



Climate change effects on population dynamics of three species of Amazonian lizards

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ABSTRACT

The scarcity of data on natural history and ecology of lizards still limits the understanding of population dynamics for many species. We attempt to evaluate possible effects of climate change on the population dynamics of three lizard species (*Ameiva ameiva*, *Gonatodes humeralis* and *Norops fuscoauratus*) in two Amazonian localities (Caxiuanã National Forest and Ducke Reserve). We calculated a tolerance index combining environmental thermal adequacy with the b-d model, which consider survival and reproductive rates to calculate population dynamics. Thus, we simulated population growth rates based on current and future environmental operative temperatures, considering an optimistic and a business-as-usual scenario of greenhouse gases emissions (GGE), and evaluate if the sensitivity of life history traits to population growth rate are likely to be triggered by climate change. Our results demonstrated that both populations of *G. humeralis* and the Ducke population of *N. fuscoauratus* may become locally extinct under both scenarios of GGE, while both populations of *A. ameiva* are likely to decrease, but without reaching a scenario of local extirpation. This study represents the first effort to evaluate the sensitivity of lizard populations and elasticity to climate change and demonstrate the geographic variability of these traits in three widespread and habitat-generalist species. We highlight the need of new studies focusing on species with different biological trait patterns, such as endemic distributions and habitat-specialists, to provide the theoretical and empirical basis for biologically informed conservation strategies and actions, in order to minimize the potential extinction of populations due to climate change.

1. Introduction

Projected changes in global mean earth surface temperatures for the late 21st century vary from 1.85 °C, in an optimistic scenario that assumes a moderate decrease in current greenhouse gases emission rates (RCP4.5), to 3.7 °C in a business-as-usual scenario (RCP 8.5), which assumes that there will be no decrease in current emission rates (Field et al., 2014). These scenarios impose to lizards (and other organisms) a balance between environmental warming, thermoregulation, behavioral flexibility, and physiological adaptation, which may play important roles in the vulnerability and adaptive capacity of a species in response to climate change (Beever et al., 2017; Gunderson and Stillman, 2015).

Lizards can evolve or express different physiological limits through phenotypic plasticity according to the environment they inhabit (Scheffers, 2014), allowing a significant influence of environmental temperature variation on their behavioral and physiological responses

(Camacho and Rusch, 2017; Clusella-Trullas and Chown, 2014; Withers, 1992). Since environmental constraints may hinder reproduction and performance of lizards at optimal levels (e.g., Irschick et al., 1999; Pianka and Parker, 1975; Shine, 1992), interactions between behavior and physiology could affect population growth rates and population persistence (Buckley et al., 2015; Porter and Tracy, 1983; Sinervo and Adolph, 1989).

Changes in local climatic patterns and occurrence of extreme climatic events may lead to strong selection on natural populations, demanding local adaptation (Campbell-Staton et al., 2017). Adaptive responses can potentially differ between major life stages of a population, so it is important to identify which life stages are more vulnerable to temperature variation (Sinclair et al., 2016). The lack of evolutionary adaptation or phenotypic plasticity in thermal tolerance and phenology of any life stage under new thermal scenarios may lead to populations decrease, and eventually to local extirpation (Ofori et al., 2017; Sinervo et al., 2010). Thus, maintenance of body temperature (T_b) within the

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species physiological limits among all life stages is essential for its individuals survival and, consequently, for long-term population persistence (Bogert, 1959).

Although most Neotropical species present T_{bs} that reflect environmental temperatures (Huey and Slatkin, 1976; Huey, 1982; Ruibal, 1961), several others may present a certain degree of active thermoregulation, by using behavioral mechanisms that result in higher T_{bs} compared to air and substrate temperatures (Kiefer et al., 2007; Vitt et al., 1998). Overall, tropical species are expected to be more vulnerable to climate change than temperate ones, since they already experience stressful environmental conditions, such as extreme temperatures and solar radiation, in both forest and open habitats (Huey et al., 2009). Knowledge about how lizards respond behaviorally or physiologically to environmental stress is crucial to estimate their tolerance and vulnerability, and to allow future predictions about the persistence of species and populations (Munoz et al., 2016; Williams et al., 2008).

Frequency of studies on natural populations have increased after the pioneering work of Blair (1960) and Tinkle (1967) on the demography and natural history of two North American lizards. However, there is limited information available on reproduction and survival rates of lizards (Dunham, 1994; Miles and Dunham, 1992, 1993; Rocha, 1998), and on the effects of climate change on the Neotropical lizard fauna (Piantoni et al., 2016; Winter et al., 2016), especially in the Amazonia rainforest (Pontes-da-Silva et al., 2018a, 2018b).

