UNIVERSIDADE DE BRASÍLIA
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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Risco de extinção e demografia de um lagarto neotropical vivíparo

Laís Pio Caetano Machado

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade de Brasília como parte dos requisitos para a obtenção do título de Mestre em Ecologia.

Orientador: Dr. Guarino Rinaldi Colli

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Introdução geral

A distribuição geográfica e a demografia estão entre os principais aspectos de caracterização e conservação das espécies. Esses atributos dependem não só da história evolutiva, mas dos requisitos e tolerâncias ambientais dos organismos (Grinnel, 1917; Irwin and Irwin, 2005). Nesse sentido, as condições do clima e da paisagem são importantes para estimar parâmetros geográficos e demográficos e para projetar suas mudanças (Brook et al., 2008; Böhm et al., 2016). Dentre as possíveis causas de alteração, estão as mudanças climáticas e o fogo, uma vez que eles afetam os animais não só diretamente, como também de forma indireta, através de seu reflexo na estrutura da vegetação e, consequentemente, na redução da qualidade do hábitat (Irwin and Irwin, 2005; Brook et al., 2008; Selwood et al., 2014; Sousa et al., 2015).

As mudanças climáticas podem ter efeito sobre os organismos em todos os ecossistemas (Parmesan, 2006; Urban, 2015; Walther et al., 2002). Isso se dá principalmente porque, apesar da distribuição geográfica de uma espécie ser determinada pela combinação de múltiplos fatores ambientais, comportamentais e fisiológicos, seu preditor mais frequente é a temperatura (Grinnell, 1917). De acordo com o Painel Intergovernamental de Mudanças Climáticas (IPCC), a temperatura da superfície global atual (2012-2020) é 1,09 °C maior do que entre 1850-1900, e essa diferença pode chegar a 5,7 °C até 2100, devido ao grande aumento nas emissões antrópicas de gases de efeito estufa (IPCC, 2021). Dessa forma, são previstas consequências para vários grupos, como plantas (Thuiller et al., 2005; Velazco et al., 2019), insetos (Boggs, 2016; Pureswaran et al., 2018), peixes (Rougier et al., 2015), anfíbios (Blaustein et al., 2010; Corn, 2005), répteis (Böhm et al., 2016; Diele-Viegas, 2018), aves (Crick, 2004; Şekercioğlu et al., 2012), mamíferos (Pacifici et al., 2018; Thuiller et al., 2006). Estimativas apontam que, até 2080, cerca de 57% das plantas e 34% dos animais podem perder mais da metade de sua área de adequabilidade climática atual (Warren et al., 2013), ou seja, locais com condições climáticas adequadas para sua sobrevivência e manutenção. Dessa forma, se não houver tempo e dispersão suficientes para os organismos adequarem-se às novas condições ou migrarem para locais mais favoráveis, as alterações no clima podem levar ao colapso demográfico e à extinção (Graham et al., 1996; Tingley et al., 2009; Sinervo et al., 2010).

O fogo é um agente natural de perturbação em diversos ecossistemas (Bond and Keeley, 2005; Walter and Ribeiro, 2010; Pivello, 2011). No entanto, sua atividade recente tem sido principalmente associada à ação antrópica (Ramos-Neto and Pivello, 2000; Pivello, 2011).

Essa influência do ser humano sobre o regime de queima é complexa, pois pode aumentar o potencial de grandes incêndios não só de forma direta, através do uso do fogo em atividades agropecuárias durante a estação seca, mas também indiretamente pelos esforços de supressão de queima (Pivello, 2011; Wu et al., 2021). Além disso, há uma relação sinérgica entre as mudanças climáticas e o fogo, uma vez que as queimadas emitem gases que intensificam o efeito estufa, bem como cenários severos de alteração no clima associam-se a projeções de maior área queimada, principalmente devido ao aquecimento e à seca (van der Werf et al., 2017; Wu et al., 2021). Ademais, o regime de queima pode ser afetado pelas mudanças previstas na vegetação em decorrência da alteração climática (Keeley and Syphard, 2016).

Frente a esses dois fatores de alteração das condições ambientais, o grau de impacto sobre os organismos pode variar com as características das espécies (Huey et al., 2012). Em relação às mudanças climáticas, animais ectotérmicos apresentam alta vulnerabilidade, pois dependem primariamente da absorção de calor do ambiente para regular sua temperatura corporal (Huey, 1982; Diele-Viegas and Rocha, 2018). Uma estimativa para lagartos projetou um nível global de extinção local de 16% até 2050 e 30% até 2080 (Sinervo et al., 2010). Adicionalmente, levando em conta que a viviparidade em lagartos geralmente é uma adaptação a climas frios, espécies vivíparas podem ter maior risco de extinção frente ao aquecimento global (Sinervo et al., 2010; Pincheira-Donoso et al., 2013; Jara et al., 2019). Além disso, a distribuição geográfica também pode ser relevante, pois lagartos tropicais experimentam menor amplitude térmica e possuem menor tolerância termal em relação aos de latitudes maiores, podendo sofrer impactos mais severos (Tewksbury et al., 2008). Já em relação ao fogo, a resposta de lagartos é bastante variada, pois enquanto algumas espécies sofrem prejuízos, outras são beneficiadas ou não são afetadas (Greenberg et al., 1994; Driscoll and Henderson, 2008; Brisson et al., 2013; Scroggie et al., 2019). Ainda, há espécies que não sofrem efeito direto da queima, mas podem ser prejudicadas por suas consequências indiretas na vegetação e no microclima em longo prazo (Costa et al., 2013; Sousa et al., 2015; Costa et al., 2020). Nesse sentido, é relevante investigar os efeitos específicos de diferentes regimes de queima para cada espécie, a fim de que sejam planejados delineamentos estratégicos de manejo de fogo e conservação (Driscoll and Henderson, 2008; Lindenmayer et al., 2008).

Considerando a origem antrópica da maioria das queimas atuais e das mudanças climáticas em curso, é de suma importância avaliar seus efeitos sobre os organismos, em especial os ectotérmicos de regiões tropicais. A maioria dos estudos que investigam o impacto das mudanças climáticas em répteis é proveniente dos Estados Unidos e da Europa, havendo uma lacuna de informação para o Hemisfério Sul (Winter et al, 2016). Dessa forma, o presente estudo teve como objetivo estimar o efeito das mudanças climáticas e de diferentes regimes de queima sobre a distribuição geográfica e a demografia de um lagarto neotropical vivíparo. Com este trabalho, buscamos um melhor entendimento acerca do efeito das mudanças climáticas e do fogo sobre a lacertofauna sul-americana, contribuindo para a elaboração de estratégias de conservação na região.

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Chapter 1. Climate change shrinks environmental suitability for a viviparous Neotropical skink

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Anthropogenic global warming and deforestation are significant drivers of the global biodiversity crisis. Ectothermic and viviparous animals are especially vulnerable since high environmental temperatures can impair embryonic development, but we lack knowledge about these effects upon Neotropical organisms. Here, we model the combined effects of climate change and deforestation on the geographic distribution of the viviparous Neotropical lizard *Notomabuya frenata* (Scincidae). This species ranges in Brazil, Argentina, Paraguay, and Bolivia. We use environmental and physiological variables (locomotor performance and hours of activity) to predict areas with suitable habitats in the present and the future, considering different scenarios of greenhouse gas emissions and deforestation. The most critical predictors of habitat suitability were: isothermality (i.e., the ratio between mean diurnal temperature range and annual temperature range), precipitation during winter, and hours of activity under lower thermal extremes. Still, our models predict a contraction of suitable habitats in all future scenarios and the displacement of these areas towards eastern South America. In addition, protected areas are not enough to conserving suitable habitats for this species. Our findings highlight the vulnerability of tropical and viviparous ectotherms and suggest that even species that are currently widely distributed, such as *N. frenata*, may have their conservation compromised shortly due to the low representativeness of their suitable habitats in protected areas combined with the synergistic effects of climate change and deforestation. We stress the need for decision-makers to consider the impact of range shifts in creating protected areas and managing endangered species.

1. Introduction

Climate change resulting from anthropogenic greenhouse gas emissions can challenge living organisms worldwide (Parmesan, 2006; Urban, 2015). In response, species can shift their ranges to reach suitable habitats in the future if dispersal is not limited (Graham et al., 1996; Araújo et al., 2006; Tingley et al., 2009; Carvalho et al., 2010). Alternatively, they can adapt to new environmental conditions through evolutionary responses, but this can take a long time (Hoffmann and Sgrò, 2011). In this sense, phenotypic plasticity is important in the face of accelerated climate change, as it allows short-term changes in organisms (Matesanz et al., 2010; Merilä & Hendry, 2014; Bonamour et al., 2019). However, the lack of adjustment can lead to local extinction as suitable habitats for many species are expected to decline due to global warming (Sinervo et al., 2010; Bonino et al., 2015; Minoli & Avila, 2017; Pontes-da-Silva et al., 2018). Thus, anticipating the challenges of climate change is essential to support adequate conservation strategies (Hannah et al., 2002).

To investigate the effects of climate change on organisms, species distribution models are a valuable tool (Hannah et al., 2002; Pearson & Dawson, 2003). Some of these models relate environmental predictors to species occurrence records (also called correlative models), often easily accessible from open-access databases (Elith & Leathwick, 2009; Peterson et al., 2015). Despite its high applicability, the complex combination of processes indirectly expressed in their predictions limits the interpretation of their results (Kearney & Porter, 2009; Pearson & Dawson, 2003). Besides, species distribution models can rely on intrinsic biological predictors (also called mechanistic or biophysical models), which increase model accuracy under novel environments and provides an understanding of the biological mechanism behind the response to environmental changes, promoting ecologically interpretable results (Kearney & Porter, 2009; Zurell et al., 2016). However, calibration of these models requires many costly parameters, absent for most organisms (Peterson et al., 2015; Urban et al., 2016). Given the shortcomings of each approach alone, these methods can be seen as complementary by comparing their results or by building hybrid models (Morin & Thuiller, 2009; Talluto et al., 2016).

Species' vulnerability to environmental changes depends on their exposure, sensitivity, resilience, and adaptation potential (Williams et al., 2008). Except for exposure, these factors are determined by intrinsic species characteristics, which can be incorporated as biological predictors in species distribution models (Williams et al., 2008). Among these are physiological (thermal tolerance, locomotor performance), ecological (habitat use, activity time), demographic (population growth, dispersal potential), and evolutionary (genetic variability, gene flow) parameters (reviewed in Urban et al., 2016). Thermal tolerance, i.e., the range of temperature the animal can tolerate, is one of the most critical factors for ectotherms since high temperatures may exceed their thermal limits, leading to a reduction in their activity time and compromising survival and reproduction (Huey & Stevenson, 1979; Sinervo et al., 2010). Thus, hours of activity and locomotor performance have often been successfully used in in mechanistic and hybrid species distribution models (Pontes-da-Silva et al., 2018; Yuan et al., 2018).

Among the intrinsic characteristics of sensitivity, ectothermic animals are particularly vulnerable to climate change since they depend primarily on heat exchange with the environment to regulate their body temperature (Angilletta et al., 2002; Huey, 1982). This physiological sensitivity may be amplified in tropical species that live in more thermally stable environments and have narrow thermal safety margins, so even slight warming can harm them (Deutsch et al., 2008; Huey et al., 2009). Moreover, small ectotherms, such as lizards, have limited dispersal ability, which makes it difficult for them to reach suitable habitats in the future in the face of accelerated climate change and habitat fragmentation (Spiller et al., 1998; Thomas et al., 2004). In the tropical region, lizards are among the vertebrates most threatened by habitat disturbances (Alroy, 2017). In this way, deforestation can increase the exposure of organisms to climate change, because in addition to intensifying greenhouse gas emissions, it reduces the availability of suitable habitats and makes dispersion difficult due to landscape fragmentation (Sala et al., 2000; Travis, 2003; Powers & Jetz, 2019). To minimize this threat, it is important that suitable habitats for lizards are effectively represented within protected areas, to contribute to the conservation of this group (Corbalán et al., 2011; de Novaes e Silva et al., 2014).

Most studies investigating the effects of climate change on reptiles are from temperate-zone species, with critical information gaps for Africa, Asia, and South America, regions that concentrate most of the global reptile richness (Böhm et al., 2016; Winter et al., 2016). Besides, the negative consequences of climate change should be more severe for tropical species because they experience environmental temperatures close to or already at their optimal temperatures (T_{opt}; Deutsch et al., 2008). As T_{opt} of tropical organisms is very close to their critical thermal maximum (CT_{max}), they have narrower thermal tolerance than high latitudes species (Deutsch et al., 2008; Tewksbury et al., 2008; Sunday et al., 2011). Here, we estimate the synergetic effects of climate change and deforestation on the geographic distribution of a viviparous Neotropical lizard, the skink *Notomabuya frenata* (Cope, 1862). This species is widely distributed in Brazil, Argentina, Bolivia, and Paraguay, primarily in the Atlantic Forest, Cerrado, Chaco, and Pantanal regions (Álvarez et al., 2009; Dirksen & Riva, 1999; Pinto et al., 2017). It occupies open and forested areas, using various microhabitats, such as fallen logs, rocks, trees, termite mounds, ground, and litter (Vitt, 1991; Colli et al., 2002; Linares & Eterovick, 2013; Vrcibradic & Rocha, 1998a). In addition, it has a diverse diet, consisting of arthropods, mainly termites (Vrcibradic & Rocha, 1998a).

