Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia

Aspectos da Ecologia Térmica de um Lagarto Neotropical

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Tese apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Ciências Biológicas da Universidade de Brasília, como requisito para a obtenção do título de Doutora em Ecologia

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“It's only in the mysterious equation of love that any logical reasons can be found.”

John Nesh

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Há seis anos, quando me deparei com a prova de seleção para o doutorado, eu estava no início de um ciclo que misturava expectativas acadêmicas com a incrível experiência de ter um bebê (eu não fazia idéia de onde estava me metendo). Ao olhar para trás, percebo como esse caminho foi permeado por desafios que, por vezes, pareciam intransponíveis e um questionamento surgiu em minha mente: "Será que vou dar conta?" e assim persistiu em todas as etapas do doutorado, nas disciplinas, nos trabalhos de campo e laboratório, no exame de qualificação durante a pandemia, quando meu prazo regular terminou e eu fiquei sem a bolsa, e ainda hoje esse pensamento paira em minha mente. Agora ele já não me amedronta mais, pois estou em paz com tudo o que consegui fazer até aqui, que vai muito além desta tese. Ver minha filha com cinco anos, feliz, confiante, construindo bases sólidas para se tornar uma pessoa segura e com senso crítico me traz uma satisfação que eu nem consigo mensurar. Mas, isso tudo que está acontecendo agora só foi possível porque muitas mãos amigas me ajudaram a transpor esse abismo que separava o sonho da realidade e é com o coração cheio de esperança e carinho que que quero agradecer:

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Ah sobre aquela pergunta, a resposta é não, não dei conta, nós demos!

Introdução Geral

Atividades humanas estão impactando negativamente o clima, causando um aumento da temperatura média do planeta e afetando diretamente diversos grupos de organismos, inclusive podendo conduzir certas espécies à extinção (Gunderson and Stillman, 2015). A temperatura tem um impacto direto e abrangente na aptidão dos ectotérmicos, influenciando a reprodução (razão sexual, número de ovos, viabilidade da prole), defesa do território, termorregulação e evasão de predadores (Herrel et al., 2007; Huey, 1982; Sannolo et al., 2019). Quando expostos a temperaturas elevadas, lagartos buscam refúgio para evitar o superaquecimento, o que reduz suas oportunidades de obter recursos e de se reproduzir (Frishkoff et al., 2015; Sinervo et al., 2010b). O aumento da temperatura também pode expor os animais aos seus limites fisiológicos, resultando em estresse e até mesmo morte (Diele-Viegas et al., 2020). Além disso, temperaturas elevadas têm o potencial de alterar as distribuições geográficas de populações ou espécies inteiras, aumentando o risco de extinção (Chevin et al., 2013; Duarte et al., 2012; Sinervo et al., 2010b). Numerosos estudos têm demonstrado que temperaturas além da tolerância térmica dos ectotérmicos podem potencialmente levá-los à extinção (Beltrán et al., 2020; Cahill et al., 2012; Deutsch et al., 2008; Sinervo et al., 2010a). Além disso, indivíduos que não conseguem manter a temperatura corporal ideal também podem experimentar uma redução em sua aptidão. Os ectotérmicos tropicais provavelmente serão os primeiros a sentir os impactos das mudanças climáticas, pois são mais sensíveis às variações de temperatura ambiental em comparação com as espécies temperadas (Deutsch et al., 2008). Esses organismos possuem uma margem térmica de segurança estreita, tornando-os suscetíveis mesmo a pequenos aumentos de temperatura (Huey et al., 2009).

Por outro lado, certas espécies têm a capacidade de reduzir potencialmente os efeitos das mudanças climáticas através de plasticidade fenotípica. Esse fenômeno envolve a variação irreversível na expressão de características durante o desenvolvimento induzida por certos fatores, como temperatura, estrutura do habitat e disponibilidade de recursos (Gunderson et al., 2017; Pigliucci, 2001; West-Eberhard, 2003). Apesar de sua importância, poucos estudos investigaram a relação entre essas características ecológicas térmicas e a plasticidade fenotípica, o que pode mudar nossa compreensão de como os ectotérmicos lidarão com as mudanças climáticas.

Além da plasticidade fenotípica, variações térmicas no ambiente podem mediar outros aspectos da ecologia do indivíduo, incluindo o seu desempenho locomotor. Dessa forma, a temperatura emerge como um fator crítico, influenciando não só a atividade metabólica, mas também a capacidade neuromuscular e a eficácia global do aparelho locomotor (Huey, 1982). Além disso, outros fatores, como a autotomia caudal, podem afetar a maneira como os lagartos se movimentam.

A autotomia caudal é uma estratégia anti-predatória notável que consiste na liberação da cauda inteira ou de parte dela (Arnold, 1984, 1987) que geralmente acontece durante o ataque de predadores podendo aumentar as chances de sobrevivência (Congdon et al., 1974). Quando confrontados com predadores, alguns lagartos usam esse mecanismo, obtendo uma vantagem significativa, pois a cauda autotomizada distrai o predador, permitindo que o lagarto escape (Medger et al., 2008). Essa estratégia é documentada em cerca de 13 das aproximadamente 20 famílias de lagartos (Downes and Shine, 2001). A autotomia geralmente ocorre por meio de planos de fratura transversais em cada vértebra, resultando na regeneração subsequente da cauda com características diferentes da original (Arnold, 1984). Embora proporcione benefícios imediatos, a perda da cauda acarreta custos, impactando o equilíbrio locomotor, energia, imunidade, crescimento e sucesso reprodutivo do organismo (Higham et al., 2013). Por sua vez, algumas espécies desenvolveram estratégias para minimizar os efeitos adversos da autotomia, incluindo o aumento na intensidade de forrageamento (Sousa et al., 2016), ajustes comportamentais para manter distância dos predadores e adaptações na movimentação e na resistência durante corridas (Domínguez-López et al., 2015). No que diz respeito ao desempenho locomotor, essa estratégia anti-predatória pode afetar diretamente a velocidade, resistência e equilíbrio dos indivíduos, com variações entre espécies e fases ontogenéticas (Bateman and Fleming, 2009). A resposta dos lagartos à autotomia caudal pode ser mediada por variações térmicas em seu ambiente, enfatizando a necessidade de considerar condições climáticas específicas ao avaliar o impacto dessa adaptação.

À medida que as mudanças climáticas induzidas pelo homem continuam a impactar o planeta, é imperativo entender como as espécies reagirão a essas condições de mudança. Organismos ectotérmicos são estreitamente dependentes do clima que os cercam e muito vem sendo estudado sobre como as mudanças climáticas afetarão a vida dos lagartos (Sinervo et al., 2010b). Porém, a maioria desses estudos ocorrem no hemisfério norte, principalmente nos EUA e Europa (Winter et al., 2016), revelando uma lacuna de conhecimento a respeito de vertebrados ectotérmicos de regiões tropicais, grupo de organismos que tem sido apontado como o primeiro a sofrer os impactos diretos de mudanças no clima (Deutsch et al., 2008; Llewelyn et al., 2018). Pesquisas que aprofundem a compreensão sobre a ecologia desse grupo são de extrema relevância, pois fornecem informações sobre como os ectotérmicos reagirão às mudanças climáticas e, consequentemente, contribuem para o melhor direcionamento dos esforços de conservação. Dessa forma, este estudo teve o objetivo de elucidar aspectos da ecologia térmica do lagarto Neotropical *Notomabuya frenata*, com o enfoque na relação entre plasticidade fenotípica e autotomia caudal, performance locomotora e aspectos ecofisiológicos.

