UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

PATRICIA MARQUES DO AMARAL OLIVEIRA

ASPECTOS ECOFISIOLÓGICOS ASSOCIADOS AO ESTADO HÍDRICO E À ECOLOGIA TÉRMICA DE LAGARTOS DA CAATINGA DE PERNAMBUCO, BRASIL

Recife
2025

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutora em Biologia Animal. Área de concentração: Ecologia

Orientador (a): Prof. Dr. Pedro Murilo Sales Nunes

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Recife

2025

.Catalogação de Publicação na Fonte. UFPE - Biblioteca Central

Oliveira, Patricia Marques do Amaral.
Aspectos ecofisiológicos associados ao estado hídrico e à ecologia térmica de lagartos da Caatinga de Pernambuco, Brasil / Patricia Marques do Amaral Oliveira. - Recife, 2025.
104f.: il.

Tese (Doutorado) - Universidade Federal de Pernambuco, Centro de Biociências, Programa de Pós Graduação em Biologia Animal, 2025.
Orientação: Pedro Murilo Sales Nunes.
Coorientação: Carlos Arturo Navas Iannini.
Inclui referências.

1. Desidratação; 2. Caatinga; 3. Mudanças climáticas; 4. Termorregulação. I. Nunes, Pedro Murilo Sales. II. Iannini, Carlos Arturo Navas. III. Título.

UFPE-Biblioteca Central

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Aprovado em: 29/07/2025.

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*Dedico esta tese à Caatinga, pelos anos
em que se tornou minha morada
cientifíca.*

AGRADECIMENTOS

Primeiramente agradeço aos meus pais, por sempre me influenciarem a estudar, pesquisar e aprender. Agradeço também a Pri, minha irmã e a Lucas, meu companheiro.

Ao Pedro Nunes por todos os anos de orientação e a Carlos Navas, por todo o suporte para fazer essa tese nascer. Agradeço também ao pessoal do laboratório de Herpetologia, os que passaram e os que continuam. Especialmente aos que foram à campo comigo: Boleno, Dália, Osmar, Fernanda, João Felipe e Duda. Agradeço a minha banca examinadora: Dra. Luisa Diele-Viegas, Dra. Marjoriane de Amaral, Dr. Marco Katzenberger, Dr. Fábio Barros, Dr. Hugo Andrade e Dr. Pedro Ivo. Agradeço ao pessoal do Catimbau, especialmente a Elitânea e sua família.

E um agradecimento especial aos meus amigos de doutorado que me acompanharam durante essa jornada desde o princípio: Bruna T., Henrique A., Clara A., Victor L. e Paulo B. E aos que chegaram no final: Thabata C. e Nathally A.

Por fim, agradeço aos órgãos de fomento: FACEPE, Capes e Propesqi. Ao PPGBA, ao Idea Wild e também ao PELD Catimbau.

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IDEA WILD

“Tudo em vorta é só beleza,
sol de abril e a mata em flor.
Mas Assum Preto, cego dos óio,
num vendo a luz, ai, canta de dor.”

Luiz Gonzaga & Humberto Teixeira, Assum Preto (1950)

RESUMO

Ambientes semiáridos, como a Caatinga brasileira, impõem desafios significativos à fauna local, especialmente aos organismos ectotérmicos, que dependem das condições do ambiente para regulação térmica e manutenção do equilíbrio hídrico. Nesta tese, investigaram-se aspectos ecofisiológicos associados ao estado hídrico e à ecologia térmica de três espécies de lagartos da Caatinga pernambucana: *Ameivula ocellifera*, *Tropidurus cocorobensis* e *Tropidurus semitaeniatus*. O estudo teve como objetivos principais caracterizar a absorção de água dessas espécies, avaliar a influência da alimentação na condição hídrica e corporal de indivíduos desidratados, examinar a escolha de temperaturas preferidas e de atividade e projetar a distribuição potencial das espécies sob cenários futuros de mudanças climáticas. Os dados foram obtidos por meio de coletas em campo, experimentos de hidratação induzida, de alimentação e modelagem ecológica. Os resultados mostraram diferenças significativas entre as espécies quanto ao índice de absorção de água, influenciado por fatores ecológicos como microhabitat e modo de forrageamento. *Ameivula ocellifera*, espécie de forrageamento ativo e mais exposta à radiação solar, apresentou maior desidratação em campo e, consequentemente, maior absorção de água nos experimentos. *Tropidurus semitaeniatus*, espécie saxícola, demonstrou menor desidratação, possivelmente devido às características do habitat rochoso que favorecem a retenção de umidade. Os testes indicaram que o consumo de alimentos, em vez de contribuir para a reidratação, pode acentuar a desidratação em algumas situações, revelando um possível custo fisiológico da digestão em condições de escassez hídrica. A modelagem de distribuição das espécies sob cenários climáticos futuros apontou para um potencial deslocamento de áreas adequadas, com redução significativa para *T. semitaeniatus* e aumento da distribuição para *T. cocorobensis*, revelando assim a influência das possíveis diferentes estratégias térmicas dessas espécies. Conclui-se que o estado hídrico e a ecologia térmica dos lagartos da Caatinga estão intrinsecamente relacionados, sendo modulados por fatores ambientais e ecológicos. Compreender essas interações é essencial para prever os impactos das mudanças climáticas sobre a herpetofauna do semiárido e propor estratégias de conservação mais eficazes.

Palavras-chave: lagartos; ecologia térmica; desidratação; Caatinga; mudanças climáticas; hidratação

SUMÁRIO

1 INTRODUÇÃO

Modelos preveem possíveis cenários com um aumento de temperatura ambiental (em torno de 6° C) na região central da América do Sul, com diminuição (de 5 a 20%) das chuvas (MARENGO et al., 2009). Essas condições de temperaturas altas e umidade reduzida ocorrem e podem ser verificadas em regiões áridas e semiáridas do planeta, como por exemplo nas Caatingas brasileiras, em particular no período de estiagem (DA SILVA et al., 2018), afetando a disponibilidade de alimentos e água para vertebrados distribuídos nesse domínio (MCLAUGHLIN, 2002). Quando se considera especificamente os lagartos, diversos efeitos dessa escassez são reconhecidos em parâmetros ecológicos e, consequentemente, fisiológicos, resultando em alterações na dieta (KOLODIUK, 2010), no forrageamento (RIBEIRO & FREIRE, 2011), ciclos reprodutivos (RIBEIRO et al., 2012), termorregulação (RIBEIRO & FREIRE, 2010) e uso de micro-habitat (SALES et al., 2011). Apesar da biodiversidade da Caatinga possuir mecanismos e estratégias que auxiliam a lidar com a seca (SANTOS et al., 2014; DA SILVA et al., 2018), cenários climáticos mostram que o aumento da aridez é uma das principais ameaças a este domínio morfoclimático (Quarto Relatório de Avaliação do PainelIntergovernamental sobre Mudanças Climáticas - AR4 IPCC, 2007).

Muitas linhagens de lagartos parecem possuir uma alta sensibilidade a temperaturas extremas, principalmente por serem animais que necessitam do ambiente para regular sua temperatura corporal e, consequentemente, realizarem suas funções básicas (HUEY, 1982). Contudo, apesar da ocorrência em ambientes com essas características implicar em desafios adaptativos significativos, algumas linhagens de lagartos têm ocupado esses ambientes, como são os casos de regiões áridas e semiáridas. A alta sazonalidade dos ambientes semiáridos, com uma longa estação seca e um curto período chuvoso, resulta em diferentes temperaturas e radiação solar ao longo de um ano e, por consequência, na busca e na manutenção da hidratação dos indivíduos que ocupam esses ambientes. Em lagartos, a exposição às condições desidratantes durante a atividade está relacionada, principalmente, aos habitats e microhabitats ocupados (HEATWOLE & VERON,

1977) e às suas atividades termorregulatórias (FOLEY & SPOTILA, 1978). Ambientes áridos e desérticos, onde os organismos são expostos à alto estresse hídrico, são importantes forças seletivas quanto à desidratação (WALDSCHMIDT & TRACY, 1983).

Os lagartos desenvolveram adaptações notáveis para sobreviver em ambientes áridos, onde a escassez de água é um desafio significativo. Essas adaptações incluem estruturas cutâneas especializadas, estratégias comportamentais e mecanismos fisiológicos que otimizam a captação e o transporte de água. Uma das adaptações mais importantes para a absorção de água é a pele microestruturada. Espécies como *Moloch horridus* (Agamidae) e *Phrynosoma cornutum* (Phrynosomatidae) apresentam micro-ornamentação em forma de favo de mel, criando uma superfície super-hidrofílica que facilita a retenção de películas de água (COMANNS et al., 2011; WITHERS, 1993). Além disso, a pele possui uma rede de canais capilares entre escamas sobrepostas, frequentemente semi-tubulares e interligados, que transportam a água passivamente. Em algumas espécies, a água é direcionada ao focinho para ingestão (COMANNS et al., 2016; JOEL et al., 2016). Entre as adaptações fisiológicas, destaca-se o uso da bexiga urinária como reservatório de água. O monstro de Gila (*Heloderma suspectum;* Helodermatidae), por exemplo, reabsorve água da bexiga para a corrente sanguínea durante a desidratação, funcionando como um amortecedor contra a perda hídrica (DAVIS & DENARDO, 2007). Além das características anatômicas e fisiológicas, muitos lagartos adotam posturas específicas para maximizar a absorção de água. O lagarto com chifres do Texas (*Phrynosoma cornutum*; Phrynosomatidae) arqueia o abdômen, estende as pernas e abaixa a cabeça e a cauda para aumentar o contato com fontes de água (JOEL et al., 2016; SHERBROOKE, 1990). Comportamentos semelhantes ocorrem em *Phrynocephalus helioscopus* (Agamidae), que achata o corpo e assume uma postura específica para coletar água (SCHWENK & GREENE, 1987).

Todas essas adaptações e estratégias visam a manutenção do equilíbrio hídrico, uma vez que lagartos sob estresse hídrico apresentam diversas respostas fisiológicas, podendo impactar seu desempenho ecológico, reprodução, forrageamento e termorregulação (HUEY et al., 2010). Em lagartos da Amazônia, a desidratação reduz o Máximo Térmico Voluntário (VTmax), alterando a percepção do risco térmico, afetando sua distribuição geográfica e aumentando sua vulnerabilidade climática (CAMACHO et al., 2023). Além disso, a desidratação leva a temperaturas corporais mais baixas e à preferência por microhabitats mais frios, indicando um trade-off entre conservação da água e termorregulação (ROZEN-RECHELS et al., 2020). O estresse hídrico também influencia a dieta, com lagartos selecionando itens mais ricos em água. Em espécies de deserto, a ingestão de vegetais é alta devido ao seu maior teor hídrico (NAGY, 1973). Além disso, mudanças na composição da dieta durante a estação seca e variações na amplitude do nicho trófico já foram documentadas (FERREIRA et al., 2017; WHITFIELD & DONNELLY, 2006). Comportamentalmente, lagartos desidratados reduzem a atividade e alteram seus padrões diários, buscando refúgios mais frescos e úmidos, o que pode afetar suas estratégias de forrageamento e fuga de predadores (ROZEN-RECHELS et al., 2020). A desidratação também aumenta a reatividade ao estresse e altera respostas ao risco de predação, destacando a interação entre hidratação e comportamento (CHABAUD et al., 2023). Apesar dos desafios da desidratação, algumas espécies apresentam respostas adaptativas que minimizam seus efeitos. Em monstros de Gila, por exemplo, a função imunológica aprimorada sugere mecanismos evolutivos para lidar com a escassez de água (MOELLER et al., 2017).

No entanto, o impacto global da desidratação reforça a importância de compreender essa dinâmica no contexto das mudanças climáticas e da conservação do habitat. Entre as influências fisiológicas mais exploradas, o impacto na ecologia térmica de lagartos, que está diretamente relacionada à termorregulação, além da área de uso e capacidade locomotora (WILSON et al., 1989), se torna importante frente às mudanças do clima. Resultados publicados por Sannolo e Carretero (2019), mostram que espécies do gênero *Podarcis* (Lacertidae) em ambientes desérticos, quando desidratados mudam sua temperatura corporal preferida, optando por se abrigarem em refúgios e em temperaturas mais baixas. A temperatura corporal preferida é definida como a faixa de temperaturas corporais mantida por um organismo em um gradiente térmico e que não fornece restrições físicas e bióticas, sendo bastante importante para estudos ecológicos e evolutivos de espécies ectotérmicas (LICHT et al.,1966). Os lagartos podem perder água, principalmente, de duas formas: pela respiração e pela pele (WEAVER ET AL., 2023), e muitas vezes processos básicos como a termorregulação e digestão estão intimamente interligados com a perda de água.

Para lagartos heliotérmicos, muitas vezes uma temperatura ideal para realizar suas funções básicas envolve exposição à luz solar e essa exposição aumenta as taxas de perda de água, trazendo assim um trade-off entre termorregular e se manter hidricamente equilibrado (ANGILLETTA ET AL., 2002). A temperatura preferida (Tp) dos lagartos influencia diretamente seu estado hídrico, regulando tanto a termorregulação quanto a perda de água por evaporação (EWL). Como ectotérmicos, esses animais ajustam seu comportamento para manter a temperatura corporal dentro de uma faixa ideal, impactando processos fisiológicos, incluindo os níveis de hidratação. A Tp varia conforme o nicho ecológico da espécie, como observado em *Darevskia praticola* (28,1°C) e *Podarcis muralis* (30,6°C) (Lacertidae), cuja diferença está relacionada às taxas de EWL e adaptações ao ambiente (ĆOROVIĆ et al., 2024). Embora a perda de água aumente com a temperatura, ambas as espécies demonstram mecanismos evolutivos para controlá-la (ĆOROVIĆ et al., 2024). Em *Psammodromus algirus* (Lacertidae), o aumento das temperaturas levou 52% dos indivíduos a ultrapassarem sua faixa térmica preferida em 2017, comparado a apenas 2% em 1997, resultando em maior seleção por microhabitats sombreados, embora estes estejam se tornando escassos (DÍAZ et al., 2022). Assim, enquanto a Tp é essencial para a manutenção da hidratação, alguns estudos indicam que a disponibilidade de água pode ser um fator ainda mais determinante para a distribuição dos lagartos, evidenciando a complexa relação entre temperatura e estado hídrico nesses organismos (CARNEIRO et al., 2017).

Situação semelhante pode ser observada na digestão de uma refeição, a depender do que foi predado, o consumo de uma refeição pode influenciar significativamente o equilíbrio hídrico em répteis, muitas vezes prejudicando-o em vez de ajudar. Répteis do deserto, como os monstros de Gila e as cascavéis, não conseguem melhorar sua hidratação por meio da ingestão de alimentos. Pelo contrário, as refeições podem levar a uma maior desidratação devido aos custos fisiológicos associados à digestão, apresentando uma osmolalidade plasmática elevada após a refeição, o que indica desidratação (WRIGHT et al., 2013). De maneira semelhante, as cascavéis que consomem alimentos não melhoram seu estado de hidratação; em vez disso, elas atingem a desidratação severa mais rapidamente do que aquelas que não se alimentam (MURPHY & DENARDO, 2019). Após a alimentação, muitos répteis exibem um aumento no comportamento de beber água, sugerindo que o consumo de alimentos aumenta suas necessidades gerais hídricas, em vez de reduzi-las (LILLYWHITE, 2017). Alguns lagartos, como o *Zootoca vivipara* (Lacertidae), podem obter hidratação suficiente através de sua dieta de insetos, ao contrário de outros répteis que dependem mais de água de fontes livres (KAY, 2023). As tartarugas do deserto podem obter hidratação de plantas suculentas, mas seu equilíbrio hídrico permanece precário, frequentemente levando a um balanço hídrico negativo durante os períodos secos (NAGY & MEDICA, 1986). Embora alguns répteis possam se adaptar para obter água de sua dieta, muitas espécies do deserto dependem principalmente de água livre, destacando os desafios de manter a hidratação em ambientes áridos.

É razoável considerar que populações de lagartos percam mais água e estejam expostos a níveis mais elevados de desidratação como uma consequência direta do aumento das temperaturas médias e irradiação solar resultante das mudanças climáticas globais das últimas décadas (HUEY et al., 2010). Entretanto, pouco se sabe sobre os limites e efeitos da desidratação nesses animais em condições naturais. Dessa forma, se torna particularmente importante compreender o grau de exposição à desidratação de lagartos em regiões que permitam a avaliação da influência das condições climáticas. Uma maior compreensão da influência da desidratação na ecologia trófica e térmica tem potencial de revelar distintos processos de ajustes individuais e, como consequência, fomentar avanços nas investigações sobre as consequências das mudanças climáticas na Caatinga e outras regiões do planeta com condições semelhantes. Complementarmente, compreender a temperatura preferida (Tp) das espécies de lagartos é essencial para prever sua distribuição futura em ambientes semiáridos, especialmente diante das mudanças climáticas. O aumento das temperaturas ameaça muitas espécies ao reduzir a disponibilidade de habitats térmicos adequados. *Colobosauroides carvalhoi* (Gymnophthalmidae), por exemplo, é restrito a fragmentos florestais mais frescos devido às suas limitações térmicas (RECODER et al., 2018).