In this study, we attempt to derive demographic indicators from thermal aspects of three lizard species, *Ameiva ameiva* (Teiidae), *Gonatodes humeralis* (Sphaerodactylidae), and *Norops fuscoauratus* (Dactyloidae), considering thermal field data obtained from populations at two localities in the Brazilian Amazonia and evaluate possible effects of climate change on their population dynamics. Although they present distinct physiology and behavior, these three species have broad geographic distributions across the Neotropics, experiencing different environmental gradients through their range extents. Thus, local populations are likely to present different responses to local environmental conditions, making them interesting study models.

We evaluate the growth rate sensitivity of populations, or the responses of the populations to perturbations in life history traits; and their elasticity, which quantifies the contribution of the life history traits to growth rates (de Kroon et al., 2000). We also simulate the populations responses to temperature increases predicted by the end of the 21st century (Field et al., 2014), allowing a preliminary evaluation of the potential impact of climate change on these populations. Thus, we aimed to answer the following questions: i) How do the growth rates of populations from these three species vary considering their tolerance index and reproductive rates? ii) To what extent are the thermal traits of each lizard species related to their population dynamics? iii) Which predictions can be drawn from the potential impacts of climate change on these lizard populations by the end of 21st century?

2. Materials and methods

2.1. Target species

Ameiva ameiva (Teiidae) occurs from Panamá, in Central America, to Northern Argentina, in South America east of the Andes, and is present both in forest and open vegetation formations. This heliothermic species frequently basks in sunny areas, resulting in T_{bs} that may exceed the air temperature up to 12 °C (Avila-Pires, 1995; Diele-Viegas et al., 2018; Duellman, 1978).

Gonatodes humeralis (Sphaerodactylidae) is widely distributed in Amazonia and in its surroundings, being considered one of the most common lizards in parts of the biome. Its distribution reaches to the north the coast of Venezuela, the Guianas and Trinidad and Tobago; and southward it extends into parts of the Brazilian Cerrado biome (Avila-Pires, 1995; Miranda et al., 2010). It is found mostly on the shaded portions of tree trunks and base of palms, up to two meters high,

in all kinds of forests and even in urban parks that present some density of trees (Avila-Pires, 1995). It is a thermoconformer, with activity T_b related to air and substrate temperatures, but usually 1–2 °C higher (Diele-Viegas et al., 2018; Vitt et al., 1997).

Norops fuscoauratus (Dactyloidae) occurs throughout Amazonia (all countries) and in part of the Atlantic Forest, along the Brazilian coast, reaching the south of Espírito Santo state (Vanzolini, 1980). It is a forest dweller, found predominantly jumping through the vegetation, mainly on trunks, branches and limbs, at a mean height of approximately 1 m above ground. *Norops fuscoauratus* is also a thermoconformer, with activity T_b related to substrate temperature, but on average 1.6 °C higher (Diele-Viegas et al., 2018; Vitt et al., 2003).

2.2. Field data

We obtained physiological data during two expeditions to Floresta Nacional de Caxiuanã, Pará, Brazil (1°27'S, 51°17'W) and one expedition to Reserva Florestal Adolpho Ducke, Manaus, Brazil (2°57'S, 59°55'W), all conducted between June 2015 and April 2016. Both localities are characterized by isothermal condition (low temperature variation), which is a consequence of the high relative air humidity throughout the year (Costa et al., 2012; Luizão and Vasconcelos, 2002). The rainy season in Caxiuanã occurs between January and June, while in Ducke it occurs between December and May. Caxiuanã presents a more intense dry season, with 2–3 months of precipitation lower than 60 mm (Am of Köppen classification), while Ducke falls in the Af category, with 3 months of precipitation lower than 100 mm (Costa et al., 2012; Luizão and Vasconcelos, 2002). In both areas, the vegetation is predominantly represented by lowland dense ombrophylous (*terra firme*) forest, with tree diversity and density being higher in Ducke than in Caxiuanã (Costa et al., 2012; Luizão and Vasconcelos, 2002; Ter Steege et al., 2003). The two areas also differ in topography—Caxiuanã elevation varies from zero to 80 m, with the majority of *terra firme* forest in elevations between 40 and 60 m; Ducke is more topographically complex, mostly with plateaus of 80–140 m (Baccaro et al., 2008).

We captured lizards through active search and funnel traps. The first method consisted of visual search on the leaf litter, tree trunks and vegetation in general, covering different microenvironments potentially occupied by *G. humeralis* and *N. fuscoauratus*, in the period between 8:00 am and 5:00 pm. Captured animals were transported to the field laboratory in cloth bags. Funnel traps were installed in open areas and had openings on both sides and baits left inside (usually crickets) to attract *A. ameiva*. The traps were opened every day at 10:00 am, and the inspections occurred at 11:00 am, 12:00 pm, 01:00 pm and 02:00 pm, peak of activity of the species. We closed traps to avoid the capture of other animals until the next day.

