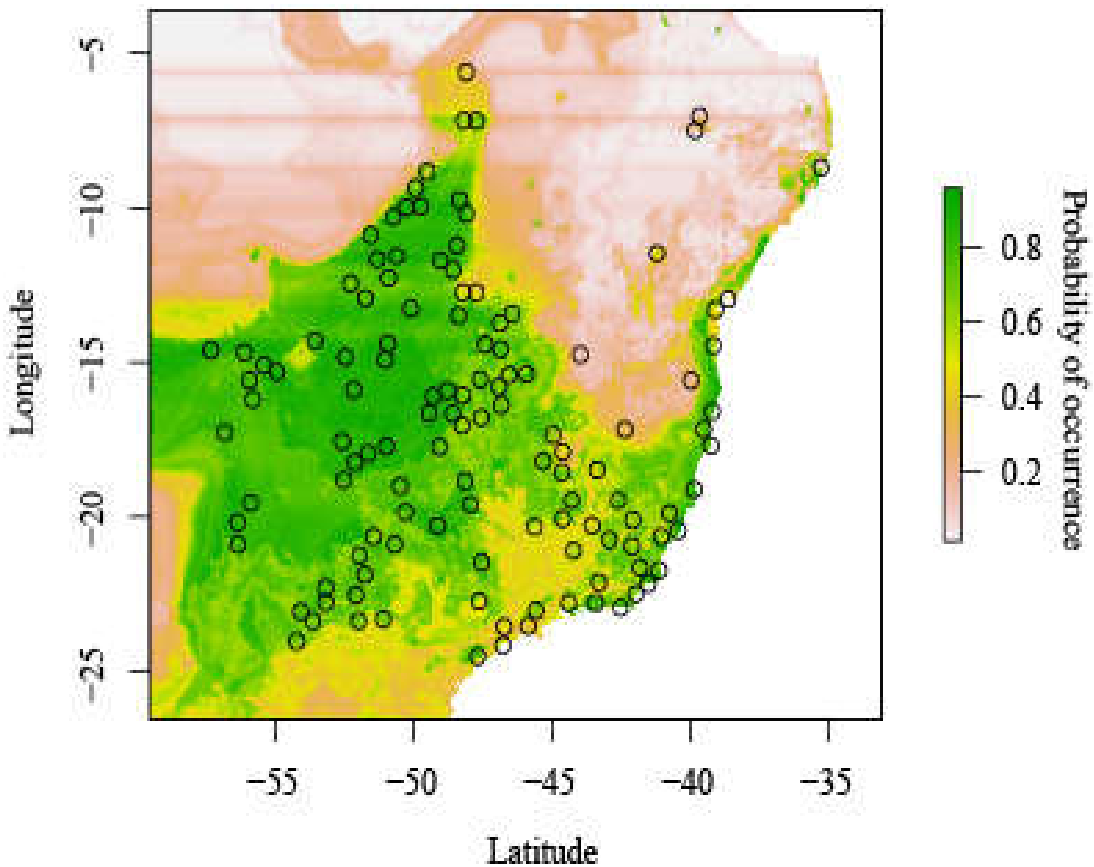


Figure 1.3. Probability of occurrence of the lizard *Tropidurus torquatus* across Brazil. Estimated using Random Forest regression of occurrence records and background points against precipitation and hours of activity. Circles represent occurrence records.

Chapter 2 - Is day length more important than climate in predicting reproductive seasonality of a lizard with a parietal eye?

Abstract

We aim to determine if geographical variation of reproductive seasonality is determined by day length in tropical lizard species with and without a parietal eye. We performed a literature search for records of reproductive individuals of both species, then used a Random Forest model to infer which environmental variables mostly influenced reproductive status for each species. The resulting model was used to predict reproduction seasonality and infer geographical variation in breeding patterns across the Brazilian Cerrado. Solar radiation and day length were the main factors determining the reproductive seasonality of *T. torquatus*, a lizard that has a parietal eye, while *A. ameiva*, which lacks this trait, was more sensitive to temperature and precipitation. Both species showed a latitudinal pattern in breeding season duration, breeding for longer as they get closer to the equator. *A. ameiva* usually had longer breeding seasons, achieving yearlong reproduction in some areas. The model yielded high predictive accuracy for *T. torquatus*, showing simple random forest regressions could be used to predict geographical variation in breeding seasonality of data deficient taxa. The parietal eye is an important anatomical structure which helps to determine geographic variation in reproductive seasonality of lizards with such structure. The presence of a functional parietal eye might have important consequences for squamates' adaptation to climate change, since the rapid shift in weather might cause a mismatch between the photoperiodic cue and optimal environmental conditions for reproduction.

Introduction

Timing of reproduction is crucial for animals living in seasonal environments. They can optimize the allocation of resources by timing life history events so each stage of development happens in optimal environmental conditions (Bradshaw & Holzapfel, 2007). Failing to do so might result in suboptimal allocation of reproductive effort or even loss of offspring, as well as affect adult survival (Corn & Muths, 2002; Goodenough *et al.*, 2010; Saino *et al.*, 2011). It has been extensively demonstrated that animals and plants may shift their breeding phenology in response to climate change (Forchhammer *et al.*, 1998; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Visser & Both, 2005).

These shifts might be adaptive if they allow the organisms to track optimal environmental conditions for breeding or offspring development. However, they can be maladaptive if they result in mismatches with the phenology of optimal environmental conditions, food sources and important interacting species (Parmesan & Yohe, 2003). Thus, the ability to accurately shift breeding periods might be crucial for the survival of a species in face of global climate change.

Many animals rely on environmental cues to time reproductive events. Day length is a highly consistent and reliable cue for climate conditions across geographical ranges, and is used by a wide variety of organisms (Bradshaw & Holzapfel, 2007). It seems to be more important for the breeding phenology of animals living at high latitudes (Angilletta, Jr., 2001; Bradshaw & Holzapfel, 2007), but few studies on have been done on tropical taxa (Hau, 2001).

Reproductive seasonality in tropical lizards has been associated with risks of egg desiccation and food availability (Colli *et al.*, 1997), both of which are influenced by climate. *Tropidurus torquatus* (Tropiduridae) and *Ameiva ameiva* (Teiidae) are two of the most widely distributed and locally abundant lizard species in the Brazilian Cerrado. Both species are typical of open areas and very abundant in this region, which consists mostly of shrublands and fields. It has been suggested that precipitation affects the seasonality of food abundance, mostly arthropods, hatchling survival and microhabitats appropriate for egg laying, and thus the reproductive cycle, of *A. ameiva* (Colli, 1991).

Data on geographical variation of reproductive phenology of tropical lizards is scarce, and most methods available are data intensive or easier applied to temperate taxa. Here we propose and evaluate a simple correlative model for predicting geographical variation in phenology that can be used in data deficient taxa and examine drivers of geographical variation in reproductive seasonality in two tropical lizards. We hope to stimulate phenological studies with tropical and data deficient taxa, which in turn would make more data available so more sophisticated methodologies might be applied or developed.

Methods

We conducted a literature search for papers providing information on reproductive status, time and location of lizards of both species. We then compiled climatic conditions (maximum month temperature, minimum month temperature, average month temperature, total month precipitation, total month solar radiation) for the locations and times when the lizards were captured, using 2.5 minute resolution climate surfaces from WorldClim 2 (Fick & Hijmans, 2017). We classified the instances found as: (1) Reproductive, if female lizards were found to have mature gonads or were bearing eggs; and (2) Non-reproductive, if a study reported none or a very small proportion of reproductive females under a reasonable sample size. We estimated day length for the same time and locations using Corripio's method (Corripio, 2003).

In addition to climatic variables, we estimated daily hours of activity for each time and location considered (Sinervo *et al.*, 2010). This method consists of simulating daily temperature variation as a sine wave ranging from daily minimum to maximum temperatures and then counting the number of hours in which those temperatures fall in the temperature range in which an animal is considered to be active. In order to obtain those temperature ranges, we placed lizards in thermal gradients for one hour and had their body temperatures registered every minute. Then we calculated the range between the 5th and 95th temperature percentile registered in the gradient and considered that as the temperature range of activity. These methods are described in detail in Caetano *et al.*, 2019.