Além disso, reconhecer traços ecofisiológicos pode ajudar a prever a vulnerabilidade dos lagartos às mudanças climáticas, permitindo a formulação de estratégias de conservação mais eficazes (CARNEIRO et al., 2017). No entanto, embora a Tp seja um fator fundamental, outros aspectos ecológicos, como disponibilidade de água e estrutura do habitat, também devem ser considerados para compreender e proteger a distribuição dos lagartos em regiões semiáridas.

Pensando nisso, selecionamos três espécies modelo de lagartos que ocorrem na Caatinga: *Ameivula ocellifera* (Spix, 1825) (Família Teiidae), *Tropidurus cocorobensis* Rodrigues, 1987 (Família Tropiduride) e *Tropidurus semitaeniatus* (Spix, 1825) (Família Tropiduridae). Essas espécies possuem algumas similaridades, como uma dieta composta principalmente por insetos (OLIVEIRA ET AL., 2022; OLIVEIRA ET AL., 2024) e são heliotérmicas (RODRIGUES, 1987; RIBEIRO ET AL., 2011; SALES & FREIRE, 2015). As três espécies possuem diferenças interessantes, como ocupação de diferentes microhabitats, onde *A. ocellifera* e *T. cocorobensis* compartilham o hábito psamófilo, e *T. semitaeniatus* é estritamente saxícola (RIBEIRO ET AL., 2011). Além da diferença no modo de forrageio, os *Tropidurus* são considerados lagartos do tipo senta-e-espera, enquanto *A. ocellifera* é uma espécie de lagarto de forrageio ativo (RODRIGUES, 1987; RIBEIRO ET AL., 2011; SALES & FREIRE, 2015).

Uma vez que espécies de lagartos são sabidamente sensíveis às mudanças climáticas, investigar os processos de desidratação dos mesmos em ambientes naturalmente secos e com sazonalidade marcada se revela particularmente importante para a compreensão de processos ecológicos envolvidos em diferentes táxons, com histórias evolutivas e características ecofisiológicas distintas. Acreditamos que averiguar a influência da desidratação na ecologia trófica e térmica dessas espécies pode nos indicar como os lagartos serão afetados com relação a composição de dieta, uso de espaço e termorregulação, em futuros cenários de altas temperaturas e aumento da aridez. Dessa forma, explorar processos fisiológicos relacionados à desidratação voluntária abre possibilidades para a compreensão de efeitos das mudanças climáticas globais em lagartos no presente e no futuro, permitindo a antecipação de situações e, eventualmente, a aplicação de medidas mitigatórias.

Nesse sentido, o presente trabalho teve como objetivos: 1) Definir o balanço hídrico de campo de indivíduos adultos de *Ameivula ocellifera*, *Tropidurus cocorobensis* e *Tropidurus semitaeniatus* em uma área de Caatinga; 2) Comparar o balanço hídrico de campo de indivíduos da espécie *Ameivula ocellifera*, *Tropidurus cocorobensis* e *Tropidurus semitaeniatus* relacionando com fatores ambientais e condição corporal; 3) Entender se o consumo de uma refeição é capaz de influenciar, positivamente ou negativamente, no balanço hídrico e na condição corporal de lagartos desidratados; 4) Explorar a escolha de temperaturas preferidas; 5) Explorar as temperaturas corporais coletadas na hora da captura de indivíduos; 6) Modelar a distribuição das espécies de *Tropidurus* de acordo com cenários futuros de mudanças de clima.

O presente estudo está organizado em três capítulos, cada um correspondente a um manuscrito produto dos dados obtidos durante o projeto de tese. O primeiro capítulo, intitulado "EXPLORING INDUCED HYDRATION IN SEMI-ARID LIZARDS", traz informações sobre o balanço hídrico de campo das três espécies de lagartos, foi aceito pelo **The Herpetological Journal** (no prelo). No segundo capítulo, intitulado "EFFECTS OF FOOD INTAKE IN WATER ABSORPTION AND BODY CONDITION OF SEMI-ARID LIZARDS", buscamos relacionar balanço hídrico e ecologia alimentar. Está submetido à revista **Journal of Herpetology** (em processo de revisão). E o terceiro capítulo, intitulado "TOO HOT TO HANDLE? PREFERRED TEMPERATURE AND FUTURE DISTRIBUTION BASED ON CLIMATE CHANGE OF TWO *TROPIDURUS* LIZARDS FROM THE BRAZILIAN SEMI-ARID REGION", nos traz resultados sobre ecologia térmica, uso do espaço e distribuição futura dos lagartos *Tropidurus*, e será submetido ao **Journal of Thermal Biology**.

2 CAPÍTULO 1 – Aceito pelo periódico *The Herpetological Journal*

Exploring induced hydration in semi-arid lizards

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Abstract. Semi-arid environments impose significant thermal stress on ectotherms, requiring specialized water acquisition strategies. This study investigated the water status of three lizard species from the Caatinga, examining the interaction between environmental factors and physiological adaptations for water acquisition. To achieve this, we combined field data—including body mass, body condition, and body temperature—with induced hydration experiments to quantify water uptake. Additionally, environmental factors such as soil and air temperature, as well as humidity, were measured. *Ameivula ocellifera* exhibited the highest water absorption, potentially reflecting greater dehydration due to its active foraging and sun exposure. Conversely, *Tropidurus semitaeniatus* absorbed less water, suggesting better hydration, possibly linked to its rocky habitat that may enhance water retention. Soil temperature and humidity significantly influenced the water status of all species, underscoring the role of ectothermy in water regulation. These findings highlight the importance of ecological context and environmental conditions in shaping water-related adaptations in semi-arid lizards.

Keywords: reptiles; Brazilian drylands; experimental hydration; body weight.

INTRODUCTION

Semi-arid regions face significant hydric challenges that affect both ecosystems and the organisms inhabiting them. These challenges stem from limited water availability, increasing aridity, and climate change, which collectively threaten biodiversity and ecosystem services (Caylor et al., 2009; Torres-García et al., 2021). Future scenarios indicate more extreme weather patterns, potentially causing sudden shifts in ecosystem dynamics and species distributions (Rathore, 2024). Desert and semi-arid regions are expected to experience significant increases in average temperatures, with pronounced warming leading to more frequent and intense extreme temperature events, as well as a reduction in precipitation (Marengo et al., 2009; IPCC, 2023). These climatic changes are expected to alter ecosystem structure and function, disrupting species interactions and the capacity of ecosystems to recover from disturbances (Tariq et al., 2006). Over time, the increasing frequency of extreme climate events may push semi-arid ecosystems toward irreversible degradation, threatening both biodiversity and human livelihoods.

The climate changes have ecological implications for the Brazilian Caatinga, a biome projected to face a warming scenario of 2°C or more by the end of this century (IPCC, 2023). The Caatinga is a morphoclimatic domain that already experiences changes in climate due to natural conditions and anthropogenic actions. Naturally, the Caatinga has a high seasonality with an average annual rainfall of 250 to 1200 mm, and a dry season that lasts six to 11 months (da Silva et al., 2018; Magalhães et al., 2022). From 1985 to 2019, there was an 11% reduction in the native vegetation of this morphoclimatic domain, mainly due to agriculture and livestock farming (Rocha et al., 2024). This degradation directly affects local climatic conditions, doubling the incidence of solar radiation compared to preserved areas (Silva et al., 2024), which significantly impacts ecosystem services and biodiversity (Rocha et al., 2024).

Some organisms are particularly sensitive to environmental conditions, especially factors related to temperature and water. For example, anurans, are highly sensitive to water loss, with projections indicating that up to 36.1% of their habitats may face more severe drought conditions by 2100 (Wu et al., 2024). Reptiles, such as the spiny-tailed lizard, experience reduced locomotor performance and foraging activity due to rising temperatures, with potential declines of 14.5% in sprint speed and 43.5% in foraging activity by 2099 (Tatu et al., 2024). Their reliance on burrows as thermal refuges may further limit their activity, exacerbating the challenges imposed by hydric stress (Tatu et al., 2024). As ectothermic organisms, lizards exhibit heightened sensitivity to environmental perturbations.

Their ecological responses to adverse environmental conditions in lizards encompass dietary shifts (Kolodiuk, 2010), novel foraging behaviours (Ribeiro & Freire, 2011), reproductive cycle alterations (Ribeiro et al., 2012), adjustments in microhabitat use (Sales et al., 2011) and activity patterns (Rossi et al., 2023; Stark et al., 2024) Furthermore, hydric stress, induced by water restriction, can affect key ecological, behavioural and physiological traits, including reproduction, foraging efficiency, and thermoregulation, with effects varying by species (Huey et al., 2010; Rozen-Rechels et al., 2020; Díaz-Ricaurte et al., 2020, 2022; Guevara-Molina et al., 2020; Camacho et al., 2023).

For instance, Dupoue et al. (2020) observed reduced longevity and compromised oxidative defences in *Zootoca vivipara* subjected to early-life hydric stress. Similarly, Sannolo & Carretero (2019) reported that dehydration in *Podarcis* lizards elicits a preference for lower body temperatures and increased refuge utilization, illustrating the impact on behaviour. While water stress is broadly detrimental, its ecological consequences for lizards remain complex. Lizards face the dual challenges of maintaining body temperature and managing water loss, both of which are influenced by microhabitat selection, movement patterns, and exposure within their environment (Foley & Spotila, 1978). In this context, the concept of thermo-hydroregulation in ectotherms becomes particularly relevant, as it refers to the integrated physiological and behavioral strategies these organisms employ to regulate both body temperature and water balance in response to environmental fluctuations. The interplay between thermoregulation (temperature control) and hydroregulation (water balance) is crucial, as both processes are interconnected and can directly influence individual performance and fitness (Rozen-Rechels et al., 2019). Especially in arid regions, and particularly with the advancement of climate change, the ability to thermo-hydroregulation may become critical for ectotherm populations, as it is highly dependent on environmental conditions (Díaz et al., 2022).

Consequently, under the ecological and climatic pressures prevalent in the Caatinga, lizards are likely experiencing increased evaporative water loss and heightened vulnerability to dehydration due to escalating temperatures and solar radiation (Huey et al., 2010). In this study, we hypothesise that different microhabitats play a crucial role in the water absorption capacity of lizards, given their ectothermic nature. We also propose that species-specific ecological traits may not optimise water retention, thus impacting their water balance in the wild. For example, species that forage actively in more exposed and warmer environments, such as *Ameivula ocellifera*, may experience greater dehydration but develop a higher water absorption capacity to compensate for this loss. To investigate this, we focused on three lizard species occupying distinct microhabitats and display different ecological strategies: *Ameivula ocellifera* (Spix, 1825; Teiidae), *Tropidurus cocorobensis* (Rodrigues, 1987; Tropiduridae), and *Tropidurus semitaeniatus* (Spix, 1825; Tropiduridae), aiming to elucidate the relationship between ecological traits and water management capabilities in the semi-arid Caatinga.

METHODS

Study Area

The study was conducted within Catimbau National Park (CNP), a protected conservation unit located within the Caatinga ecoregion (Latitude: from -8.4° to -8.6°, Longitude: from -37.15° to -37.2333°) in the state of Pernambuco, Brazil. CNP encompasses approximately 62,000 hectares, with elevations ranging from 700 to 1,000 metres above sea level. The climate is classified as hot semi-arid (BSh) according to the Köppen-Geiger system (Peel et al., 2007), characterized by an average annual precipitation of 600 mm and a mean annual temperature of 26°C (Gomes et al., 2006). The CNP area features sandstone outcrops and sandy soils, supporting a xeromorphic vegetation typical of the Caatinga biome. Dominant plant families include Cactaceae, Euphorbiaceae, Mimosaceae, and Fabaceae (Gomes et al., 2006). The CNP landscape exhibits a pronounced seasonality, with deciduous leaf shedding during the dry season and subsequent regrowth and flowering during the rainy period, accompanied by the ephemeral formation of flooded areas. For the duration of this study, environmental data were collected at two sampling points. Point 1 exhibited an mean air temperature of 32.62°C and an mean relative humidity of 45.90%, while Point 2 recorded an mean air temperature of 31.73°C and a mean relative humidity of 54%.

Natural History of Compared Species

The teiid lizard *Ameivula ocellifera* (Spix, 1825) is an active forager inhabiting the Restinga, Cerrado, and Caatinga environments (Sales and Freire, 2015). This species is associated with sandy microhabitats, a characteristic shared with *Tropidurus cocorobensis* Rodrigues, 1987 (Pedrosa et al., 2014), the second species examined in this study. *Tropidurus cocorobensis* is a heliophilic, sit-and-wait foraging tropidurid lizard with a relictual distribution in the Caatinga, restricted to the states of Alagoas, Bahia, and Pernambuco (Rodrigues, 1987; Ribeiro et al., 2012). The third species, *Tropidurus semitaeniatus* (Spix, 1825), is readily distinguished by its flattened body and head, adaptations associated with its rock crevice affinity and saxicolous habits (Ribeiro et al., 2011). This species is found in the northeastern Caatinga and Atlantic Forest (Roberto, 2017). All three species are primarily insectivorous, although plant material consumption is frequent among tropidurids (Sales and Freire, 2015; Oliveira et al., 2022). These species were selected due to their shared dietary preferences, yet divergent in foraging behaviours, as well as their occupation of different microhabitats. Furthermore, analysis of two species from the same genus provides a reliable framework for comparative analyses. This combination of ecological and phylogenetic attributes facilitates a comprehensive discussion of the study's findings.

Data Collection

Individuals of *A. ocellifera* and *T. cocorobensis* were collected during two expeditions to the CNP in November 2020 (dry season) and January 2021 (end of dry season), while *T. semitaeniatus* individuals were collected in January 2022 (end of dry season) and June 2022 (wet season). Collection methods varied based on species' ecology: pitfall traps were employed for the psammophilous *A. ocellifera* and *T. cocorobensis* (Foster, 2012), while noosing techniques were used for the saxicolous *T. semitaeniatus* (Fitzgerald, 2012). The traps were set up in the morning, with individuals being removed immediately after capture and their body temperatures measured using a cloacal thermometer (WT-1B Digital Thermometer, High Precision -50°C to 300°C). This procedure was typically conducted swiftly enough to prevent thermal shifts caused by the temperature of the trap bucket or sun exposure, and only data gathered under these conditions were included (in cases of delays, individuals were released without data collection). For the saxicolous individuals, cloacal temperature was recorded immediately after they were noosed. Adult individuals, including males and females, were subjected to the experiments. Specimens of *T.*

cocorobensis and *T. semitaeniatus* were considered adults if males displayed black spots on the thighs. For females, the presence of eggs or mature ovaries was used as the criterion. For *A. ocellifera*, snout-vent length was used to determine adulthood, with males measuring over 45.55 mm and females over 41.60 mm (Sales and Freire, 2015). Air and soil temperatures, as well as humidity, were recorded at the collection sites using a thermo-hygrometer (Incoterm 7666.02.0.00, Accuracy: ±5% RH, Accuracy int/ext: ±1°C from 0°C to 50°C), immediately after collecting an individual.

Sample sizes were as follows: 31 *A. ocellifera* (15 in the first expedition, 15 in the second, and 1 in the fourth), 57 *T. cocorobensis* (30 in the first, 23 in the second, and 4 in the fourth), and 46 *T. semitaeniatus* (29 in the third and 17 in the fourth). Following data collection, lizards were transferred to a shaded, enclosed location with minimal ventilation for water absorption experiments. After the experiments, lizards were euthanized using a lethal dose of 2% lidocaine hydrochloride, fixed in 10% formalin, and stored in 70% ethanol. The specimens were deposited in the Herpetological Collection of the Federal University of Pernambuco (CHUFPE), with some used for the methodology described by Oliveira et al., 2022, as well as for another manuscript to be submitted. Collections were authorised by Brazilian environmental agencies (SISBIO permits #73617, #79254-1), and all experimental procedures were approved by the Animal Use Ethics Committee of UFPE (CEUA-UFPE processes 0004/2020 and 0065/2021).

Experimental Procedures

Immediately following capture, the lizards were weighed in the field to determine their initial body mass (BM1) using a precision scale (model: Bel S, accuracy: 0.001 g) under controlled conditions to ensure consistency and minimise external influences (as all the experimentation was carried out in the field, the conditions we were able to control were the passage of people and other animals, ventilation, and solar incidence). Initial weights were recorded prior to the experimental hydration procedure. All experimental procedures were conducted at the collection site, in a shaded, enclosed area, with the aim of obtaining data at the time of capture without interference from transportation to a laboratory. This approach ensured that the natural environmental conditions of the lizards were maintained during the experiment, minimising additional stress and potential variations in environmental parameters that might occur during transportation.