Viviparity has independently evolved many times among squamate reptiles and is often interpreted as a critical adaptation to cold climates (Shine, 2014; Wright et al., 2015). *Notomabuya frenata* is part of a lineage that dispersed from Africa ca. 18 mya and diversified in South America and the Caribbean, so it evolved in warm climates (Hedges & Conn, 2012; Miralles & Carranza, 2010). Thus, viviparity is presumably advantageous for enabling females to control thermal conditions during embryogenesis in both cold and warm conditions, enhancing the fitness of offspring (Ji et al., 2007; Shine, 1995). However, despite this control through maternal thermoregulation, the harmful consequences of climate change may be worrying for viviparous species because thermal conditions during gestation can affect embryo viability and offspring phenotype, so high heat exposure can compromise embryonic development and young's performance after birth (Beuchat, 1986; Lourdais et al., 2004; Jara et al., 2019; Shine & Harlow, 1993).

Thus, we aim to estimate how climate change and deforestation affect the geographic distribution of the viviparous Neotropical lizard *Notomabuya frenata*. Considering what was presented above about the high vulnerability of tropical and viviparous organisms, we hypothesize that climate change will reduce the geographical distribution area of this species and that deforestation will exacerbate this threat. Therefore, we expect to test the relative contributions of physiological and environmental predictor in our hybrid models. We hypothesize that the physiological variables will have the most outstanding contribution to the model, as they consider specific traits of the species.

2. Methods

2.1. *Environmental variables*

We retrieved historical (1970-2000) and future (2041-2060, 2061-2080, and 2081-2100) climatic and elevation data at a 2.5-min resolution from the WorldClim 2.1 database (Fick & Hijmans, 2017). These variables comprised elevation, total monthly precipitation, minimum and maximum monthly temperatures, and 19 derived bioclimatic variables (Hijmans et al., 2005). We cropped rasters to the spatial extent of South America (between 10° and -40° latitude and between -80° and -30° longitude). Regarding the future climate projections, we used two shared socioeconomic pathways (SSP2-4.5 and SSP5-8.5), which estimate how different socioeconomic contexts can lead to different greenhouse gas emission scenarios (Riahi et al., 2017). Besides, we use eight general circulation models (GCMs), which calculate climatic parameters considering different physical processes. Using several SSP and GCMs, we incorporated uncertainty due to different climate change scenarios in our modeling (van Ulden & van Oldenborgh, 2006).

To reduce multicollinearity among spatially correlated variables, which can cause instability in parameter estimation (Dormann et al., 2013), we used a mask whose extent was the same as that of the environmental variables (above) and extracted values of the historical environmental variables for 1000 random points with package DISMO (Hijmans et al., 2017). Next, we used a stepwise approach to eliminate highly collinear variables based on the variance inflation factor (VIF) with package USDM (Naimi, 2015). The procedure consisted of calculating VIF for all variables, excluding the one with the highest VIF (> 10), and repeating the procedure until no variables with VIF > 10 remained.

2.2. *Thermal performance variables*

We collected 32 individuals of *Notomabuya frenata* using pitfall traps in cerrado *sensu stricto* and gallery forest habitats at Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística - IBGE (15°56'41" S, 47°53'07" W), Distrito Federal, Brazil. It is a protected area within the Cerrado biome in central Brazil, with Aw climate in Köppen’s classification (Alvares et al., 2013; Nimer, 1989). In the cerrado *sensu stricto* habitat, we opened the pitfall traps monthly and checked them for six days in a row, while in the gallery forest habitat, the traps were always open and checked twice a week. We measured the snout-vent length (with a ruler to the nearest 1 mm) and mass (with a Pesola Micro Line spring scale to the nearest 0.1 g) of all captured individuals.

We brought lizards to the laboratory to collect physiological data. All procedures were approved by the Animal Use Ethics Committee of the University of Brasília (process 33786/2016). All the following physiological experiments were performed with all 32 individuals collected. First, we estimated the preferred temperature (T_{pref}) of each lizard using a thermal gradient consisting of an MDF plywood terrarium with eight compartments (each 100 × 15 × 30 cm – l × w × h) with a 60-W incandescent lamp at one end and an ice pack on the other, generating a ~20-50 °C thermal gradient (Paranjpe et al., 2012). We recorded lizard body temperature every minute for one hour by a 36 ga thermocouple (Omega 5SC-TT-T-36-72) taped to their abdomen and connected to a data acquisition module (Omega TC-08 8 Channel Thermocouple USB Data Acquisition Module), using the mean to estimate T_{pref}. We allowed a 5-min acclimatization period in the gradient before recording body temperatures. We observed no impairment of lizard movements during the experiments due to thermometers.

We estimated thermal performance by inducing lizards to run on a track (200 × 30 × 40 cm – l × w × h) at three body temperatures in the following order: room temperature, 5 °C below, and 5 °C above the room temperature. Lizards ran two times at each test temperature, and there was a 30-min interval between tests. Room temperature was the body temperature of each individual at the end of the T_{pref}. experiment (ranged from 23,0 to 35,6 ºC). As we did not standardize room temperature, we could examine the sprint speed of the species over a range of temperatures, not just three, to obtain sufficient variation for subsequent regression analyses (Appendix S1). We used gel ice packs and incandescent lamps to alter the lizards' body temperature, monitored with an L-K industries Miller & Weber T-6000 Cloacal 0/50 ºC thermometer. We recorded all runs with a high-speed digital camera (Casio EX-FH25 10.1MP) at 420 fps and processed videos with Tracker 4.11.0 to obtain the maximum sprint speed for each individual at each temperature.

One hour after the last run, we measured the critical thermal minimum (CT_{min}) and maximum (CT_{max}) temperatures with a one-hour interval between them. We always measured CT_{min} before CT_{max}, since the last may be more stressful. We exposed lizards to the sources of heat and cold mentioned above until they lost the righting response, i.e., when lizards placed on their dorsum could not flip over to their venter.

We generate a thermal performance curve (Appendix S1; Huey & Stevenson, 1979) using a generalized additive mixed model – GAMM (Wood, 2017; Zajitschek et al., 2012). This model used the maximum running speed as the response variable, body temperature as a fixed effect, and SVL as a covariate. We included the lizard identification as a random effect. From the thermal performance curve, we estimated thermal performance breadth and optimal temperature for performance (Huey & Stevenson, 1979). The GAMM allowed us to extrapolate thermal performance spatially and temporally based on the historical and biologically relevant future temperature data (monthly average minimum and maximum temperatures, and bioclimatic variables related to the minimum and maximum temperatures at specific times of the year – BIO5, BIO6, BIO8, and BIO9), using package MAPINGUARI (Caetano et al., 2019). Just as we did with the environmental variables, we built a mask, selected 1000 random points, and extracted thermal performance values for each point. Then, we eliminated highly collinear variables using the stepwise VIF approach as above.

2.3. Hours of activity variables

We used data collected at Reserva Ecológica do IBGE (above) and in a gallery forest at Estação Ecológica do Jardim Botânico de Brasília (15°51'12" S, 47°49'14" W), Distrito Federal, Brazil. To estimate the hours of activity, we recorded the daily temperature experienced by lizards in the field (operative environmental temperature) and the temperature range in which they are active (Caetano et al., 2020). The latter corresponds to the difference between the minimum and maximum voluntary temperatures, i.e., the lowest and highest temperatures recorded in the T_{pref} experiment. We used data loggers (Onset HOBO Pro v2 2x External Temperature Data Logger U23-003) to estimate the operative environmental temperature with sensors inserted into PVC models of equivalent size and color to *Notomabuya frenata* (2.0 cm diameter x 6.0 cm length; brown and gray; Appendix S2). We placed the models in microhabitats used by the species: bare ground (N = 62), leaf litter, termite mounds (N = 22), logs (N = 33), trees (N = 13), burrows (N = 22), and shrubs (N= 8). Among all microhabitats sampled, the models were under varying degrees of sunlight exposure. We deployed data loggers in August 2013, January 2014, and April-July 2014, recording temperatures every minute. In this way, we recorded the temperature variations which animals could experience in each microhabitat. This protocol for estimating operational temperature has been validated for small ectotherms, such as lizards (Pontes-da-Silva et al., 2018; Sinervo et al., 2010). Further, we recorded variation in air temperature every minute at the same time and locations using 21 data loggers (Onset HOBO Pro v2 Temperature/Relative Humidity Data Logger U23-001-A) placed inside a PVC cover, fixed to a metal pole at 50 cm above the ground. There was no contact between metal poles and data collectors; therefore, there was no interference in the collection of air temperature.

We estimated the daily hours in which the operative temperature in each microhabitat is within the species' voluntary temperature range. We considered the average among microhabitats as the number of hours of activity of *Notomabuya frenata*. Then, we built a generalized linear model with Poisson errors relating hours of activity to maximum daily air temperature recorded in the field (Appendix S3). As this model estimates the hours of activity based on air temperature, we use historical and future biologically relevant temperature data (monthly average minimum and maximum temperatures, BIO5, BIO6, BIO8, and BIO9) to extrapolate the hours of activity spatially (in South America) and temporally (current and future) using the package MAPINGUARI (Caetano et al., 2019). Thus, each pixel of the temperature rasters had its estimated value of hours of activity. Similar procedures have been used previously (e.g., Kirchhof et al., 2017; Caetano et al., 2020). As with the environmental and thermal performance variables, we used a stepwise VIF approach to exclude highly collinear variables.

2.4. Species occurrence records

We obtained 245 occurrence records of *Notomabuya frenata* from the literature and herpetological collections. Then, we removed duplicate records using the DISMO package to avoid spatial autocorrelation, leaving 200 records. Next, we used the four least collinear environmental variables (VIF < 2) to filter the records using the *EnvSample* function to avoid environmental bias (Varela et al., 2014), leaving 130 records.

2.5. Land cover data

To account for deforested areas, we obtained land cover data from Broxton, Zeng, Sulla-Menashe, and Troch (2014) for the present, based on ten years (2001-2010) of data from the "5.1 Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type MCD12Q1" collection. We considered 12 classes of land cover as natural vegetations (evergreen needleleaf, evergreen broadleaf, deciduous needleleaf, deciduous broadleaf, mixed forests, closed shrublands, open shrublands, woody savannas, savannas, grasslands, permanent wetlands, and snow/ice) and four classes as deforested (croplands, urban and built up, cropland/natural vegetation, and barren). For the future, we obtained land-use projections made by Li et al. (2017) for 2050 and 2100 under the greenhouse gas emission scenarios B1 and A2. As we considered three future periods in our analyses, we made a linear interpolation between these data to estimate the land use in 2070, using the *interpolate_linear* function of the THINGS package (Baumgartner & Wilson, 2015). We considered tree classes of land cover as natural vegetations (water, forest, and grassland) and three classes as deforested (farmland, urban, and barren).

2.6. Protected areas data

To assess the effectiveness of protected areas in conserving sites with habitat suitability for *Notomabuya frenata*, we obtained protected areas data in Brazil, Argentina, Paraguay, and Bolivia from the World Database on Protected Areas - WDPA (UNEP-WCMC, 2022). We considered all protected areas that overlap the current habitat suitability area for the species, including all International Union for Conservation of Nature and Natural Resources (IUCN) management categories (Dudley, 2008).

2.7. Habitat suitability modeling

Using the stepwise procedure described above, we pooled the selected environmental, thermal performance, and hours of activity variables and excluded those with VIF > 5 to reduce collinearity. The following variables were retained: BIO2, BIO3, BIO14, BIO15, BIO18, and BIO19; thermal performance based on BIO5; and hours of activity based on BIO6 and BIO8 (Appendix S4-13). Then, we used these nine variables as predictors and the 130 species occurrence records as a response variable to build a model to predict areas of habitat suitability in the present, using package BIOMOD2 (Thuiller et al., 2020). As our data consisted only of presence records and we needed absence records, we generated pseudoabsence records (background) randomly sampled across the study area (VanDerWal et al., 2009). Next, we used ten algorithms to build the habitat suitability models. Because the number of pseudoabsences can significantly affect model accuracy depending on the algorithm (Barbet-Massin et al., 2012), we used ten thousand pseudoabsences for six algorithms (Generalized Linear Models - GLM, Generalized Additive Models - GAM, Artificial Neural Network - ANN, Surface Range Envelope - SRE, Functional Data Analysis - FDA, Multivariate Adaptive Regression Splines - MARS and Maximum Entropy - MAXENT.Phillips), and 130 pseudoabsences (= number of presences) for three algorithms (Random Forest - RF, Classification Tree Analysis - CTA, and Generalized Boosting Models - GBM).