In a field laboratory, captured lizards were individually kept in plastic containers with water available to avoid dehydration and holes in the lid to allow air exchange. Animals were maintained in captivity without access to food until the end of the tests, which were conducted during their activity period. After experiments, we measured snout-vent length of each animal (SVL, in mm), sexed and released them in their original capture site. Up to ten individuals of each species were deposited at the herpetological collections of Museu Paraense Emílio Goeldi (MPEG) and Instituto Nacional de Pesquisas da Amazônia (INPA-H) as vouchers. We captured and tested 22 individuals of *A. ameiva* in Caxiuanã and twenty in Ducke; sixty-one individuals of *G. humeralis* in Caxiuanã and thirty-four in Ducke; and forty-five individuals of *N. fuscoauratus* in Caxiuanã and fifty in Ducke.

We measured VT_{max} in plywood compartments of 1.5 m × 0.35 m × 0.4 m (length x width x height), in which the lizards were individually housed during the experiment (Diele-Viegas et al., 2018; Paranjpe et al., 2012). We created in each compartment a thermal gradient by using a heating lamp ~100 W at one end and ice pack at the other end of the gradient. We maintained the temperature of

the thermal gradient varying approximately from 15 °C to 40 °C, since thermal preferences of all three species is inside this range (Diele-Viegas et al., 2018). We monitored the lizards body temperature inside the structure during 120 min by measuring it every 3 min with an infrared digital thermometer. We pointed the laser to the medial portion of the animal body, from about 45 cm. The use of infrared thermometers to measure body temperature was validated with data on *Zootoca vivipara*, which present body size similar to *Ameiva ameiva* (Diele-Viegas et al., 2018). We found a high correlation between core and surface temperatures by measuring T_b of 34 individuals with both cloacal and infrared thermometers (0.85, $p < 0.001$; Diele-Viegas et al., 2018). We started monitoring the animal T_b after five minutes of the animal allocation in the gradient, but we only account for thermal preference after 30 min of monitoring to allow the individuals to reach their preferences. Thus, we recovered a total of 30 measurements per individual. We choose to consider VT_{max} as the upper bound of the measurements made in the thermal gradient (i.e., third quartile; Kubisch et al., 2016), since we observed that most individuals (mainly from *G. humeralis* and *N. fuscoauratus*) started to move inside the gradients to avoid warming when body temperatures reached these values (pers. comm).

To measure the set of available temperatures in the microhabitat used by the active animal (T_e) and determine the spatial and temporal heterogeneity of microenvironmental temperatures, we installed twenty temperature sensors (HOBO 2 × External Temperature Data Logger) with lizard PVC models that are similar in size and shape to the analyzed species (Paranjpe et al., 2012; Pontes-da-Silva et al., 2018a, 2018b). Smaller models ($N = 10$) were placed in the forest, near roots, fallen trunks and litter, embracing the microhabitat used by *G. humeralis* and *N. fuscoauratus*, while bigger models ($N = 10$) were placed in forest edge and open areas, embracing the microhabitat used by *Ameiva ameiva*. Environmental temperatures were measured every two minutes during approximately 20 days in each locality. Since both localities presented similar isothermal condition and were sampled in a time period with typical weather, we found no differences between T_e recovered by small and big models (t -test, $t(172.35) = 1.28$, $p = 0.19$). Thus, we averaged the measurements made during the activity period of the species (08:00 am to 05:00 pm) to get an estimate of T_e per locality.

2.3. Life table

We built life tables based on the literature and field data. We categorized age groups based on literature data on snout-vent length (SVL) related to reproductive condition for each species, since direct data on age is not available. We considered hatchlings as age group 0, juveniles after reaching sexual maturity as age group 1 and adults as age group 2. Considering the scarcity of data and associated uncertainties, population growth rates were interpreted with caution and alternative possibilities were tested. For *A. ameiva*, we considered as age group 0 individuals with SVL lower than 88 mm; age group 1 individuals with SVL equal to or above 88 mm and lower than 125 mm; and age group 2 individuals with SVL equal to or above 125 mm (Colli, 1991; Vitt and Colli, 1994). For *G. humeralis*, we considered as age group 0 individuals with SVL lower than 31 mm; age group 1 individuals with SVL equal to or above 31 mm and lower than 35 mm; and age group 2 individuals with SVL equal to or above 35 mm (Avila-Pires, 1995; Vitt et al., 1997). For *N. fuscoauratus*, we considered as age group 0 individuals with SVL lower than 37 mm; age group 1 individuals with SVL varying from 37 mm to 40 mm; and age group 2 individuals with SVL equal to or above 40 mm (Avila-Pires, 1995; Vitt et al., 2003).