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Capítulo 1. Phenotypic plasticity in thermal traits of a Neotropical lizard across a short environmental gradient

(Submetido a Austral Ecology)

Abstract

In light of the challenges posed by climate change and escalating environmental pressures, it is crucial to understand the interplay between temperature-related traits and phenotypic plasticity to help us to undertake effective conservation strategies. We studied the phenotypic plasticity of temperature-related traits in *Notomabuya frenata* (Scincidae), a lizard species that inhabits both open (cerrado *sensu stricto*) and forested (gallery forests) habitats within the Brazilian Cerrado. Our research was conducted at the IBGE Ecological Reserve in Brasília, Brazil, where we gathered ecophysiological and morphological data from 15 individuals collected in cerrado *sensu stricto* and 16 from gallery forests. We used Generalized Additive Mixed Effects Models and Generalized Linear Models to model the role of phenotypic plasticity in ecophysiological parameters of *N. frenata*. Contrary to our initial expectations, individuals from gallery forests exhibited a notably superior locomotor performance independently of temperatures when compared to their cerrado *sensu stricto* counterparts. Gallery forest lizards have a wider tolerance for both maximum and minimum critical temperatures and prefer higher temperatures. Our findings indicate that *N. frenata* display phenotypic plasticity in temperature-related traits. Gallery forest individuals in the face of climate change might be better equipped to cope with the deleterious effects of increasing temperatures. Unfortunately, most individuals of *N. frenata* are found in open areas of the Cerrado biome which is increasingly imperiled by conversion into pasture and agricultural lands.

Keywords: Cerrado, Lizards, Thermal-tolerance, Temperature, Climate change.

1. Introduction

Human activities are disrupting the global climate, causing an elevation of the average temperature, especially in terrestrial environments (Gunderson and Stillman 2015), which are expected to suffer twice the warming rate when compared to aquatic environments (Diffenbaugh and Field 2013). Temperature has a direct and multifaceted impact on the fitness of ectotherms influencing reproduction (sex ratio, number of eggs, offspring viability), territory defense, thermoregulation, and predator avoidance (Booth 2018; Herrel *et al.* 2007; Huey 1982; Sannolo *et al.* 2019). When exposed to high temperatures, ectotherms seek refuge to mitigate the risk of overheating, reducing their opportunities to obtain resources and reproduce (Frishkoff *et al.* 2015; Sinervo *et al.* 2010b). Elevated temperature can also expose animals to overheating by surpassing their physiological limits, leading to stress and death (Diele-Viegas *et al.* 2020). Furthermore, elevated temperatures can disrupt the geographic distributions of entire populations or species, thereby increasing the extinction risk (Chevin *et al.* 2013; Duarte *et al.* 2012; Sinervo *et al.* 2010b). Tropical ectotherms will probably be the first organisms to suffer the impacts of climate change since they are more susceptible to environmental temperature variations compared to temperate species (Deutsch *et al.* 2008). These organisms possess a narrow thermal safety margin making them susceptible to even minor temperature increments (Huey *et al.* 2009).

As human-induced climate change continues to impact the planet, it is imperative to understand how species will react to these changing conditions. This understanding might help us better target conservation efforts. A possible strategy is adaptation, but as it results from natural selection, it may not occur in time to avoid the losses of rapid climate change (Gotthard and Nylin 1995). Alternatively, certain species may possess adaptive mechanisms to cope with the detrimental effects of climate change by irreversibly modifying their development in response to environmental stimuli. This phenomenon—phenotypic plasticity—refers to variation in the expression of specific characteristics induced by various environmental factors, such as temperature, habitat structure, and resource availability (Gunderson *et al.* 2017; Pigliucci 2001; West-Eberhard 2003). For example, butterflies can change color, flies can change the size of their wings, and some reptiles can have their sex determined by the temperature they experience during embryonic development (Booth 2018; Powell *et al.* 2010; Solensky and Larkin 2003). Phenotypic plasticity can be inferred using five approaches: "animal model" analyses, common garden studies, experimental manipulations, refined population responses, and measures of individual plasticity (Merilä and Hendry 2014).

Some key traits that affect the fitness of ectotherms and that can be used to predict how well ectotherms will respond to climate change are maximum and minimum thermal tolerances (temperature range that an animal can tolerate without suffering physiological stress), preferred temperature (optimal temperature for normal functions), and thermal performance (how animals perform under different temperatures). Numerous studies have demonstrated that temperatures beyond the thermal tolerance of ectotherms can potentially lead to extinction (Beltrán *et al.* 2020; Cahill *et al.* 2012; Deutsch *et al.* 2008; Sinervo *et al.* 2010a). Furthermore, individuals that fail to maintain optimal body temperatures may also experience a reduction in their fitness. Despite their importance, few studies investigated the relationship between these thermal ecological traits and phenotypic plasticity, which might change our understanding of how well ectotherms will cope with climate change.

Ectotherms that live in open areas have higher body temperatures than those in forested environments due to direct sunlight availability (Lanna *et al.* 2022). Additionally, ectotherms found in open areas have more opportunities to thermoregulate, allowing them to adjust their body temperatures to preferential values. On the other hand, forested environments tend to be more shaded and humid, resulting in fewer opportunities to thermoregulate. Consequently, species living in forested environments tend to have lower body temperatures and a narrower body temperature variation (Huey and Slatkin 1976). Because of these characteristics, forested areas ectotherms are more likely to suffer from the consequences of climate change (Neel *et al.* 2021). For instance, a study of two species of anole lizards demonstrated that the forest-dwelling species is substantially more vulnerable to climate change than the closely related species that lives in forest-edge habitats (Neel *et al.* 2021).

Examining a single species that inhabits distinct environments enables a better comprehension of the effects of climate change on squamates. Here we assess the presence of phenotypic plasticity in the thermal ecological traits of the lizard *Notomabuya frenata*, a geographically widespread species that occurs in savanna (e.g., cerrado *sensu stricto*) and forested habitats (e.g., gallery forests) in the Cerrado biome. This species has low dispersion capability and individuals often use a single type of environment throughout life (Vrcibradic and Carlos Frederico Duarte 1998). We investigate a single population in contrasting but adjoining habitats—cerrado *sensu stricto* and gallery forest—with no barriers to the flow of individuals and genes between them. Therefore, we assume panmixia and that differences between individuals collected in the two habitats reflect phenotypic plasticity. We hypothesize that the contrasting thermal environments across the forest-savanna gradient will elicit phenotypic plasticity in *N. frenata*. We also predict that individuals captured in open habitats will exhibit a higher (*i*) preferential and (*ii*) critical temperature while having an (*iii*) smaller thermal safety margin when compared to individuals captured in closed environments.

2. Methods

2.1.Species

The skink *Notomabuya frenata* is a small, viviparous, diurnal, and heliothermic lizard (Vrcibradic and Rocha 1998a) with a wide distribution throughout South America, including Brazil, Bolivia, Paraguay, and Argentina. In Brazil, it occurs in various states, such as Brasília, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Piauí, Rio de Janeiro, Rio Grande do Sul, Rondônia, São Paulo, and Tocantins (Bérnils and Moura-Leite 1990; Colli 2002; Costa *et al.* 2008; Gainsbury and Colli 2003; Lema 1994; Pinto *et al.* 2017; Sazima and Haddad 1992; Vitt 1991; Vrcibradic 2006; Vrcibradic and Rocha 1998a; b; Whiting *et al.* 2006). This species can be found in different habitats of the Cerrado biome, characterized by unique vegetation (forests, savannas, and grasslands) but subjected to the same macroclimatic conditions. Several reproductive and survivorship aspects of this species are directly affected by environmental temperature. For instance, male spermatogenic activity increases with lower ambient temperature (Vrcibradic and Duarte 1998), while high temperatures can compromise embryonic development and offspring performance (Beuchat 1986; Jara *et al.* 2019; Lourdais *et al.* 2004; Shine and Harlow 1993).

2.2.Study area and sampling of individuals

We performed the study at the Reserva Ecológica do IBGE (15°56’06” S, 47°52’09” W), a protected area in Brasília, Distrito Federal, Brazil, situated in the core of Cerrado. Originally occupying around 23% of the Brazilian territory, with approximately two million square kilometers in central Brazil (de Oliveira *et al.* 2019), the Cerrado is the largest and richest Neotropical savanna with one of the highest levels of endemicity in the world (Myers *et al.* 2000). Cerrado is marked by a rainy season from October to April and a dry season from May to September (Alvares *et al.* 2013; Kottek *et al.* 2006; Nimer 1989) with habitats encompassing a mosaic of grasslands, savannas, and forests (Ribeiro and Walter 2008).