We used 75% of the 130 occurrence records to build the models as a training data set and the remaining 25% as the test data set. We repeated this process ten times. To reduce the uncertainty associated with the choices made for each model (Buisson et al., 2010), we evaluated their quality using the following indexes: KAPPA, TSS, ROC, ACCURACY, BIAS (Allouche et al., 2006; Qiao et al., 2015). Next, we derived an ensemble of the model predictions with $TSS \geq 0.8$, weighing their contribution to the set according to the TSS value, using package BIOMOD2. Then, we calculated predictor importance with the *variables_importance* function of the same package to investigate which type of predictor (environmental or biological) had the most outstanding contribution to models. This function uses Pearson's correlation between reference predictions (i.e., with unchanged values) and the prediction with the investigated variable randomly permuted (Thuiller et al., 2020). Predictor importance is then estimated as 1 - Pearson's correlation, so the lower the correlation, the more significant the influence of the predictor. We repeated this randomization procedure ten times and averaged the importance values for each variable.

We combined the occurrence data of *Notomabuya frenata* and the model predictions to calculate an occurrence threshold using the Maximum Sensitivity plus Specificity (maxSSS) method (Liu et al., 2016). The threshold obtained was 0.51, so we considered the pixels with a habitat suitability value above that threshold as presences and those below it as absences. Then, we transformed the habitat suitability predictions into binary surfaces with packages BIOMOD2 and PRESENCEABSENCE (Freeman & Moisen, 2008). Finally, we calculated the pixel size and multiplied it by the number of presence pixels to obtain the total area of habitat suitability for the present, subtracting the deforested areas by 2010 (Broxton et al., 2014).

We did a gap analysis to assess the effectiveness of protected areas for *Notomabuya frenata*. So, we overlapped the habitat suitability raster and the polygons of the protected areas and then calculated the number of overlapping pixels with package EXACTEXTRACTR (Baston, 2021). Next, we calculated the pixel size and multiplied it by the number of pixels to calculate the amount (in km^2) and proportion (%) of suitability area that is under protected areas.

We used the ensemble model to project habitat suitability areas into the future using the same nine predictors we used to build the model. Then, we transformed all projections into binary geographic surfaces and calculated the total area of habitat suitability for the future, disregarding the expected deforestation (Li et al., 2017). For each period considered — 2041-2060, 2061-2080, and 2081-2100 — we subtracted the projected deforestation for 2050, 2070, and 2100, respectively. Regarding the emission of greenhouse gases, for the projections of habitat suitability in the SSP2-4.5 and SSP5-8.5 scenarios, we used the land use projections for B1 and A2, respectively, due to the greater similarity between them (van Vuuren & Carter, 2014). Finally, we calculated the difference between the current predicted area and future projections to assess gains and losses of habitat suitability for *Notomabuya frenata* due to climate change. We conducted all statistical analyses described above in the R environment (R Core Team, 2020).

3. Results

Regarding the preferred temperature and critical thermals of *Notomabuya frenata*, the average T_{pref} for all individuals was 33.53 ± 3.88 °C, the average CT_{min} was 14.04 ± 2.87 °C, and the average CT_{max} was 41.60 ± 3.37 °C. The preferred temperature range, i.e., the central 50% of all preferred temperature records (Hertz et al., 1993; Huey et al., 2009), was 28.89-37.40 °C. The median of preferred temperature records was 35.60 °C. The optimal temperature (T_{opt}), i.e., the best-performance body temperature, was 31.80 °C (Appendix S1). Regarding the sprint speed of the species, the maximum value was 20.23 cm/s.

Among the algorithms used to build the model, three had TSS values ≥ 0.8: RF, GBM, and GAM (Table 1). Therefore, we combined their predictions to estimate the current habitat suitability area for *Notomabuya frenata* and project it into the future. Isothermality (BIO3) made the most outstanding contribution to the model, followed by precipitation of the coldest quarter (BIO19) and hours of activity based on the minimum temperature of the coldest month (BIO6; Fig. 1; Appendix S14).

Excluding areas deforested between 2001 and 2010, we estimated the current suitable area at 3,686,948 km² (Fig. 2). However, our gap analysis showed that only 159,209.6 km^2 of this habitat suitability is within protected areas, which corresponds to only 4.32% of the total area (Fig. 2).

We obtained 48 projections for the future forecasts, 16 for each period (2041-2060, 2061-2080, and 2081-2100; Appendix S15-17). Although the results showed substantial variation due to the combination of SSPs, GCMs, years, and deforestation, habitat suitability in the future was smaller than the present in all projections, suggesting a negative effect of climate change on the species (Appendix S18).

The average contraction in suitable habitats on the SSP2-4.5 scenario and its deforestation projection, the average reduction was estimated at 38.16% for 2041-2060, 54.35% for 2061-2080, and 58.50% for 2081-2100. Based on the SSP5-8.5 scenario and its respective deforestation, the average reduction was estimated at 55.54% for 2041-2060, 79.94% for 2061-2080, and 89.66% for 2081-2100. Among the GCMs, the maximum reduction was projected with CanESM5 in the SSP5-8.5 scenario, with 86.33% for 2041-2060, 95.15% for 2061-2080, and 99.17% for 2081-2100.

As for the geographic location of suitable habitats for *Notomabuya frenata* in the future, its expansion was concentrated in small regions in northeastern Brazil and northern Argentina (Fig. 4). Contrarily, its contraction occurred in large areas of central Brazil, eastern Bolivia, and northern and western Paraguay.

4. Discussion

4.1. Contribution of predictor variables

The most important predictor of habitat suitability was isothermality (BIO 3), i.e., the ratio between the mean diurnal temperature range and the annual temperature range. The distribution of *Notomabuya frenata* is associated with areas of intermediate to high isothermality, mainly in the portion corresponding to the Cerrado biome. This greater thermal stability may be reflected in the high diversity of viviparous skinks in central Brazil, harboring at least four often sympatric species (Hedges & Conn, 2012). Although we have not tested these parameters, the importance of isothermality for *N. frenata* may be related to the influence of incubation temperature variability in increasing gestation duration and reducing offspring locomotor performance, as observed in other viviparous lizards (Ji et al., 2007; Ma et al., 2018). This finding suggests that the distribution of *N. frenata* is mainly limited by the thermal stability of the environment, which can influence thermoregulation behavior, life history patterns, and phenotypic plasticity (Clarke & Zani, 2012; Ma et al., 2018; Noble et al., 2018). This variable also has a dominant effect on the distribution of other tropical organisms, such as plants, mammals, and other lizards (Huang et al., 2021; Santos et al., 2014; Varela et al., 2009).

The precipitation of the coldest quarter (BIO19) was second in importance for predicting the habitat suitability for *Notomabuya frenata*. Its distribution is mainly concentrated in areas with low or no precipitation in winter, as in the Cerrado and northern Chaco (Appendix S14; Reboita et al., 2010). Thus, the range of this species seems to be strongly associated with regions of Aw climate in Köppen’s classification, characterized by a dry winter (Peel et al., 2007). In this scenario, viviparity can be advantageous to buffer environmental fluctuations, ensure good hydric conditions for embryonic development, and avoid eggs’ desiccation risk if they are deposited on dry soils (Shine & Brown, 2008). In addition, hatchlings usually occur between the end of the dry season and the beginning of the rainy season, coinciding with the increase in insect abundance in the Cerrado, which is the main component of the species' diet (Pinheiro et al., 2002; Vrcibradic & Rocha, 1998a, 1998b). Thus, the importance of precipitation in determining the distribution of *Notomabuya frenata* seems to be related to intrinsic traits that configure adaptive advantages to the seasonality of water and food. Previous studies also show precipitation as a determining predictor for the distribution of reptiles, including lizards that occur in Brazil (Bradie & Leung, 2017; Caetano et al., 2020; Winck et al., 2014).

Biological predictors also contributed to the species distribution model of *Notomabuya frenata*. Hours of activity based on the minimum temperature of the coldest month (BIO 6) was the third most relevant predictor (Fig. 1). This finding indicates that the limitation of their activity time due to climatic extremes is also a determining factor for their distribution. However, unlike other lizard species, the distribution of *N. frenata* appears to be limited mainly by lower temperatures, which reduce its activity (Appendix S14; Medina et al., 2016; Monasterio et al., 2013). As local adaptations can promote intraspecific variations in the thermal physiology of ectotherms, the biological predictors used in this work have the limitation of being based on only one site (Herrando-Perez et al., 2019; Pontes-da-Silva et al., 2018). This stems from the challenge of obtaining ecophysiological data for sufficient sites for comprehensive coverage due to wide distribution and time and resource constraints (Peterson et al., 2015; Urban et al., 2016).

Models based on environmental predictors deal with species realized niche, inferring the environmental requirements for their occurrence, and models based on biological predictors deal with species fundamental niche, modeling distribution based on knowledge of their physiology (Morin & Thuiller, 2009; Peterson et al., 2015). Thus, the use of hours of activity and thermal performance enables a more detailed identification of the processes that can limit species distributions because these variables are closely linked to vital organism processes, such as feeding, considering the foraging time; survival, through the escape of predators, and reproduction, through the meeting of partners (Irschick & Losos, 1998; Robson & Miles, 2000).

4.2. Protected areas

We estimated the current suitable area for *Notomabuya frenata* at 3,686,948 km², but only 4.32% of this total is within protected areas, which corresponds to 159,209.6 km^2. This finding indicates the low effectiveness of protected areas in conserving suitable habitats for this species, mainly because its main threats are deforestation for agriculture and pasture, in addition to mining, road construction, and fires (Ribeiro-Júnior & Amaral, 2017). This result can be more worrying given that all types of IUCN protected areas were considered; therefore, some of them allow different levels of human use (Dudley, 2008).

As there are few protected areas, several South American species have a very small portion of their distribution protected, such as Chaco reptiles in several countries (Bax & Francesconi, 2019), Paraguayan reptiles (Cacciali, Cabral, & Yanosky, 2015), lizards endemic to the Cerrado (de Novaes e Silva et al., 2014), and Amazonian lizards (Ribeiro-Júnior & Amaral, 2017), for example. Like us, Ribeiro-Júnior and Amaral (2017) observed a low proportion of the *Notomabuya frenata* distribution within protected areas, but specifically for the Brazilian Amazonia in their work. In addition, the authors highlighted that 52% of the area of occurrence of this species within Amazonia has been deforested, as it coincides with the “arc of deforestation” (Ribeiro-Júnior & Amaral, 2017).

4.3. Climate change and geographic distribution

Our models predicted an extensive contraction of suitable habitats in all scenarios, indicating that climate change will severely impair *Notomabuya frenata*. The most significant area reduction was predicted for the last two decades of the 21st century under the most pessimistic scenario of greenhouse gas emissions, when an average increase of 4 °C in the temperature of South America is estimated (Magrin et al., 2014). This result highlights the importance of mitigating these emissions to avoid drastic changes in the planet’s temperature and guarantee biodiversity’s future (Warren et al., 2013).

In this sense, our results add to other studies that project a contraction in the future geographic distribution of lizards from tropical regions (Berriozabal-Islas et al., 2018; Pontes-da-Silva et al., 2018), reinforcing the concept that species from lower latitudes have high vulnerability to climate change (Tewksbury et al., 2008). In addition, this study shows one more viviparous lizard that is potentially vulnerable to climate change, as has been discussed in other works (Jara et al., 2019).

The models identified changes in the geographic location of areas of suitable habitats for *Notomabuya frenata* in the future. A dominant pattern is a cumulative reduction in the suitable area with increased greenhouse gas emissions (Fig. 4). We found that areas of habitat suitability are restricted to southeastern and parts of southern and northeastern Brazil, coinciding with Atlantic Forest areas, which may be related to the moderated temperature in the microclimate due to the wetter climate and forest vegetation (Ewers & Banks-Leite, 2013). However, this is also the most degraded biome in Brazil, with about 12% of its original area remaining (Ribeiro et al., 2009), which reduces the buffering of the microclimate temperature (Ewers & Banks-Leite, 2013) and threatens the availability of areas for *N. frenata*.

4.4. Land-use changes

Changes in land use have intensified the effects of climate change on *Notomabuya frenata*, as its projections have further reduced the areas available for the survival and maintenance of this species in the future. This reinforces the threat of synergistic effects of climate and landscape changes on biodiversity (Sala et al., 2000; Travis, 2003). The four countries that make up the distribution of the species accounted for 80% of all deforestation in South America and the Caribbean between 2001 and 2010 (Aide et al., 2013). In the Chaco areas of northern Argentina, 1.4 million hectares were deforested between 1972 and 2007 (Gasparri & Grau, 2009). More than 50% of the Cerrado has been converted and fragmented to create farming areas (Klink & Machado, 2005; Sano et al., 2008). Thus, even if our models predict small expansions of habitat suitability areas for *N. frenata* in the future, the reach of these sites will be hampered not only by the limited capacity of the lizards to disperse but by the loss and fragmentation of habitats (Thomas et al., 2004).