To assess which environmental variables drove the reproductive phenology of each species, we used a Least Absolute Shrinkage and Selection Operator (LASSO) procedure to a Generalized Linear Mixed Model (GLMM) regression using R package *glmLasso* (Schelldorfer *et al.*, 2014) between reproductive status records, minimum month temperature, maximum month temperature, average month temperature, total month precipitation, using a logit link function. We performed a 5-fold cross validation using R package *cvms* (Olsen, 2016) to assess model accuracy.

We then fitted GLMMs with only the variables selected in LASSO to make predictions for the Cerrado, using the WorldClim monthly climate surfaces, so we could examine model-predicted geographical patterns in breeding season duration. We chose the Cerrado to make our projections

because it is the major region of range overlap between our focal species, where both are very abundant. All analyses were performed in the R programming environment, version 3.5.0 (R Development Core Team, 2018).

Results

We found 9 studies containing data on 16 populations of *T. torquatus* and 10 studies containing data on 15 populations of *A. ameiva*, although only 7 of the *A. ameiva* studies included information on the reproductive status of lizards for the whole year. These data are summarized in tables 1 and 2.

Solar radiation and day length were the only predictors for which coefficients were not reduced to zero on the LASSO procedure for *T. torquatus*, indicating those are the best predictors of reproduction timing for this species, in agreement with previous reports for a population in central Cerrado (Wiederhecker *et al.*, 2002). The only important predictor for *A. ameiva* was linear precipitation, also agreeing with previous reports (Colli, 1991; Vitt & Colli, 1994). Cross-validation yielded an AUC of 0.840 for the *T. torquatus* model, indicating the model has high predictive power, while the *A. ameiva* model had less support (AUC = 0.645), indicating there are other drivers of breeding phenology not captured in the model. Overall, *T. torquatus* was predicted to have more variation than *A. ameiva* in breeding seasonality, along a latitudinal gradient with longer breeding seasons in the north, while *A. ameiva* (Figure 1) showed longitudinal gradient with longer breeding seasons in the west.

Discussion

Neither lizards' phenology showed correlation with temperatures, unlike what has been found for many ectotherms (Conover & Present, 1990; Grant & Dunham, 1990; Sinervo & Doyle, 1990; Adolph & Porter, 1993; Bernardo, 1994), including *A. ameiva* (Fitzgerald *et al.*, 1999). Another thermally related variable, time of activity, was not strongly correlated with reproductive phenology for either species in our study, but it has been shown to be important in other ectotherms (Sinervo &

Adolph, 1989, 1994, Adolph & Porter, 1993, 1996). Precipitation showed a positive correlation with *A. ameiva* breeding phenology, indicating it prefers to breed in the rainy season, as reported by previous studies (Colli, 1991; Vitt & Colli, 1994). Studies on other tropical species found similar correlations to precipitation, with lizards reproducing continuously wherever there was enough rainfall (Watling *et al.*, 2005). *Ameiva ameiva* was predicted to breed for longer in the border of the Cerrado with the Amazon and Atlantic rainforests (Figure 1), in accordance to what was observed in a previous study (Colli, 1991). The same study however, reported longer breeding seasons at the semi-arid regions to the east as well, the opposite of what our model predicted. That study associated breeding season duration with predictability of rainfall, a temporal dynamic that was not included in our modeling.

The selection of day length and solar radiation for *T. torquatus* and precipitation for *A. ameiva* suggest the influence of the parietal eye mechanism in driving the breeding phenology of *T. torquatus*. While very common in Tropicuridae, including *T. torquatus*, all Teiidae lack a functional parietal eye, including *A. ameiva* (Gundy & Wurst, 1976). The parietal eye is an important photoreceptive organ that can detect day length. It is usually located in forehead and attached to the pineal gland, which can trigger important hormonal changes based on the day length. For instance, it influences patterns of thermoregulation, circadian cycles and reproductive physiology (Tosini, 1997). Through the modulation of melatonin brought by the pineal organ, the parietal eye can affect gonadal condition and mating behavior (Clausen & Poris, 1937; Haldar & Thapliyal, 1977, 1981; Underwood, 1985; Nelson *et al.*, 1987; Crews *et al.*, 1988; Haldar & Pandey, 1989a,b; Mendonça *et al.*, 1996). Intensity of solar radiation has been associated with behavioral changes intermediated by the parietal eye (Glaser, 1958; Stebbins & Eakin, 1958).

Relying on photoperiodic cues to time their reproductive seasonality could have important consequences for *T. torquatus* and other lizards with parietal eyes, in face of climate change, since cue and environment might be mismatched if climate shifts faster than an animal can adapt its photoperiodic response (Caprioli *et al.*, 2012). However, studies on other species with parietal eyes found substantial plasticity in reproductive phenology in response to temperature variations

(Ljungström *et al.*, 2015; Rutschmann *et al.*, 2016), indicating the photoperiodic response might not be so restrictive.

A fundamental question in life history studies is if variation among populations is caused by environmental constraints or by adaptation (Adolph & Porter, 1996). This distinction can have important consequences for a species response to climate change. If that variation is caused by the species struggling with restricting conditions and resource limitation, climate change might bring further stress and hamper reproductive efforts. If that variation is caused by adaptation or plasticity, it is an indicator of breeding strategy malleability that might be adaptive to face new conditions brought by climate change. While we found that somewhat rigid variables predict timing of reproduction in *T. torquatus*, the species shows substantial variation in other aspects of its life history, such as clutch size, mass and frequency (Vitt & Goldberg, 1983; Wiederhecker *et al.*, 2002; Kiefer *et al.*, 2008). If that is due to plasticity or adaptive capacity, *T. torquatus* might be able to buffer the effects of climate change on breeding season duration in time to adapt its photoperiodic response to new climate conditions (Caprioli *et al.*, 2012).

Our results suggest geographical variation of reproductive seasonality can vary substantially between tropical lizard species. One of the probable causes of such differences is the presence of parietal eyes on some species, such as *T. torquatus*. Future studies on breeding phenology should consider photoperiodic responses as a candidate driver of breeding phenology for species having this structure. This is especially important on studies about climate change effects, since reliance on a mechanism dependent on somewhat inflexible environmental cues could make the species unable to adjust their breeding phenology to new conditions.

Tables and Figures

Breeding season duration of two lizard species across the Brazilian Cerrado

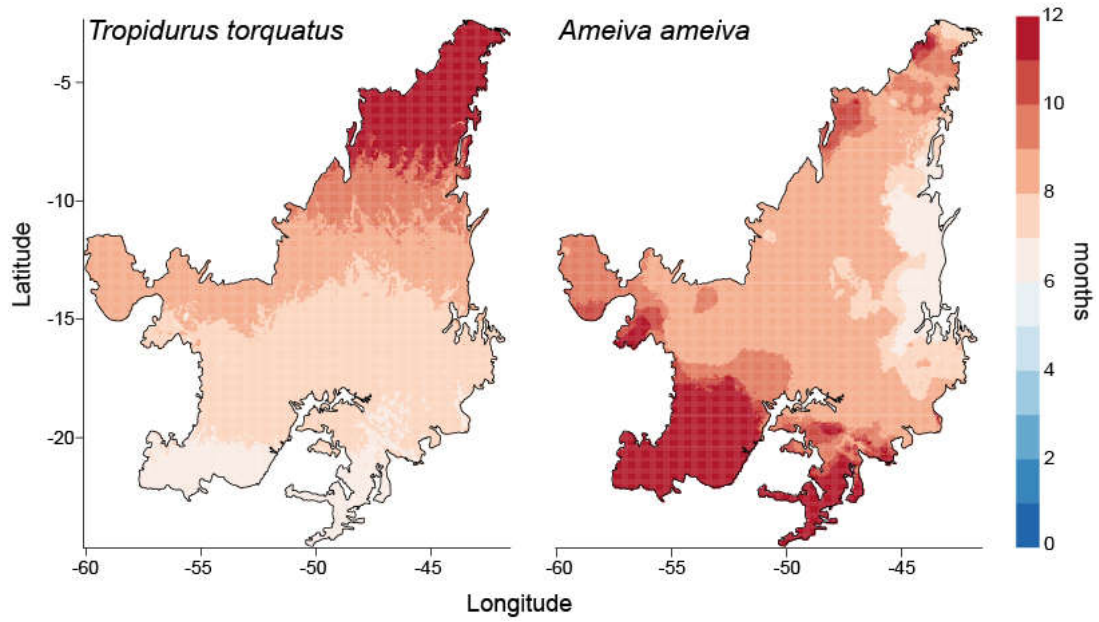


Fig 1. Breeding season duration for *Tropidurus torquatus* and *Ameiva ameiva* across the Brazilian Cerrado estimated with a generalized linear mixed model, with average month day length and total month solar radiation as predictors for *T. torquatus* and total month precipitation for *A. ameiva*.