Reproductive rates were also obtained from literature data. Clutch size varies geographically and is related to SVL in *A. ameiva* (Vitt and Colli, 1994). We considered the reproductive data of two populations from the study of Vitt and Colli (1994) based on the geographical proximity and landscape similarity with both populations analyzed

here: Santa Cruz da Serra (Rondônia) and Rio Xingú, next to Altamira (Pará). In Rondônia, the population had a mean SVL of 114 mm, minimum SVL at maturity of 88 mm and mean clutch size of 3.2 eggs, while in Xingu these numbers were respectively 125.3 mm, 109 mm and 4.4 eggs. Based on these data and assuming one clutch per year for age group 2, we estimated a reproductive rate of 3.2 eggs in age group 1 (88 mm ≤ SVL < 125 mm) and 4.4 in age group 2 (SVL ≥ 125 mm).

Although females of *G. humeralis* produce only one egg at each reproductive event, they usually return to the nest at least once, at short intervals, to oviposit additional eggs (Avila-Pires, 1995; Mesquita et al., 2015; Vitt et al., 2000). Larger females invest relatively less in producing each egg, which suggests that they could produce eggs more frequently, resulting in a larger reproduction rate than smaller females (Vitt et al., 1997). Thus, we evaluate two possibilities of reproductive rates for this species: b_x1) No differences between smaller and larger females, with both producing two eggs per year, considering one return to the nest; b_x2) smaller females producing two eggs per year, with one return to the nest, and larger females producing three eggs per year, with two returns to the nest.

The available information for *N. fuscoauratus* shows that females can lay only one egg per clutch, although depositing up to three clutches per year (Mesquita et al., 2015; Vitt et al., 2008). Considering the lack of evidence for a relation between SVL and clutch size for this species, but the general tendency of relation between these traits (Winck and Rocha, 2012), we evaluated two possibilities: b_x1) equal reproductive rates for both smaller and larger females, with both producing three eggs per year; b_x2) smaller females producing one egg per year and larger females producing three eggs per year.

Since field-based (e.g., capture-mark-recapture studies) estimates on population survival rates for the target taxa are not available, we estimated a tolerance index based on the concept of voluntary thermal tolerance as an approximation of survival (the upper and lower bound of stressful temperatures; Camacho and Rusch, 2017; Huey, 1982). We considered the tolerance index as the relationship between the upper temperature limit of the animal activity restriction (maximum voluntary temperature, VT_{max}) and the environmental temperature of the microhabitat in which this animal occurs. Thus, we combined the concept of environmental thermal adequacy with the b-d model and considered the tolerance index as a vital trait to calculate population dynamics. The concept of thermal adequacy considers that habitats would be thermally ideal if T_e is within the range of voluntary temperatures (Hertz et al., 1993). The b-d, or birth-death model consider, in turn, the relationship between survival and reproductive rates as vital traits to calculate population dynamics (Stadler, 2009; Volkov et al., 2003).

We thus estimated the tolerance index considering thermal physiology data from the analyzed populations, by using the following formula:

$$t_x = \frac{V_x}{N_x} \quad (1)$$

where t_x is the tolerance index in age group x ; V_x is the number of individuals in this age group whose VT_{max} exceeds the T_e in the population microhabitat; and N_x is the total number of individuals in this age group. The VT_{max} correspond to the upper limit of animal activity restriction (Kubisch et al., 2016), which means that environmental temperatures that are above this value exceed the ideal temperature for animals to stay active. Thus, we considered that only animals with $VT_{max} > T_e$ would be thermally adapted to the environment and thus should tolerate the environmental temperature.

2.4. Data analysis

We conducted all analyses in the statistical software environment R 3.5.1 (R Core Team, 2018). To estimate the population growth rate (λ), we first calculated the population size at the next reproductive event (re

+ 1). To do that, we considered as total number of individuals in age group 0 at $re + 1$ the product of total number of individuals in age group 1 and age group 2 at re and their reproductive rates [$Ag0_{re+1} = (b_j \times Ag1_{re}) + (b_a \times Ag2_{re})$]; the number of individuals in age group 1 as the product of the number of individuals in age group 0 at re and its tolerance index [$Ag1_{re+1} = (t_j \times Ag0_{re})$]; and the total number of individuals in age group 2 as the product of the number of individuals in age group 1 and age group 2 and their tolerance rates [$Ag2_{re+1} = (t_j \times Ag1_{re}) + (t_a \times Ag2_{re})$]. Then we calculated λ as a function of the number of individuals in one re to the re before. Also, we were not able to take other pressures under account (e.g., ageing and predation), so we considered λ as an upper bound for population growth rate.