4.5. Overview and recommendations

In summary, our work indicates that environmental variables had a more significant contribution to the distribution model of *Notomabuya frenata*. However, environmental and biological predictors proved to be essential in estimating the effect of climate change on habitat suitability for this lizard. The modeling approach we use is still scarce for species from the Neotropical region. In addition, temperature variability, precipitation during winter, and lower thermal extremes are among the main limitations for the distribution of this and other species. Moreover, we found low effectiveness of protected areas in conserving current suitable habitats for *N. frenata*. Finally, our findings indicate that climate change and its effects on biological parameters of the species may cause a drastic reduction in its potential range in the future, supporting the hypothesis of the high vulnerability of tropical and viviparous lizards to local extinctions. Considering projected deforestation for the future showed that the suitable habitats are much smaller than projected, indicating how the growing land-use change can exacerbate the threat of climate change to biodiversity. Our work suggests that even species that are currently widely distributed, such as *N. frenata*, may have their conservation compromised soon due to the low representativeness of their habitat suitability in protected areas combined with changes in climate and landscape. Therefore, we highlight the need for decision-makers to consider this and other works in creating protected areas and other conservation projects.

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Table 1. Quality of the algorithms for building the ensemble model considering five evaluation metrics.

Algorithm	Accuracy	BIAS	KAPPA	ROC	TSS
RF	0.92351	0.99628	0.84683	0.96614	0.84683
GBM	0.91751	0.99659	0.83487	0.96327	0.83487
GAM	0.98700	0.88518	0.36179	0.94180	0.82212
MARS	0.98745	0.90887	0.35430	0.94313	0.78697
MAXENT.Phillips	0.99290	0.99038	0.69088	0.89907	0.76401
CTA	0.86909	0.91824	0.73818	0.87893	0.73818
GLM	0.98723	0.71190	0.26180	0.90627	0.73554
ANN	0.98700	0.20593	0.19801	0.89671	0.73542
FDA	0.98829	0.97427	0.36526	0.92838	0.73490
SRE	0.98974	0.65031	0.58703	0.80912	0.61831

*The models that have been combined (TSS ≥ 0.8).

RF, Random Forest; GBM, Generalized Boosting Models; GAM, Generalized Additive Models; MARS, Multivariate Adaptive Regression Splines; MAXENT.Phillips, Maximum Entropy; CTA, Classification Tree Analysis; GLM, Generalized Linear Models; ANN, Artificial Neural Network; Functional Data Analysis – FDA; SRE, Surface Range Envelope.

Figures

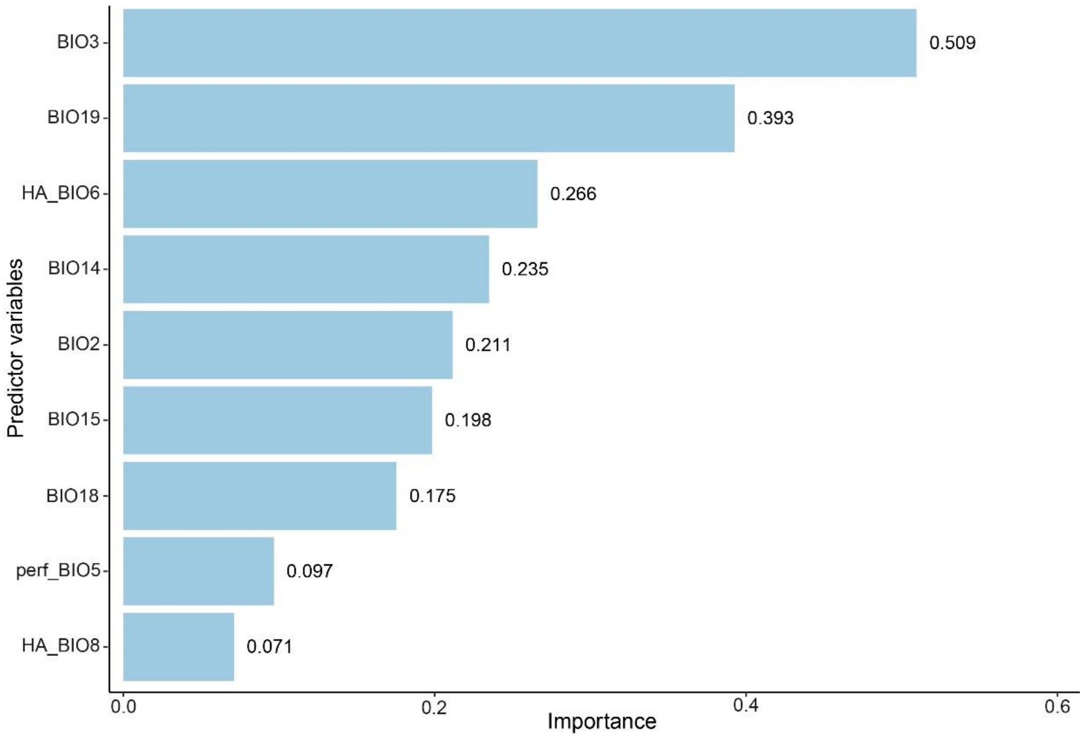

Figure 1. Importance of the predictor variables for the *Notomabuya frenata* distribution model. The numbers indicate the proportion of contribution, calculated by 1 - Pearson's correlation between reference prediction (i.e., with unchanged values) and the prediction with the investigated variable randomly permuted. In the figure, BIO3 = isothermality; BIO19 = precipitation of the coldest quarter; HA_BIO6 = species' hours of activity based on the minimum temperature of the coldest month; BIO14 = precipitation of the driest month; BIO2 = mean diurnal range; BIO15 = precipitation seasonality (coefficient of variation); BIO18 = precipitation of the warmest quarter; perf_BIO5 = thermal performance of the species based on the maximum temperature of the hottest month; HA_BIO8 = species' hours of activity based on the mean temperature of the wettest quarter.

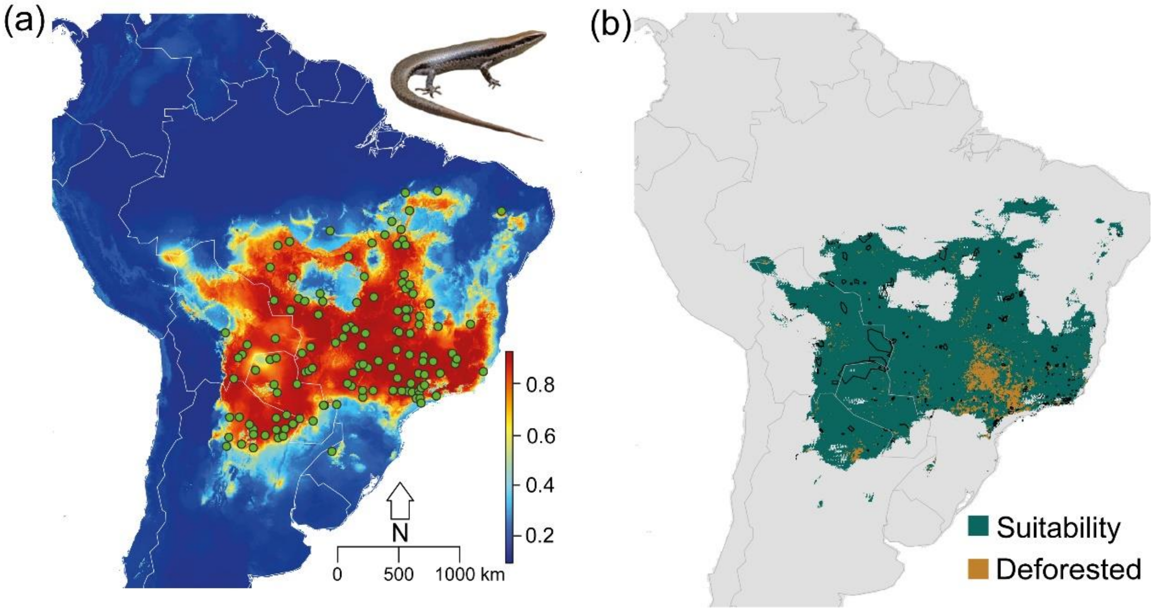

Figure 2. Predicted area of habitat suitability for *Notomabuya frenata* at present (3,686,948 km²). In (a), the closer to red, the greater the habitat suitability of the site for the species. The green points are the occurrence records of the species used in our analyses. In (b), the binary image is represented, where green indicates the area of habitat suitability for the species and brown represents the deforested area between 2001 and 2010. The black polygons represent the boundaries of protected areas.

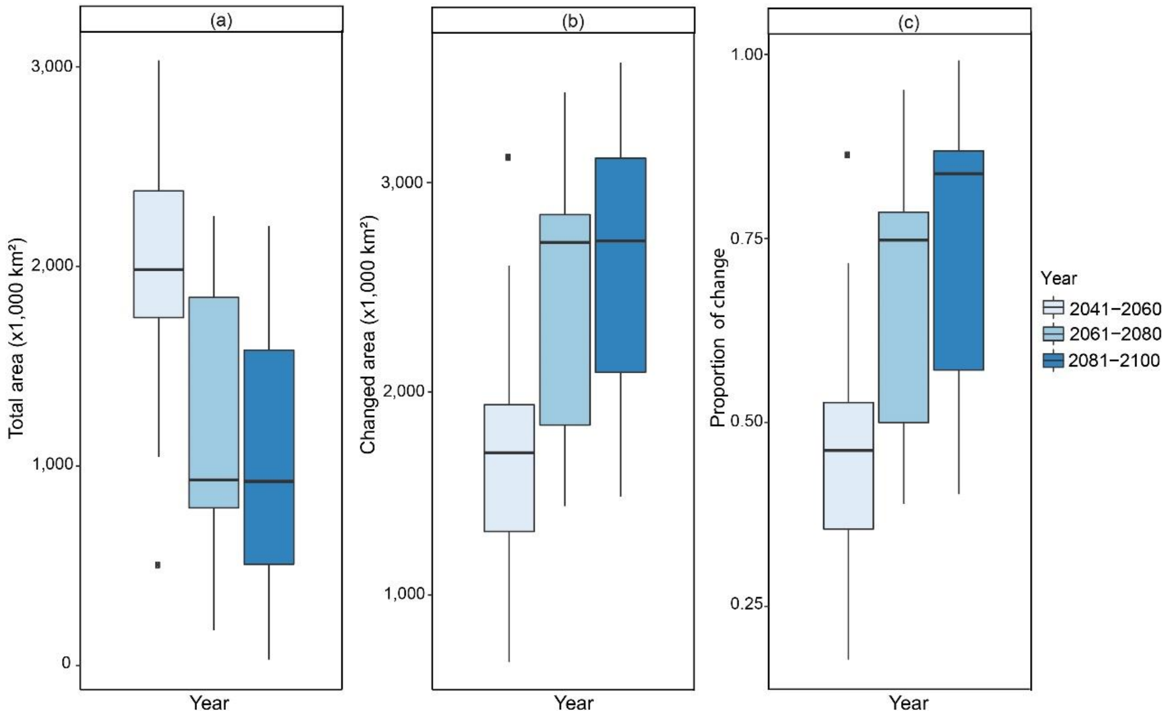

Figure 3. Area of habitat suitability for *Notomabuya frenata* projected for the years 2041-2060, 2061-2080, and 2081-2100, considering eight general circulation models (GCMs) and two shared socioeconomic pathways (SSP2-4.5 and SSP5-8.5). The values of the graph represent (a) total suitable area in the future, subtracting the projected deforestation for 2050, 2070, and 2100, respectively; (b) the changing suitable area (reduced in all cases) between current and future, subtracting current and projected deforestation, respectively, and (c) proportion of the change shown in (b).