Chapter 3 - Using physiology and phenology to estimate geographical variation and climate change effects on the population dynamics of a tropical lizard

Abstract

We aim to understand geographical variation in survival, recruitment and population growth of a tropical lizard across its range, using physiological and phenological information, and assess which demographic rates are more important for the effect of climate change in those populations. We conducted a mark and recapture study of a *T. torquatus* population in central Brazil for 12 years. We examined the influence of climate and time of activity, interacting with breeding phenology, in population survival and recruitment. We then extrapolated demographic rates across the species range by applying the relationships observed to spatial predictors of the same variables. We obtained population growth projections by summing the survival and recruitment projections. Then, we evaluated the accuracy of projections by comparing population growth rates to known points of occurrence. Monthly survival was correlated with time of activity and precipitation, both interacting with breeding phenology, while monthly recruitment was correlated with temperature and precipitation, with no breeding season interaction. Population growth projections were not correlated with occurrence records, indicating that spatial predictions were unreliable. Physiology and phenology add important information to the estimation of demographic rates at local scales but proved unreliable predictors for spatial extrapolation of those rates. Local variation in how populations respond to climate has an important influence in demographic rates that was not captured in our model and is possibly the most important venue to be pursued for model improvement. This variation could be due to environmental variation, adaptation, plasticity or species interactions. We suggest possible venues for incorporating those processes and improving similar analysis.

Introduction

It is well documented now that climate change has severe effects on biodiversity (Pearson et al., 2004), such as changing species distribution, phenology, communities composition and ecosystem

dynamics (Walther et al., 2002). Organisms responses to climate change are likely to be mediated by mechanisms like physiology, dispersal, species interaction, evolution, responses to environmental variation and demography (Urban, Tewksbury, & Sheldon, 2012; Zarnetske, Phoebe et al., 2012; Rissler et al., 2017a), thus it is crucial that we seek to incorporate those as possible in biogeography studies. Understanding biological mechanisms underlying species responses to the environment is essential to predict a species range (Kearney & Porter, 2004), yet 77% of species distribution models published don't incorporate any biological mechanism (Petchey et al., 2015b). Moreover, a model based on processes might be made without distribution information. This provides the advantage of revealing the fundamental niche of the species and examining why this niche is not realized can reveal important constraints brought by species interactions and dispersal abilities (Buckley, 2007; Buckley et al., 2010).

One of the most common mechanisms incorporated in species distribution modelling is physiology (Urban et al., 2016). Physiology acts as a filter of immediate physical conditions on organismal responses, such as phenology changes and dispersal, which, in turn, influence population dynamics and species persistence (Kearney & Porter, 2009). Thermal physiology is especially relevant for ectotherms, since temperature influences their activity and performance and as a result, their survival, growth and reproduction (Porter et al., 1973; Sinervo & Adolph, 1989, 1994; Adolph, 1990; Adolph & Porter, 1993; Deutsch et al., 2008). Temperature can directly determine time of activity in ectotherms (Porter et al., 1973; Grant & Dunham, 1988; Grant, 1990; Adolph & Porter, 1993; Kearney & Porter, 2009; Sinervo et al., 2010), and through it, affect life history, demography and distribution (Porter et al., 1973; Huey, 1991; Walther et al., 2002; Kearney & Porter, 2009).

Another crucial process that will be affected by climate change is species breeding phenology. Changes in the timing of life history events affect the reproductive output of individuals (Massot, Clobert, & Ferrière, 2008) their interaction with other species (Durant, Hjermmann, Ottersen, & Stenseth, 2007) and consequently, can have important impacts in population dynamics (Miller-Rushing, Høye, Inouye, & Post, 2010). Climate change has already altered plants and animal phenologies (Root, Price, Hall, & Schneider, 2003), causing mismatches between life history stages

and environmental conditions adequate for reproduction (Parmesan & Yohe, 2003). We must predict how life history phenology is changing in space and time to accurately assess the effect of climate change in species demography and distribution, so we are better informed to design conservation measures.

Spatial extrapolation of demographic rates can help us understand which aspects of population dynamics are driving species distribution and make also make inferences about metapopulation dynamics. Climate has complex effects on population dynamics (Crozier & Dwyer, 2006), therefore, analysis that can discriminate the effects of climate change in different demographic rates can be crucial for improving predictions and informing policy. For example, if it is predicted that climate change will cause a population to decline mostly by affecting recruitment rates, conservation efforts might be directed to sites and times of the year more relevant for the species reproduction. Having such information would help save resources and greatly increase conservation efficacy.

One technique that could be harnessed for spatial extrapolation of demography is mark and recapture analysis. This type of analysis is widely used in demographic, dispersal and meta-population dynamics studies in a wide range of taxa (Hill, Thomas, & Lewis, 1996; Sweanor, Logan, & Hornocker, 2000; Wiederhecker, Pinto, Paiva, & Colli, 2003; Straley, Quinn, & Gabriele, 2009). They provide estimates of demographic rates for species with difficult detection, providing an invaluable tool for understanding population dynamics of such taxa. Population dynamics is what ultimately determine species range, since a species ability to inhabit a location depends upon whether individuals can survive, reproduce or migrate to nearby sites in sufficient numbers (Holt, 2003; Holt & Keitt, 2005).

Here, we aim to determine if populations of the lizard *Tropidurus torquatus* in Brazil will be able to persist across the species' current range through 2070, under different carbon emission scenarios. We developed a model of population dynamics that incorporates species physiology, phenology and demography independent of species occurrence records. Geographical models of population dynamics incorporating physiology and life history have been used before for insects (Crozier & Dwyer, 2006) and lizards (Buckley, 2007). Those studies relied on very specific

mechanistic models of how those physiology and life history drive demographic rates, which are likely to have low transferability. Our model is the first to do so using mark and recapture population models, a more general methodology which allow the estimation of demographic rates without making many assumptions about underlying mechanisms of climate effects on those rates.

Methods

Study species:

Tropidurus torquatus Wied, 1820 (Squamata, Tropiduridae) is a locally abundant lizard, common in urban areas, which occurs in Brazil, Uruguay, Paraguay and Argentina; in Brazil, it occurs throughout the Cerrado region and in some areas of the Atlantic Forest (Rodrigues, 1987). Its local abundance and conspicuousness make it a convenient model for ecological studies, and its wide distribution makes it a good candidate for testing if biogeographical methodologies are applicable over large areas. Moreover, it is one of the most well studied South American lizards, so it is a prime candidate for studies involving literature reviews, such as this one. Its demography has been studied before and populations have shown high turnover rates resulting from high investment in reproduction, low investment in survival and short life cycles (Wiederhecker et al., 2003), a pattern which is expected to be replicated across the species range if demographic projections are accurate.