The study area is part of a long-term monitoring of squamates involving pitfall traps to capture individuals. Each trap consists of four 35-liter buckets arranged in a “Y” shape, with one bucket in the center and three at the ends. The buckets are buried in the ground and connected by three 6-meter galvanized sheets that function as guides. We used 50 pitfall traps installed in five transects in cerrado *sensu stricto* (savanna-like vegetation) and 20 traps in one transect in a gallery forest. We checked the cerrado *sensu stricto* traps once a month for a week but checked the gallery forest traps twice weekly (every Tuesday and Friday). In the field, we recorded the snout-vent length using a metal ruler (1 mm precision) and the body mass with a Pesola Micro Line spring scale (0.1 g precision) for every individual we captured. We uniquely marked each lizard by toe-clipping (no more than two per member), which meets ethical expectations and does not impair skinks' capture probabilities (Jones and Bell 2010; Perry *et al.* 2011).

The two transects (cerrado *sensu stricto* and gallery forest) are separated on average by 1.76 km, with the minimum and maximum distance between them being 1.54 km and 2.05 km, respectively. It is important to highlight that there are no barriers to the flow of individuals and genes between the two habitats, which is why we assume panmixia. However, as all collected individuals were marked, data collected over the years of this monitoring show that there was no recapture of individuals between habitats. This may reflect the restricted home range and dispersal ability of the species (Vrcibradic and Duarte 1998).

We transported animals to the University of Brasília laboratory and placed them in individual terrariums with vermiculite substrate and water *ad libitum*. Within up to 24 hours after capture, we performed ecophysiological trials and promptly released the individuals near the traps where we captured them.

2.3.Thermal performance

We collected all physiological data in the laboratory (Animal Use Ethics Committee of the University of Brasilia permit # 33786/2016). We determined the preferred temperature for each lizard by employing a thermal gradient setup within an MDF plywood terrarium, which featured eight compartments (each measuring 100 x 15 x 30 cm in length, width, and height). We established the gradient by placing a 60-W incandescent lamp at one end and an ice pack at the other, generating a temperature range of ~20–50 ºC (Paranjpe *et al.* 2012). Lizard body temperatures were recorded every minute for an hour using a 36-ga thermocouple (Omega 5SC-TT-T-36-72) affixed to their abdomen. We connected thermocouples to a data acquisition module (Omega TC-08 8-Channel Thermocouple USB Data Acquisition Module) and used the mean temperature to estimate the preferred temperature. Before recording body temperatures, we allowed a 5-minute acclimatization period in the gradient. We observed no hindrance to lizard movements during the experiments due to the thermocouples. We used the lowest and highest temperatures recorded during the preferred temperature experiment to estimate the minimum and maximum voluntary temperatures.

Then, we induced lizards to run on a wooden track (200 cm x 30 cm x 40 cm) under three different temperatures: ambient (~25 ºC), hot (= ambient +5 ºC), and cold (= ambient -5 ºC), which impact the sprint's speed (Angilletta Jr. 2009). We used the ambient temperature as a parameter so that individuals did not reach their thermal limits. We exposed each lizard to a heat source (60 W incandescent lamp) or ice packs to reach the desired temperatures while monitoring its temperature with a single-channel fast-reading digital cloacal thermometer. Subsequently, the individual was placed on the track and induced to run as fast as possible by manual stimulation to simulate a predatory pursuit and verify the maximum speed reached on the course. Each lizard ran twice at each temperature, totaling six runs. Temperature measurements were taken immediately before the race with a quick-reading cloacal thermometer. The minimum critical temperature considered is where the lizards, placed in an ice box, lost the ability to return to the prone position when turned supine (without killing the animal). The maximum critical temperature is where the lizards, heated with the aid of an incandescent lamp, lose the ability to return to the prone position when turned supine (without killing the animal). We conducted the runs with at least one-hour intervals between them. We took all body temperatures with the quick-reading cloacal thermometer Omega Engineering HH-91 (0.1 ºC precision).

We recorded runs at 420 frames per second (fps) with a Casio HS EX-FH25 digital camera, supported by an aluminum tripod 1.5 m high, positioned in the center of the track. To measure the running speed of each lizard in each run, we used the Tracker 4.80 software (https://physlets.org/tracker/).

2.4.Statistical analyses

To examine the impact of habitat on the locomotor performance of *Notomabuya frenata*, we built Generalized Additive Mixed Effects Models – GAMMs (Wood 2017) with the package MGCV (Wood 2011). Through GAMMs, we generated performance curves and evaluated the influence of predictors on their shape and location. Due to non-parametric data smoothing functions, GAMMs allow for non-linear and flexible responses (Wood 2006). We used the maximum running speed as the response variable (highest running speed value for each temperature), individual identity as a random factor, and SVL and habitat (cerrado *sensu stricto* and gallery forest) as fixed factors. To determine predictor importance, we built a less complex null model composed only of the response variable and intercept. Then, we employed a dual approach involving model selection and averaging, based on the Akaike Information Criterion adjusted for small samples (AICc) with the MuMIn package (Barton 2009).

Furthermore, we built generalized linear models (GLMs) to assess between-habitat differences in the thermal tolerance (critical thermal minimum and maximum) and preferred temperature. In the complete model, we tested whether minimum critical temperatures, maximum critical temperatures, and preferred temperatures were explained by habitat and SLV. We conducted all statistical analyses with the R platform (R Core Team 2018).

3. Results

We obtained data from 15 individuals collected in cerrado *sensu stricto* and 16 collected in gallery forest (Table 1). The average of critical temperatures (minimum and maximum) and preferred temperature of individuals collected in the cerrado *sensu stricto* were 15.06 ºC, 40.34 °C and 33.2 ºC, respectively, and 13.42 °C, 42.58 °C and 35.28 °C for lizards from the gallery forest (Table 1). The likelihood-ratio test indicated that our full GAMM differed significantly from a null model and adequately fitted the data ($\chi^2 = 61.47$, $p < 0.01$, r^2-adjusted = 0.65). The GAMM indicated differences in the locomotor performance between individuals collected in different habitats and that temperature is the only relevant predictor tested (Table 2). Model selection and averaging showed that habitat and temperature are the most important predictors of locomotor performance in *Notomabuya frenata*, followed by the interaction between temperature and habitat (Table 3). The GAMM predicted maximum locomotor performance around 31 ºC (Fig. 1) and that lizards from gallery forest had higher locomotor performance than lizards from cerrado *sensu stricto* regardless of the temperature (Fig. 1). Finally, the GLMs revealed (1) a difference in thermal tolerances between individuals from gallery forest and cerrado; (2) that habitat and SVL were significant predictors ($p < 0.05$) of maximum critical temperature; and (3) that habitat had a great influence on the differences in critical thermal minimum and preferred temperature ($p = 0.06$ and $p = 0.08$, respectively; Table 4). Individuals from the gallery forest have greater critical thermal tolerance for maximum and preferred temperature values and smaller thermal critical tolerance for minimum compared to individuals from the cerrado *sensu stricto* (Table 1).

4. Discussion

Our results show that exposure to different habitats impacts the thermal and ecological traits of *Notomabuya frenata* and modulates the development of the individuals, corroborating our hypothesis of phenotypic plasticity. We found a significant influence of habitat and temperature on the reptile's locomotor performance, with gallery forest individuals outperforming those from cerrado *sensu stricto*. Additionally, we recorded distinct thermal tolerances between these habitats, with gallery forest lizards showing broader tolerances for critical thermal maximum but a more confined tolerance for critical thermal minimum and preferred temperatures. and evidence that individuals living in the gallery forest have an advantage in coping with rising ambient temperatures caused by climate change.