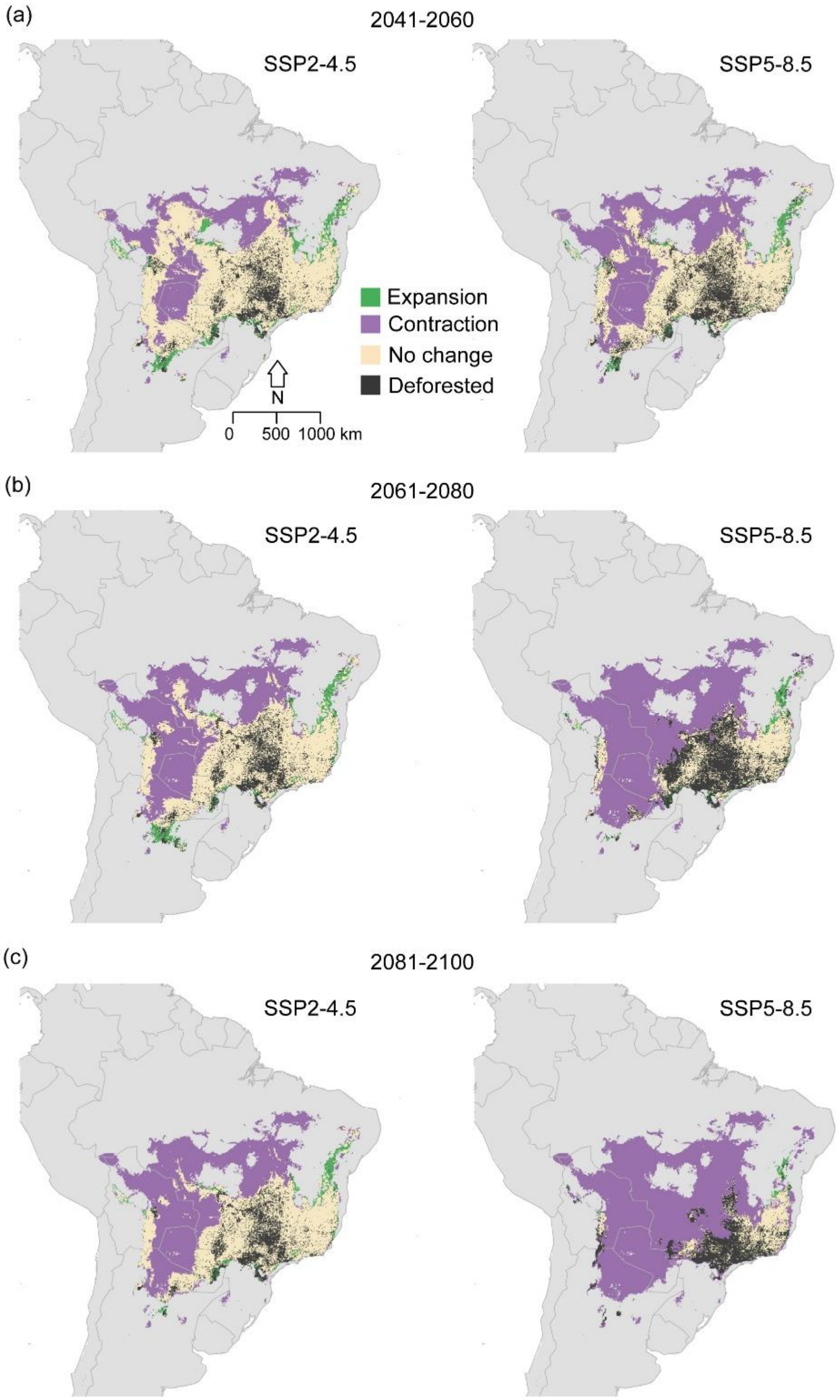

Figure 4. Geographic location of the average expansion (green) and contraction (purple) of the area of habitat suitability for *Notomabuya frenata* in (a) 2041-2060, (b) 2061-2080, and (c) 2081-2100. In the figure, the suitable habitats that was not altered between the current and the future is represented in beige, while the deforested area projected for 2050, 2070, and 2100 is represented in black.

Chapter 2. Long-term effects of different fire regimes on the demography of the lizard *Notomabuya frenata* (Squamata, Scincidae)

Abstract

Studies carried out on large temporal scales are essential to investigate the effect of environmental disturbances, such as fire, on the demographic aspects of species. We investigated the long-term effects of climate variation and different fire regimes on the population dynamics of *Notomabuya frenata*, a Neotropical viviparous lizard from the Cerrado of central Brazil. Over fifteen years, we carried out a mark-recapture study in five plots of cerrado *sensu stricto* submitted to different fire regimes. Then, we built Cormack-Jolly-Seber demographic models and implemented model selection with an information theory approach to investigate the effect of fire regimes and climate seasonality on survival and capture probabilities. The life cycle of *N. frenata* is longer than one year, with overlapping generations. Fire regimes had little influence on the age structure, which was mainly influenced by seasonality and insolation. However, intermediate to severe fire regimes impaired capture probabilities, which may result from indirect effects of fires on the vegetation structure. Precipitation positively influenced the survival and negatively the captures of this species, which may be related to increased food availability during the rainy season in the Cerrado, contributing to the survival of individuals and reducing the foraging distance. Thus, for population maintenance of this species, integrated fire management should preferably occur at the beginning of the dry season, when fire intensity is lower.

1. Introduction

Large-scale temporal or spatial studies represent a challenge for science. Among their main difficulties is the maintenance of the experiment's structure, the modification of the methodology throughout the study, the variation in the sampling frequency, and the demand for expensive financial and human resources (Driscoll et al., 2010; Magurran et al., 2010). However, they are of paramount importance in ecology because many complex processes can only be detected over large timescales (Lindenmayer et al., 2010; Hughes et al., 2017; Kuebbing et al., 2018). In addition, long-term monitoring is critical to investigate the effect of environmental disturbances on species' demographics, as these are highly variable over the years after habitat change (Driscoll et al., 2010; Haslem et al., 2011; Kuebbing et al., 2018). Thus, population studies generally require at least ten years to have consistent results and may take even longer if carried out in highly variable environments (Cusser et al., 2021).

The population dynamics of a species results from the balance between the entry and exit of individuals, i.e., birth, death, immigration, and emigration rates (Dunham et al., 1989; Begon et al., 1996). These demographic parameters, in turn, depend on factors such as foraging, mating, and avoiding predation (Dunham et al., 1989). These activities can be influenced by abiotic factors, such as climate, landscape, and disturbances since they alter the quantity and quality of the habitat and can restrict populations to intervals or refuges of environmental suitability (Dunham et al., 1989; Letnic et al., 2004; Brook et al., 2008). Thus, estimating the variation in demographic rates can indicate, more precisely, the mechanisms by which the viability of natural populations is affected by human pressures (Selwood et al., 2014).

Fire is an environmental disturbance that can significantly influence the demography of organisms (Lenic et al., 2004; Brook et al., 2008). It acts as a natural agent of disturbance in some ecosystems, such as savannas and grasslands (Bond & Keeley, 2005; Walter & Ribeiro, 2010; Pivello, 2011). Natural fires have a lower intensity and are mainly caused by lightning in the rainy season or in the transition between the dry and the rainy season, which characterizes the highly seasonal climate of the savannas (Ramos-Neto and Pivello, 2000; Peel et al., 2007; Silva et al., 2008; Pivello, 2011). Thus, natural fires maintain a vegetation mosaic in savannas (Moreira, 2000; Mystri et al., 2010; Walter & Ribeiro, 2010; Pivello, 2011).

However, due to increasing human occupation, most current fires result from anthropic actions, characterized by greater extensions and higher intensities (Ramos-Neto & Pivello, 2000; Pivello, 2011). One strategy for preventing such disastrous fires and maintaining desirable fire regimes is an integrated fire management (IFM) approach. Rural and indigenous communities originally used the fires to protect housing areas, stimulate plant regrowth or flowering, increase the supply of nutrients in the soil, and clean areas for planting, among others (Pivelo, 2011; Schmidt et al. al., 2016). Currently, much attention has been invested in IFM, which considers ecological, cultural, and political aspects in prescribing fires as a means of protecting fauna and flora (Coutinho, 2000; Myers, 2006; Miranda et al., 2002; Dias & Miranda, 2010; Schmidt et al., 2016).

As a natural agent of environmental disturbance, fire has acted as a selective pressure for thousands of years (Miranda et al., 2002; Bond & Keeley, 2005). In this sense, several organisms have an evolutionary history closely related to fires in savanna environments, influencing ecological aspects, such as habitat use, reproductive rate, survival, and dispersal capacity (Roberts, 2000; Miranda et al., 2002). The response of lizard populations to fire can vary over time and between species (Driscoll & Henderson, 2008). For those species harmed by fire suppression, IFM benefits their population parameters (Greenberg et al., 1994; Brisson et al., 2013; Scroggie et al., 2019). Despite suffering little or no direct effects from fires, other species suffer long-term indirect consequences, such as changes in microclimate, vegetation cover, and resource availability (Costa et al., 2013, 2020; Sousa et al., 2015). This diversity of lizard responses highlights the importance of carrying out studies on the populations of many species so that strategic IFM can be carried out (Driscoll & Henderson, 2008; Driscoll et al., 2010).

Here we investigate the long-term effects of different fire regimes and climate variation on the population dynamics of the lizard *Notomabuya frenata* (Cope 1862) in the Cerrado of central Brazil. This skink is viviparous, has a long gestation period (about nine months), and produces only one litter each year (Vitt, 1991; Vrcibradic & Rocha, 1998b). Studies that provide demographic information on viviparous reptiles are relevant, as viviparity in Squamata has a complex evolutionary history, occurring in about 20% of species but having independently evolved more than 100 times in the group (Blackburn, 1985, 2014; Wright et al., 2015). *Notomabuya frenata* ranges in four countries in South America, occurring mainly in the Cerrado, Chaco, and Atlantic Forest (Álvarez et al., 2009; Dirksen & Riva, 1999; Pinto et al., 2017). Except for the last biome, the species occurs mainly in environments with highly seasonal precipitation, characterized by cold, dry winters and hot, humid summers (Reboita et al., 2010).

Taking into account the life habits of the species and its evolutionary history linked to fire-prone environments and strongly seasonal climates, we investigate two hypotheses: (1) Considering that the abundance of *Notomabuya frenata* increases after the fire but peaks at intermediate fire regimes (Costa et al., 2013, 2020), environments with extreme fire regimes (intense fire and no fire) should reduce the survival and capture of the species; (2) Considering the importance of precipitation on the population dynamics of organisms, as well as the effect of humidity on the composition of Cerrado lizard assemblages (Brown & Shine, 2006; Ogutu et al., 2008; Altwegg & Anderson, 2009; Costa et al., 2020), the survival and capture of *N. frenata* should be influenced by seasonal precipitation.

2. Material and methods

2.1. Study area and data collection

We conducted the study in an area of cerrado *sensu stricto* at Reserva Ecológica do IBGE (15°56'41" S, 47°53'07" W), Distrito Federal, Brazil (Ribeiro, 2011). The area was protected from fires between 1971 and 1988 (17 years) when a prescribed burning study started. In this study, carried out between 1988 and 2008, five 200 x 500 m plots were established in the cerrado *sensu stricto* physiognomy (Fig. 1), each submitted to a specific fire regime (Dias & Miranda, 2010). Fire severity increased along the following sequence: no burning (Control), burning every four years in the mid-dry season (Quadrennial), burning every two years at the beginning of the dry season (Early Biennial), burning every two years in the mid dry season (Middle Biennial), and burning every two years at the end of the dry season (Late Bienal). Apart from the Control plot, all others were adjacent, separated by 5 m wide dirt roads. In 2011, an unplanned fire partially burned the Late Biennial and wholly burned the Control plot. As the plots had the same vegetation and shared the same burning history before the onset of the experiment, we assumed that the differences between them over time resulted from the different prescribed fire regimes. Importantly, our study could not be replicated due to the costs of replicating large-scale ecological studies and the legal issues associated with burning vegetation in protected areas (Carpenter, 1990; Oksanen, 2001). Long-term experiments, such as ours, are scarce and play a key role in ensuring the availability of adequate treatment levels (Driscoll et al., 2010).

Since December 2005, we have been monitoring the population of *Notomabuya frenata* in the study area using 50 pitfall traps, which we opened and checked monthly for six consecutive days. For each captured individual, we measured the snout-vent length (SVL) with a ruler (nearest 1mm) and the mass with a spring scale (Pesola Micro Line spring scale to the nearest 0.1 g). We sexed lizards through hemipenis eversion (males) and palpation of the abdomen to assess the presence of enlarged vitellogenic follicles or oviductal eggs (gravid females). We considered as juveniles those small-sized individuals that we could not sex at capture or in subsequent recaptures. Next, we uniquely marked each lizard by toe-clipping (no more than two per member) and released them close to the point of capture. Toe-clipping meets legal and ethical expectations and does not impair skinks' survival or capture probabilities (Jones & Bell, 2010; Perry et al., 2011; Hoehn et al., 2015). Through this identification, we could record subsequent recapture events and the variation of SVL over time.

To assess the sexual maturity of individuals in the evaluation of the population age structure, we obtained data from 30 gravid females (SVL and number of embryos) and 83 males (SVL and testes volume) of *Notomabuya frenata* collected during the filling of the Serra da Mesa reservoir, Minaçu, Goiás (13°50’00” S, 48°23’00” W), ca. 460 km from Reserva Ecológica do IBGE. The specimens are deposited in the Coleção Herpetológica da UnB (CHUNB). We considered the SVL of the smallest gravid female or the smallest male with enlarged testes and convoluted epididymis as the size at sexual maturity for each sex.