We also calculated the sensitivity of reproductive rate and tolerance index to population growth rate changes by the characteristic equation, deducted from the life table, which calculates the λ derivative in relation to the vital character through the Lotka and Euler equation (Wallinga and Lipsitch, 2007):

$$1 = \sum_{x=0}^L b_x \cdot t_x \cdot e^{-(\ln \lambda) \cdot x} \tag{2}$$

Based on the life tables of the populations analyzed, we used the following characteristic equation:

$$\lambda^2 - t_0 \cdot b_1 \cdot \lambda - t_0 \cdot t_1 \cdot b_2 = 0 \tag{3}$$

where t_0 is the tolerance of the age group 0, t_1 is the tolerance of the age group 1, b_1 is the fertility of age group 1 and b_2 is the fertility of age group 2. We obtained the λ derivative in relation to the different vital traits (a_i s) through the implicit function theorem (Lima, 2011), which predicts that all partial derivatives of λ in order to the a_i s can be obtained by deriving in relation to each a_i and dividing the result by the characteristic equation derivative in relation to the λ , as described below:

$$\frac{\partial f(\lambda, a_i)}{\partial s_0} = -b_1 \cdot \lambda - b_2 \cdot t_1 \tag{4}$$

$$\frac{\partial f(\lambda, a_i)}{\partial s_1} = -b_2 \cdot t_0 \tag{5}$$

$$\frac{\partial f(\lambda, a_i)}{\partial b_1} = -t_0 \cdot \lambda \tag{6}$$

$$\frac{\partial f(\lambda, a_i)}{\partial b_2} = -t_0 \cdot t_1 \tag{7}$$

$$\frac{\partial f(\lambda, a_i)}{\partial \lambda} = 2 \cdot \lambda - b_1 \cdot t_0 \tag{8}$$

We then calculated the sensitivity as:

$$S(a_i) = -\frac{\frac{\partial f(\lambda, a_i)}{\partial a_i}}{\frac{\partial f(\lambda, a_i)}{\partial \lambda}} = -\frac{\partial \lambda}{\partial a_i} \tag{9}$$

And elasticity as:

$$E(a_i) = S(a_i) \cdot \frac{a_i}{\lambda} \tag{10}$$

Lastly, we simulated an increase of 10% in a_i , in order to allow the estimation of the absolute and relative variation that this would cause in λ , respectively:

$$V_{absolute} \lambda = S \left(\frac{a_i}{10} \right) \tag{11}$$

$$V_{relative} \lambda = 10 \cdot E \tag{12}$$

To investigate the effects of future climate change on population dynamics, we measured future T_e s as the sum of current T_e and the difference between predicted and current mean annual temperature

(Bio1, WorldClim) of the FLONA Caxiuanã and Reserva Ducke, through the packages raster (Hijmans, 2017), rgdal (Bivand et al., 2017) and gtools (Warnes et al., 2015). To do that, we used the MPI-ESM-LR (Max Planck Institute Earth System Model) climate layer at 0.0083333 degrees resolution (downscaled to 1×1 km grid cells), which is the climate model that best captured the patterns of temperature and precipitation during the control period at global scales (Anav et al., 2013).

We measured future T_e s for the decades of 2060–2080, referred to as 2070, under an optimistic scenario of greenhouse gases emissions (GGE), which is referred to as Representative Concentration Pathway (RCP) 4.5 and represents a reduction of current emissions, and a business-as-usual scenario of GGE, which represents the maintenance of current emission rates and is referred to as RCP 8.5 (van Vuuren et al., 2014). We recovered an increase in annual mean temperature of 2.61 °C in Caxiuanã considering RCP 4.5 and 3.65 °C considering RCP 8.5. For Ducke, we recovered an increase of 2.87 °C and 4.59 °C for the RCPs 4.5 and 8.5, respectively. Finally, we performed a Jeffreys-Rule Prior analysis to calculate a Bayesian posterior distribution for each tolerance index considered here, in order to evaluate whether the changes in λ and the predicted decline of populations occurred due to random effects in the data.

3. Results

The populations were experiencing an average T_e of 26.9 °C at Caxiuanã, varying from 25.3 °C to 28.8 °C, and 27.9 °C at Ducke, varying from 23.9 °C to 30.3 °C. By 2070, individuals would experience an average T_e of 29.49 °C at Caxiuanã and 30.80 °C at Ducke, in the optimistic scenario; and 30.53 °C at Caxiuanã and 32.52 °C at Ducke, in the business-as-usual scenario. Life tables for all populations are represented in Table 1, including VT_{max} , t_x and b_x for all evaluated scenarios and possibilities of reproductive rates.