For the hydration experiment, each lizard was placed in an individual, shaded container with water covering approximately half of its ventral body surface. This setup was maintained for two hours to standardise hydration levels across individuals. After this hydration period, each lizard was carefully removed from the container, externally dried with absorbent paper to remove surface water, and weighed again (BM2). Following the initial post-hydration weighing, the lizards were kept dry and individually isolated in separate containers to avoid external influences. Additional weight measurements were performed at 15-minute intervals over the next hour, recorded as BM3 (15 minutes), BM4 (30 minutes), BM5 (45 minutes), and BM6 (60 minutes). This protocol was developed based on pilot studies conducted by the authors, in which we observed that weight fluctuations stabilised around BM3 and BM4. To account for individual size variation, the snout-vent length (SVL) of each lizard was measured using digital callipers (accuracy: 0.01 mm). SVL was used as a covariate in our analyses to control for potential body size effects.

Calculation of Water Absorption Index (WAI)

To estimate the Water Absorption Index (WAI) of the lizards, we focused on weight measurements taken after hydration. Specifically, we calculated the average of the two stable weights recorded at 15 and 30 minutes post-hydration (BM3 and BM4) and subtracted the initial body mass measured in the field (BM1). The formula used to obtain the Water Absorption Index (WAI) was:

$$WAI=(BM3+BM4)/2-BM1$$

WAI reflects the difference between the initial field body mass and the stable post-hydration mass. A higher WAI indicates a greater amount of water absorbed during the experimental hydration, suggesting the lizard initially contained less water in its body, thereby indicating a higher level of dehydration in the field.

Body Condition Index (BCI)

As our analysis of water balance heavily relies on the initial weight of field individuals (BM1), we deemed it necessary to also consider a measure of body condition. We calculated a Body Condition Index (BCI) based on the residuals (Ri) of an ordinary least squares (OLS) regression using the log-transformed snout-vent length (SVL) and the initial weight in the field (BM1) for each individual. Regressions were conducted separately for each studied lizard species (Gaston and Vaira, 2020).

The BCI integrates elements of body structure, composition, and nutritional state for each individual, making it a potential correlate of the Water Absorption Index. Accordingly, we performed a Spearman correlation between BCI and WAI to evaluate their relationship.

Data Analysis

Normality of weight data was assessed using Shapiro-Wilk tests (Shapiro & Wilk, 1965). Due to non-normality, we used the Kruskal-Wallis test to test for differences between the three species in SVL, body temperature, and WAI. Wilcoxon signed-rank tests were used to compare body mass before (BM1) and after induced hydration (mean of BM3 and BM4). A linear mixed-effects model was employed to examine differences in body mass before and after induced hydration across the three species (Harrison et al., 2018). Multiple linear regression was used to evaluate the relationship between weight difference and potential predictor variables: body condition index, body temperature, air temperature, soil temperature, and relative humidity. Species was not included as an interaction term in this analysis. Additionally, a fixed-effects model was applied to assess the interaction between species and predictor variables. All statistical analyses were conducted using R software (version 3.5.1) with the 'vegan' (Oksanen et al., 2019) and 'lme4' packages. Data visualization was performed using the 'ggplot2' package in R 3.5.1.

RESULTS

We found between-species differences in median body lengtth (SVL: KW $\chi^2 = 11.058$, df = 2, p = 0.0040), field body temperature (BT: KW $\chi^2= 48.56$, df = 2, p = 2.849×10-11), and Water Absorption Index (WAI: KW $\chi^2 = 30.56$, df = 2, p = 2.312×10^{-7}) (see Fig. 1). The largest species was *T. semitaeniatus*, followed by *T. cocorobensis*, and then *A. ocellifera* (Table 1). The latter and smaller species displayed the highest average body temperature (BT), followed by *T. cocorobensis* and *T. semitaeniatus* (Table 1). Lizards of all species gained weight after experimental hydration (Table 1, Fig. 1); *T. semitaeniatus* had the smallest weight difference, followed by *T. cocorobensis*, while *A. ocellifera* had the greatest body mass gain. The variability considering all individuals from the three species was significant, with an estimated variance of 35.081 and a standard deviation of 5.923 (Fig. 2). The body condition indices of the lizards subjected to the experiment ranged from -2 to 3.

Furthermore, there was no correlation between the individuals' body condition and their WAI in all three species (*A. ocellifera*, p = 0.9303; *T. cocorobensis*, p = 0.1330; *T. semitaeniatus*, p = 0.2775) (Fig. 3). Considering the environmental conditions at the time of data collection and experiments, soil temperature and air humidity were important for understanding the variations in WAI among all individuals ($F = 9.138$, $p = 4.786 \times 10^{-9}$). The latter variable positively affected WAI (0.0032), while soil temperature had a negative effect (-0.0230). When considering the species factor, only soil temperature was statistically related to the difference in WAI ($p = 6.263 \times 10^{-6}$) (Fig. 3).

DISCUSSION

Our study investigates the hydration states of lizard species from the Caatinga, based on the premise that greater dehydration in the field would lead to a higher Water Absorption Index (WAI). During the experiment, the lizards were exposed to conditions that allowed them to collect water through their ventral surfaces, which were covered with water over approximately half of their body. The water collected in this way was not only actively ingested but may also have been absorbed through microstructured scales (passive water collection) that facilitate the passive transport of water into the capillaries between the scales and eventually to the mouth (Comanns et al., 2015; Commans, 2018). *A. ocellifera*, the species with the highest WAI, may be active in a state of lower body water content, followed by *T. cocorobensis*, and finally the saxicolous species *T. semitaeniatus*, which exhibited the lowest WAI and consequently appeared to have more water. Proportionally, individuals of *A. ocellifera* were the smallest compared to the other species. These results highlight the relevance of body size, which is mechanically linked to water loss through respiration and skin, processes that, in turn, are functions of lung size and body surface area (Mautz, 1982). Furthermore, smaller animals have a less favourable surface-to-volume ratio and tend to lose water at relatively higher rates (Turk et al., 2010). Consequently, as also observed in our results (Figure 1), considering body shape, the impact of body size on water loss can be particularly significant.

Lizards primarily lose water through cutaneous evaporation and respiration (Le

Galliard et al., 2021), and water loss is associated with various environmental factors such as high temperatures and low humidity (Weaver et al., 2023; Davis et al., 2024), as well as biological/ecological factors like morphology, life stage, habitat use, and activity period (Le Galliard et al., 2021). The species *A. ocellifera* is known to be an active forager, which implies longer activity periods and greater exposure to sunlight and higher temperatures, especially in the semi-arid environment of the Caatinga (Sales and Freire, 2015). This may explain the high average body temperature observed in its individuals and, consequently, the greater amount of water absorbed in the experiment compared to the other two model species, *Tropidurus cocorobensis* and *T. semitaeniatus* (Table 1, Figure 1), which are sit-and-wait foragers (Rodrigues, 1987). Despite being more exposed, active foraging species can "select" their prey more effectively and find a greater diversity of items, and for some vertebrates, water obtained in the diet and/or the consumption of an ideal meal can help obtain more water (Karasov, 1893; Znari and Nagy, 1997).

Other factors may be more closely associated to water loss and absorption, such as species-specific behaviours (Guevara-Molina et al., 2020), thermal tolerance (Díaz-Ricaurte et al., 2022), and microhabitat characteristics (Bodineau et al., 2024), particularly in semi-arid environments where lizards employ various strategies to maintain water balance. These strategies include behavioural adaptations, such as increased shelter use and reduced thermoregulation during droughts (Bodineau et al., 2024), as well as physiological aspects like thermal tolerance (Camacho et al., 2023), which is linked to habitat factors such as water and ambient temperature (Chabaud et al., 2022). The target species of this study remain largely unexplored in terms of their physiological aspects, with most research focusing on their ecological traits. Therefore, it is important to understand how these factors may be associated with water absorption and, more importantly, how their behaviours, strategies, and microhabitats contribute to water balance.

Although body condition and energy are important for absorbing more water, for ectothermic animals, environmental conditions appear to be the primary influencers (Lillywhite, 2017; Rozen-Rechels et al., 2020). As suggested by our results, body condition does not influence the Water Absorption Index; however, water loss can affect physiological and behavioural aspects that reduce reptiles' energy gain (Rozen-Rechels et al., 2020; Camacho et al., 2023), and despite being well adapted to arid environments, these animals are still subject to dehydration and its consequences

(Munsey, 1972). Environmental conditions are considered predictors of various ecological aspects of lizards, such as thermoregulation, foraging, feeding, growth rate, reproduction, and life cycle (Ribeiro et al., 2012; Sannolo et al., 2020). Our results revealed that the Water Absorption Index in lizards was significantly influenced by soil temperature (Figure 3, and in this context, it is crucial to consider the type of microhabitat used by lizard species, primarily because reptiles are ectothermic organisms that rely on external temperatures to regulate their body temperature. Essentially, temperature alters some physiological, biochemical, and morphological mechanisms, such as plasma osmolality and body mass (Kearney et al., 2018), being a variable with a direct effect on metabolism and water loss.

Reptiles, as ectothermic organisms adapted to a wide range of environments, have developed distinct strategies to maintain their hydration in often challenging conditions. Environmental water is an important source of water intake for these animals. However, in many cases, semi-arid environments can go months without precipitation, significantly reducing the available water (McLaughlin, 2002; Da Silva, 2018). One of the most relevant strategies to minimise loss and find water is movement between different habitats (Dezetter et al., 2023). Our model species occupy various microhabitats; however, *T. semitaeniatus* stands out by exclusively inhabiting rock outcrops and crevices (Rodrigues, 1987). Initially, we expected this territorial "limitation" to make this species more susceptible to dehydration, but our results indicated the opposite (Table 1, Figure 1). It is important to note that, at the collection site, the extensive rocky outcrops create microenvironments with low and medium vegetation, forming various shaded areas that are crucial for maintaining water balance (Huey & Tewksbury, 2009). Additionally, temporary pools form, providing water for a longer period than the microenvironments found in the soil (Ribeiro & Freire, 2009). We highlight that most individuals of this species were collected at the end of the dry season, as the rains began, leading to higher body water content. This could explain the negative values observed exclusively in this species (Figure 3), suggesting some individuals had significant water reserves. This pattern was not observed in individuals collected during the dry season expeditions.

The negative association between soil temperature and the water absorption index (WAI) suggests that individuals captured in areas with higher soil temperatures had more water in their bodies. Similarly, the positive correlation between ambient humidity and WAI indicates that individuals exhibited greater water absorption under higher humidity conditions, which implies lower initial body water content (Figure 3). It is important to emphasize that the temperature and humidity data were recorded at the exact moment each individual was captured, reflecting the environmental conditions at that specific time. This could be related to the species' activity patterns, as lizards might be more active when temperatures are slightly higher (Filogonio et al., 2010; Caldas et al., 2015; Martins et al., 2018) increasing the likelihood of encountering resources and maintaining their hydration status. We specifically captured individuals during their active periods, meaning the recorded soil temperature reflects the temperature of the environment where the lizards were active. Regarding the positive relationship between humidity and WAI, this trend was particularly notable in *Tropidurus semitaeniatus* individuals, and not in the other species (Figure 3). Most individuals of this species were collected during the rainy season when humidity levels remained elevated throughout most of the expedition, and environmental conditions were favourable with available water.

A key point to consider is that there are more precise methodologies for measurements such as water balance and dehydration (Dupré and Crawford, 1986; Johnson and Propper, 2000; Moeller et al., 2023). For example, osmolality measurement is useful for understanding an organism's ability to cope with different osmotic pressures and manage fluids internally, making it an important tool for the physiological aspects of organisms (Dupré and Crawford, 1985; Davis and DeNardo, 2007; Guzman et al., 2011; Perry et al., 2021). Direct osmometry is considered a more accurate technique, as it provides a direct measurement of the number of dissolved particles in a liquid, while calculated methods may be more prone to errors due to variability in the parameters used for the calculations. In contrast, the approach of the present study, observing hydration behaviours or other adaptations without directly measuring osmolality, may not fully capture how the animal regulates fluid balance at the cellular level. This methodological difference may lead to significant variations in the results interpreted, as what is observed through direct osmolality measurement more specifically reflects the internal physiology of the animals, while approaches considering water absorption do not provide as precise a view of the underlying physiological processes, such as internal osmotic regulation. However, the approach adopted in the present study, focusing on observing hydration behaviour and water absorption, offers a complementary perspective that may also be relevant for understanding the behavioural adaptations of lizards to water scarcity.

The experimental results presented here suggest that the model species may face challenges in maintaining water balance during the dry season in the Caatinga. We did not address dehydration tolerance or test the impacts of dehydration on performance, so we lack information on how critical the dehydration states reported here may have been. Therefore, future studies exploring the extent of dehydration, its consequences, and the strategies employed by these species would be highly valuable. In particular, understanding the challenges posed by low water source is crucial, as maintaining water balance is often vital for lizards (Lorenzon et al., 1999; Zylstra et al., 2013), and dehydration has well-documented ecological consequences. For example, Wilson et al. (1989) found that dehydration reduces the running capacity of *Uta stansburiana* Baird and Girard, 1852 (Phrynosomatidae). Water imbalance may also affect growth rates (Lorenzon et al., 1999), interfere with oxidative status in gravid females, and reduce egg production (Dupoué et al., 2020). Additionally, it can lead to reduced space use, increased refuge use, and changes in thermoregulatory behaviours (Sannolo & Carretero, 2019; Camacho et al., 2023). Our data also reinforce that hydration status directly affects thermal responses, supporting findings that dehydration reduces Voluntary Thermal Maximum (VTmax), limiting thermoregulatory efficiency in various organisms, including amphibians and reptiles (Camacho et al., 2023). They also support the importance of microhabitat selection in maintaining water balance (Weaver et al., 2023; Bodineau et al., 2024).

Our results on the hydration states of lizards from the Caatinga provide valuable insights into how these animals cope with the challenges of a semi-arid environment, particularly considering that water balance significantly influences their performance and strategies (Lillywhite, 2017; Rozen-Rechels et al., 2020). While body size influences water loss through respiration and cutaneous evapotranspiration, our findings suggest that the surface area-to-volume ratio in smaller lizards may increase relative dehydration rates. Furthermore, behavioural and ecological factors, such as active foraging versus sit-and-wait strategies, play intricate roles in maintaining water balance. While these animals adopt various strategies and adaptations to cope with climate change, studies indicate that reptiles are less likely to develop temperature-related traits. This is primarily because their generation time is long, making adaptation slower in comparison to the rapid pace of climate change (Sinervo et al., 2010). We also note that this study highlights the importance of considering the microhabitat used by lizard species, as differences in these environments can have direct implications for their thermal and, consequently, water regulation.

ACKNOWLEDGEMENTS

The authors are thankful to the Instituto Chico Mendes de Conservação da Biodiversidade and to the Comitê de Ética em Uso Animal of the Universidade Federal de Pernambuco for animal collection and handling permits permissions (ICMBio permits nº 79254-1; CEUA-UFPE nº 0065/2021). The authors are also thankful to the Projeto Ecológico de Longa Duração-PELD/CNPq Catimbau and its coordinator M. Tabarelli for lodging and equipment used during field work. PMAO is thankful to Pro-reitoria para Assuntos de Pesquisa e Pós-Graduação da UFPE, Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (IBPG-1566-2.04/19) and Idea Wild for financial support. PMAO is thankful to Elitânea’s family for logistical support. PMSN is grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq Fellowship #313622/2018-3).

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Funding: This work was supported by to Conselho Nacional de Desenvolvimento Científico e Tecnológico CNPq [Fellowship #313622/2018-3] and Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco [IBPG- 1566-2.04/19].