2.2. Data analysis

We conducted all analyses described below on the R platform (R Core Team, 2022).

2.2.1. Population monitoring

Initially, we screened demographic data to identify potential errors and outliers, which were later corrected. This step was necessary given the dataset’s large size and the study’s long duration. We removed inconsistent records from the sample set for which there was no solution, as they represented a minimal part of the total (79 records, representing 7% of the total dataset). The inconsistencies included the absence of all body measurements (i.e., SVL, mass, and tail length), smaller size at recapture compared to the previous capture, and a very long time between captures (> 3 years). For missing or outlying (probability less than 0,01% of occurring by chance) SVL records, we imputed values considering body mass, sex, and length of the intact tail as predictors, using the MISSFOREST package (Stekhoven & Bühlmann, 2012).

To investigate the variation in the number of captures and recaptures of individuals between the study plots, we used sequential chi-square tests, removing plots with higher chi-square residues until the difference between them was non-significant (Zar, 2010). To verify whether there was a difference in the mean values of SVL between plots over time, we tested whether the data followed a normal distribution and whether their variances were homoscedastic. As the first assumption was not met, we used the non-parametric Kruskal-Wallis test (McKight & Najab, 2010).

2.2.2. *Age structure*

To identify seasonal patterns and trends in the age structure of the *Notomabuya frenata* population, we transformed the monthly averages of SVL into time series. As time series analysis does not allow for missing data, and we had no captures in some months and plots, we used multiple imputations (Rubin, 1996; Zhang, 2003) to replace missing data and estimate statistical parameters with the AMELIA II package (Honaker et al., 2012). To improve the prediction of imputations (Honaker et al., 2012), we included monthly averages of precipitation, relative humidity, insolation, and maximum air temperature as covariates. We obtained these climate variables from the Instituto Nacional de Meteorologia (INMET) at the Brasília meteorological station (83377), which is close to the study area (approximately 19 km). For the selection of variables, we eliminated highly collinear ones (VIF > 10), based on the variance inflation factor (VIF), using the USDM package (Naimi, 2015). We have decomposed the time series into seasonal, trend, and residual components (Cowpertwait & Metcalfe, 2009).

Additionally, we evaluated the influence of selected climate variables on the monthly averages of SVL. To account for the effect of seasonality, which generates autocorrelation between data closer in time, we created cyclic patterns of sine and cosine waves over months and years (Crawley, 2013). We included these patterns in linear mixed-effects models relating monthly averages of SVL to climate variables using the LME4 package (Bates et al., 2015). We used the year as a random factor in the models to account for the temporal pseudo-replication resulting from repeated sampling of plots throughout the study (Crawley, 2013). We used an information theory approach to perform model selection (Burnham & Anderson, 2002) based on the Akaike information criterion corrected for reduced sample sizes (AIC_c) with the MUMIN package (Bartón, 2022). We exhaustively evaluated all possible models to assess predictor importance, determined as the sum of the Akaike weights for all models containing the predictor, retaining those with $\Delta AIC_c \leq 2$ (Burnham & Anderson, 2002).

2.2.3. *Demographic model*

We use the capture history of *Notomabuya frenata* from December 2005 to December 2020 to build Cormack-Jolly-Seber demographic models fitted with maximum likelihood estimation using the MARKED package (Laake et al., 2013). To investigate the effect of fire regimes and precipitation seasonality on the population parameters of the species, we considered plots and precipitation as covariates of survival (ϕ) and capture (p) probabilities. In the analysis, the plot was considered fixed for each individual since there were no recaptures in different plots, while the precipitation varied over the study period. From there, we created models with all combinations of these parameters and performed model selection based on the Akaike information criterion (AIC). Because of the uncertainty associated with choosing only one model, we retained all models in which $\Delta\text{AIC} \leq 4$ (Burnham & Anderson, 2002).

3. Results

From December 2005 to December 2020 (15 years), we obtained a total of 1194 occurrences of *Notomabuya frenata*, with 1018 capture events and 176 recapture events, resulting in an average of 0.147 recaptures per individual. Among the 1018 individuals sampled, 86.15% (n = 877) were captured only once, 11.19% (n = 114) were captured twice, 1.87% (n = 19) were captured three times, and only 0.79% (n = 8) had four captures. The frequency of captures and recaptures was significantly lower in the Late and Middle Biennial plots (Fig. 2; LB: captures: $\chi^2_4 = -7.798$, $P < 0.001$; recaptures: $\chi^2_4 = -4.090$, $P < 0.001$; MB: $\chi^2_3 = -7.010$, $P < 0.001$; recaptures: $\chi^2_3 = -3.125$, $P < 0.001$).

Overall, we captured more adults at the beginning and juveniles at the end of each year; however, generation overlap was extensive (Fig. 3). Recruitment peaked from September to December, during the transition between the dry and rainy seasons (Fig. 4). The seasonal and trend components of the SVL time-series were minor, while the residual (stochastic) component was more pronounced (Fig. 5). There was no difference in SVL between plots ($\chi^2_4 = 4.891$, $P = 0.299$; Fig. 6), indicating that fire regimes had little effect on the population's age structure. Model selection retained seven models with $\Delta\text{AIC} \leq 2$ relating climatic variables to monthly averages of SVL (Table 1). Among these models, seasonality (cosine wave) and insolation were the most important predictors of SVL.

The selection of demographic models relating survival (ϕ) and capture (p) probabilities to fire regime and precipitation seasonality returned five models with $\Delta\text{AIC} \leq 4$ (Table 2). The best model had precipitation as a covariate of both ϕ and p. Moreover, precipitation influenced p in all retained models and ϕ in three models. While it influenced p negatively, its effect on ϕ was positive (Figure 7; Table 3). The fire regime influenced p in two models and ϕ in one model. Both demographic parameters were higher in the Control and Early Biennial plots (Table 3). Two models showed constant survival probability.

4. Discussion

According to our results, the absence of burning increased the frequency of captures and recaptures of *Notomabuya frenata* in the study area. However, fire regimes did not represent a determining factor in the age structure of this population, which was mainly influenced by seasonality and insolation. Our demographic models indicated that survival and capture probabilities are influenced by fire regimes and, mainly, by precipitation.

4.1. Life cycle and age structure

The life cycle of *Notomabuya frenata* was longer than one year, and there was an overlap of generations, which may reflect the long gestation period of the species, which lasts on average nine months (Vrcibradic & Rocha, 1998b). The population's age structure was negatively influenced by seasonality but positively by insolation. Thus, the greater the insolation, the greater the body size, which may result from increased opportunities for effective thermoregulation influencing population parameters, such as growth, survival, age structure, and female reproductive (Marquis et al., 2008; Hare & Cree, 2010; Sousa et al., 2015). Insolation also proved to be one of the most important climatic variables for the body size of *Micrablepharus atticolus,* a lizard endemic to the Cerrado (Sousa et al., 2015).

Fire regimes had little influence on the age structure of *Notomabuya frenata*. This finding may be related to the fact that this is a generalist species in terms of habitat use and diet (Vrcibradic & Rocha, 1998a; Costa et al., 2013). In this sense, the ability to explore different types of shelters, such as termite nests, rock crevices, and holes in the ground or logs, can contribute to fire survival (Driscoll & Henderson, 2008; Costa et al., 2013). In the Cerrado, the temperature below ground suffers slight thermal variation during wildfires; therefore, burrows are an important refuge for lizards (Miranda et al., 1993; Frizzo et al., 2011). In addition, the variety of arthropods that make up the diet of *N. frenata* contributes to the nutrition and growth of individuals, although the availability of resources varies throughout the post-fire stages (Pianka, 1996; Driscoll & Henderson, 2008).

4.2. Fire's effect on demography

Fire regimes affected the survival and, mainly, the capture probabilities of *Notomabuya frenata*. Capture probabilities were higher in plots with less severe fire regimes (Control and Early Biennial). Conversely, capture probabilities were lower in plots under more severe fire regimes (Late Biennial and Middle Biennial). Thus, our hypothesis that extreme fire regimes affect the demographic parameters of *N. frenata* was partially supported because intense fire regimes harmed the species' demography, but the absence of fires favored it. These results indicate that this lizard can be affected by direct or indirect consequences of fire. Considering that vertebrates are rarely affected by direct effects of fire, such as burns and deaths, and that the short-term effect on *N. frenata* is a reduction in its activity, it is unlikely that this species will be affected by direct effects of fire (Lyon et al., 1978; Frizzo et al., 2011; Costa et al., 2013). This immobility behavior is known from other skinks, and, despite decreasing the chances of capture, it can contribute to the survival of individuals by reducing the risks related to the fire itself and increased post-fire predation (Fenner & Bull, 2007; Costa et al., 2013).

The main effects of wildfires on vertebrates are the indirect consequences of changed habitat structure (Lyon et al., 1978; Lindenmayer et al., 2008; Frizzo et al., 2011; Costa et al., 2013). The reduction in leaf litter and tree cover and greater exposure and darkening of the ground can alter temperature and humidity in microhabitats, impairing activity patterns (Lyon et al., 1978; Costa et al., 2020). In this sense, increased vegetation covers due to less intense fire regimes reduces the consequences on the microclimate, allowing individuals to remain more active, foraging in a greater variety of microhabitats (Costa et al., 2020). In addition, greater plant complexity reduces the risk of predation, preventing them from having to remain in refuges, migrate or forage in distant locations, increasing their likelihood of recapture (Verdolin, 2006; Shepard, 2007; Leahy et al., 2015).

4.3. Precipitation's effect on demography

Our results supported our hypothesis that precipitation affects the demography of *Notomabuya frenata*. Regarding species survival probability, it was positively influenced by precipitation. This favoring may be related to the expansion of insect abundance during the rainy season in the Cerrado, which provides an abundant supply and availability of food for adults and young of this species (Vrcibradic & Rocha, 1998a, 1998b; Pinheiro et al., 2002). This nutritional expansion of adults is relevant to ensuring investment in reproduction, given that precipitation is a crucial factor for this parameter in reptiles (Colli, 1991; Rocha, 1992;

Mesquita & Colli, 2003; Marquis et al., 2008). In the case of this genus of lizard, nutrition through the placenta accounts for almost the entire mass of the young (Blackburn & Vitt, 1992; Ramírez-Pinilla, 2014). Thus, the feeding of females is essential for the nutrition of embryos throughout the gestational period and also for the accumulation of energy in fat bodies, which are mobilized for the offspring mainly in the last months of gestation, when there is a rapid embryonic growth (Vitt & Blackburn, 1983; Blackburn & Vitt, 1992; Vrcibradic & Rocha, 1998b; Ramírez-Pinilla, 2014). Additionally, precipitation also contributes after the birth of the young, which occurs in the months of the beginning of the rainy season, so the greater availability of food in this period contributes to their nutrition and growth, which may favor their survival (Vrcibradic & Rocha, 1998b). In addition, precipitation prevents dehydration, which could impair lizard growth and activity patterns (Lorenzon et al., 1999).

In contrast, precipitation negatively affected the probability of capture of *Notomabuya frenata*. This result may also reflect the greater abundance of food during the rainy season in the Cerrado, as it reduces the species' home range, as the foraging distance required to obtain nutrition is shorter (Simon, 1975; Stehle et al., 2017). In addition, diurnal and heliothermic reptiles, such as *N. frenata*, rely heavily on solar energy to warm up, and their capture rate is impaired with increased precipitation (Vrcibradic & Rocha, 1998a; Spence-Bailey et al., 2010). This pattern, in turn, can affect their demography, as evidenced by the positive relationship between insolation and growth of *N. frenata*. Thus, cloud cover during the rainy season can impair the lizards' opportunity for thermoregulation, consequently reducing their activity and likelihood of recapture (Vitt et al., 1997; Hare & Cree, 2010).

5. Conclusion

Knowledge of the effects of fires upon animal populations is critical to effective conservation planning and managing ecosystems adapted to fire. Considering that intermediate to intense fire regimes impair demographic parameters of *Notomabuya frenata*, efforts to reduce the intensity of fires can contribute to the survival and, mainly, to the activity of this species. In addition, macroclimatic variables, such as insolation and precipitation, were closely linked to the demography of this lizard, which may be related to the fact that it is a heliothermic and viviparous species. Thus, understanding how climatic seasonality modulates species' life histories is essential for IFM. Thus, as fire is a disturbance closely related to the evolutionary history of the Cerrado, we emphasize the importance of its management through appropriate temporal and spatial scales, occurring preferably at the beginning of the dry season, when the fire intensity is lower due to the lower amount of organic matter that serves as fuel.

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Table 1. Akaike information criterion adjusted for small samples (AIC_c), coefficients and relative importance of the predictors (Imp.) of seven linear models with $\Delta AIC_c \leq 2$. The models relate monthly means of snout-vent length of *Notomabuya frenata* to variables from December 2005 to December 2020 at Reserva Ecológica do IBGE, Brasília, Brazil.