Population monitoring:

A population of *T. torquatus* was monitored in the gallery forest of the Monjolo creek at Reserva Ecológica do Roncador (RECOR), a protected area in Brasília, Distrito Federal, at the central region of the Brazilian Cerrado (15°55'51.37" S, 47°53'1.99" W). Lizards were trapped with 20 arrays of pitfall traps, which were visited twice a week, every week, from June 2000 to May 2012. Each array consists of one 30-liter central plastic bucket buried in the ground, surrounded by three more buckets 6 m away from the center. The peripheral buckets are connected to the central one by 6 m long and 0.5 m high galvanized foil fences, angled 120° from each other, forming an “Y” figure to the array. Captured lizards were given a permanent, individual numerical identities by toe clipping, so they could later be

identified if recaptured. The capture history of individuals was kept in a binomial record, assigning the value “1” to each individual in the months it was captured and “0” in the months it was not captured. Individuals were released in the same area immediately after marking and performing morphological measurements. We obtained maximum temperature and total precipitation data for each month on the study period from RECOR's weather station, to be used later on demographic modeling.

Time of activity estimates:

We estimated daily hours of activity for the population monitoring site along the study period (Sinervo et al., 2010) implemented in package *Mapinguari* (Caetano, Santos, Miles, Colli, & Sinervo, 2019). This method consists of simulating daily temperature variation as a sine wave ranging from daily minimum to maximum temperatures and then counting the number of hours in which those temperatures fall in the temperature range in which an animal is active based on laboratory behavioral studies.

We collected animals in the Brazilian municipalities of Brasília (15.7998° S, 47.8645° W) at Distrito Federal; Nova Xavantina (14.6644° S, 52.3585° W), Alta Floresta (9.8765° S, 56.0855° W) and Gaúcha do Norte (12.9656° S, 53.5636° W) at the state of Mato Grosso; and Lagoa da Confusão (10.9201° S, 50.1833° W) at the state of Tocantins. Those sites cover a variety of environments across the species range such as core savannah areas and savannah-rainforest interfaces, potentially sampling relevant variations on the species physiology. Animals were captured using the same kind of pitfall traps used for population monitoring, and by noosing and manual capture.

To determine suitable temperatures for activity, we performed thermal gradient preference experiments (Caetano, Santos, Miles, et al., 2019). We placed captured lizards on a temperature gradient created by a 60-watt incandescent lamp on one end and an ice pack on the other end. The gradient floor was made of aluminum, for better temperature conductance and the walls were made of smooth plywood to avoid climbing. Lizards could choose their position in the gradient for one hour while their body temperature was recorded every minute by a thermocouple attached to their abdomen insulated with surgical tape and connected to a data logger (Eltek® 1000 Series Squirrel Meter Data

Logger 64K, 10 Channel 1001WD)(Paranjpe et al., 2013). We excluded the temperature measurements during the first ten minutes, in which the individual was acclimating to the gradient. Then we calculated the range between the 5th and 95th temperature percentile registered in the gradient and considered that as the temperature range of activity. Those percentiles were calculated from the pooled temperatures measured for all lizards, which generates better predictors for species distribution (Caetano *et al.*, 2019a).

Demographic modelling:

We fitted mark and recapture models of the capture history of individuals monitored at RECOR with the weather station data and hours of activity estimates for the same period, to identify the best predictors of demographic rates, using the package *RMark* (Laake, 2013), which builds models for the Program MARK (White & Burnham, 1999). We used Pradel open population model (Pradel, 1996) due to its ability to estimate both survival (*Phi*) and *per capita* recruitment (*f*) in open populations. We used a logistic link function for survival and exponential for recruitment. Before fitting the models we tested if the data met the assumptions of no transience (animals have different survival probabilities) and no trap-dependence (animals have different capture probabilities) (Cooch & White, 2006), using standard tests in the program RELEASE (Burnham, Anderson, White, Brownie, & Pollock, 1987).

We fitted 16 Pradel models for survival and recruitment in *RMark* with different combinations of predictors. Each model had a thermally-related term, average temperature or time of activity, and a precipitation term, as predictors for *Phi* and *f*. Temperature predictors included quadratic terms to simulate parabolic thermal performance curve type of responses, in which the demographic trait decreases as temperature moves away from an optimum in both directions. We created a categorical variable assigning different values for months of the breeding season (August to February) and months of the non-breeding season (March to July) (Wiederhecker et al., 2002). We included models in which the breeding variable interacts with the climatic predictors. We also fitted a fully saturated (time as a

categorical variable) and a null model (intercept only) for comparison. We let detection probability remain saturated in every model. The list of models fitted can be verified in Table 3.1.

We then selected the models based on the Akaike information criterion corrected for finite sample sizes (AIC_c) (Burnham & Anderson, 2002, 2004). We set aside models less than 2 difference in AIC_c to the best model (Burnham & Anderson, 2004). We assessed the goodness-of-fit of the best models by calculating the model's deviance R^2 , calculated by dividing the difference of the log-likelihood of the candidate model and the null model by the difference of the log-likelihood of the saturated model and the null model.

Phenology projections:

We conducted a literature search for papers providing information on reproductive status, time and location of *T. torquatus* lizards. We classified the instances found as: (1) Reproductive, if female lizards were found to have mature gonads or were bearing eggs; and (2) Non-reproductive, if a study reported none or a very small proportion of reproductive females under a reasonable sample size. We then compiled environmental conditions (maximum month temperature, minimum month temperature, total month solar radiation) for the locations and months when the lizards were captured, using 2.5 minutes resolution climate surfaces from WorldClim 2 (Fick & Hijmans, 2017). We estimated day length for the same time and locations using Corripio's method (Corripio, 2003). In addition to climatic variables, we generated monthly time of activity estimates, using the method described above over Worldclim maximum and minimum temperature data at 2.5 arc minutes resolution, with the sinusoidal model described in (Sinervo et al., 2010), with limits defined by the 5% and 95% voluntary minima and maxima from the study of thermoregulation in the laboratory gradient.

We performed a Random Forest (RF) regression on package *randomForest* (Breiman & Cutler, 2012) between the reproductive status records obtained from literature and solar radiation, day length and time of activity, variables which are good predictors for *T. torquatus* breeding phenology (Caetano, Santos, Miles, et al., 2019). Then, we used this model to predict breeding season timing across the species range (Caetano, Santos, Miles, et al., 2019). We projected the predictions of the

models across WorldClim monthly climate surfaces for the study area at 2.5 arc minutes resolution. We classified areas at each month as breeding if the predicted probability was greater than 0.5 and non-breeding if it was less.

Demographic projections:

The coefficients for each variable on the mark and recapture model were applied to spatial predictors corresponding to the variables selected in the demographic analysis, obtained as described above for the phenological modeling, allowing us to create spatial projections of survival and recruitment. For the variables that contained breeding season interactions, we used the spatial projections of phenology described above to determine the coefficients to be used. We obtained estimates of discrete population growth rate by summing survival and recruitment projections (Cooch & White, 2006). We restricted projections to areas in which environmental variables were inside the ranges experienced by the population during the monitoring period.

Since we only have one population monitoring site, validation of demographic spatial projections is difficult. To increase confidence in the results, we assessed if known occurrence records were correlated to positive population growth rate. Lizards are unlikely to disperse more than a few dozen to hundreds of meters in a year (Doughty & Sinervo, 1994; Olsson, Gullberg, & Tegelström, 1996; Olsson & Shine, 2003), so populations in areas predicted to not sustain population growth should be rare if projections are accurate. We used population growth projections to determine areas where growth was higher than one and those that were lower, and then used this as a predictor of population occurrence in a GLMM model, implemented in package SPAMM (Rousset and Ferdy 2014), using a Matern autocorrelation structure to account for spatial autocorrelation. We used 100 different sets of pseudoabsences in those regression models, each with 1000 pseudoabsences. Pseudoabsences were generated by environmental profiling with One-Classification Support Vector Machine (OCSVM), using the R package *mopa*, (Senay et al., 2013; Iturbide et al., 2015). All analyses were made in the software R, version 3.5.0 (R Development Core Team, 2018).