Figures

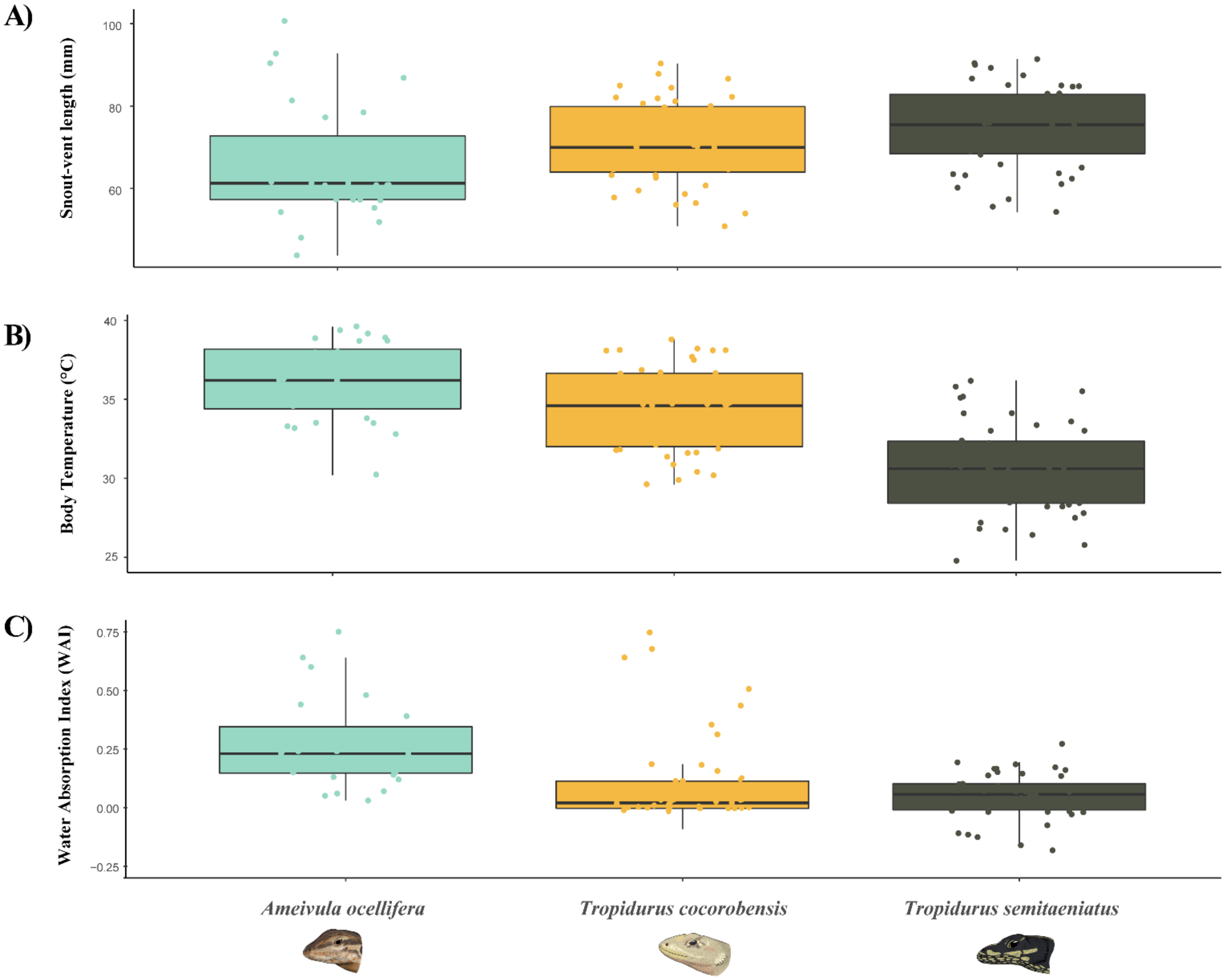

Figure 1. Boxplot graphs showing the distribution of Snout-Vent Lengths (A), Field Body Temperatures (B), and Water Balances, values representing the gained mass values after experimental hydration (C) of *Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus*. Each box represents the median and data dispersion.

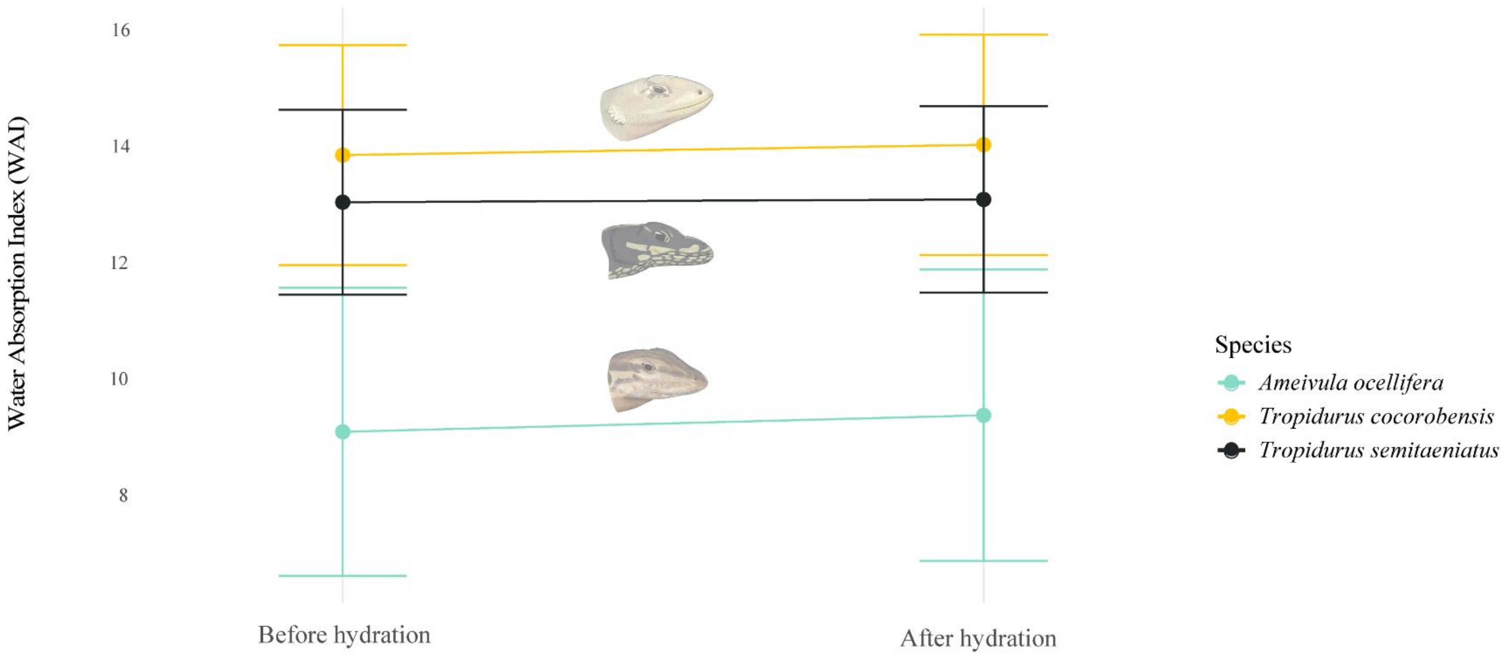

Figure 2. Variation in the average weight of the species *Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus* before and after the induced hydration experiment. The graph compares the average weight of individuals from the three species, highlighting the changes associated with the hydration process.

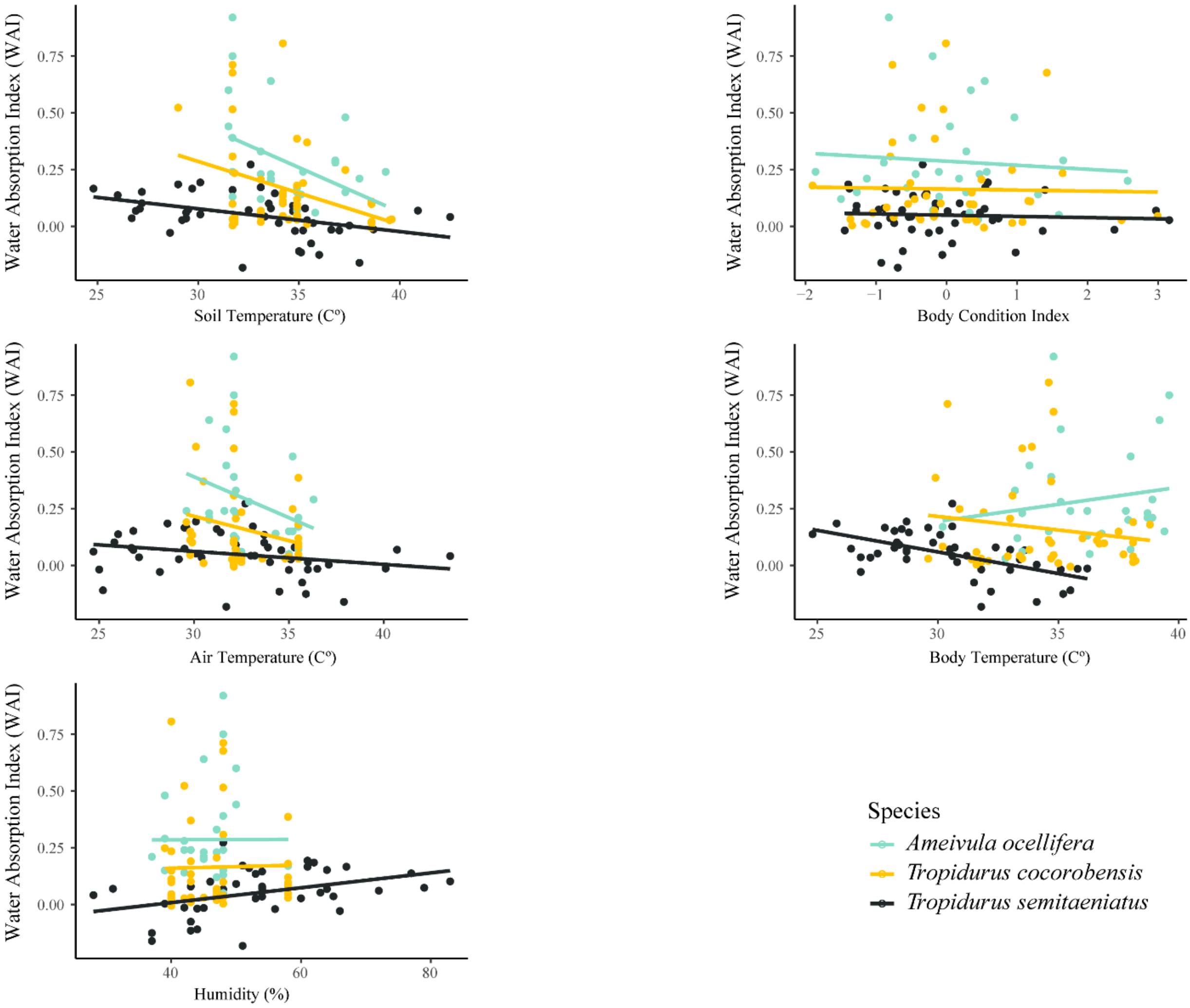

Figure 3. Relationship between water balance and influencing variables for the lizard species *Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus*. The graphs show the variation in water balance as a function of air temperature, soil temperature, humidity, body condition index, and body temperature.

Table 1. Mean and standard deviation of snout-vent length (SVL), body temperature (BT), body mass (before and after induced hydration). Also, the difference between these body masses and the data from the Wilcoxon nonparametric test. Values were rounded to the second decimal place.

Species	**SVL (mm)**	**Body Temperature (°C)**	**Body Mass (g)**			***v-value***	***p***
			Before hydration	**After hydration**	**Water Balance**		
Ameivula ocellifera	66.43 ± 13.75	36.21 ± 2.51	9.11 ± 6.27	9.38 ± 6.34	0.27	430	< 0.0001
Tropidurus cocorobensis	71.32 ± 10.06	34.32 ± 2.60	13.89 ± 6.01	14.00 ± 6.18	0.11	1060	< 0.0001
Tropidurus semitaeniatus	74.73 ± 9.92	30.51 ± 2.85	13.03 ± 5.35	13.08 ± 5.35	0.05	241.5	< 0.05

3 CAPÍTULO 2 – Em processo de revisão pelo periódico *Journal of Herpetology*

Effects of food intake in water absorption and body condition of semi-arid lizards

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Abstract

The study examines water absorption related to meal consumption in three lizard species from the Caatinga biome (*Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus*). The individuals were subjected to 10 days without water, followed by an experimental hydration process. During this process, some individuals received an insect-based meal, while others remained unfed. The goal was to determine whether meal consumption would affect the amount of water absorbed. The results indicate that *T. semitaeniatus*, which is restricted to rocky microhabitats, exhibited greater water loss compared to the other two species that occupy sandy microhabitats. Meal consumption did not significantly alter the water balance in *T. semitaeniatus*, suggesting that microhabitat conditions—such as the availability of shelter—may better support hydration needs. Conversely, *A. ocellifera* and *T. cocorobensis*, which share similar sandy habitats, showed lower water absorption in the fed group, possibly as a compensatory mechanism for their arid environment. Notably, the Body Condition Index (BCI) did not differ significantly between fed and unfed groups for any of the species, implying that short-term feeding may not affect overall energetic status under dehydration. The findings underscore the interaction between microhabitat occupancy and water balance strategies, which could become increasingly critical as climate change exacerbates aridity. For lizards already living under "limiting" conditions, such as the dry season in Brazil's semi-arid region, understanding these adaptive strategies becomes crucial for conservation efforts.

Keywords: dehydration; Caatinga; diet; feeding ecology

Lizards are sensitive to extreme temperatures, primarily because they depend on environmental thermal heterogeneity to regulate their body temperature within ranges necessary for basic physiological functions (Huey, 1982; Huey et al., 2010). Despite the climatic constraints in regions with pronounced seasonality, lizard lineages have successfully adapted to such environments, including the seasonally dry tropical forests of semi-arid regions. In these reptiles, exposure to dehydrating conditions during activity is largely determined by the habitats and microhabitats they utilize (Heatwole and Veron, 1977) and by their thermoregulatory behaviors (Foley and Spotila, 1978). Consequently, arid environments, where organisms experience intense water stress, exert strong selective pressures (Waldschmidt and Tracy, 1983). In line with these physiological and ecological constraints, recent studies have extensively examined how Caatinga’s climatic seasonality influences lizard ecology (Kolodiuk et al., 2009; Ribeiro et al., 2011; Sales et al., 2011; Oliveira et al., 2024).

In some sympatric species, such as *Tropidurus hispidus* and *Tropidurus semitaeniatus*, changes in foraging behaviors can be observed according to the climatic seasons of the region, allowing them to coexist in limiting conditions during the water deficit season (Kolodiuk et al., 2009). Dietary shifts have also been well documented. For example, Ferreira et al. (2017) found that during the dry season, there are changes in the selection of prey items compared to the rainy season. Sales et al. (2011) observed that *Ameiva ameiva* (Teiidae) individuals in a Caatinga area of Rio Grande do Norte exhibit more individual dietary specializations during the dry season, resulting in a broader trophic niche during that time compared to the rainy season when they specialize in eating larvae and pupae. Changes in feeding behavior are also seen in prey selection (Nagy, 1973), especially because the consumption of certain meals can help offset the water deficit that some species experience in desert environments (Cooper 1985; Znari and Nagy, 1997; Henen et al., 1998; Ostrowski et al., 2002). For instance, desert lizards often consume more plant-based items to obtain more water (Nagy, 1973).

In terms of basic functions, food provides necessary energy, and water consumption complements hydration. However, in many natural environments, free water can be scarce, and dietary water (acquired through prey) can play an essential role in hydration (Golightly and Ohmart, 1984; Nagy and Medica, 1986). As a result, some species, especially those in desert and seasonally dry environments, tend to adjust their diets, searching for prey that offers more water (Cooper 1985; Znari and Nagy, 1997; Henen et al., 1998; Ostrowski et al., 2002). Nonetheless, some desert reptile species, such as *Heloderma suspectum* (Helodermatidae) and Crotalus atrox (Viperidae), cannot fully balance their hydration by consuming a meal (Wright et al., 2013; Murphy and DeNardo, 2019). On the other hand, the desert tortoise *Gopherus agassizii* (Testudinidae) relies entirely on dietary water to avoid water deficits (Henen et al., 1998).

Although digestion may aid in balancing hydration, its energetic cost is high (Lillywhite, 2017). Reptiles often require slightly higher temperatures to digest food, and depending on their condition, exposure to high temperatures can cause further water loss (Lillywhite, 2017). However, despite the costs, eating can improve body condition, providing more energy reserves to face challenges like water scarcity in the environment (Chabaud et al., 2023). Therefore, this study aims to understand how water balance relates to the feeding ecology of three species of Caatinga lizards by testing three main hypotheses: (i) Can dehydrated lizards improve their body condition by feeding? (ii) Is water balance affected by meal consumption? (iii) Will species occupying different microhabitats respond differently to these questions? Ultimately, we found that species-specific strategies for dealing with water stress highlight the intricate balance between physiology, behavior, and environmental constraints, reinforcing the importance of integrating ecological context into physiological studies.

METHODS

Study Area. - The study was conducted in the Catimbau National Park (hereafter referred to as PARNA Catimbau), a conservation unit located in the Caatinga ecoregion between the geographical coordinates 08°24''S and 08°36'S and 37°09'W and 37°14'W, in the state of Pernambuco, Brazil. The Park covers approximately 62,000 hectares, with elevations ranging between 700 and 1000 meters. The region's climate is classified as hot semi-arid (BSh) according to the Köppen classification, with an average annual precipitation of 600 mm and an average annual temperature of 26 °C (Gomes et al., 2006). The park's landscape includes sandy soil and conglomerate sandstone outcrops (Projeto RadamBrasil, 1983), and the vegetation is typical of the Caatinga biome, dominated by xerophytic species, with families such as Cactaceae, Euphorbiaceae, Mimosaceae, and Fabaceae being the most common (Gomes et al., 2006). Generally, the PARNA landscape follows typical Caatinga characteristics: during the dry season, plants appear dry, leafless, and the environment is hot and arid, while during the rainy season, the vegetation fully blooms, leaves sprout, and some areas may become flooded due to rainwater accumulation.