Except for the Caxiuanã population of *A. ameiva*, all evaluated populations showed a high confidence level regarding the variation of lambda in both analyzed RCPs and reproductive rates (Fig. 1, Table 2). The Ducke population of *A. ameiva* is likely to decrease by 2070 only in RCP 8.5. Both Caxiuanã and Ducke populations of *G. humeralis* are predicted to decrease over time, considering the RCP 4.5 and both possibilities of reproductive rates investigated. Considering the RCP 8.5, they may reach an immediate collapse by 2070, assuming no acclimatization or local adaptation. For *N. fuscoauratus*, we predicted that

Table 1
Life tables of analyzed populations.

		AG	t_x (cs)	t_x (os)	t_x (bu)	b_{x1}	b_{x2}	N_0
<i>Ameiva ameiva</i>	Caxiuanã (29.22 °C)	0	1	1	0.5	0	-	7
		1	0.71	0.29	0.21	3.2	-	14
	Ducke (29.75 °C)	2	0	0	0.5	4.4	-	1
		0	0.83	0.5	0.17	0	-	6
		1	0.5	0.5	0.38	3.2	-	8
		2	0.5	0	0.5	4.4	-	6
<i>Gonatodes humeralis</i>	Caxiuanã (26.24 °C)	0	0.5	0	0	0	0	8
		1	0.47	0.1	0	2	2	30
	Ducke (28.26 °C)	2	0.46	0.08	0	2	3	13
		0	0.37	0	0	0	0	8
		1	0.5	0.2	0	2	2	10
		2	0.69	0.19	0.13	2	3	16
<i>Norops fuscoauratus</i>	Caxiuanã (28.52 °C)	0	1	1	1	3	1	3
		1	1	1	1	3	3	38
	Ducke (28.58 °C)	2	0.79	0.55	0.53	3	3	9
		0	0.6	0.1	0	0	0	9
		1	1	0.1	0.1	3	1	9
		2	0.59	0.1	0.1	3	3	32

Legend: AG = age groups; t_x = tolerance indexes (cs = current scenario; os = optimistic scenario; bu. = business-as-usual scenario), b_{x1} = equal reproductive rates, b_{x2} = smaller females producing lower number of eggs, N_0 = sample size. Maximum voluntary temperature (VT_{max}) are in parentheses.

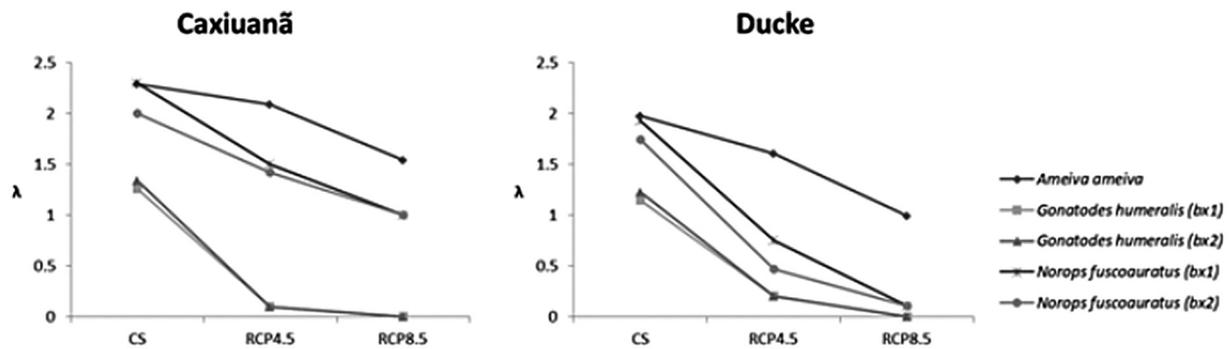


Fig. 1. Population growth rates (λ) of *Ameiva ameiva*, *Gonatodes humeralis* and *Norops fuscoauratus* from Caxiuanã and Ducke. CS = Current Scenario, RCP 4.5 = optimistic scenario of greenhouse gases emissions (GGE) by 2070, RCP8.5 = business-as-usual scenario of GGE by 2070. bx1 and bx2 = evaluated reproductive rates.

only the Ducke population growth rate might decrease over time, considering both RCPs and reproductive rates investigated.

All populations presented higher sensitivities for age groups 0 and 1 (Table 3). Also, with exception of the second possibility of reproductive rate (i.e., b_{x2} , smaller females producing one egg per year and larger females producing three eggs per year) evaluated for *N. fuscoauratus*, all populations presented higher elasticity for tolerance of the age group 0 and reproduction rates of the age group 1 (Table 3). Considering a hypothetical relative variation of 10% on population growth rate, we predicted that the most impacted vital rate would be the tolerance of the age group 0 for all populations (Table 3).