Results

The data satisfied the assumption of no transience ($\text{Chi}^2 = 0.486$, $\text{df} = 1$, $p = 0.486$) and no trap-dependence ($\text{Chi}^2 = 1.804$, $\text{df} = 10$, $p = 0.998$). Only one model was selected using the AICc criterium established (Table A4). The best predictors of survival were time of activity and precipitation, both interacting with breeding season, and for recruitment, temperature and precipitation, with no interaction (Table A4). Survival was negatively correlated with time of activity during the breeding season and positively correlated during the non-breeding season and precipitation was positively correlated in both seasons, but with a bigger coefficient during the non-breeding season. Recruitment had a negative parabolic relationship with temperature and a negative correlation with precipitation (Table 3.2). The saturated model and null models had an AICc much larger than the models selected (difference in AICc > 1900), indicating that including the predictors selected added valuable information (Table 3.1). The best model had a deviance R-squared of 0.88, indicating a good fit.

Survival was projected to be moderate in most of the range, while recruitment was higher in the south of the Cerrado, towards higher elevations (Figure 3.1). Because there was much more spatial variation in predicted recruitment than survival, predicted values of population growth essentially reflected spatial patterns of recruitment rates. Only 45 of 100 test sets showed correlation between occurrence and positive population growth, indicating the model does not perform reliably. Overall, the results indicate the demographic rates did a poor job of predicting the species distribution (Figure 3.1).

Discussion

At the population monitoring site, time of activity ranked better than environmental temperatures as a predictor of survival, and variables with breeding season interaction performed better than those without, but recruitment responded mostly to pure climatic variables with no breeding season interaction (Table 3.1). This indicates that including thermal physiology and phenology in demographic models can improve survival predictions, but not as much for recruitment. Climate

effects on survival were quite distinct from the effects on recruitment, showing it is important to seek methods to make those differences explicit to understand the effects of climate change in populations.

The unreliable correlation between occurrence records and areas able to sustain population growth show the model was unsuccessful in extrapolating the demographic rates from the population monitoring sites, and that relationships between climate, physiology and phenology are not similar across the species range. Hereafter, we examine four important factors that are likely to be varying across the species range and could lead to the observed results: environmental variation, adaptation, plasticity and species interactions (Urban et al., 2016), and suggest ways in which they could be included in future analysis.

Environmental characteristics not directly related to weather, such as habitat structure, thermal opportunities and water availability, could be an important source of demographic variation. Those are likely to be very different from the center of the species distribution, in the savannah-like Cerrado environment, to the border with other biomes such as the Amazon rainforest to the northwest and the semi-arid Caatinga to the northeast. Another factor likely to be important is anthropization. Our model was fitted to a natural population, but *T. torquatus* is well-known to thrive perianthropic areas (Nogueira, Valdujo, & França, 2005). So, data from population monitoring studies in urban environments (Wiederhecker et al., 2003) and in the border with other biomes could be employed to generate a similar models. Then, the predictions for those models could be compounded using spatial projections of vegetation structure, aridity and anthropization as weights.

Plastic and adaptative responses to climate variation is poorly studied in reptiles (Sinervo et al., 2018), especially in thermal physiology (but see Leal & Gunderson, 2012; Moritz et al., 2012; Clusella-Trullas & Chown, 2014) which could have important consequences for the effects of thermal environments on *T. torquatus* demographic rates. Those two mechanisms could produce similar changes in thermal physiology, so laboratory studies are likely the best option to determine which one is most prevalent in the study species. Raising individuals from different populations in a range of temperature conditions could help us separate the effects of plasticity from adaptation and determine how environmental variation affects thermal ranges, similarly to plasticity studies commonly done on

the effect of temperature on lizards life histories (Sinervo & Adolph, 1994; Sorci, Clobert, & Belichon, 2006) of the impact of maternal environment and thermal preference on progeny thermal preference (Paranjpe et al., 2013). A model that accounts for such mechanisms must be able to correlate environmental conditions with expected variation in thermal traits under such mechanisms to be able to accurately project physiological variables.

Species interactions are known to have severe impacts on demographic rates (McPeck & Peckarsky, 1998; Miller-Rushing et al., 2010). We must identify the most important interacting species to test if they are indeed affecting geographical variation in demographic rates. Likely candidates for *T. torquatus* are congeneric competitors, such as *Tropidurus hispidus*. *T. torquatus* is replaced by *T. hispidus* in the northeast in environments similar to the ones it usually inhabits (Rodrigues, 1987). Competing species could exclude *T. torquatus* from important territories and food resources at the interfaces of the distributions of both species. Competition can interact with climate and physiology, since suboptimal environmental conditions could affect *T. torquatus* thermal performance, making them poorer competitors. Moreover, Sinervo et al. (2010) demonstrate that while 2/3 of the observed extirpations of Mexican *Sceloporus* lizards could be explained by their thermal ecophysiological limits being exceeded, 1/3 of the extinctions were unexplained by the ecophysiological model. Instead, in 6 of the 8 unexplained cases, they observed range expansion into the extirpation site by a potential competitor with a superior thermal niche, suggesting that competition impacted demography (Sinervo et al., 2018). The distribution of competing species could be used to constrain the range in which we make demographic projections, but a more direct way to measure the effect of competition would be to have monitor populations in the contact area of both species' distributions. In that way, fluctuations in the demography of both species could be used as predictors for each other in demographic models, and climate interactions could be included as well.

The incorporation of the factors cited here seem to require the deployment of several multi-species population monitoring studies across the species range, which could be impractical due to high cost and time necessary to accumulate data. However, some of those studies have already been conducted for *T. torquatus* (urban environment: Wiederhecker et al., 2003; interface with the Amazon:

Campelo, 2017) and this data could be harnessed in such effort. Other taxa, such as birds are more well studied and could be used to test this methodology. Alternatively, the methodology could be applied to extreme endemic species with more restricted distributions and specialized habitat uses, like the endangered lizard *Liolaemus lutzae*, which lives only on sand dunes in a small coastal stretch in southeast Brazil (Carlos F. D. Rocha, Siqueira, & Ariani, 2010). For such species, it is likely that environmental variation, adaptation, plasticity and species interactions do not change a lot across their range, since they will live in similar habitats throughout. Previous studies have identified areas with suitable climate for this species (Winck, Almeida-Santos, & Rocha, 2014), but our methodology, if validated for such species, could reveal underlying demographic causes of habitat suitability. *L. lutzae* species has been transplanted to a location outside its natural range in an effort to establish a population in an area with less anthropic pressure (Soares & Araujo, 2009), and the projection of demographic rates could better inform similar practices.

Our results stress the importance physiology and phenology in mediating the effect of climate in population dynamics at local scales, but we couldn't assess if those process have utility in spatial extrapolation of population dynamics. The methodology used here seems to be limited in its spatial extrapolation, which show the importance of local conditions and variation in population responses for making accurate predictions. Incorporating this into future analysis is an important venue for future research. There are many challenges to overcome when spatially projecting demographic rates, but the potential benefits of doing so accurately can greatly improve information for conservation efforts. Attempts such as the one conducted here are useful to identify shortcomings and direct future efforts in the area.

Tables and Figures

Table 3.1. List of best mark and recapture Pradel demographic models for a population of *Tropidurus torquatus* in Brasília, Brazil, monitored from May 2000 to June 2012. Displayed are the predictors for survival (Φ), recruitment (f) for each model, number of parameters (n_{par}), Akaike information criterion corrected for finite sample sizes (AIC_c), difference in AIC_c from the best model

(DAIC_c), model weight and deviance. Also included are the same data for a saturated, fully time-dependent model (time as a factor), and a null model (intercept only).