Natural History of the Species Compared. - *Ameivula ocellifera* (Spix, 1825) is an active foraging lizard species from the family Teiidae, found in Restinga, Cerrado, and Caatinga environments (Menezes et al., 2006; Sales and Freire, 2015). This species is associated with sandy microhabitats, similar to *Tropidurus cocorobensis* Rodrigues, 1987 (Pedrosa et al., 2014), the second model species in this study. *Tropidurus cocorobensis* is a heliophilic lizard from the Tropiduridae family, classified as a sit-and-wait forager and has a relictual distribution in the Caatinga, found only in the states of Alagoas, Bahia, and Pernambuco (Rodrigues, 1987; Ribeiro et al., 2012). The third model species in this study is *Tropidurus semitaeniatus* (Spix, 1825), another Tropiduridae lizard easily recognized by its flattened body and head, which allow it to use rock crevices as refuges (Vanzolini, 1976; Vitt, 1981; Ribeiro et al., 2011). This species shows saxicolous habits, specializing in rocky microhabitats, and is found in the Caatinga and northeastern Atlantic Forest (Rodrigues, 2003; Roberto, 2017). These lizard species share similar diets, primarily consisting of arthropods, particularly insects, and among tropidurids, the consumption of plant material is also common (Ribeiro and Freire, 2011; Sales and Freire, 2015; Oliveira et al., 2022). All three model species occur in sympatry in PARNA Catimbau (Pedrosa et al., 2014).

Data Collection. - Individuals of *Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus* were collected during two expeditions in PARNA Catimbau using pitfall traps with drift fences (Cechin and Martins, 2000; Foster, 2012) and noosing (Fitzgerald, 2012). The traps were opened in the morning and monitored throughout the active period by a researcher. Upon capturing a target species, we immediately removed the specimen and measured its body temperature using a cloacal thermometer, ensuring that bucket temperature or sunlight did not influence the reading. Specimens for which temperature could not be taken immediately were released without data collection.

Adult males of *T. cocorobensis* and *T. semitaeniatus* were identified by the presence of black thigh spots, and females were identified using snout-vent length (SVL) and the presence of eggs (Rodrigues, 1987). For *A. ocellifera*, maturity was determined based on SVL (adult males >45.55 mm; adult females >41.60 mm, following Sales and Freire, 2015). After data collection, all lizards were anesthetized and euthanized using a lethal dose of 2% lidocaine hydrochloride. The specimens were then fixed in 10% formalin and preserved in 70% ethanol. Collected specimens were deposited in the Herpetological Collection of the Federal University of Pernambuco (CHUFPE). Collection was authorized by Brazilian environmental agencies (SISBIO permits #73617, #79254-1), and experimental procedures were approved by the Animal Ethics Committee of UFPE (CEUA-UFPE protocols 0004/2020, 0065/2021).

Water Absorption and Feeding. - After collection, all individuals of each species were housed in individual boxes with access to natural light and kept for 10 days without water and food. After this initial period, the animals were transferred to the experimental site, where temperature and light were controlled. In this environment, half of the individuals of each species were fed Tenebrio molitor beetle larvae for four days, receiving a total of 0.800 g of food per individual (equivalent to approximately 6.05% of the average weight of the lizards). These individuals continued without access to water and formed the Fed Group. The other half of the individuals remained without water and food for four days as well, constituting the Non-Fed Group.

At the end of this period, all lizards were weighed again (BME1) and subjected to an experimental hydration process. This process involved placing them individually in containers with water, covering up to half of their bodies, for two hours. After hydration, the lizards were carefully dried with absorbent paper to remove any excess surface water that could interfere with the measurement, and then weighed again (BME2). Additional weighings were performed at 15-minute intervals over the next hour: BME3 (15 minutes), BME4 (30 minutes), BME5 (45 minutes), and BME6 (60 minutes). This sequential weighing protocol was based on preliminary observations from pilot studies, which indicated weight fluctuations immediately after hydration, stabilizing between BME3 and BME4. Furthermore, the snout-to-vent length (SVL) of each lizard was measured using high-precision digital calipers (0.01 mm accuracy). This measurement was used as a covariate in the analyses to control for the effects of body size on the results.

Body Condition Index (BCI). - For a better analysis of water balance, it is important to consider the influence of body size (SVL) and initial/natural weight (BM1). To this end, we calculated the Body Condition Index (BCI) using the residuals (Ri) from an ordinary least square (OLS) (Schulte-Hostedde et al., 2004) regression between snout-vent length (SVL) and the logarithmic transformations of: initial/natural body mass (BM1), which is considered the ideal BCI, body mass after 10 days without water (BM2), and body mass after feeding (BME1) for each individual. The regressions were conducted separately for each lizard species studied (Lagrue and Poulin, 2015; Warner et al., 2016; Gastón and Vaira, 2020). Since the body condition index encompasses parameters of body structure (in this case, snout-vent length and body mass in nature) for each studied individual, it becomes crucial for a more precise comparison of the species’ water balance in the field, as this state changes depending on the lizard's size and weight. Additionally, we will compare the body conditions of individuals in nature, after ten days of dehydration, and after feeding.

Calculation of the Water Absorption Index (WAI). - To estimate the Water Absorption Index (WAI) of the lizards, body mass measurements taken after the induced hydration process were used. The calculation was based on the average of the two stable weights recorded at 15 minutes (BME3) and 30 minutes (BME4) after hydration. This average was then subtracted from the body mass measured before hydration, after the feeding or non-feeding period, according to the previously established experimental groups (BME1). The formula used for this calculation was:

$$\mathbf{WAI=(BM3+BM4)/2-BME1}$$

This metric reflects the difference between the initial body mass of the lizards and the stable body mass recorded after hydration. Higher WAI values indicate that the lizards absorbed a greater amount of water during the experiment, suggesting that they initially had a lower body water content. Throughout the experiment, the individuals were kept in two separate experimental groups (Fed Group and Non-Fed Group). These conditions were carefully controlled to assess potential differences in water balance between the groups.

Data Analysis. - To calculate the water balance, we subtracted the initial weight

(BME1) from the average of the third and fourth weights (BME3, BME4—15 and 30 minutes, respectively, after hydration) for each individual. We used the average of these weights because, in this interval starting from the third measurement, the body mass of the individuals generally stabilized. The primary idea is that the greater the state of water loss in the wild, the more water the lizard would be able to absorb after induced hydration. Before all analyses, we performed Shapiro-Wilk tests to understand the distribution of the data, allowing us to use appropriate statistical tests (Shapiro and Wilk, 1965). We conducted a Kruskal-Wallis test to determine if the difference in weight lost during dehydration was statistically different among the species. We used a non-parametric Wilcoxon test to compare body masses before (BM1) and after induced hydration (average of BM3 and BM4), separating the individuals by species. ANOVA was used to test for significant differences among species' water balance, and we used post hoc tests to identify which species or groups (with food and without food) differed from each other. Additionally, we utilized the Friedman Test to detect statistically significant variations in the different body condition indices calculated for each species (Conover, 1999). All graphs displaying our results were created using the 'ggplot2' package in R 3.5.1 (R Core Team, 2022).

RESULTS

During ten days of dehydration, individuals of *T. semitaeniatus* lost more water (11.65%) compared with individuals of *A. ocellifera* (5.24%) and *T. cocorobensis* (6.34%) and this difference is statistically significant (Kruskal-Wallis chi-squared = 22.484, $p < 0.05$) (Figure 1). After dehydration, the experiment was conducted with 19 individuals of *Tropidurus semitaeniatus* (11 - Fed Group, eight - Non-Fed Group), 20 individuals of *Tropidurus cocorobensis* (10 - Fed Group, 10 - Non-Fed Group) and 20 individuals of *Ameivula ocellifera* (10 - Fed Group, 10 - Non-Fed Group). The fed group of *T. semitaeniatus* absorbed more water during experimental hydration compared to the non-fed group (Table 1, Figure 1); however, this difference is not statistically significant (p-value = 0.591). To *A. ocellifera* and *T. cocorobensis* individuals of “no food group” absorbed more water (Table 1, Figure 1), and this difference is significant (*A. ocellifera*: p-value = 0.017; *T. cocorobensis*: p-value = 0.019). Considering all three lizard species and their water balance, we observed that the 'species' factor has a significant effect on water balance, meaning the species differ significantly in this aspect ($p < 0.05$). The Body Condition Index (BCI), considering body mass in nature, dehydrated and in experiment, does not differ significantly within the three conditions for the three species (*A. ocellifera*: p = 0.522; *T. cocorobensis*: p = 0.638; *T. semitaeniatus*: p = 0.104) (Figure 2).

DISCUSSION

Our results indicate that, relative to the other two species, *Tropidurus semitaeniatus* lose water at a faster rate, and their water balance remains unaffected by meal consumption. In contrast, *Ameivula ocellifera* and *Tropidurus cocorobensis* retain water more effectively, and only fed individuals—but not their unfed counterparts—exhibit a reduction in water absorption under similar treatments. A comparable pattern in *T. semitaeniatus* has been documented for *Zootoca vivipara* (Chabaud et al., 2023) and *Tropidurus catalanensis* (Padilla Perez et al., 2021). Water loss in lizards is influenced by a complex interaction between physiological adaptations, environmental conditions, and behavior. Studies indicate that a species' climatic niche has a greater influence on evaporative water loss (EWL) than intrinsic physiological traits, with EWL rates increasing with temperature and varying with humidity (Salazar and Miles, 2024; Davis et al., 2024; Weaver, 2023). Cutaneous evaporative water loss (CEWL) represents a significant part of this process and can rapidly adjust to thermal fluctuations (Davis et al., 2024). Body mass and body condition also influence this dynamic, as CEWL rates vary across different body regions (e.g., dorsum and ventrum) and are modulated by factors such as lizard size and the environmental conditions at the time of capture (Weaver et al., 2022).

Body condition remains stable across all three species, even after meal consumption, but its interpretation requires attention to the time scale. We calculated BCI immediately after feeding, so that longer-term values may differ. In fact, other lizard species do increase BCI as a response to meals (Padilla Perez et al., 2021), potentially offsetting the energetic costs associated with limited water availability (Chabaud et al., 2023). Yet, a BCI based on natural weight, provides an important ecological reference, reflecting the field status of individuals, their energy reserves, and influences life history events such as migration and reproduction (Gallagher et al., 2014). This variable is particularly informative, as lizards depend on external abiotic conditions to regulate their body temperature with impacts on physiology and time budgets. Therefore, microhabitat use must relate to the interspecific differences here reported. Whereas *Ameivula ocellifera* and *Tropidurus cocorobensis* share a sandy microhabitat and its associate resources (Oliveira et al., 2022), *Tropidurus semitaeniatus* is restricted to rocky outcrops (Ribeiro and Freire, 2011) likely more favorable for water balance. Here, a possible link between field conditions and laboratory experiments is that higher absolute values of water loss would be expected under higher hydration levels prior to dehydration.

Regarding the experimental availability of meals, one shall consider that the three studied species are predominantly insectivorous and adjust their diets based on field food conditions (Ribeiro and Freire, 2011; Oliveira et al., 2022; Oliveira et al., 2024), likely aligning their dietary composition with the impacts of local seasonality on productivity (Ferreira et al., 2017; Oliveira et al., 2024). The water costs of digestion can cancel out the benefits of water in the diet, as observed in studies with Heloderma suspectum, where meal consumption did not maintain water balance over time (Wright et al., 2013). In some snakes, for example, large carnivorous meals require high postprandial body temperatures and significant energy expenditure, two factors that would oppose water conservation (Lillywhite, 2017). Back to our study, the stability of BCI as reported suggests that feeding does not negatively impact the lizards' energetic state. We acknowledge the complexity of the relationships under analysis, particularly for BCI reflects both the ecological history of an individual—for example the quality of its recent diet—and its current physiological state, with these factors being interdependent (Lagrue and Poulin, 2015; Warner et al., 2016; Gastón and Vaira, 2020). In addition, the exclusively insectivorous diet offered in this study may have been insufficient to alter the water balance, precisely because of the high metabolic cost associated with digestion.

With the above discussion in mind, the types of food consumed in the wild can indicate—even if indirectly—lizard strategies to enhance water absorption. Teiid lizards do not frequently ingest high-water-content items, and plant material is less common in their diets, often consisting of only small fragments (Sales et al., 2012; Oliveira et al., 2022). In contrast, the diets of *T. cocorobensis* and *T. semitaeniatus* in Caatinga areas include a considerable frequency of plant consumption, especially leaves, with records of these species consuming all parts of such items (Barros-Ribeiro et al., 2008; Fonseca et al., 2012; Oliveira et al., 2022; Bezerra-Silva et al., 2024; Oliveira et al., 2024). For some species, this consumption of plant material is essential, as seen in desert iguanas, which obtain substantial hydration from succulent vegetation (Minnich and Shoemaker, 1970). For dehydrated individuals of *Tropidurus catalanensis* reduced their consumption of animal items and invested in a proportionally more plant-rich diet, suggesting that plant-based foods may be a viable alternative under water-scarce conditions (Fernandes et al., 2024). On the other hand, while plant-based meals may provide hydration, they can also impose osmotic challenges that lead to dehydration in certain reptiles, such as the chuckwalla lizard, which, despite frequently consuming fruits, experiences significant body mass loss due to dehydration (Smiths, 1985). Therefore, the role of diet as an influencer of water balance is complex and species-dependent.

The results presented here, are derived from laboratory experiments applied just after capture, a traditional proposal regarding body temperature, that open avenues for future investigation in terms of water balance. Species occupying the same microhabitat my converge in responses to water stress, using meal consumption as a coping strategy, yet this possible generalization does not apply to broader views on habitat, as the Caatinga. in *Tropidurus semitaeniatus*, meal consumption does not influence water absorption, suggesting that microhabitat conditions—particularly the availability and accessibility of shelters—play a more effective role in maintaining water balance. While consuming high-water-content food items may help mitigate water deficits, this strategy loses effectiveness in critical periods, such as the driest months in the Caatinga, when overall dietary resources become scarce. In contrast, psammophilous species may struggle with shelter availability and instead rely on alternative strategies, such as increasing energy reserves through feeding to sustain activity. Understanding these physiological and behavioral strategies is crucial in the face of climate change, particularly for species already persisting under limiting conditions, like those imposed by the dry season in the Brazilian semi-arid region.

ACKNOWLEDGEMENTS

The authors are thankful to the *Instituto Chico Mendes de Conservação da Biodiversidade* and to the *Comitê de Ética em Uso Animal of the Universidade Federal de Pernambuco* for animal collection and handling permits permissions (ICMBio permits nº 79254-1; CEUA-UFPE nº 0065/2021). The authors are also thankful to the *Projeto Ecológico de Longa Duração-PELD/CNPq* Catimbau and its coordinator M. Tabarelli for lodging and equipment used during field work. PMAO is thankful to *Pro-reitoria para Assuntos de Pesquisa e Pós-Graduação da UFPE*, *Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco* (IBPG-1566-2.04/19) and Idea Wild for financial support. PMSN is grateful to *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq Fellowship #313622/2018-3).

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Figures

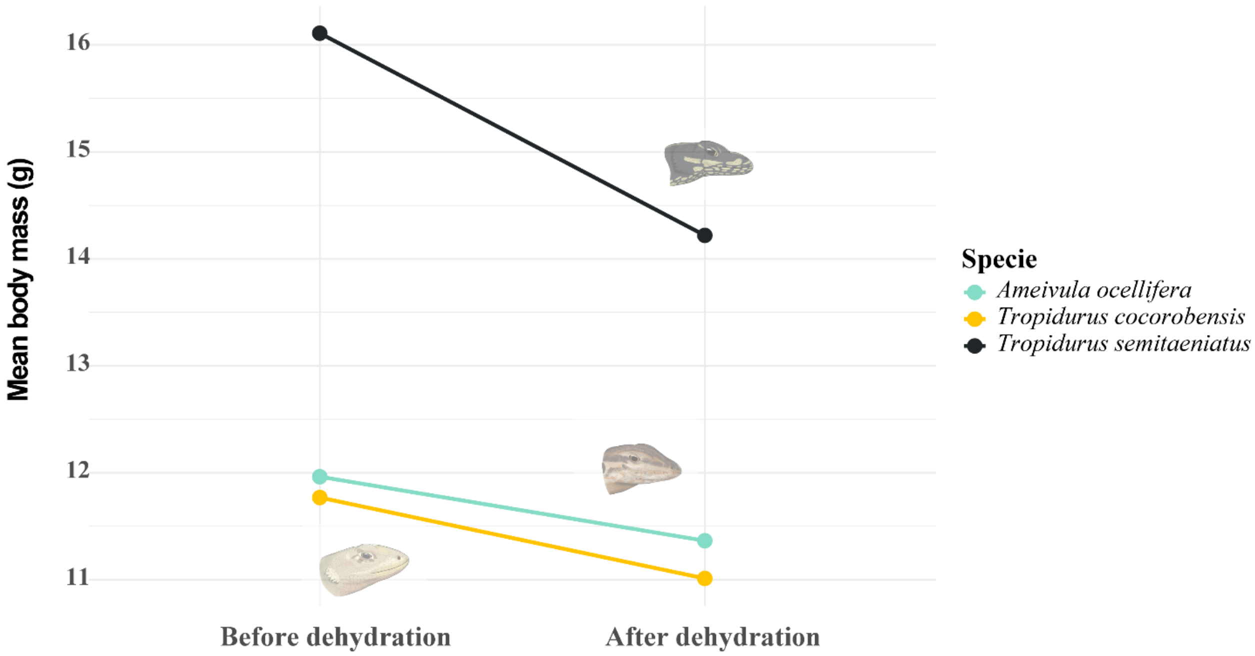

Figure 1. Mean body masses before and after experimental dehydration of individuals from *Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus*.