Our findings highlight that temperature plays a crucial role in influencing the locomotor abilities of *Notomabuya frenata*, like its impact on other lizard species (Beltrán *et al.* 2020; Silva *et al.* 2021; Sinervo *et al.* 2010a). The GAMM analysis confirmed the influence of habitat and temperature on the maximum locomotor performance, showcasing its critical role in the species' daily activities, such as foraging, mating, and evading predators. Lizards from the gallery forest exhibited superior locomotor performance compared to their counterparts from the cerrado *sensu stricto* across varied temperatures. Additionally, we found a significant distinction in the thermal tolerances between individuals from different habitats. The gallery forest lizards displayed wider tolerances for critical thermal maximum but a narrowed tolerance for critical minimum and preferred temperatures compared to those from cerrado *sensu stricto*. These results suggest that individuals living in gallery forests are better equipped to handle increases in ambient temperature caused by climate change. This result is surprising because *Notomabuya frenata* is primarily found in open habitats (Vrcibradic and Carlos Frederico Duarte 1998). Thus, we anticipated that lizards from the cerrado *sensu stricto* would exhibit superior thermal performance compared to their counterparts in gallery forests.

The intraspecific variation observed in climate-relevant traits and their association with habitat and temperature are indicators that this species can adjust the trait to different conditions because of phenotypic plasticity (Llewelyn *et al.* 2016). This conclusion is possible because the observed variation occurs within the same population, as there are no barriers to the flow of genes between the two habitats, but no recapture of individuals was observed between the habitats. Phenotypic plasticity is favored in more predictable environments (Reed *et al.* 2010). In this sense, the plasticity observed in *Notomabuya frenata* may be related to the predictability of climate variations in the Cerrado, where the annual thermal amplitude is low and the seasonal variation has two clearly defined seasons with little stochastic variation (Macena *et al.* 2008).

A higher preferred temperature observed in individuals from the gallery forest may be linked to limited opportunities for thermoregulation. Consequently, when this resource (heat) becomes available in the environment, they seize the chance to elevate their body temperature. This adaptation may reflect the scarcity of this resource in gallery forests. On the flip side, this behavior could also reflect the thermal stress individuals from the cerrado *sensu stricto* might face due to recent climate changes. It is well-established that animals in tropical areas are more susceptible to climate change because their preferred temperature is closer to their maximum thermal limit, which limits your thermal safety margins (Deutsch *et al.* 2008; Gunderson and Stillman 2015; Huey *et al.* 2009; Tewksbury *et al.* 2008). In other words, tropical species have a narrower thermal safety margin. We can draw an analogy between individuals from the gallery forest and those from the cerrado *sensu stricto*, indicating that the latter are more vulnerable than their counterparts in the gallery forest. In this way, adaptation and mitigation strategies might need to prioritize the cerrado *sensu stricto* habitats, preserving microhabitats, fostering connectivity, and minimizing anthropogenic stressors.

Recent work has shown that environmental factors play a more significant role than physiological variables in shaping the geographic distribution of *Notomabuya frenata* (Machado *et al.* 2023). Considering this, projections for the future indicate a large reduction in areas with environmental suitability for this species due to the combined impacts of climate change and extensive deforestation (Machado *et al.* 2023). This is worrying because conservation units currently protect only 4.32% of suitable habitats for this species. Added to this, its future areas of suitability appear to be shifting to forest environments, potentially occupying what is currently the Atlantic Forest, the most deforested biome in Brazil (Machado *et al.* 2023; Ribeiro *et al.* 2009). Therefore, the loss of future areas of environmental suitability together with the physiological impacts due to climate change poses significant challenges to the conservation of this species.

Considering this, our findings suggest a more optimistic future for *Notomabuya frenata*, since species with phenotypic plasticity are expected to be more capable of surviving ecological catastrophes and avoiding extinctions, as they can express different phenotypes depending on environmental conditions (Ma *et al.* 2018; Merilä and Hendry 2014). This may be especially relevant considering that the species has limited dispersal capacity, so it is unlikely to be able to mitigate the consequences of climate change by dispersing to locations with more suitable environmental conditions (Vrcibradic and Duarte 1998). However, it is important to keep in mind that plasticity may not be enough to buffer climate change (Gunderson and Stillman 2015; Urban *et al.* 2014).

While our study provides valuable insights, it is crucial to acknowledge its limitations. Firstly, while our study has effectively covered thermal ecology and phenotypic plasticity in *Notomabuya frenata* across two habitats, these habitats are only a subset of the diverse ecological conditions within the Cerrado biome. Hence, generalizations across the entire biome should be made cautiously. Additionally, our reliance on short-term physiological experiments, though standard in ecological studies, might not entirely capture these lizards' long-term adaptive or acclimatization responses to sustained environmental changes. Lastly, while our sample size was adequate for statistical robustness, increasing the sample size in future endeavors might provide deeper insights and accommodate broader inter-individual variability.

The broader implications of our findings extend beyond the specific case of *Notomabuya frenata*. Understanding the thermal adaptations of lizard species in different habitats is fundamental for conservation efforts, especially in the context of climate change. Our results underscore the importance of considering habitat-specific strategies when formulating conservation plans. Moreover, the observed phenotypic plasticity suggests that species capable of adjusting their development might have a better chance of coping with the ongoing impacts of climate change. From a broader perspective, studies like ours underscore the significance of preserving ecological heterogeneity, as this could be the buffer against which many species rally their defenses against human-induced climatic change. On a practical note, conservationists and policymakers can utilize these insights to prioritize habitats and draft focused intervention strategies.

In this way, we conclude that *Notomabuya frenata* exhibits phenotypic plasticity, and individuals living in the gallery forest have better conditions to cope with rapid climate changes. However, this adaptability is not necessarily favorable for the species, given that it predominantly occupies open areas in the Cerrado biome. The Cerrado has undergone severe conversions of its territory for pasture and agriculture, leaving few forest remnants for the species to shelter in the face of more severe warming. Such knowledge is indispensable for informed biodiversity conservation strategies, especially when facing the imminent challenges of global climate change. Future research could delve deeper into the genetic basis of this phenotypic plasticity, exploring how gene expression varies across habitats and temperatures. Additionally, long-term monitoring might provide insights into how these thermal traits evolve in response to sustained environmental changes.

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Tables

Table 1. Summary statistics of the ecophysiological parameters of *Notomabuya frenata* from cerrado *sensu stricto* and gallery forest in Brasília, Brazil. Values represent the mean ± one standard deviation. SVL: snout-vent length.

Parameter	**Cerrado *sensu stricto***	**Gallery forest**
Sample size	15	16
SVL (mm)	59.13 ± 8.41	59.88 ± 5.92
Sprint speed maximum (cm/s)	5.76 ± 4.96	5.94 ± 5.96
Critical thermal minimum (ºC)	15.06 ± 2.67	13.42 ± 2.05
Critical thermal maximum (ºC)	40.34 ± 3.84	42.58 ± 2.01
Body temperature during runs (ºC)	26.89 ± 8.83	27.5 ± 11.1
Preferred temperature (ºC)	33.2 ± 3.65	35.28 ± 2.61

Table 2. Full generalized additive mixed-effects Model (GAMM) relating predictors of locomotor performance (running speeds) in the lizard *Notomabuya frenata*. **SVL**: snout-vent length. Habitat: cerrado *sensu stricto*/gallery forest. **Edf:** expected degrees of freedom.

Parametrics Terms				
Term	Estimate	Std. Error	*t*	*P*
Intercept	4.8284	0.4655	10.372	< 0.00001
Habitat	1.9594	0.6613	2.963	0.00362
Smooth Terms				
Term	Edf	Ref. df	*F*	*P*
s(Temperature)	5.744	5.744	41.32	< 0.00001
s(SVL)	1.384	1.384	0.16	0.796

Table 3. Model selection and averaging of generalized additive mixed-effects models (GAMMs) relating predictors to locomotor performance of the lizard *Notomabuya frenata.* Models depicted are those with DAICc < 10. Temp: temperature, df: degrees of freedom, AICc: Akaike information criterion corrected for small samples, DAICc: difference between given and best model, wAICc: Akaike weight.