4. Discussion

This is the first study integrating population-level parameters to estimate thermal sensitivity of Amazonian lizards to climate change. Our interpretations were based on indirect estimates of tolerance to warming, considering an index that embraces both environmental thermal adequacy and birth-death model to predict population dynamics. Especially in recent years, a body of studies has sought to understand the relationships between environmental warming, thermoregulation, physiological adaptation, vulnerability and persistence/extinction of native populations and species of lizards (e.g., Buckley et al., 2015; Buckley and Huey, 2016; Munoz et al., 2016), but none of them incorporate population dynamic parameters. Therefore, the present study is pioneering in the search for a relationship between thermal physiology and population growth rates through demographic analysis.

Table 2

Confidence intervals for population growth rates.

		<i>Ameiva ameiva</i>		<i>Gonatodes humeralis</i>		<i>Norops fuscoauratus</i>		
		CI	λ	CI	λ	CI	λ	
b_{x1}	Caxiuanã	Scenario						
		CS	2.97–4.10	2.29	0.67–1.99	1.26	1.88–3.77	2.30
		RCP4.5	2.61–3.76	2.09	0.003–0.62	0.10	0.30–2.82	1.50
		RCP8.5	0.60–2.65	1.54	0.001–0.54	0.00	0.01–1.94	1.00
	Ducke	Scenario	CI	λ	CI	λ	CI	λ
		CS	1.88–3.82	1.98	0.47–1.82	1.15	1.34–3.47	1.93
RCP4.5		0.92–3.26	1.61	0.004–0.71	0.20	0.001–0.78	0.75	
	RCP8.5	0.20–2.23	0.99	0.001–0.58	0.00	0.001–0.73	0.11	
b_{x2}	Caxiuanã	Scenario	CI	λ	CI	λ	CI	λ
		CS	–	–	0.76–2.14	1.34	1.07–2.29	2.00
		RCP4.5	–	–	0.005–0.65	0.10	0.29–1.79	1.42
		RCP8.5	–	–	0.001–0.53	0.00	0.02–1.33	1.00
	Ducke	Scenario	CI	λ	CI	λ	CI	λ
		CS	–	–	0.54–1.96	1.23	0.91–2.13	1.74
RCP4.5		–	–	0.006–0.75	0.20	0.001–0.35	0.47	
	RCP8.5	–	–	0.001–0.60	0.00	0.001–0.35	0.11	

Legend: b_{x1} = equal reproductive rates, b_{x2} = smaller females producing lower number of eggs, CI = Confidence Interval, λ = population growth rate. λ in bold presented high level of confidence ($p < 0.05$).

Table 3

Sensitivity and elasticity of vital traits from evaluated populations, with simulation of a 10% increase of relative variation in λ in relation to current population growth rate.

	VR	Caxiuana							Ducke					
		A_i	S	E	V_{abs}	V_{rel}	λ_{sim}	A_i	S	E	V_{abs}	V_{rel}	λ_{sim}	
<i>Ameiva ameiva</i>	bx1	t_h	1.00	7.61	3.33	0.69	33.27	2.98	0.83	6.59	2.77	0.55	27.71	2.53
		t_j	0.71	3.20	1.00	0.23	9.99	2.52	0.50	2.83	0.71	0.14	7.14	2.12
		b_j	3.20	1.66	2.33	0.53	23.28	2.82	3.20	1.27	2.06	0.41	20.57	2.39
		b_a	4.40	0.52	1.00	0.23	9.99	2.52	4.40	0.32	0.71	0.14	7.14	2.12
<i>Gonotodes humeralis</i>	bx1	t_h	0.50	2.28	0.91	0.11	9.07	1.37	0.38	2.12	0.69	0.08	6.91	1.23
		t_j	0.47	0.66	0.25	0.03	2.46	1.29	0.50	0.48	0.21	0.02	2.09	1.18
		b_j	2.00	0.42	0.66	0.08	6.61	1.34	2.00	0.28	0.48	0.06	4.82	1.21
		b_a	2.00	0.15	0.25	0.03	2.46	1.29	2.00	0.12	0.21	0.02	2.09	1.18
	bx2	t_h	0.50	2.43	0.90	0.12	9.04	1.46	0.38	2.31	0.70	0.09	7.04	1.32
		t_j	0.47	0.89	0.31	0.04	3.10	1.38	0.50	0.66	0.27	0.03	2.66	1.26
		b_j	2.00	0.40	0.59	0.08	5.94	1.42	2.00	0.27	0.44	0.05	4.37	1.29
		b_a	3.00	0.14	0.31	0.04	3.10	1.38	3.00	0.11	0.27	0.03	2.66	1.26
<i>Norops fuscoauratus</i>	bx1	t_h	1.00	6.20	2.70	0.62	27.01	2.92	0.60	4.26	1.32	0.26	13.23	2.19
		t_j	1.00	1.88	0.82	0.19	8.19	2.49	1.00	0.87	0.45	0.09	4.51	2.02
		b_j	3.00	1.44	1.88	0.43	18.82	2.73	3.00	0.56	0.87	0.17	8.72	2.10
		b_a	3.00	0.63	0.82	0.19	8.19	2.49	3.00	0.29	0.45	0.09	4.51	2.02
	bx2	t_h	1.00	1.67	0.83	0.17	8.34	2.17	0.60	1.65	0.57	0.10	5.67	1.84
		t_j	1.00	1.00	0.50	0.10	5.00	2.10	1.00	0.62	0.36	0.06	3.59	1.80
		b_j	1.00	0.67	0.33	0.07	3.33	2.07	1.00	0.36	0.21	0.04	2.08	1.78
		b_a	3.00	0.33	0.50	0.10	5.00	2.10	3.00	0.21	0.36	0.06	3.59	1.80