Parameter	**Model 1**	**Model 2**	**Model 3**	**Model 4**	**Model 5**	**Model 6**	**Model 7**	**Imp.**
AIC_c	1122.12	1122.43	1123.53	1123.74	1123.92	1123.92	1124.05	-
Intercept	63.59	51.99	53.60	77.72	63.25	63.40	65.39	-
Cosine wave	-3.41	-4.10	-4.34	-4.30	-3.63	-4.82	-3.35	1.0
Insolation	0.03	0.03	0.02		0.03		0.03	0.79
Max. temperature	-0.47			-0.47	-0.42		0.48	0.56
Sine wave			-0.78		-0.47			0.23
Humidity				-0.12		0.09		0.21
Precipitation							-0.10	0.10

Table 2. Selection of Cormack–Jolly–Seber demographic models for the lizard *Notomabuya frenata* between 2005 and 2020, in control and treatment plots with different burn severities, in an area of cerrado *sensu stricto* at Reserva Ecológica do IBGE, Brasília, Brazil. Only the best models (ΔAIC < 4) are presented, where: Φ = survival probability; p = capture probability; prec = precipitation.

Model	**AIC**	**ΔAIC**	**wAIC**
Φ(~ prec) p(~ prec)	2,005.56	0	0.329
Φ(~ prec) p(~ plot + prec)	2,006.45	0.89	0.210
Φ(~ 1) p(~ prec)	2,006.80	1.24	0.177
Φ(~ 1) p(~ plot+ prec)	2,007.65	2.09	0.116
Φ(~ plot+ prec) p(~ prec)	2,008.24	2.68	0.086

Table 3. Demographic analysis of the lizard *Notomabuya frenata* between 2005 and 2020, in control and treatment plots with different burn severities, in an area of cerrado *sensu stricto* at Reserva Ecológica do IBGE, Brasília, Brazil. The values represent estimates of demographic parameters and coefficients of the covariates of the second-best Cormack-Jolly-Seber model selected: *Φ(~ precipitation) p(~ plot+ precipitation)*. Coefficients (β) *Φ*: survival probability; *p*: capture probability.

	Parameter	Estimation	β (± sd)
Φ			
	Intercept	0.862	1.836 ± 0.238
	Precipitation	0.501	0.004 ± 0.003
p			
	Intercept (Middle Biennial)	0.026	-3.638 ± 0.259
	Early Biennial	0.529	0.119 ± 0.281
	Late Biennial	0.325	-0.729 ± 0.439
	Control	0.513	0.053 ± 0.277
	Quadrennial	0.437	-0.255 ± 0.302
	Precipitation	0.499	-0.002 ± 0.001

Figures

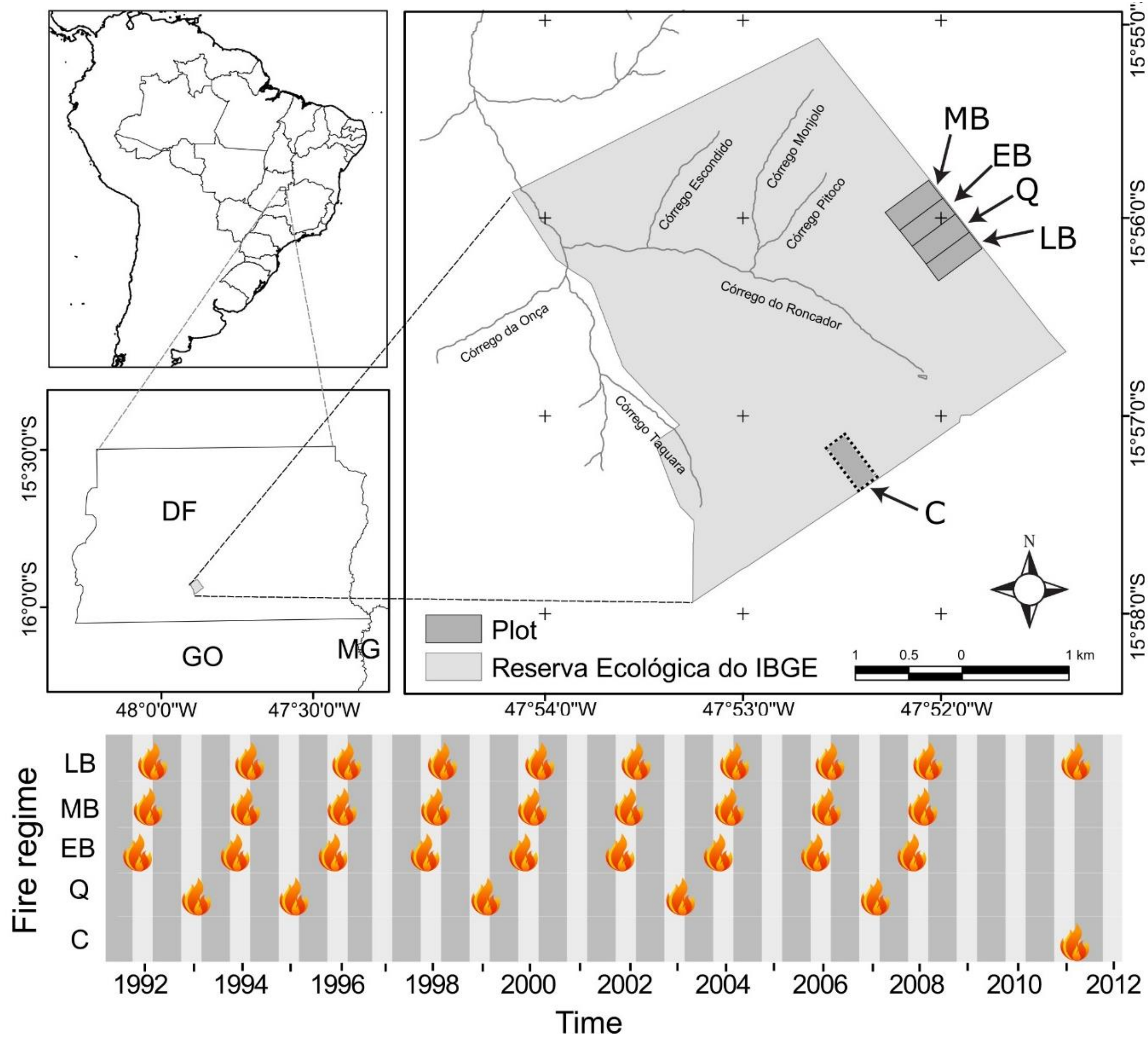

Figure 1. Study area at Reserva Ecológica do IBGE, Brasília, Brazil. Map with location of the studied plots: late biennial (LB), middle biennial (MB), early biennial (EB), and quadrennial (Q) burns and the control without fire until 2011 (C). Adapted by: Sousa et al. (2015).

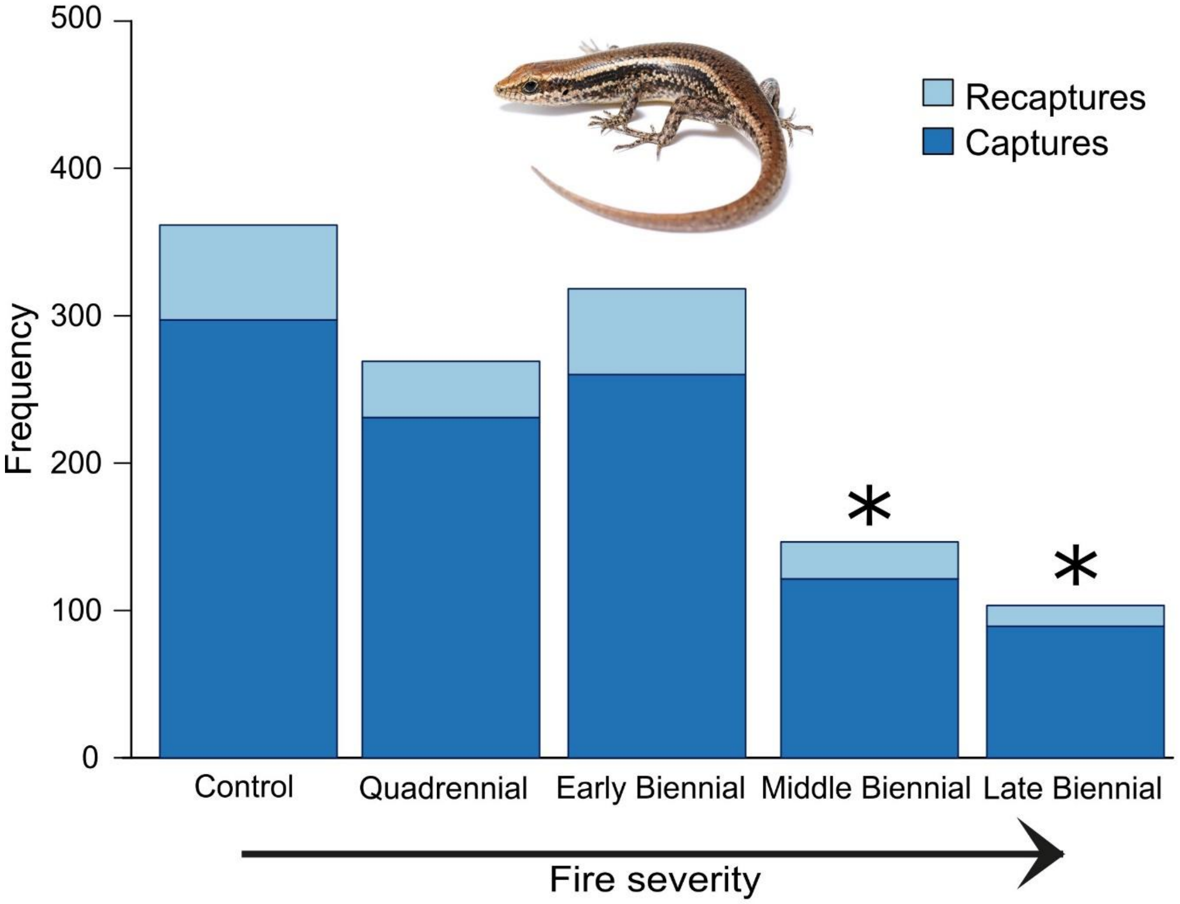

Figure 2. Captures and recaptures of *Notomabuya frenata* in control and treatment plots with different burn severities, in an area of cerrado *sensu stricto* in central Brazil. The asterisk indicates the plot where captures and recaptures differed significantly (P < 0.001) from the rest. Species photo by: Luis Felipe Carvalho de Lima.

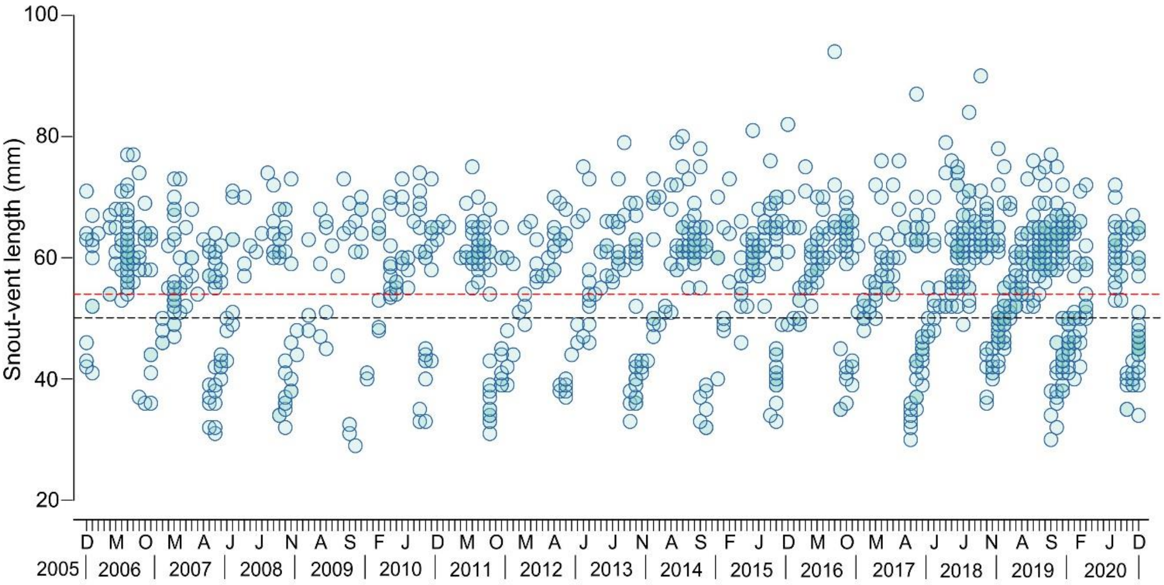

Figure 3. Snout-vent length (SVL) of *Notomabuya frenata* captured from 2005 to 2020, in control and treatment plots with different burn severities, in a cerrado *sensu stricto* area in central Brazil. The dashed lines indicate the SVL at sexual maturity for females (SVL = 54 mm; red) and males (SVL = 49 mm; black), that is, the SVL value of the smallest gravid female or the smallest male with enlarged testes and convoluted epididymis.