Model Selection					
Model	**df**	**logLik**	**AICc**	**DAICc**	**wAICc**
habitat+s(temp)+s(temp*habitat)	8	-373.280	763.7	0.00	0.788
habitat+s(temp)	6	-377.463	767.6	3.90	0.112
habitat+s(temp)+s(size)+s(temp*habitat)	10	-373.276	768.3	4.60	0.079
habitat+s(temp)+s(size)	8	-377.462	772	8.36	0.012
habitat+s(temp)+s(size)+s(temp*habitat)+ s(size*habitat)	12	-373.276	773	9.35	0.007

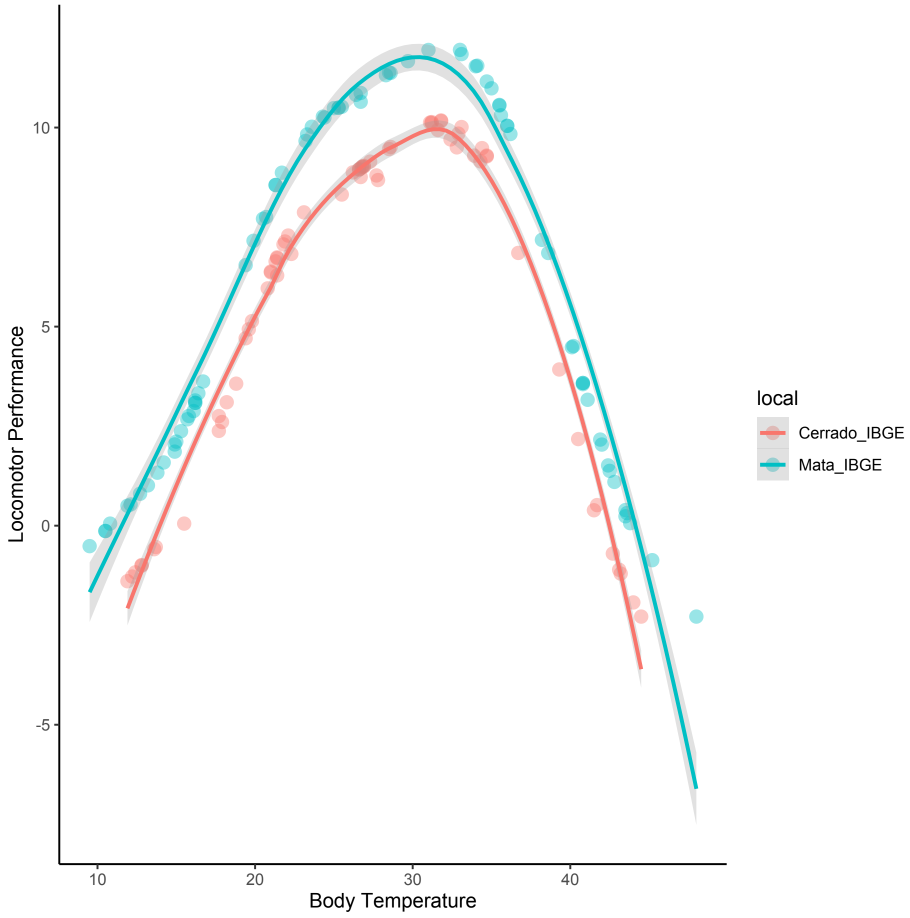
Model Average					
Importance	**habitat**	**s(temp)**	**s(temp*habitat)**	**s(size)**	**s(size*habitat)**
Sum of weights	1	1	0.87	0.1	<0.01
Number of containing models	9	6	3	6	3

Table 4. Generalized linear models (GLMs) relating predictors of thermal tolerance (minimum critical temperatures, maximum critical temperatures and preferred temperatures) in the lizard *Notomabuya frenata*. **SVL**: snout-vent length. **Habitats**: cerrado *sensu stricto*/gallery forest.

Critical Thermal Minimum				
	Estimate	Std. Error	*t*	*P*
Intercept	13.40880	3.70651	3.618	0.00116
Habitats	-1.66470	0.86578	-1.923	0.06473
SVL	0.02801	0.06179	0.453	0.65389
Critical Thermal Maximum				
	Estimate	Std. Error	*t*	*P*
Intercept	28.72152	4.20199	6.835	<0.00001
Habitats	2.09320	0.98152	2.133	0.04186
SVL	0.19642	0.07005	2.804	0.00907
Preferred Temperature				
	Estimate	Std. Error	*t*	*P*
Intercept	29.57162	4.89827	6.037	<0.00001
Habitats	2.03767	1.14416	1.781	0.0858
SVL	0.06139	0.08166	0.752	0.4585

Figure Legends

Figure 1. Locomotor performance (sprint speed) of the lizard *Notomabuya frenata* as a function of body temperature. Points represent partial residuals of a generalized additive mixed model (GAMM), while lines and bands represent the predictions and confidence limits, respectively. The upper green dots and lines represent lizards from the gallery forest, while the lower red dots and lines represent lizards from the cerrado sensu stricto.



Capítulo 2. Caudal Autotomy and Locomotor Performance in the Neotropical Lizard Notomabuya frenata (Cope, 1862)

(Submetido a Journal of Thermal Biology)

Abstract

While caudal autotomy is a prevalent anti-predatory strategy in lizards, its consequences for autothomized individuals remains poorly understood. This study investigates the impact of caudal autotomy on the locomotor performance of *Notomabuya frenata* of individuals collected in two distinct habitats, the central Cerrado and the Cerrado-Amazon ecotone. We investigated how locomotor performance varies in relationship to body size, locality and tail condition. Surprisingly, size had no impact on locomotor performance, challenging conventional expectations. We found an influence of temperature and locality on locomotor performance with lizards from the Cerrado-Amazon transition zone exhibiting superior locomotor performance. Additionally, individuals with regenerated tails displayed unexpectedly enhanced locomotor performance compared to those with intact or broken tails which suggest a potential compensatory mechanism or phenotypic plasticity in response to caudal autotomy. This study contributes to the broader understanding of anti-predatory adaptations in lizards, emphasizing the importance of considering specific environmental contexts in evaluating the consequences of autotomy. Future studies should delve into genetic aspects, behavioral adaptations, and potential compensatory mechanisms to comprehensively unravel the intricate relationship between caudal autotomy and locomotor performance in *N. frenata*.

Key words: Temperature, morphology, Cerrado, Lizards.

1. Introduction

Predation is one of the major evolutionary forces driving morphological adaptations to increase the likelihood of obtaining food or decrease the chances of becoming prey (Dawkins and Krebs, 1979). Squamates have several anti-predatory morphological adaptations to avoid direct contact with predators, such as cryptic or warning coloration (Mappes et al., 2005; Ruxton et al., 2004). If confrontation with predators cannot be avoided, some squamates use defensive strategies such as biting and trashing or even purposedly removing their tail, a phenomenon known as caudal autotomy (Arnold, 1987). This anti-predatory strategy involves the complete or partial voluntary removal of the tail, which allows the tail to distract the predator while the lizard escapes (Arnold, 1984, 1987; Congdon et al., 1974).

Interestingly, caudal autotomy may also occur in intra-specific conflicts (Bateman et al., 2014).

Caudal autotomy can be observed in various groups of squamates and appears to exhibit a phylogenetic pattern, emerging as a predominant predator evasion strategy. Notably, this occurs among 13 of approximately 20 lizard families, such as Gekkonidae, Scincidae, and Gymnophthalmidae (Downes and Shine, 2001). In most lizards, autotomy occurs through transversely located fracture planes in each vertebra (Arnold, 1984). The autotomized tail usually regenerates but acquires different shape, size, and function characteristics than the original tail (Higham et al., 2013). During the regeneration process, the vertebra is replaced by a cartilage tube that can become calcified (Arnold, 1984). Removing the tail in response to an imminent threat provides a significant advantage, as it may allow the organism a valuable opportunity to escape predators (Bateman and Fleming, 2009).