Legend: VR = vital character, t_x = tolerance indexes, b_x = reproductive rates, A_i = vital character values, S = sensitivity, E = elasticity, V_{abs} = absolute variation in λ , V_{rel} = relative variation in λ , λ_{sim} = simulated population growth rate, with V_{rel} of 10%.

extinction of *G. humeralis* in both evaluated populations due to the absence of tolerance to warming of the age group 0 may indicate additive factors influencing their vulnerability, such as proximity to the Arc of Deforestation, for the population of Caxiuana, and to an urban environment, for the population of Ducke.

The ways that organisms may cope with changing environmental conditions by behavioral flexibility is not unique and vary among species in terms of their adaptive capacity in face of climate change (Beever et al., 2017). It is important to note that even though both *A. ameiva* populations may experience a decrease in their growth rates, estimates do not reach a scenario of potential local extinction, as predicted for *G. humeralis* and *N. fuscoauratus*. Lizards with broader thermal preferences, such as *A. ameiva*, are likely to be favored by selection, allowing it to persist in altered thermal environments through evolutionary adaptation (Gilbert and Miles, 2017). On the other hand, response to selection may be too slow for anoles and other lizards with lower thermal preferences, so evolutionary change in *G. humeralis* and *N. fuscoauratus* is unlikely to occur considering current rates of environmental change (Logan et al., 2018; Martins et al., 2018).

The most sensitive vital trait for all populations to both scenarios of greenhouse gases emissions was the tolerance of age group 0, which was also the most impacted vital trait considering a hypothetical variation in population growth rate. These results were evidenced by the simulations of predicted changes on population dynamics due to climate change. The scarcity of data on lizards natural history and ecology still limits the understanding of demography parameters for many species, restricting deeper population analyzes, especially for megadiverse regions whose species are relatively poorly known (Dunham, 1994). Despite this lack of information, our results are consistent with the idea that increases in environmental temperatures caused by climate change have the potential to influence the population dynamics of reptiles (Lelièvre et al., 2010).

Although active thermoregulators can usually cope with changing environmental conditions through behavioral flexibility and adaptive capacity (Grant, 1990; Grant and Porter, 1992), thermal performance of ectotherms as a function of T_b has been considered fixed through the ontogeny (Beever et al., 2017; Heatwole and Taylor, 1987; Sinclair et al., 2016). Factors such as circadian rhythm of behavioral thermoregulation operate distinctly among different age groups and may play

an important role in species thermal adaptation (Akashi et al., 2016). In addition, clutch size, age at sexual maturity and species longevity may decrease with increasing environmental temperatures when the influence of T_b (and factors influencing it) on lizard ecology and natural history is tested (Meiri et al., 2013).

We conclude that populations of the thermoregulatory species *A. ameiva* would probably be more resistant to predicted temperature increases in both optimistic and business-as-usual scenarios of greenhouse gases emissions. Both Caxiuana and Ducke populations of *G. humeralis*, as well as Ducke population of *N. fuscoauratus*, may collapse within few generations, assuming no acclimatization or local adaptation. This study represents the first effort to evaluate population sensitivity and elasticity to climate change and demonstrate the geographic variability of these characters in three widespread and habitat-generalist species. We highlight the need of new studies focusing on species with different biological trait patterns, such as endemic and habitat-specialists, to provide the theoretical and empirical basis for biologically informed conservation strategies and actions, in order to minimize the chances that the most pessimistic forecasts materialize, leading many species and populations of lizards to extinction.

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