Phi	f	npar	AICc	DAICc	weight	deviance
ha_b + prec_b	temp² + temp + prec	153	4951.227	0	0.686	972.766
temp²+temp+prec	temp²+temp+prec	152	4954.429	3.202	0.138	979.565
temp²_b+temp_b+prec_b	temp²+temp+prec	155	4955.557	4.330	0.079	969.854
ha_b+prec_b	temp²_b+temp_b+prec_b	156	4955.611	4.384	0.076	966.261
temp²+temp+prec	temp²_b+temp_b+prec_b	155	4959.346	8.118	0.012	973.642
ha+prec	temp²+temp+prec	151	4959.995	8.767	0.009	988.712
temp²_b+temp_b+prec_b	temp²_b+temp_b+prec_b	158	4967.743	16.516	0	971.052
ha+prec	temp²_b+temp_b+prec_b	154	4967.874	16.648	0	985.800
ha_b+prec_b	ha_b+prec_b	154	4990.543	39.316	0	1008.469

temp²_b+temp_b+prec_b	ha_b+prec_b	156	4994.825	43.597	0	1005.475
temp²+temp+prec	ha_b+prec_b	153	4996.373	45.145	0	1017.912
temp²_b+temp_b+prec_b	ha+prec	154	5001.727	50.500	0	1019.653
temp²+temp+prec	ha+prec	151	5001.812	50.585	0	1030.530
ha_b+prec_b	ha+prec	152	5001.868	50.641	0	1027.005
ha+prec	ha_b+prec_b	152	5009.102	57.875	0	1034.239
ha+prec	ha+prec	150	5031.471	80.244	0	1063.755
time	time	430	7447.836	2496.60 9	-	852.961
null	null	3	5455.386	1992.45 0	-	1882.072

Table 3.2. Coefficients for survival and recruitment estimated in a mark and recapture Pradel model for a population of *Tropidurus torquatus* monitored in Brasília, Brazil, from June 2000 to May 2012. *temp* represents maximum temperatures, *prec* represents precipitation and *ha* represents hours of activity. Variables with subscript *b* are averaged for the breeding season,

with subscript *nb* are averaged for the non-breeding season and subscript *year* are averaged for the whole year. Also displayed are standard errors for the estimate (SE), lower confidence limit (LCL) and upper confidence limit (UCL)

variable	coefficient	SE	LCL	UCL
<u>Survival</u>				
Intercept	2.289	1.560	-0.761	5.340
ha_b	-0.144	0.108	-0.355	0.067
ha_{nb}	0.173	0.329	-0.471	0.817
prec_b	0.009	0.002	0.004	0.013
prec_{nb}	0.0206	0.148	-0.270	0.311
<u>Recruitment</u>				
Intercept	61.568	0.717	60.2	62.973
temp²	0.089	0.002	0.085	0.093
temp	-4.851	0.027	-4.900	-4.798
prec	-0.014	0.009	-0.003	0.004

**Demographic rate projections for *Tropidurus torquatus* populations
across Central Brazil**

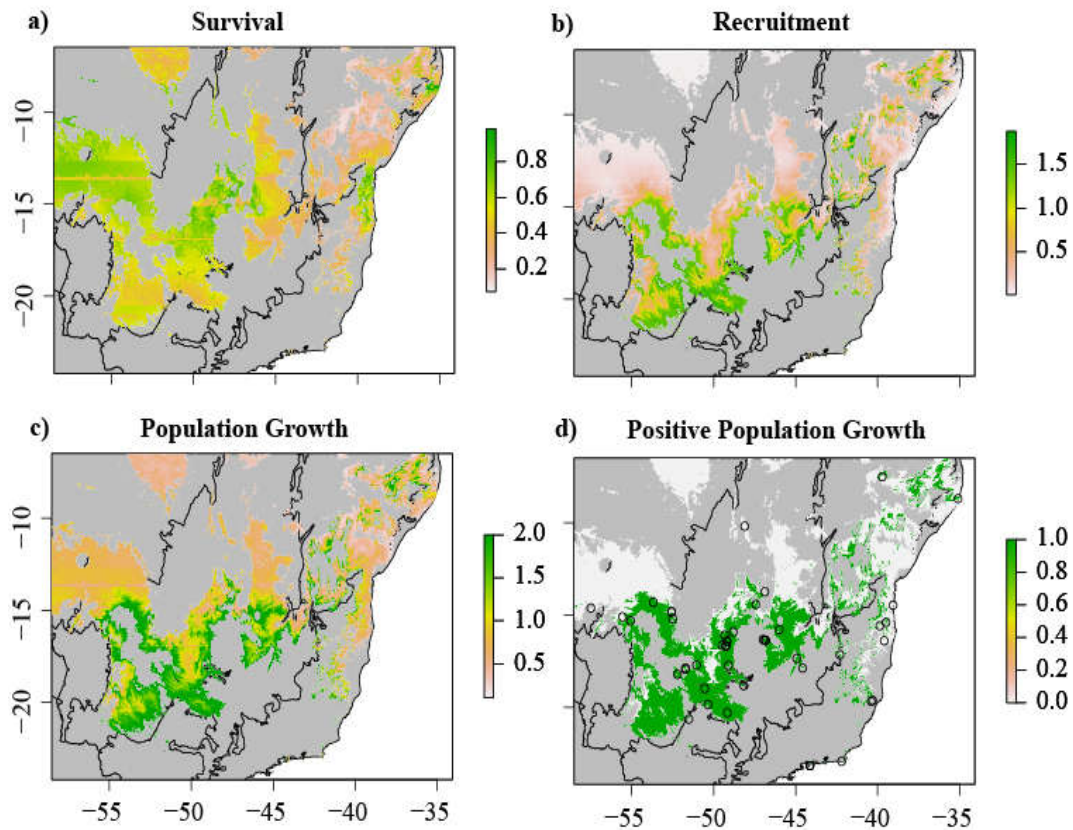


Figure 3.1. Projected demographic rates for *Tropidurus torquatus* populations across Brazil. (a) Probability of surviving to the next year. (b) *Per capita* recruitment per year. (c) Instantaneous population growth rate. (d) Areas with positive population growth rate. Blue circle represents site of population monitoring. Black circles represent known sites of species occurrence.

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Appendix

Table A1. Description of time of activity estimates for the lizard *Tropidurus torquatus* across known occurrence points. Sinusoidal method measured hours above or between temperature thresholds by simulating daily temperature variation from macroclimate data. Operative temperature method used on site measures of daily temperature variation at different microhabitats and then extrapolated those measures to areas not sampled. Microclim used the microclimate surfaces developed by Kearney *et al* (2014), which simulate temperature variation at different shade levels. Each method counted the number of hours spent at specific body temperature ranges, obtained either from laboratory gradient experiments or field observations: above preferred temperature (lab: $T_{pref}=31.5^{\circ}\text{C}$, field: $T_{pref}=32.6^{\circ}\text{C}$), between interquartile temperatures (lab: $T_{50_lwr}=26.7^{\circ}\text{C}$, $T_{50_upr}=36.6^{\circ}\text{C}$, field: $T_{50_lwr}=30.9^{\circ}\text{C}$, $T_{50_upr}=34.6^{\circ}\text{C}$) or between 90th quantile temperatures (lab: $T_{90_lwr}=12.4^{\circ}\text{C}$, $T_{90_upr}=47.2^{\circ}\text{C}$, field: $T_{90_lwr}=25.2^{\circ}\text{C}$, $T_{90_upr}=40.2^{\circ}\text{C}$). For the operative and microclim methods, we also created versions of the variables that simulate thermoregulation, by choosing whichever microhabitat allowed the most time of activity at each time step, instead of averaging across microhabitats.