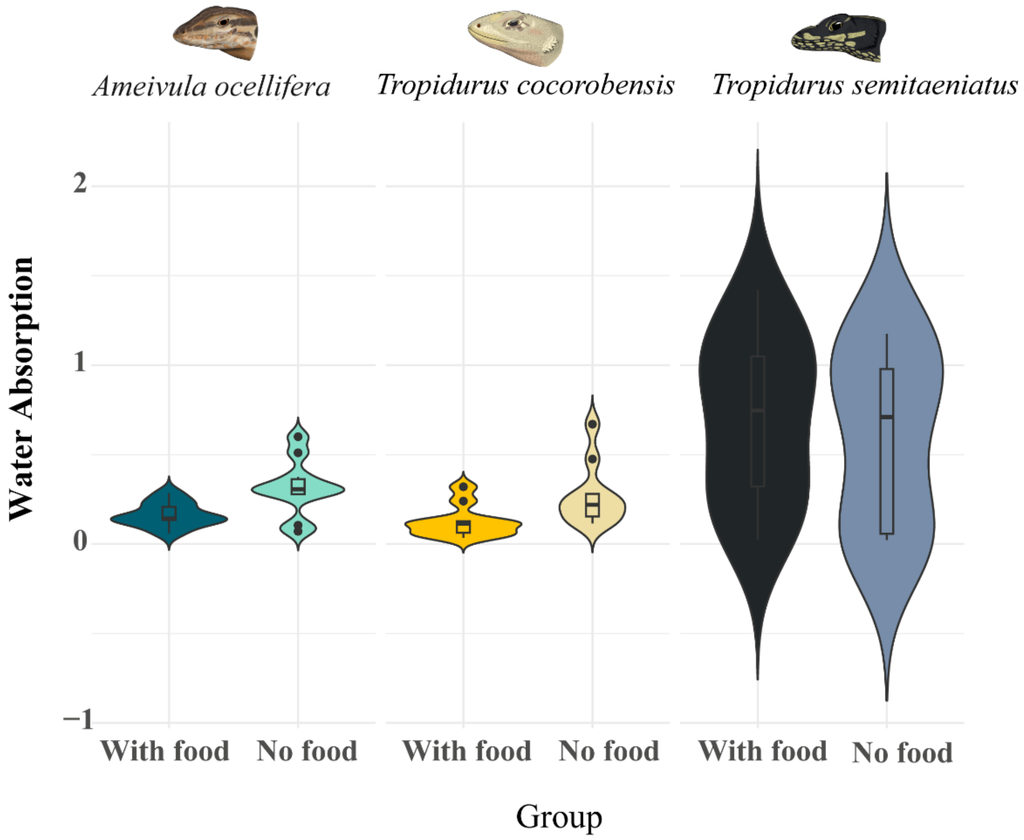

Figure 2. Water Absorption of individuals from *Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus* subjected to experiments, with data separated into fed and unfed individuals.

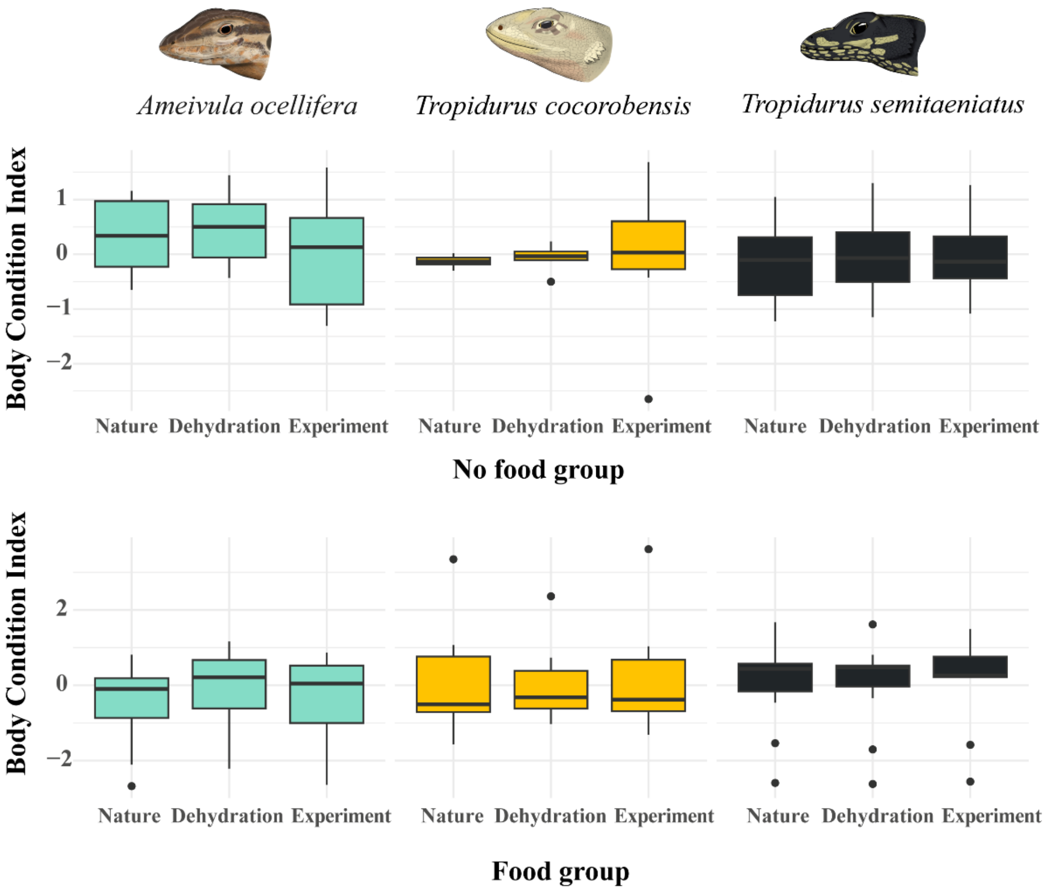

Figure 3. Body condition indices based on body mass in the wild, after dehydration, and after feeding or non-feeding (Unfed Group and Fed Group) of individuals from *Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus*.

Table 1. Mean and standard deviation of body mass (g) of individuals from *Ameivula ocellifera*, *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus* subjected to the water balance experiment.

		Body Mass (g)		
	Group	**Before Hydration**	**After Hydration**	**Water Absorption**
Ameivula ocellifera ***(N=20)***	With food	12.07 ± 2.90	12.23 ± 2.90	0.16
	No food	11.72 ± 2.09	12.03 ± 2.14	0.32
Tropidurus cocorobensis ***(N=20)***	With food	12.22 ± 2.62	12.34 ± 2.65	0.13
	No food	11.82 ± 1.73	12.09 ± 1.83	0.27
Tropidurus semitaeniatus ***(N=19)***	With food	14.27 ± 2.44	14.97 ± 2.47	0.70
	No food	14.00 ± 1.70	14.60 ± 1.95	0.60

4 CAPÍTULO 3 – A ser submetido no *Journal of Thermal Biology*

Too hot to handle? Preferred Temperature and Future Distribution based on Climate Change of two *Tropidurus* Lizards from the Brazilian Semi-Arid Region

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Abstract

Climate change is reshaping the thermal landscapes available to ectotherms, particularly in semi-arid environments such as the Caatinga biome of Brazil. In this study, we investigate the thermal ecology and projected distributional responses of two sympatric heliothermic lizard species—*Tropidurus cocorobensis* and *Tropidurus semitaeniatus*—which occupy distinct microhabitats. Using ex-situ thermal gradient experiments, we determined the preferred body temperatures ($T_p$ref) of both species, and integrated these data with species distribution models (SDMs) based on current and future climate scenarios (SSP 245, 370, and 585 for 2050 and 2090). *T. cocorobensis* exhibited a mean selected body temperature of 33.37 °C and a broader thermal response, with projections indicating potential range expansions of up to 81%. In contrast, *T. semitaeniatus* showed a lower $T_p$ref (32.34 °C) and is projected to lose up to 54% of its suitable habitat, shifting eastward toward the Atlantic Forest. Behavioral observations suggest that differences in microhabitat use and thermoregulatory strategies may contribute to these divergent responses. Our findings highlight how eco-physiological traits and habitat specificity influence species' vulnerability or resilience to climate change. These results underscore the importance of integrating physiological data and climate projections to guide conservation strategies for ectothermic species in warming and increasingly arid regions.

Keywords: climate change; Caatinga; thermoregulation; temperature

Introduction

Thermoregulation is essential for ectothermic vertebrates like lizards, which depend on external conditions to maintain body temperatures within functional limits (Huey, 1982; Huey et al., 2010). It influences key physiological processes and behaviors such as reproduction, territorial defense, and predator avoidance (Black et al., 2019). Deviations from optimal temperatures can impair neuromuscular function and locomotion (Bennett, 1980; Huey, 1982), limiting the ability to capture prey, defend territories (Marler and Moore, 1988), or evade predators (Hertz et al., 1982). Suboptimal temperatures may also disrupt hormonal regulation of reproductive behaviors (Crews, 1980; Moore and Marler, 1987). Thermoregulatory efficiency is often inferred by how closely a lizard’s body temperature (Tb) matches its preferred temperature (Tpref), both of which shape its ecological niche and geographic distribution (Navas, 2002). Habitat and microhabitat selection are driven by thermal resource availability, and when species share similar thermal preferences and activity periods, competition for optimal microhabitats may occur. Heliothermic lizards, which rely on solar radiation for thermoregulation, may face increasing competition as climate warming reduces the availability of cooler microhabitats (Kearney, 2013).

For instance, heliothermic lizards—those that depend on solar radiation for thermoregulation—may face increased challenges as climate warming alters the thermal landscape, reducing the availability of cooler microhabitats (Kearney, 2013). From a mechanistic perspective, such changes can lead to mismatches between the fundamental thermal niche—defined by the range of body temperatures in which physiological performance is maximized—and the realized thermal niche, which is constrained by actual environmental temperatures (Huey et al., 2012; Sunday et al., 2014). Operative environmental temperatures, which integrate radiation, convection, and conduction in a specific habitat, often serve as a proxy for the thermal conditions available to an ectotherm (Bakken, 1992). When operative temperatures exceed the upper limits of thermal performance or reduce the time available within the thermal optimum, lizards may be forced to reduce activity, shift behavior, or abandon otherwise suitable habitats—even in the absence of direct competition. Thus, climate change can restrict activity windows and reshape thermal niches (Sinervo et al., 2018; Doucette et al., 2023).

In arid regions, vegetation shade plays a crucial role in thermoregulation. Shaded microhabitats provided by vegetation are essential for maintaining activity budgets, especially under future climate scenarios (Grimm-Seyfarth et al., 2017). Beyond simply offering refuge, vegetation buffers operative environmental temperatures by reducing incident solar radiation and increasing humidity, thereby softening thermal extremes throughout the day (Chamaillé-Jammes et al., 2006; Sears et al., 2011). This thermal buffering effect extends the temporal window of thermally suitable conditions, allowing heliothermic lizards to remain active for longer periods without exceeding critical thermal limits (Scheffers et al., 2014). In some systems, shaded microhabitats created by vegetation can reduce operative temperatures by several degrees, significantly altering the availability of preferred thermal microenvironments (Grimm-Seyfarth et al., 2017).

Climate change is altering the spatiotemporal availability of thermally suitable microhabitats, especially in open and arid environments. Rising air and surface temperatures, along with reduced daily thermal variation, limit lizards' ability to maintain optimal body temperatures (Huey et al., 2012; Kearney et al., 2009). These shifts can shorten activity windows and compress or shift thermal niches, prompting behavioral adjustments in habitat use, activity times, or thermoregulatory effort (Sunday et al., 2014; Bonino et al., 2015; Gunderson and Leal, 2016; Díaz et al., 2022). High-altitude populations may shift upward, though extreme elevations bring additional physiological challenges (Jiang et al., 2023). Temperate lizards face both thermal and hydric stress, while tropical and subtropical species are especially vulnerable to rising temperatures (Mi et al., 2022). However, vertical migration is also limited by habitat structure, resource availability, and landscape connectivity, which may not align with elevational gradients (Freedman and Portier, 2019; Buckley and Jetz, 2007). Tropical regions like the Caatinga already present thermal challenges for ectotherms (Da Silva et al., 2018; Scholes, 2020). This exclusively Brazilian biome, with a semi-arid climate, is marked by extreme dry and rainy seasons, high solar radiation, elevated temperatures, and low precipitation (Gomes et al., 2006). Such conditions impose strong physiological stress, especially on lizards that rely on behavioral thermoregulation to maintain optimal body temperatures (Ribeiro and Freire, 2010; Ferreira et al., 2014). Thermal stress can restrict foraging and social interactions during peak heat (Huey et al., 2010; Sunday et al., 2014), reducing energy intake and thereby limiting growth and reproductive output (Angilletta et al., 2002). High body temperatures also impair digestion and metabolism (Huey and Slatkin, 1976), and prolonged exposure can decrease sperm quality and clutch viability, reducing reproductive success (Lorenzon et al., 2001; Dupoué et al., 2017).

Furthermore, the Caatinga is considered one of the most vulnerable Brazilian biomes to extreme climate variability, with projections indicating reduced rainfall, temperature increases of up to 4 °C under the pessimistic scenarios, heightened aridity, and a high risk of desertification (Marengo et al., 2017; IPCC, 2023). While these projections are robust at the regional scale, their translation to the thermal ecology of lizards remains uncertain. However, such warming trends may narrow the thermal safety margins of heliothermic species, especially those already operating near their upper thermal limits (CTmax). This could reduce the time available for daily activity, disrupt energy acquisition, and increase vulnerability to local extinction (Sinervo et al., 2010; Sunday et al., 2014). Currently, approximately 94% of the region is classified as having moderate to high susceptibility to desertification (Vieira et al., 2021). These climate-related pressures are compounded by ongoing anthropogenic impacts, such as deforestation and habitat fragmentation, which have transformed the original landscape into highly heterogeneous mosaics (Andrade et al., 2005).

Given these environmental and physiological pressures, Caatinga lizards provide a valuable model for examining fine-scale physiological and behavioral responses to thermal stress. Such investigations can yield insights into the mechanisms that shape resilience and adaptive potential in lizard populations inhabiting semi-arid environments, under both current and projected climate conditions, thereby informing broader questions in thermal ecology and species persistence. In this context, our study aims to explore aspects of thermal ecology linked to factors of preferred body temperature and responses to climate change projected for the coming decades in two species of heliothermal lizards from the Caatinga—*Tropidurus cocorobensis* and *Tropidurus semitaeniatus*—which occupy different microhabitats. Specifically, we aim to answer: What is the preferred temperature of each species? How will the distribution of each species be altered by climate change? What is the relationship between the preferred temperatures of each species and their predicted responses? To do this, we use two distinct approaches. First, we use ex-situ experiments to identify the preferred temperature of each species, and then we build species distribution models (SDM) to project species distributions for future climate change scenarios.

Methods

Study Area

The study was conducted in the Catimbau National Park (hereafter referred to as PARNA Catimbau), a conservation unit located in the Caatinga ecoregion, state of Pernambuco, northeastern Brazil (08°24''S and 08°36'S and 37°09'W and 37°14'W). The Park covers approximately 62,000 hectares, with elevations ranging between 700 and 1000 meters. The region's climate is classified as hot semi-arid (BSh) according to the Köppen classification, with an average annual precipitation of 600 mm and an average annual temperature of 26 °C (Gomes et al., 2006). The park's landscape includes sandy soil and conglomerate sandstone outcrops and the vegetation is typical of the Caatinga biome, dominated by xerophytic species, with families such as Cactaceae, Euphorbiaceae, Mimosaceae, and Fabaceae being the most common (Gomes et al., 2006). Generally, the PARNA landscape follows typical Caatinga characteristics: during the dry season, plants appear dry, leafless, and the environment is hot and arid, while during the rainy season, the vegetation fully blooms, leaves sprout, and some areas may become flooded due to rainwater accumulation.

Natural History of the Species Compared

Tropidurus cocorobensis Rodrigues, 1987 is a heliophilic lizard from the Tropiduridae family, classified as a sit-and-wait forager, associated with sandy environments and endemic of Caatinga. It is found only in the states of Alagoas, Bahia, and Pernambuco, inhabiting areas with shrubby vegetation that provide essential microhabitats for thermoregulation (Rodrigues, 1987; Ribeiro et al., 2012). The other target species is *Tropidurus semitaeniatus* (Spix, 1825), also from the Tropiduridae family, easily recognized by its flattened head and body, which allow it to use rock crevices as refuges (Ribeiro et al., 2011). This species displays saxicolous habits, specializing in rocky microhabitats (Passos et al., 2016), and is found in both the Caatinga and the northeastern Atlantic Forest (Rodrigues, 2005; Roberto, 2017). *T. semitaeniatus* maintains a body temperature (Tb) below its preferred temperature (Tp), with a high tolerance to heating, indicating a robust capacity to withstand temperature fluctuations (Bruinjé et al., 2024). Both target species occur in sympatry within the Catimbau National Park (PARNA Catimbau) (Pedrosa et al., 2014).