However, the loss of the tail has costs, impacting several aspects of the organism, from its locomotor balance to factors such as energy, immunity, growth, and reproductive success (Arnold, 1984, 1987). Additionally, caudal autotomy can impact the survival of autotomized individuals, as it requires energy allocation mainly to regenerate a new tail—a trait associated with long-term survival and reproductive success (Lynn et al., 2013; Maginnis, 2006). For instance, the lacertid *Takydromus viridipunctatus* suffers a high cost from caudal autotomy, especially in males during the reproductive period, when a reduction of more than 30% in their survival is observed (Lin et al., 2017). However, the mortality rate in *T. viridipunctatus* decreases significantly as the new tail regenerates, demonstrating the long-term benefits of this evolutionary strategy (Lin et al., 2017). Some species develop mechanisms to minimize the adverse effects of tail loss. Some strategies may be to increase the intensity of foraging by autotomized individuals (Sousa et al., 2016) or adjust their behaviors by maintaining a greater distance from predators compared to individuals with an intact tail (Domínguez-López et al., 2015). Autotomized males of *Lacerta monticola* spend less time moving, employ short and more paused movements, and exhibit a smaller home range (Martin and Salvador, 1997).

Many lizards use their tail during locomotion and may lose balance and momentum after its loss, as the tail serves as a counterbalance between the head and body. The lizard tail generates friction as it is dragged along the ground, propelling the animal forward, positioning the individual's center of mass near the hind limbs to enable greater propulsion force on the substrate (Arnold, 1984, 1987; McElroy and Bergmann, 2013). In the absence of the tail during a run, most of the weight is transferred to the front limbs, making the run less efficient (Arnold, 1987). Consequently, it is reasonable to assume that caudal autotomy impacts the locomotor performance, affecting speed, resistance, and balance (Bateman and Fleming, 2009). Several species show a decrease in running speed after tail loss (Cooper et al., 2004; Lin and Ji, 2005). However, the opposite can also happen, where some species may not experience changes in speed or even become faster after caudal autotomy (Brown et al., 1995; Cooper et al., 2004; Lin and Ji, 2005). Another physiological aspect that can be affected is resistance, resulting from increased pauses during running, which may reflect the additional effort required to run without the tail, as well as the loss of energy reserves stored in the tail (Brown et al., 1995; Lin and Ji, 2005). In the lizard *Niveoscincus metallicus*, the cost of caudal autotomy in females is reduced endurance, while males experience a reduction in running speed (Chapple et al., 2002). This lack of consensus on speed sprint can be explained by differences in each species' lifestyle, size, or the intensity of predation throughout ontogeny (Bateman and Fleming, 2009; Sousa et al., 2015).

Several essential traits that influence the locomotor performance of ectotherms are crucial for predicting how lizards will respond to caudal autotomy. Among these traits, morphology, including size and body mass, plays a direct and fundamental role in movement efficiency and balance (Clusella-Trullas and Chown, 2014). Temperature emerges as a critical factor, influencing not only metabolic activity but also neuromuscular capacity and the overall effectiveness of the locomotor system (Huey, 1982). Lizards' response to caudal autotomy may be mediated by thermal variations in their environment, emphasizing the need to consider specific climatic conditions when assessing the impact of this adaptation. Therefore, lizard populations occupying different localities provide the opportunity to observe how environmental variation in ambient temperature affects locomotor performance in ectotherms. Thus, we explore how caudal autotomy influences the locomotor performance of *Notomabuya frenata* (Squamata, Scincidae) across two distinct regions, one situated in the central Cerrado and the other in the transition zone between Cerrado and Amazonia. Our study investigates geographical and temperature influences, considering a positive correlation between body size and locomotor performance. We also assess whether the impact of autotomy on locomotor performance is proportional to the size of the remaining or regenerated tail section. Specifically, we expect that lizards with intact tails outperform those with broken or regenerating tails, and individuals with regenerated tails show superior locomotor performance compared to those with broken tails.

2. Material and methods

2.1.Species

The skink *Notomabuya frenata* exhibits a broad distribution (e.g., Brazil, Argentina, Bolivia, and Paraguay) along the diagonal of open formations in South America (Costa et al., 2008; Vrcibradic, 2006; Vrcibradic and Carlos Frederico Duarte, 1998). Despite being associated with different habitats, including dense savannas and forests, the species is restricted to regions with particular macroclimatic conditions (Machado et al., 2023). This heliothermic and diurnal lizard forages in low vegetation, shrubbery, rocks, and dead tree trunks, feeding mainly on arthropods (Vitt, 1991; Vrcibradic and Carlos Frederico Duarte, 1998). It is viviparous and produces only one litter per year, with a gestation period of approximately nine months (Vrcibradic and Rocha, 1998). It is a small skink, averaging approximately 55 mm in snout-vent length and 4 g in body mass (Nappo et al., 2023). The average incidence of tail autotomy in this species is 35.4% among individuals in populations, although this value can vary from 0% to 100% depending on the population (Nappo et al., 2023; Van Sluys et al., 2002).

2.2.Study area and sampling of individuals

We conducted the study in two distinct regions, one located in the core of the Cerrado and the other in the transition between Amazonia and Cerrado. In the first region, we sampled lizards at the Reserva Ecológica do IBGE (15º56’06” S, 47º52’09” W) within the Área de Proteção Ambiental das Bacias Gama e Cabeça de Veado, a protected area in Brasília, Distrito Federal, Brazil. This study area was selected as part of an ongoing squamate monitoring program. As for the second region, we sampled lizards at the guesthouse Praia Alta (-10.749612475 S, -49.845514710 W), a private property in the municipality of Lagoa da Confusão, Tocantins, Brazil. For individual capture, we employed pitfall traps. Each pitfall trap consisted of four 35-liter buckets arranged in a “Y” shape, with one bucket at the center and three at the endpoints. These containers were buried in the ground and interconnected by three 6-meter galvanized sheets or black tarps serving as guides. In Brasília, we installed 50 pitfall traps across five transects in cerrado *sensu stricto* (savanna-like vegetation) and positioned 20 traps along a single transect within a gallery forest. We checked traps in the cerrado *sensu stricto* once a month for a week; we inspected those in the gallery forest twice weekly. As for Lagoa da Confusão, we sampled the study area during a field expedition in 2016. We used 13 pitfall traps installed in one transect in cerrado sensu stricto (savanna-like vegetation) and 12 traps in one transect in a forest area (cerradão vegetation). We arranged 25 pitfall traps along a vegetation continuum from cerrado *sensu stricto* to cerradão, where we checked twice daily for ten days. For each captured lizard, we measured with a ruler (1 mm accuracy) their snout-vent length (SVL), tail length, and length of the regenerated portion of the tail (if any), and with a spring scale (Pesola Micro Line accuracy of 0.1 g) we recorded their body mass.

2.3. Ecophysiological tests

We took the collected lizards to the laboratory for physiological trials (Animal Use Ethics Committee of the University of Brasilia permit # 33786/2016). We tested the locomotor performance of full-tailed and autotomized lizards by inducing individuals to run on a wooden 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, with a 30-minute interval between tests. We used gel ice packs and incandescent lamps to alter the lizards' body temperature, monitored with a cloacal thermometer (L-K industries Miller & Weber T-6000 Cloacal 0/50 ºC). We recorded all runs with a high-speed digital camera (Casio EX-FH25 10.1MP) at 420 fps. The camera was supported by an aluminum tripod 1.5 m high, positioned in the center of the track. We processed the videos with Tracker 4.11.0 to obtain the maximum sprint speed for each individual at each temperature.

The day after collecting locomotor performance data, we obtained data on critical temperatures. To measure the critical thermal minimum (CT_{min}), we placed each lizard on a plastic box along with an ice gel pack to lower its body temperature, whereas to measure the critical thermal maximum (CT_{max}), we used a heat source (60 W incandescent bulb) to increase its body temperature slowly. We observed its behavior and checked its ability to return to the upright position when placed supine. Upon losing this capacity, we immediately recorded the lizard's body temperature with a cloacal thermometer. We collected CT_{max} data at least one hour after obtaining CT_{min}.