Name	Method	Temperature range	Origin	Thermoregulation
<i>sin_tp_lab</i>	Sinusoid	$T_b > T_{pref}$	lab pooled	no
<i>sin_tp_lab_ind</i>	Sinusoid	$T_b > T_{pref}$	lab individual	no
<i>sin_tp_field</i>	Sinusoid	$T_b > T_{pref}$	field	no
<i>sin_t50_lwr_lab</i>	Sinusoid	$T_b > T_{50_lwr}$	lab pooled	no

<i>sin_t50_lwr_lab_ind</i>	Sinusoid	$T_b > T_{50_lwr}$	lab individual	no
<i>sin_t50_lwr_field</i>	Sinusoid	$T_b > T_{50_lwr}$	field	no
<i>sin_t90_lwr_lab</i>	Sinusoid	$T_b > T_{90_lwr}$	lab pooled	no
<i>sin_t90_lwr_lab_ind</i>	Sinusoid	$T_b > T_{90_lwr}$	lab individual	no
<i>sin_t90_lwr_field</i>	Sinusoid	$T_b > T_{90_lwr}$	field	no
<i>sin_t50_upr_lab</i>	Sinusoid	$T_b > T_{50_upr}$	lab pooled	no
<i>sin_t50_upr_lab_ind</i>	Sinusoid	$T_b > T_{50_upr}$	lab individual	no
<i>sin_t50_upr_field</i>	Sinusoid	$T_b > T_{50_upr}$	field	no
<i>sin_t90_upr_lab</i>	Sinusoid	$T_b > T_{90_upr}$	lab pooled	no
<i>sin_t90_upr_lab_ind</i>	Sinusoid	$T_b > T_{90_upr}$	lab individual	no
<i>sin_t90_upr_field</i>	Sinusoid	$T_b > T_{90_upr}$	field	no
<i>sin_t50_lab</i>	Sinusoid	$T_{50_lwr} < T_b < T_{50_upr}$	lab pooled	no

<i>sin_t50_lab_ind</i>	Sinusoid	$T_{50_lwr} < T_b < T_{50_upr}$	lab individual	no
<i>sin_t50_field</i>	Sinusoid	$T_{50_lwr} < T_b < T_{50_upr}$	field	no
<i>sin_t90_lab</i>	Sinusoid	$T_{90_lwr} < T_b < T_{90_upr}$	lab pooled	no
<i>sin_t90_lab_ind</i>	Sinusoid	$T_{90_lwr} < T_b < T_{90_upr}$	lab individual	no
<i>sin_t90_field</i>	Sinusoid	$T_{90_lwr} < T_b < T_{90_upr}$	field	no
<i>op_tp_lab_avg</i>	Operative	$T_b > T_{pref}$	lab pooled	no
<i>op_tp_lab_ind_avg</i>	Operative	$T_b > T_{pref}$	lab individual	no
<i>op_tp_field_avg</i>	Operative	$T_b > T_{pref}$	field	no
<i>op_t50_lwr_lab_avg</i>	Operative	$T_b > T_{50_lwr}$	lab pooled	no
<i>op_t50_lwr_lab_ind_avg</i>	Operative	$T_b > T_{50_lwr}$	lab individual	no
<i>op_t50_lwr_field_avg</i>	Operative	$T_b > T_{50_lwr}$	field	no

<i>op_t90_lwr_lab_avg</i>	Operative	$T_b > T_{90_lwr}$	lab pooled	no
<i>op_t90_lwr_lab_ind_avg</i>	Operative	$T_b > T_{90_lwr}$	lab individual	no
<i>op_t90_lwr_field_avg</i>	Operative	$T_b > T_{90_lwr}$	field	no
<i>op_t50_upr_lab_avg</i>	Operative	$T_b > T_{50_upr}$	lab pooled	no
<i>op_t50_upr_lab_ind_avg</i>	Operative	$T_b > T_{50_upr}$	lab individual	no
<i>op_t50_upr_field_avg</i>	Operative	$T_b > T_{50_upr}$	field	no
<i>op_t90_upr_lab_avg</i>	Operative	$T_b > T_{90_upr}$	lab pooled	no
<i>op_t90_upr_lab_ind_avg</i>	Operative	$T_b > T_{90_upr}$	lab individual	no
<i>op_t90_upr_field_avg</i>	Operative	$T_b > T_{90_upr}$	field	no
<i>op_t50_lab_avg</i>	Operative	$T_{50_lwr} < T_b < T_{50_upr}$	lab pooled	no
<i>op_t50_lab_ind_avg</i>	Operative	$T_{50_lwr} < T_b < T_{50_upr}$	lab individual	no

<i>op_t50_field_avg</i>	Operative	$T_{50_lwr} < T_b < T_{50_upr}$	field	no
<i>op_t90_lab_avg</i>	Operative	$T_{90_lwr} < T_b < T_{90_upr}$	lab pooled	no
<i>op_t90_lab_ind_avg</i>	Operative	$T_{90_lwr} < T_b < T_{90_upr}$	lab individual	no
<i>op_t90_field_avg</i>	Operative	$T_{90_lwr} < T_b < T_{90_upr}$	field	no
<i>op_tp_lab_min</i>	Operative	$T_b > T_{pref}$	lab pooled	yes
<i>op_tp_lab_ind_min</i>	Operative	$T_b > T_{pref}$	lab individual	yes
<i>op_tp_field_min</i>	Operative	$T_b > T_{pref}$	field	yes
<i>op_t50_lwr_lab_max</i>	Operative	$T_b > T_{50_lwr}$	lab pooled	yes
<i>op_t50_lwr_lab_ind_max</i>	Operative	$T_b > T_{50_lwr}$	lab individual	yes
<i>op_t50_lwr_field_max</i>	Operative	$T_b > T_{50_lwr}$	field	yes
<i>op_t90_lwr_lab_max</i>	Operative	$T_b > T_{90_lwr}$	lab pooled	yes

<i>op_t90_lwr_lab_ind_max</i>	Operative	$T_b > T_{90_lwr}$	lab individual	yes
<i>op_t90_lwr_field_max</i>	Operative	$T_b > T_{90_lwr}$	field	yes
<i>op_t50_upr_lab_min</i>	Operative	$T_b > T_{50_upr}$	lab pooled	yes
<i>op_t50_upr_lab_ind_min</i>	Operative	$T_b > T_{50_upr}$	lab individual	yes
<i>op_t50_upr_field_min</i>	Operative	$T_b > T_{50_upr}$	field	yes
<i>op_t90_upr_lab_min</i>	Operative	$T_b > T_{90_upr}$	lab pooled	yes
<i>op_t90_upr_lab_ind_min</i>	Operative	$T_b > T_{90_upr}$	lab individual	yes
<i>op_t90_upr_field_min</i>	Operative	$T_b > T_{90_upr}$	field	yes
<i>op_t50_lab_max</i>	Operative	$T_{50_lwr} < T_b < T_{50_upr}$	lab pooled	yes
<i>op_t50_lab_ind_max</i>	Operative	$T_{50_lwr} < T_b < T_{50_upr}$	lab individual	yes
<i>op_t50_field_max</i>	Operative	$T_{50_lwr} < T_b < T_{50_upr}$	field	yes

<i>op_t90_lab_max</i>	Operative	$T_{90_lwr} < T_b < T_{90_upr}$	lab pooled	yes
<i>op_t90_lab_ind_max</i>	Operative	$T_{90_lwr} < T_b < T_{90_upr}$	lab individual	yes
<i>op_t90_field_max</i>	Operative	$T_{90_lwr} < T_b < T_{90_upr}$	field	yes
<i>mc_tp_lab_avg</i>	Microclim	$T_b > T_{pref}$	lab pooled	no
<i>mc_tp_lab_ind_avg</i>	Microclim	$T_b > T_{pref}$	lab individual	no
<i>mc_tp_field_avg</i>	Microclim	$T_b > T_{pref}$	field	no
<i>mc_t50_lwr_lab_avg</i>	Microclim	$T_b > T_{50_lwr}$	lab pooled	no
<i>mc_t50_lwr_lab_ind_avg</i>	Microclim	$T_b > T_{50_lwr}$	lab individual	no
<i>mc_t50_lwr_field_avg</i>	Microclim	$T_b > T_{50_lwr}$	field	no
<i>mc_t90_lwr_lab_avg</i>	Microclim	$T_b > T_{90_lwr}$	lab pooled	no
<i>mc_t90_lwr_lab_ind_avg</i>	Microclim	$T_b > T_{90_lwr}$	lab individual	no