Data Collection for physiological data

Individuals of *Tropidurus cocorobensis*, and *Tropidurus semitaeniatus* were collected during two expeditions in PARNA Catimbau using pitfall traps with drift fences (Cechin and Martins, 2000; Foster, 2012) and noosing (Fitzgerald, 2012). The traps were opened in the morning and monitored throughout the active period by a researcher. Upon capturing a target species, we immediately removed the specimen and measured its body temperature using a cloacal thermometer, ensuring that bucket temperature or sunlight did not influence the reading. Specimens for which temperature could not be taken immediately were released without data collection.

Adult males of *T. cocorobensis* and *T. semitaeniatus* were identified by the presence of black thigh spots, and females were identified using snout-vent length (SVL) and the presence of eggs (Rodrigues, 1987). After data collection, all lizards were anesthetized and euthanized using a lethal dose of 2% lidocaine hydrochloride. The specimens were then fixed in 10% formalin and preserved in 70% ethanol. Collected specimens were deposited in the Herpetological Collection of the Federal University of Pernambuco (CHUFPE). Collection was authorized by Brazilian environmental agencies (SISBIO permits #73617, #79254-1), and experimental procedures were approved by the Animal Ethics Committee of UFPE (CEUA-UFPE protocols 0004/2020, 0065/2021).

Preferred Body Temperature

The individuals were subjected to a thermal gradient experiment to determine their preferred body temperature (T_pref), understood here as the range of body temperatures selected through active thermotactic behavior under non-restrictive thermal conditions (Sannolo and Carretero, 2019; Taylor et al., 2021). This approach assumes that the observed temperatures reflect behavioral choices made in response to thermal cues, rather than random occupation of space (Navas et al., 2022). We adapted the methodology from Sannolo and Carretero (2019). In this case, a “track” (116 x 30 x 40 cm) was set up with an artificial substrate of bricks. An infrared lamp of

250 W was suspended above one end of the track to establish a temperature gradient along the designated space. The average temperatures for each of the six gradients were: 48.7ºC; 41.5ºC; 35.5ºC; 28.6ºC; 26.6ºC; 25.9ºC. The experiment took place in a temperature-controlled room set at 26 °C, with natural light entering through windows to synchronize the photoperiod with outdoor conditions.

After capture and before the start of the experiment, the group of lizards was kept in the “track” with free access to water for 24 hours to acclimate to the environment. Following acclimatization, the lights on the tracks remained on for 9 hours a day (09:00 – 18:00), and between 12:00 and 18:00, the skin surface temperatures of the specimens were measured hourly using an infrared thermometer with a measurement range of -50ºC to 400ºC and an accuracy of ± 1.5ºC. Surface temperature data were collected over 2 days, totaling 14 measurements for each individual. The entire data collection and experimental procedure was submitted to the Animal Use Ethics Committee of the Federal University of Pernambuco (registration number 0026/2023).

Species Distribution Modeling

Occurrence records for *Tropidurus semitaeniatus* and *Tropidurus cocorobensis* were obtained from online databases, including GBIF (Global Biodiversity Information Facility, www.gbif.org), speciesLink (www.specieslink.net), VertNet (www.vertnet.org), SiBBr (Sistema de Informação sobre a Biodiversidade Brasileira, www.sibbr.gov.br), and the ICMBio Biodiversity Portal (https://portaldabiodiversidade.icmbio.gov.br). Initially, all available occurrence records up to 2025 were compiled. A rigorous quality control process was then performed to remove duplicate records, imprecise data, and points georeferenced in administrative centers (e.g., state or municipal capitals), as well as those located in institutions (e.g., universities, museums) or outside Brazilian borders. This step employed the CoordinateCleaner package (Zizka et al., 2019) in the R environment. To reduce spatial bias, records were thinned to a minimum distance of 5 km using the spThin package (Aiello-Lammens et al., 2015). Additionally, we applied an environmental filter to exclude occurrences with identical bioclimatic values, using 12 environmental similarity classes through the flexsdm package (Velazco et al., 2022). Only records collected between 1970 and 2025 were considered. After filtering, we retained 98 records for *T. semitaeniatus* and 24 for *T. cocorobensis* for distribution modeling.

We used bioclimatic variables from the WorldClim database (version 2.1), a global reference for ecological modeling. The 19 standard bioclimatic variables (BIO1–BIO19) available in WorldClim version 2.1 (Fick and Hijmans, 2017), were selected at a spatial resolution of 2.5 arc-min (~4.5 x 4.5 km at the equator), representing climate averages for the 1970–2000 period. These variables include key climatic parameters such as mean temperatures, temperature extremes, and precipitation patterns, which are fundamental for understanding the distribution of *Tropidurus* lizards. To avoid multicollinearity, a spearman correlation analysis was performed, and variable pairs with |r| > 0.7 were excluded, retaining those with the highest ecological relevance for the species (Supplementary Material 1).

To assess future climate change impacts, we incorporated WorldClim projections for 2050 (2041–2060) and 2090 (2081–2100), considering three Shared Socioeconomic Pathways (SSPs): optimistic (SSP245), intermediate (SSP370), and pessimistic (SSP585). We used five General Circulation Models (GCMs) ACCESS-CM2, BCC-CSM2-MR, CMCC-ESM2, EC-Earth3-Veg, MIROC6, and MRI-ESM2-0 — and subsequently calculated ensemble means for each scenario. This ensemble approach helps reduce uncertainty inherent in individual models, producing more robust projections. All climate data were processed and standardized in R. Layers were cropped to the region of interest (Area delimited for each species, see below), reprojected to a common coordinate system, and resampled to a uniform spatial resolution. For future scenarios, scale corrections were applied to ensure comparability with current data.

Species distribution models (SDMs) were developed using the Maxent algorithm, a widely used method for ecological niche modeling based on presence-only data. This algorithm compares known occurrence sites with background points sampled from a defined study area. Proper delineation of this area is essential, as it must represent the region the species could potentially colonize if environmental conditions were suitable (Anderson and Raza, 2010). To represent species dispersal potential at evolutionary scales, we implemented a procedure to define geographic limits based on Searcy and Shaffer (2014). First, we calculated the distance between the two most distant points, then divided that distance by two and used it as a buffer around all native points of the species. This approach allows us to define an area that includes all known points of the species used in the construction of the models.

However, future projections were designed in larger rasters (delimitation of Brazil) to identify possible new areas and geographical changes in the future distributions of the species studied.This approach assumes that throughout their evolutionary history, the species could have occupied the entire region between known populations, provided favorable conditions.

To address the limitations of random background point selection, which can introduce sampling bias, we adopted a more robust strategy using target-group background points (Phillips et al., 2006). Specifically, we used all available records for each species, ensuring that background points were drawn from areas effectively surveyed by researchers. This approach increases model reliability by accounting for true sampling effort.

To ensure maximum robustness and accuracy of the distribution models, we implemented a parameter optimization protocol. Recognizing that Maxent's default settings may not be ideal for all species, we systematically adjusted key parameters. First, we tested two feature configurations: (1) Maxent's default setting, which automatically selects features based on the training data, and (2) a custom configuration using combinations of linear (L), quadratic (Q), and product (P) features, known to produce smoother and more ecologically plausible response curves.

We also evaluated regularization multipliers by testing 45 values ranging from 0 to 1 (in 0.2 increments), and from 1 to 20 (in 0.5 increments). This wide range enabled precise identification of the optimal regularization level for each species, balancing model complexity and predictive power. Model selection was based on the corrected Akaike Information Criterion (AICc), which penalizes overfitting by incorporating model complexity. Model validation was performed using 10-fold cross-validation, randomly dividing occurrence data into 10 subsets, using 9 for training and 1 for testing in each iteration. We calculated the mean Area Under the ROC Curve (AUC), a robust metric for assessing model performance. AUC values close to 1 indicate excellent discriminatory ability, while values near 0.5 indicate random performance. We also calculated the True Skill Statistic (TSS), which ranges from –1 to 1; values near 0 or negative indicate poor predictive ability, whereas values above 0.5 are considered acceptable and values near 1 are considered very good (Allouche et al., 2006).

Models were projected onto future climate scenarios, and we calculated the area of suitable habitat for each scenario to assess potential range expansion and contraction. Additionally, we generated maps of climatically stable areas by overlapping binary projections for each future scenario. These binary maps were created using the Lowest Presence Threshold (LPT), which sets the threshold at the lowest suitability value associated with a known presence, converting continuous suitability maps into binary presence–absence maps.

Data Analysis

To assess whether selected body temperatures varied throughout the day, we measured the surface body temperature of *Tropidurus cocorobensis* and *T. semitaeniatus* individuals every hour from 12:00 to 18:00 over the course of two consecutive days. These data were analyzed using linear mixed-effects models, with 'hour', 'day', and their interaction as fixed effects, and 'individual' as a random effect to account for repeated measures. The factor 'hour' was treated as categorical to allow flexible modeling of non-linear thermal variation across time. Similarly, 'day' (day 1 vs. day 2) was also modeled as a categorical variable. The interaction term (hour × day) was included to evaluate whether the daily thermal profiles differed between the two days (i.e., non-parallel temporal trends). The models were fitted using the lmer function from the lme4 package in R. Type III ANOVA with Satterthwaite's approximation for degrees of freedom was performed using the lmerTest package (Kuznetsova et al., 2017), as this approach allows assessment of marginal effects in the presence of interaction terms and potential unbalanced data. Statistical significance was assessed at $\alpha = 0.05$.

To evaluate whether body temperatures differed between species at the time of capture, we used cloacal temperature data collected immediately after individuals were captured in the field. Normality of the temperature distributions was tested using the Shapiro-Wilk test. Since data for *T. cocorobensis* did not follow a normal distribution ($W = 0.95812$, $p = 0.04652$), we applied a non-parametric Wilcoxon rank-sum test (Mann-Whitney U test) to compare temperatures between species. All statistical analyses were conducted in R (R Core Team, 2024).

Results

Thermal Ecology

The average surface body temperature selected by *T. cocorobensis* (N=10) individuals was 33.37 °C and for *T. semitaeniatus* (N=10), it was 32.34°C. Their average cloacal temperatures at the time of capture were 33.97 °C and 30.33 °C, respectively (Table 1). The analysis of variance performed separately for each species showed that, for *T. cocorobensis*, there was no significant effect of time of day on the body temperatures selected by the lizards ($F_{6,117}$ = 1.14, p = 0.346), indicating temperature selection remained stable from 12:00 to 18:00. No significant difference was found between the two experimental days ($F_{1,117}$ = 0.14, p = 0.712), and the interaction between time of day and day was also non-significant ($F_{6,117}$ = 0.39, p = 0.885). In contrast, for *T. semitaeniatus*, there was no significant main effect of Hour (treated as a categorical variable with 7 levels; $F_{6,117}$ = 1.00, p = 0.432) or Day (two-level factor representing the two consecutive sampling days; $F_{1,117}$ = 0.42, p = 0.521) on selected body temperatures. However, the interaction between Hour and Day was significant ($F_{6,117}$ = 2.68, p = 0.018), indicating that the thermal selection pattern across the day differed between the two sampling days (Figure 1). This result suggests a potential influence of daily environmental variation on thermoregulatory behavior, even under similar experimental conditions.

Cloacal body temperatures of *Tropidurus cocorobensis* (N=53) and *T. semitaeniatus* (N=64) individuals were compared using a Wilcoxon rank-sum test due to the non-normal distribution of temperature data for *T. cocorobensis*. The test revealed a significant difference between the two species (W = 3181.5, $p < 0.001$), indicating that cloacal temperatures measured immediately after capture differ significantly between *T. cocorobensis* and *T. semitaeniatus* (Figure 2).

Model Performance

The models exhibited moderate to high predictive performance, with robust median values: AUC = 0.829 and TSS = 0.625 for *Tropidurus semitaeniatus*, and AUC = 0.765 and TSS = 0.554 for *Tropidurus cocorobensis*. These results indicate that the models possess good discriminatory ability and consistent performance in projecting climatically suitable areas for the analyzed species.

Impact of Climate Change on Species Distribution

Under future climate scenarios (SSP 245, 370, and 585), projections for 2050 and 2090 revealed contrasting patterns between *Tropidurus semitaeniatus* and *Tropidurus cocorobensis*, resulting in a reshaping of the distribution ranges of these endemic lizards from Northeastern Brazil. *Tropidurus cocorobensis*, which appears to be more resilient, may benefit from rising temperatures and the expansion of open habitats. According to the climatic models, this species showed a potential expansion in its distribution, colonizing new areas toward the western Caatinga. The projected increase in suitable areas ranged from 13% to 81%, depending on the scenario considered (Figure 3 and Table 2). In contrast, *T. semitaeniatus*, which is more dependent on specific microhabitats, is projected to experience a contraction in its distribution range (Figure 4). The species is expected to shift eastward, toward the Atlantic Forest biome. Depending on the climate scenario, *T. semitaeniatus* is projected to lose between 33% and 54% of its suitable habitat (Figure 5, Table 2, and Supplementary Material 1).

Discussion

We observed that the species *Tropidurus cocorobensis* and *T. semitaeniatus* exhibit high mean selected body temperatures (Figure 1). As previously described in the literature, individuals of *T. semitaeniatus* prefer higher temperatures and display high thermal tolerance; however, the presence of a narrow thermal safety margin may represent a limiting factor and a risk under scenarios of extreme warming (Ribeiro and Freire, 2010; Bruinjé et al., 2024). The thermal ecology of *T. cocorobensis* remains poorly understood, but in general, species of the genus *Tropidurus* show potential to expand their thermal suitability, especially in areas with natural vegetation. This potential is related to the fact that they are generalist lizards, with high dominance and frequency in the Caatinga (Passos et al., 2016; Maia-Carneiro and Rocha, 2020; Santos et al., 2025). Although physiological traits are fundamental, they are not the sole determinants of thermal fitness in lizards. Behavioral variables, microhabitat use, and phenotypic plasticity also exert significant influence and interact in complex ways, particularly when considering the challenges imposed by future climate scenarios (Angilletta et al., 2002; Maia-Carneiro and Rocha, 2020). The target species of the present study, although occurring in sympatry at the study site, occupy distinct microhabitats (Rodrigues, 1987; Ribeiro and Freire, 2011; Pedrosa et al., 2014). Sandy areas are capable of absorbing and retaining heat for longer periods, leading to higher surface temperatures. The same may occur in rocky outcrops; however, their structural complexity can provide more shade and cooler sites, which may explain the greater variation in temperatures recorded for individuals of *T. semitaeniatus* (Figure 2).

Microhabitat selection by lizards is often influenced both by the thermal quality of the environment and by the species' daily activity patterns (Melville and Schulte, 2001). In the present study, we observed that *Tropidurus semitaeniatus* tends to alternate between lower and higher temperatures between 12:00 PM and 4:00 PM, stabilizing its thermal preference between 5:00 PM and 6:00 PM. In contrast, *T. cocorobensis* exhibited the opposite behavior: it maintained relatively constant temperatures between 12:00 PM and 3:00 PM and began to alternate its thermal choices more widely after that period. Although the data were obtained under controlled laboratory conditions, these patterns may reflect natural behaviors. Considering that sand—a typical substrate of *T. cocorobensis* habitats—absorbs more heat, has greater solar exposure, and offers fewer thermal refuges, this species appears to adopt a strategy of maintaining lower average body temperatures during the hours of peak solar radiation. On the other hand, *T. semitaeniatus* seems to alternate between shaded and warmer areas throughout the day, which could reflect a behavioral tendency to select higher body temperatures—a pattern already described by Ribeiro and Freire (2010), Maia-Carneiro and Rocha (2020), and Bruinjé et al. (2024). This behavioral flexibility may allow individuals of *T. semitaeniatus* to exploit microhabitats with varying thermal conditions, returning to cooler locations as needed. In contrast, *T. cocorobensis*, although it does not appear to select higher temperatures throughout the morning or afternoon, shows a pattern that suggests tolerance to higher body temperatures than *T. semitaeniatus*, at least within the environmental context of the study site.

These differences in thermal use patterns and microhabitat selection observed between the two species provide important insights into their potential responses to climate change scenarios. When integrated with species distribution modeling results (Figures 3, 4, 5), these traits may help explain why *T. cocorobensis* tends to expand its climatic suitability under future warming scenarios (Figure 3)—a pattern also reported by Almeida et al. (2025)—while *T. semitaeniatus* shows a projected contraction in its potential range (Figure 4). The combination of greater tolerance to warm environments, preference for open substrates, and low dependence on milder microclimates may favor the potential persistence and dispersal capacity of *T. cocorobensis* in regions expected to become hotter and drier. In contrast, the reliance on more complex microhabitats and a narrow thermal safety margin may render *T. semitaeniatus* more vulnerable to climate change, potentially limiting its future distribution in areas where warming exceeds its physiological tolerance and compensatory behavioral capacity.