2.4. Statistical analyses

To assess the effects of tail autotomy upon the locomotor performance of *Notomabuya frenata*, we generated a thermal performance curve (Huey and Stevenson, 2015) using a generalized additive mixed model – GAMM (Wood, 2017). We first created a full model in which the maximum running speed was the response variable; body temperature, SVL, mass, condition of the tail (broken, regenerated, or whole), tail length, length of the regenerated portion of the tail, and local (Brasília and Lagoa da Confusão) were fixed effects; and individual (identity) was a random effect. In the analysis, the condition of the tail and habitat were parametric terms, while body temperature, SVL, mass, tail length, and length of the regenerated portion of the tail were smooth terms. We used an information theory approach to perform model selection (Burnham and Anderson, 2002) based on the Akaike information criterion corrected for reduced sample sizes (AICc) with the MuMIn package (Barton, 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 (Burnham and Anderson, 2002).

3. Results

We obtained ecophysiological data from 19 lizards from Brasília and 12 lizards from Lagoa da Confusão (Table 1). The average critical temperatures (minimum and maximum) of *N. frenata* from Brasília were 17.16ºC and 37.95 ºC, respectively, and 16.42 ºC and 43 ºC for lizards from Lagoa da Confusão (Table 1).

The likelihood-ratio test indicated that our full GAMM differed significantly from a null model and adequately fitted the data ($\chi^2 = 47.062$, $p < 0.001$, r^2-adjusted = 0.481). None of the parametric terms in the model were significant, although the condition of the regenerated tail had a considerable influence on the performance of *N. frenata* ($p = 0.07$). Among smooth terms, only temperature was significant (Table 2). Model selection and averaging indicated that temperature, local, and tail condition, in this order, were the most important predictors of locomotor performance in *N. frenata* (Table 3). The GAMM predicted maximum locomotor performance around 30ºC (Fig. 1A). Lizards with regenerated tails had better locomotor performance than those with whole or broken tails (Fig. 1B). Finally, lizards from Lagoa da Confusão achieved higher performance when compared to lizards from Brasília (Fig. 1C).

4. Discussion

Considering several covariates, we investigated the impact of caudal autotomy on the locomotor performance of *Notomabuya frenata*. Our findings shed light on the factors affecting the locomotor performance of *N. frenata,* with temperature, location, and tail condition as decisive elements. We found that temperature is a key determinant of locomotor performance, reaching its peak around 30 °C. Surprisingly, body size showed no correlation with performance, and individuals with intact tails did not outperform those with broken or regenerated tails, contradicting our hypotheses. Contrary to our expectations, lizards with regenerated tails performed better than those with intact or broken tails. We also found that lizards from the transitional area of Lagoa da Confusão outperformed their counterparts from the central Cerrado.

Body temperature plays a crucial role in the locomotor performance of *Notomabuya frenata*, a result that is in accordance with most of the ecophysiological studies on ectotherms (Gangloff et al., 2019; Huey, 1982; Sinervo et al., 2010). The optimum temperature for the performance around 30 °C corresponds to the species' natural habitat preferences, as this lizard is diurnal and primarily found in open habitats (Vrcibradic and Carlos Frederico Duarte, 1998). Body temperature directly influences muscular efficiency and neuromuscular activity, and a higher metabolic rate can positively affect locomotor performance (Bennett, 1990). The higher body temperatures in Lagoa da Confusão, approximately 5 °C above those recorded in Brasília, emerge as a crucial factor that potentially shapes the locomotor performance of *N. frenata*. This thermal disparity between sites reinforces the idea that thermal sensitivity in locomotor performance may be adaptive, with organisms adjusting their optimal performance temperatures to prevailing field conditions (Angilletta Jr., 2009; Pontes-da-Silva et al., 2018). The observed results align with studies demonstrating a positive relationship between organisms' maximum performance and higher temperatures (Huey and Stevenson, 2015; Silva et al., 2021). These thermal variations underscore the complexity of interactions between organisms and their environments, emphasizing the need to account for specific climatic conditions when interpreting differences in locomotor performance among geographically distinct populations. Taking into consideration how temperature changes can disrupt lizards' activity patterns, should always be a concern when delineating conservation strategies that account for the preservation of ectotherms.

Despite the importance of the tail in lizards (Arnold, 1984), we found no measurable impact of caudal autotomy on *Notomabuya frenata.* This lizard species predominantly inhabits terrestrial environments (Vrcibradic and Carlos Frederico Duarte, 1998), frequently navigating the leaf litter, where the presence of a tail may not significantly affect its balance. Another plausible explanation lies in the dual role of the tail: while it can potentially enhance locomotor performance by aiding in movement, it may simultaneously increase friction with the substrate. In this context, autotomized individuals might experience reduced friction with the substrate (Arnold, 1987). Consequently, when comparing individuals with and without tails, the impact of tail loss may not be evident using the ecophysiological methods employed in this study. Interestingly, our findings revealed that individuals with regenerated tails exhibited superior locomotor performance, suggesting a more favorable trade-off between friction and the tail's locomotion-assisting function. Caudal autotomy in *N. frenata* may incur additional costs, such as impacts on endurance, reproduction, or other variables not explored in this study.

We found no correlation between body size (SVL, CC, RC, and mass) and performance, which has already been observed for some populations of other lizards that occur in Brazil, such as *Kentropyx calcarata* (Pontes-da-Silva et al., 2018). However, it is essential to note that our analyses did not encompass other morphological variables, such as forelimb and hind-limb length. These traits are known for their positive impact on locomotor performance (Kohlsdorf and Navas, 2012; Miles, 1994). Therefore, different lengths of the limbs among populations could explain, in part, the intraspecific differences in locomotor performance. The capacity to undergo tail autotomy is phylogenetically constrained (Arnold, 1984). It is plausible that phylogenetic factors may exert a more substantial influence than morphological factors in elucidating the caudal autotomy's impact on locomotor performance observed in *Notomabuya frenata*. However, it is imperative to validate these explanations through rigorous experimental testing. Given the complex interplay between caudal autotomy, morphological variables, and locomotor performance in *Notomabuya frenata*, this study provides significant insights, but certain considerations warrant attention. General implications underscore the importance of temperature and locality in determining locomotor performance, emphasizing the need to account for specific climatic factors when assessing the impact of autotomy. However, morphological variables did not exhibit significance, indicating potential functional compensation. Population differences suggest a substantial influence of the local environment. Limitations include considering other ecological, genetic, and behavioral factors that may modulate these relationships. In conclusion, lizards with regenerated tails displayed superior performance, defying expectations. Future research should explore the genetic influence on autotomy response, investigate specific behavioral adaptations in different habitats, and address potential functional compensation at more detailed levels. These directions are crucial for a comprehensive understanding of the evolutionary ecology of *N. frenata* and provide a robust foundation for future studies on the dynamics of caudal autotomy in lizards.

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Table 1. Summary statistics of the morphological and ecophysiological parameters of *Notomabuya frenata* from Brasília and Lagoa da Confusão, Brazil. Values represent the mean ± one standard deviation. SVL: snout-vent length.