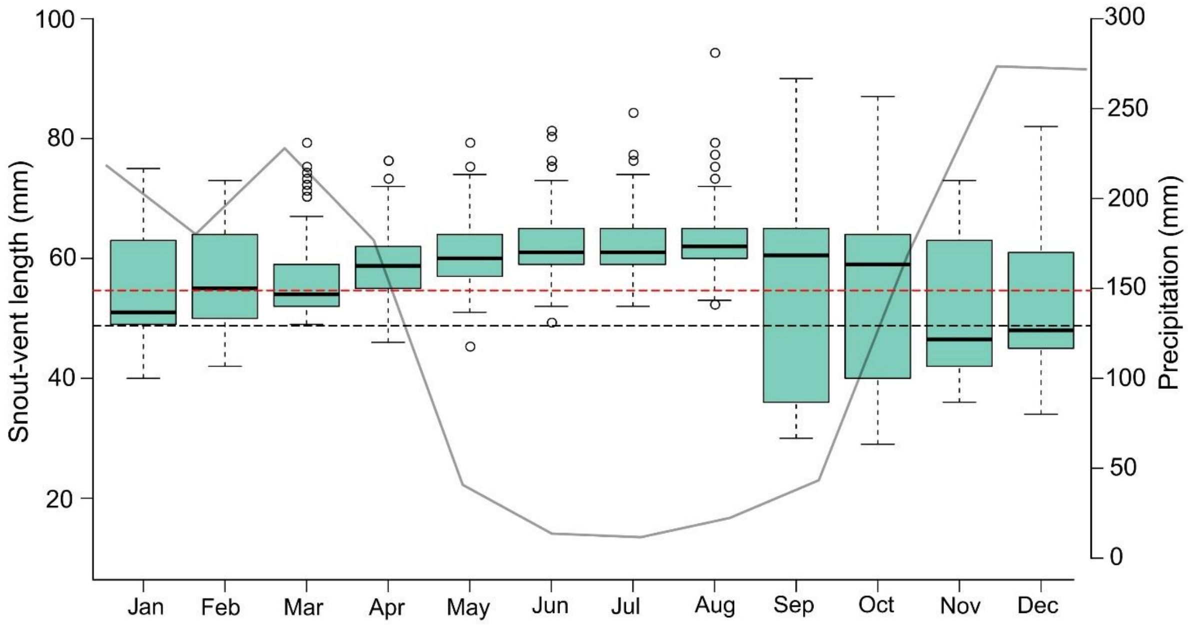

Figure 4. Monthly snout-vent length (SVL) of *Notomabuya frenata* between 2005 and 2020, in control and treatment plots with different burn severities, in a cerrado *sensu stricto* area in central Brazil. The solid gray line represents the average monthly precipitation in that period. The dashed lines indicate the SVL at sexual maturity for females (SVL = 54 mm; red) and males (SVL = 49 mm; black), that is, the SVL value of the smallest gravid female or the smallest male with enlarged testes and convoluted epididymis.

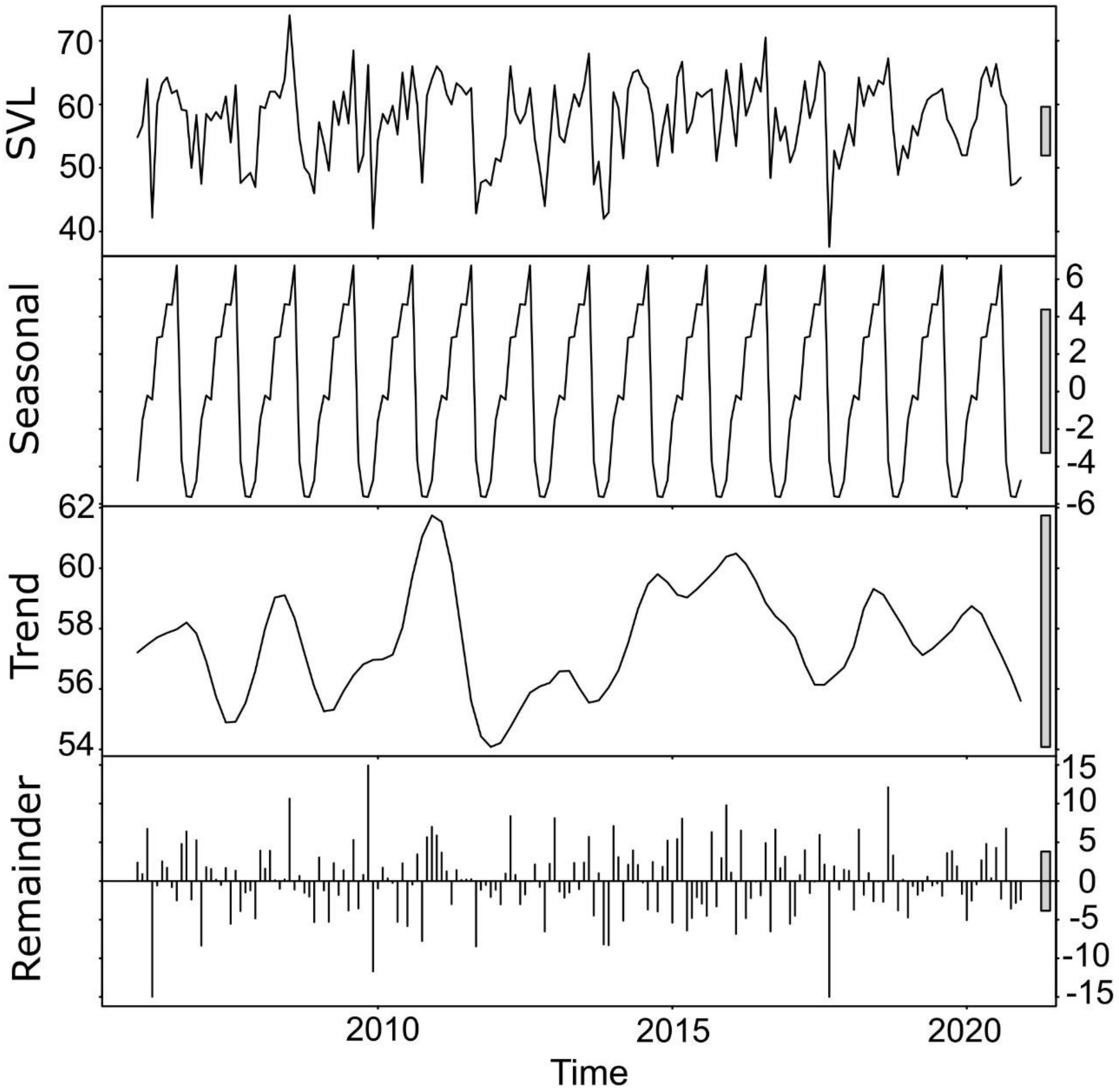

Figure 5. Decomposition of the snout-vent length (SVL) time series of *Notomabuya frenata* between 2005 and 2020, in control and treatment plots with different burn severities, in an area of cerrado *sensu stricto* in central Brazil. The bars on the right side indicate the variation attributed to each component, having the SVL data bar as the unit of measurement (upper graph). The more similar the bar size of the SVL data is, the greater the variation that the component explains.

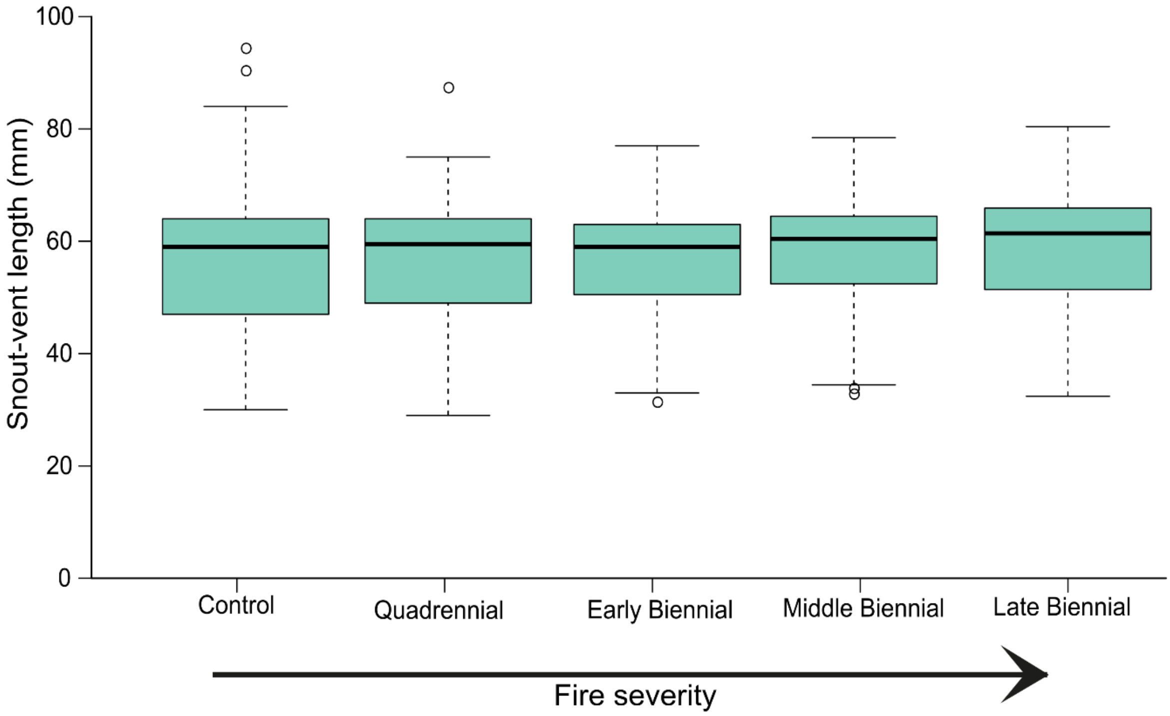

Figure 6. Variation of snout-vent length (SVL) of *Notomabuya frenata* in control and treatment plots with different burn severities, in an area of cerrado *sensu stricto* in central Brazil.

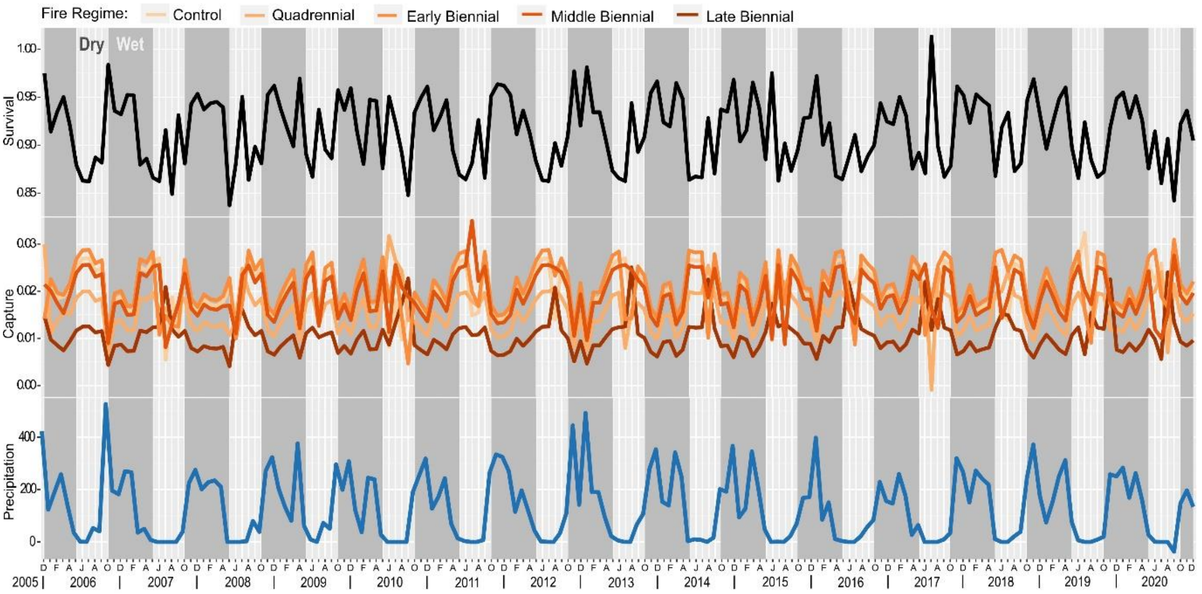

Figure 7. Estimates of apparent survival and capture probability of *Notomabuya frenata* in control and treatment plots with different burn severities, in an area of cerrado *sensu stricto* in central Brazil, from 2005 to 2020. The blue line indicates the monthly variation of the precipitation.