<i>mc_t90_lwr_field_avg</i>	Microclim	$T_b > T_{90_lwr}$	field	no
<i>mc_t50_upr_lab_avg</i>	Microclim	$T_b > T_{50_upr}$	lab pooled	no
<i>mc_t50_upr_lab_ind_avg</i>	Microclim	$T_b > T_{50_upr}$	lab individual	no
<i>mc_t50_upr_field_avg</i>	Microclim	$T_b > T_{50_upr}$	field	no
<i>mc_t90_upr_lab_avg</i>	Microclim	$T_b > T_{90_upr}$	lab pooled	no
<i>mc_t90_upr_lab_ind_avg</i>	Microclim	$T_b > T_{90_upr}$	lab individual	no
<i>mc_t90_upr_field_avg</i>	Microclim	$T_b > T_{90_upr}$	field	no
<i>mc_t50_lab_avg</i>	Microclim	$T_{50_lwr} < T_b < T_{50_upr}$	lab pooled	no
<i>mc_t50_lab_ind_avg</i>	Microclim	$T_{50_lwr} < T_b < T_{50_upr}$	lab individual	no
<i>mc_t50_field_avg</i>	Microclim	$T_{50_lwr} < T_b < T_{50_upr}$	field	no
<i>mc_t90_lab_avg</i>	Microclim	$T_{90_lwr} < T_b < T_{90_upr}$	lab pooled	no

<i>mc_t90_lab_ind_avg</i>	Microclim	$T_{90_lwr} < T_b < T_{90_upr}$	lab individual	no
<i>mc_t90_field_avg</i>	Microclim	$T_{90_lwr} < T_b < T_{90_upr}$	field	no
<i>mc_tp_lab_min</i>	Microclim	$T_b > T_{pref}$	lab pooled	yes
<i>mc_tp_lab_ind_min</i>	Microclim	$T_b > T_{pref}$	lab individual	yes
<i>mc_tp_field_min</i>	Microclim	$T_b > T_{pref}$	field	yes
<i>mc_t50_lwr_lab_max</i>	Microclim	$T_b > T_{50_lwr}$	lab pooled	yes
<i>mc_t50_lwr_lab_ind_max</i>	Microclim	$T_b > T_{50_lwr}$	lab individual	yes
<i>mc_t50_lwr_field_max</i>	Microclim	$T_b > T_{50_lwr}$	field	yes
<i>mc_t90_lwr_lab_max</i>	Microclim	$T_b > T_{90_lwr}$	lab pooled	yes
<i>mc_t90_lwr_lab_ind_max</i>	Microclim	$T_b > T_{90_lwr}$	lab individual	yes
<i>mc_t90_lwr_field_max</i>	Microclim	$T_b > T_{90_lwr}$	field	yes
<i>mc_t50_upr_lab_min</i>	Microclim	$T_b > T_{50_upr}$	lab pooled	yes

<i>mc_t50_upr_lab_ind_min</i>	Microclim	$T_b > T_{50_upr}$	lab individual	yes
<i>mc_t50_upr_field_min</i>	Microclim	$T_b > T_{50_upr}$	field	yes
<i>mc_t90_upr_lab_min</i>	Microclim	$T_b > T_{90_upr}$	lab pooled	yes
<i>mc_t90_upr_lab_ind_min</i>	Microclim	$T_b > T_{90_upr}$	lab individual	yes
<i>mc_t90_upr_field_min</i>	Microclim	$T_b > T_{90_upr}$	field	yes
<i>mc_t50_lab_max</i>	Microclim	$T_{50_lwr} < T_b < T_{50_upr}$	lab pooled	yes
<i>mc_t50_lab_ind_max</i>	Microclim	$T_{50_lwr} < T_b < T_{50_upr}$	lab individual	yes
<i>mc_t50_field_max</i>	Microclim	$T_{50_lwr} < T_b < T_{50_upr}$	field	yes
<i>mc_t90_lab_max</i>	Microclim	$T_{90_lwr} < T_b < T_{90_upr}$	lab pooled	yes
<i>mc_t90_lab_ind_max</i>	Microclim	$T_{90_lwr} < T_b < T_{90_upr}$	lab individual	yes
<i>mc_t90_field_max</i>	Microclim	$T_{90_lwr} < T_b < T_{90_upr}$	field	yes

Table A2. Published papers containing data on *Tropidurus torquatus* reproduction timing. All locations are in Brazil include the initials for the state it is located.

Location	Longitude	Latitude	Reproductive	Non-Reproductive	Reference
Trancoso, BA	-39.1833	-16.4333	Nov – Mar	Apr – Oct	(Kiefer et al., 2008)
Prado, BA	-39.2167	-17.3000	Nov – Mar	Apr – Oct	(Kiefer et al., 2008)
Guriri, ES	-39.7333	-18.7500	Nov – Mar	Apr – Oct	(Kiefer et al., 2008)
Setiba, ES	-40.4500	-20.5833	Nov – Mar	Apr – Oct	(Kiefer et al., 2008)
Praia das Neves, ES	-40.9667	-21.2500	Nov – Mar	Apr – Oct	(Kiefer et al., 2008)
Grussai, RJ	-41.0333	-21.7333	Nov – Mar	Apr – Oct	(Kiefer et al., 2008)
Jurubatiba, RJ	-41.6833	-22.2833	Nov – Mar	Apr – Oct	(Kiefer et al., 2008)
Grumari, RJ	-43.5000	-23.0833	Nov – Mar	Apr – Oct	(Kiefer et al., 2008)
Santa Maria, RS	-53.8736	-29.6269	Sep – Jan	Feb – Aug	(Arruda, 2009)
Juiz de Fora, MG	-43.5921	-21.8076	Aug – Dec	Jan – Jul	(Gomides, Ribeiro, Peters, & Sousa, 2013)

Alegrete, RS	-55.4164	-29.9783	Sep – Dec	Jan – Aug	(Vieira, Felappi, Caruccio, & Verrastro, 2011)
Barra de Marica, RJ	-42.8333	-22.9500	May – Dec	Jan – Apr	(Van Sluys, Martelotte, Kiefer, & Rocha, 2010)
Corrientes, Argentina	-58.7467	-27.4306	Jul – Feb	Mar – Jun	(Ortiz, Álvarez, Boretto, Iburgüengoytía, & Piantoni, 2014)
Brasília, DF	-47.9167	-15.7833	Aug – Feb	Mar – Jul	(Wiederhecker et al., 2002)
Exu, PE	-40.0167	-7.4167	Aug – Jan	Dec – Jul	(Vitt & Goldberg, 1983)
Arraial D'Ajuda, BA	-39.0833	-16.6500	Nov - Jul	Aug – Oct	(Freitas, Teixeira, & Ferreira, 2012)

Table A3. Published papers containing data on *Ameiva ameiva* reproduction timing. All locations in Brazil include the initials for the state it is located.

Location	Longitude	Latitude	Reproductive	Non-Reproductive	Reference
Barra de Maricá, RJ	-42.8333	-22.9500	Jun – Jan	Feb – May	(Carlos Frederico Duarte Rocha, 2008)
Exu, PE	-39.7167	-7.5167	Dec – Oct	Nov	(Vitt, 1982; Vitt & Colli, 1994)

Brasilia, DF	-47.9167	-15.7833	Oct – Apr	May – Sep	(Colli, 1991; Vitt & Colli, 1994)
Jaru, RO	-62.4500	-10.4333	Jun – Jul, Oct – Nov		(Vitt & Colli, 1994)
Boa Vista, RR	-60.6667	2.8167	Jul		(Vitt & Colli, 1994)
Altamira, PA	-52.2000	-3.2000	Jan		(Vitt & Colli, 1994)
Santa Rita do Araguaia, GO	-53.2000	-17.3167	Feb, Mar, Jul		(Vitt, 1991; Vitt & Colli, 1994)
Macapá, AP	-51.0500	0.0333		Sep – Oct	(Vitt & Colli, 1994)
Humaitá, PA	-63.0333	-7.5167		Oct – Nov	(Vitt & Colli, 1994)
Santa Cecília, Ecuador	-76.9925	0.0850	May – Dec	Jan – Apr	(Simmons, 1975)
Tabajara, MG	-41.7626	-19.5865	Mar		(Costa et al., 2010)
Alter do Chão, PA	-55.0000	-2.5000	Oct – Jun	Jul – Sep	(Magnusson, 1987)
Recife, PE	-34.8770	-8.0476	Apr – Oct	Nov – Mar	(Gillett & da Cruz, 1981)

Iquitos, Peru	-73.25	-3.7333	Jan-Dec		(Dixon & Soini, 1986)
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