Parameter	Brasília	Lagoa da Confusão	Total
Sample size	19	12	31
Mass (g)	4.47 ± 1.55	5.12 ± 2.72	4.72 ± 2.10
SVL (mm)	59.32 ± 7.58	65.00 ± 20.63	61.52 ± 14.34
Tail length (mm)	69.68 ± 25.88	63.08 ± 31.62	67.13 ± 28.32
Relative tail length	1.16 ± 0.38	0.94 ± 0.38	1.08 ± 0.40
Length of regenerated portion of tail (mm)	3.11 ± 9.24	29.17 ± 32.88	13.19 ± 25.07
Relative length of regenerated portion of tail	0.05 ± 0.16	0.40 ± 0.47	0.19 ± 0.36
Sprint speed maximum (cm/s)	9.16 ± 2.83	9.03 ± 2.95	9.11 ± 2.86
Critical thermal minimum (ºC)	17.16 ± 5.47	16.42 ± 3.18	16.88 ± 4.67
Critical thermal maximum (ºC)	37.95 ± 7.05	43.00 ± 2.43	39.91 ± 6.18
Body temperature during runs (ºC)	27.27 ± 5.32	28.06 ± 6.70	27.58 ± 5.87

Table 2. Full generalized additive mixed-effects model (GAMM) relating predictors of locomotor performance (running speeds) in the lizard *Notomabuya frenata*. **CCr**: total tail length, **RCr**: length of the regenerated portion of the tail, **SVL**: snout-vent length. **Edf:** expected degrees of freedom.

Parametrics Terms				
Term	Estimate	Std. Error	*t*	*P*
Intercept	2.9575	1.7205	1.719	< 0.0878
Local - Lagoa da Confusão	1.4927	0.9721	1.535	0.1269
Tail condition - Regenerated	2.8594	1.5740	1.817	0.0714
Tail condition - Whole	2.2303	2.2354	0.998	0.3201
Smooth Terms				
Term	Edf	Ref. df	*F*	*P*
s(Temperature)	5.059	5.059	29.525	< 0.00001
s(CCr)	1	1	0.661	0.418
s(RCr)	1	1	0.518	0.473
s(SVL)	1	1	0.492	0.484
s(Mass)	1	1	0.667	0.415

Table 3. Model selection and averaging of generalized additive mixed-effects models (GAMMs) relating predictors to locomotor performance of the lizard *Notomabuya frenata*. Models depicted are those with DAICc < 4. **Temp:** temperature, **RCr**: length of the regenerated portion of the tail, **SVL**: snout-vent length df: degrees of freedom, **AICc**: Akaike information criterion corrected for small samples, **DAICc**: difference between given and best model, **wAICc:** Akaike weight.

Model Selection					
Model	**df**	**logLik**	**AICc**	**DAICc**	**wAICc**
s(Temp)	5	-424.96	860.32	0.00	0.20
Local+s(temp)	6	-424.01	860.59	0.27	0.18
s(Temp)+Tail condition	7	-423.42	861.60	1.28	0.11
Local+s(temp)+ Tail condition	8	-422.76	862.50	2.18	0.07
s(RCr)+s(Temp)	7	-424.26	863.27	2.96	0.05
s(Mass)+s(Temp)	7	-424.28	863.33	3.01	0.05
s(SVL)+s(Temp)	7	-424.32	863.40	3.09	0.04
Local+s(Mass)+ s(Temp)	8	-423.51	864.01	3.69	0.03
Local+s(SVL)+ s(Temp)	8	-423.60	864.19	3.87	0.03

Model Average							
Importance	**s(Temp)**	**local**	**Tail condition**	**s(Mass)**	**s(SVL)**	**s(RCr)**	**s(CCr)**
Sum of weights	1	0.42	0.29	0.14	0.13	0.13	0.11
Number of containing models	64	64	64	64	64	64	64

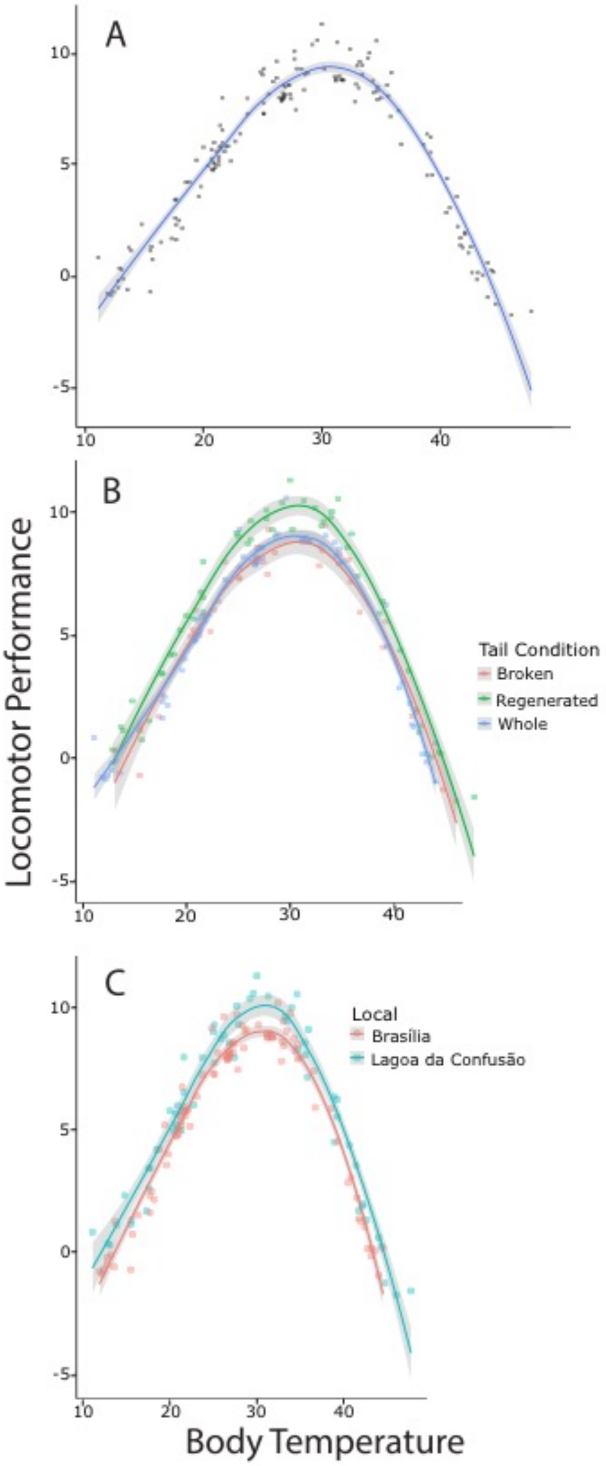

Figure 1. Locomotor performance (sprint speed) of the lizard *Notomabuya frenata* as a function of (A) body temperature, (B) body temperature and tail condition (broken, regenerated and whole), and (C) body temperature and geography (Brasília and Lagoa da Confusão). Points represent partial residuals of a generalized additive mixed model (GAMM), while lines and bands represent the predictions and confidence limits, respectively.

Considerações finais

De maneira geral, podemos concluir que fatores ambientais foram mais significantes para o desempenho locomotor de *Notomabuya frenata*, no entanto, fatores biológicos também são primordiais para a compreensão de sua ecologia térmica. *Notomabuya frenata* possui plasticidade fenotípica, evidenciando que os indivíduos na floresta de galeria possuem melhores condições para lidar com mudanças climáticas rápidas. Contudo, essa adaptabilidade pode não ser favorável à espécie, dada sua ocupação predominante em áreas abertas do Cerrado, bioma que vem sofrendo severas conversões do seu território para pastagem e agricultura, sobrando poucos remanescentes florestais para abrigar a espécie diante de aquecimento mais severo. Em relação a autotomia caudal, lagartos com caudas regeneradas exibiram desempenho superior, desafiando expectativas. A temperatura e a localidade destacam-se na determinação do desempenho locomotor, ressaltando a necessidade de considerar fatores climáticos específicos ao avaliar o impacto da autotomia. Pesquisas futuras podem aprofundar a base genética da plasticidade fenotípica e da autotomia caudal em *N. frenata*, explorando como a expressão gênica varia entre habitats e temperaturas. Além disso, o monitoramento de longo prazo pode fornecer insights sobre como esses traços térmicos evoluem em resposta a mudanças ambientais sustentadas. Finalmente, ressaltamos que o conhecimento produzido neste trabalho é crucial para aprimorar estratégias de conservação da biodiversidade, especialmente diante dos desafios iminentes das mudanças climáticas globais e perdas de áreas de adequabilidade da espécie.