Studies suggest that the ability to adjust thermal preferences or critical tolerance through acclimation or evolutionary plasticity may be essential for the persistence of ectotherms under warming scenarios (Gunderson and Stillman, 2015; Logan et al., 2014). However, this plasticity has associated limits and costs. Although *T. semitaeniatus* exhibits a certain degree of behavioral flexibility, its low thermal safety margin may indicate narrow limits for effective physiological plasticity in the face of increasing extreme temperatures. Moreover, tropical lizards appear to have lower metabolic plasticity compared to lizards from temperate regions, suggesting reduced thermal resilience (Christian et al., 2024). This is especially relevant because environmental heterogeneity and the availability of thermal refuges are critical factors for lizard survival in arid environments (Scheffers et al., 2014; Kearney et al., 2009), and for much of the year the Caatinga presents a homogeneous, drier environment with little to no rainfall (Silva et al., 2018). *T. semitaeniatus*, by inhabiting rocky areas, can access varied microclimates that allow for more efficient thermoregulation. However, in a severe warming scenario, even these refuges may become less effective in maintaining adequate thermal conditions. In contrast, *T. cocorobensis*, which inhabits open sandy areas, may rely less on these microclimates and thus potentially respond better to more homogeneous and warmer environments.

Beyond the natural environmental conditions and the biology of the lizards, changes in land use and fragmentation of natural habitats can also impact species dispersal and the maintenance of their distributions (Sinervo et al., 2010; Urbina-Cardona and Loyola, 2008). The potential expansion of *T. cocorobensis* may be facilitated by its tolerance to anthropized environments, a trait observed in other *Tropidurus* species, such as *Tropidurus hispidus* (De Andrade, 2020). However, the contraction of *T. semitaeniatus* could be exacerbated if areas of rocky outcrops are degraded or isolated, reducing its ability to move between suitable microhabitats. The thermal data collected from individuals distributed within the PARNA Catimbau highlight and reinforce the modeling results, corroborating other well-known studies on the eco-physiological aspects and microhabitat use of these species. However, it is important to emphasize that, although the projections indicate clear trends of expansion and contraction of suitable areas for the studied species, models based solely on climatic variables do not incorporate factors such as ecological interactions, geographic barriers, land use, and dispersal (Elith and Leathwick, 2009). Therefore, these results should be interpreted as potential indicators, and future studies that consider vegetation cover, biomass, availability of food, and shelters may provide valuable additional data for discussion.

In summary, our results highlight how eco-physiological, behavioral, and microhabitat use differences between *Tropidurus cocorobensis* and *T. semitaeniatus* can shape their responses to projected climate change. The integration of body temperature data at the time of capture, thermal behavior, and distribution modeling reinforces the importance of considering multiple dimensions of thermal ecology when assessing the vulnerability of ectothermic species. Although *T. cocorobensis* shows potential for persistence in warming scenarios, benefiting from more homogeneous and warmer environments, *T. semitaeniatus* may face restrictions in its distribution and potential areas, related to the loss of suitable microclimates and the degradation of specific habitats. These findings indicate the importance of conservation strategies that incorporate environmental heterogeneity, habitat connectivity, and thermal monitoring of populations. Within the context of semi-arid protected areas, such as Catimbau National Park, these results emphasize the relevance of management actions focused on protecting microhabitats and maintaining functionally connected landscapes, thereby promoting thermal and ecological resilience of species in the face of rapid climate change.

ACKNOWLEDGEMENTS

The authors are thankful to the *Instituto Chico Mendes de Conservação da Biodiversidade* and to the *Comitê de Ética em Uso Animal of the Universidade Federal de Pernambuco* for animal collection and handling permits permissions (ICMBio permits nº 79254-1; CEUA-UFPE nº 0065/2021). The authors are also thankful to the *Projeto Ecológico de Longa Duração-PELD/CNPq* Catimbau and its coordinator M. Tabarelli for lodging and equipment used during field work. PMAO is thankful to *Pro-reitoria para Assuntos de Pesquisa e Pós-Graduação da UFPE*, *Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco* (IBPG-1566-2.04/19) and Idea Wild for financial support. PMSN is grateful to *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq Fellowship #313622/2018-3).

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Figures

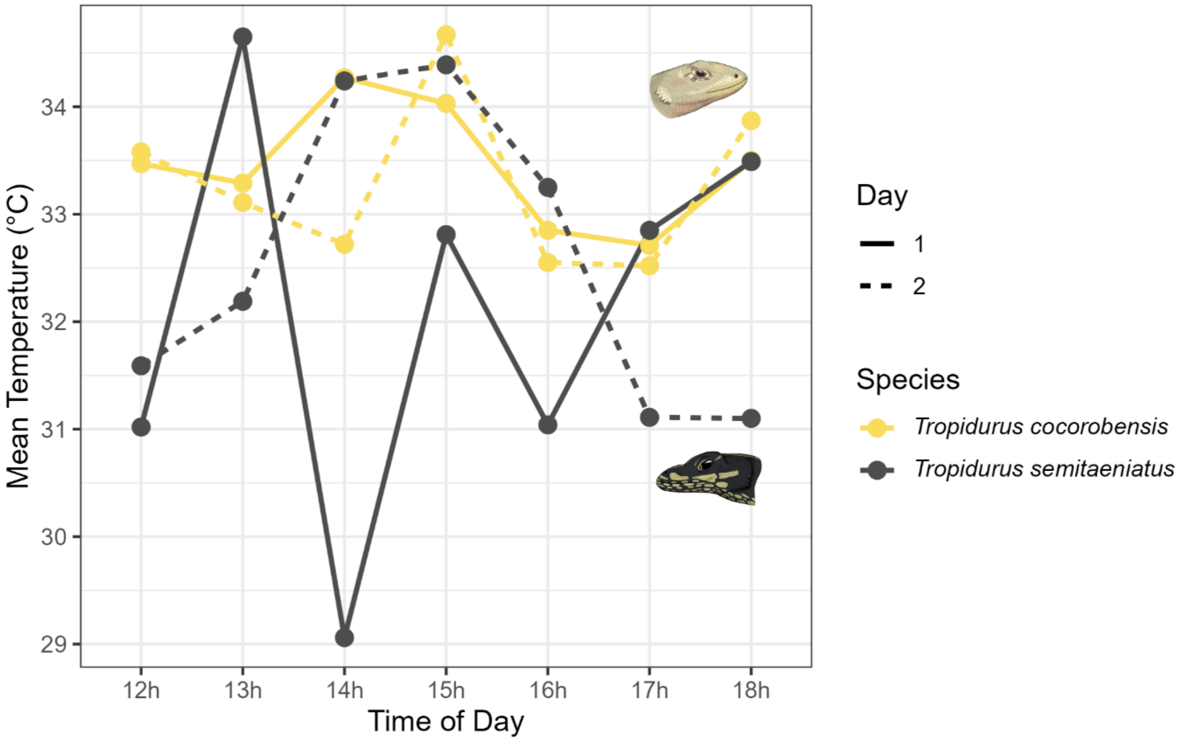

Figure 1. Comparison of mean surface body temperatures among individuals of *Tropidurus cocorobensis* and *Tropidurus semitaeniatus* throughout the experimental period.

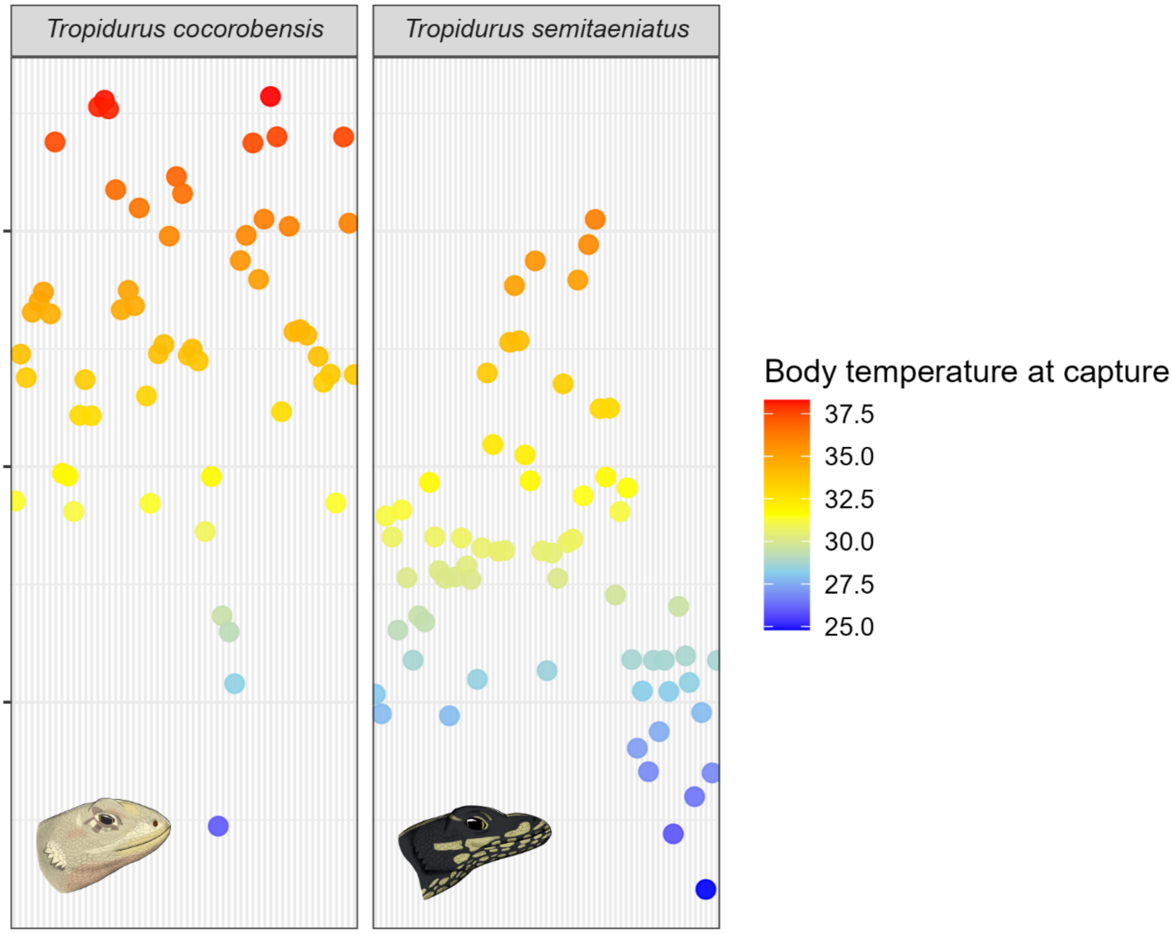

Figure 2. Mean of body temperature at capture of *Tropidurus cocorobensis* and *Tropidurus semitaeniatus* individuals.

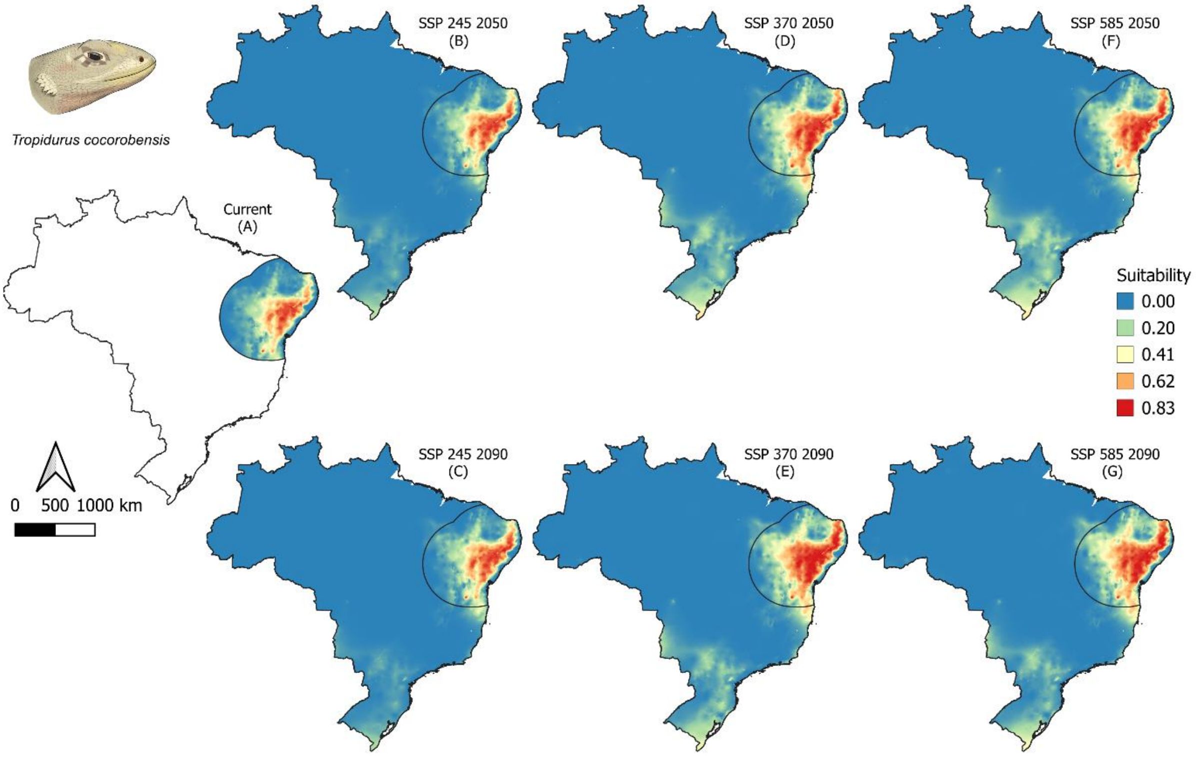

Figure 3. Current distribution and future projections of climatic suitability for *Tropidurus cocorobensis* under SSP 245, SSP 370, and SSP 585 scenarios for the years 2050 and 2090. Blue areas indicate regions currently unsuitable for the species, while red areas represent areas projected to have climatic suitability.

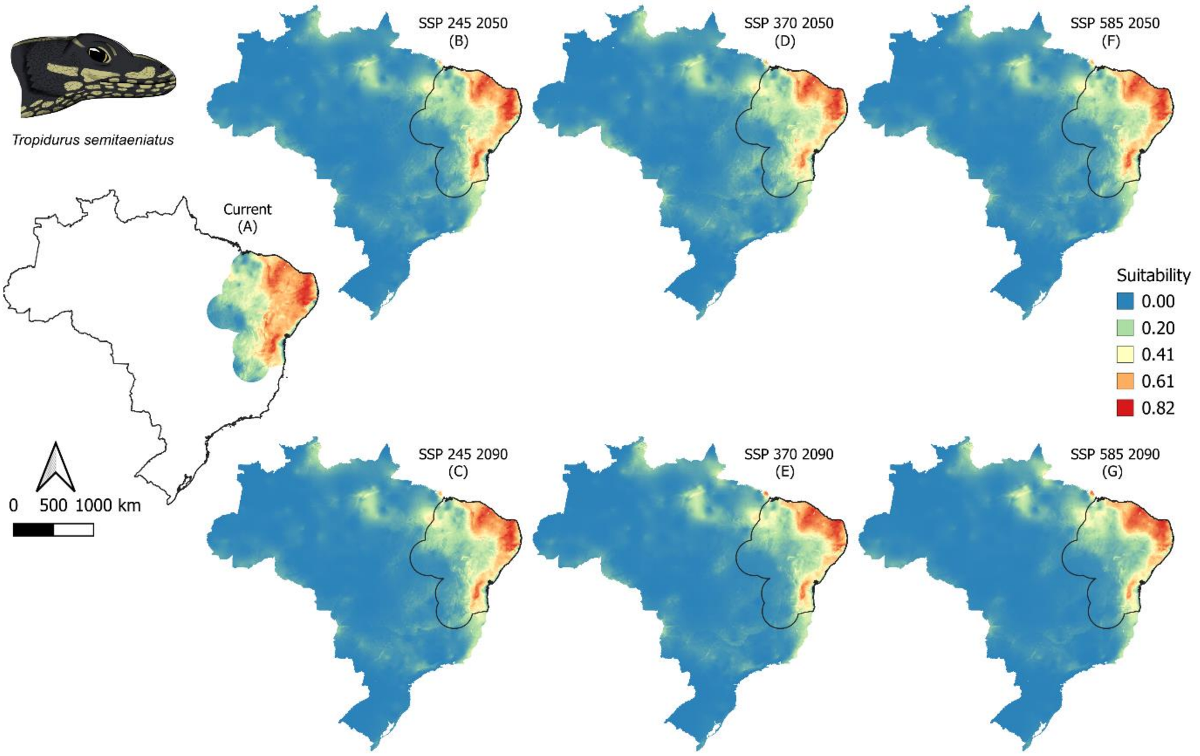

Figure 4. Current distribution and future projections of climatic suitability for *Tropidurus semitaeniatus under* SSP 245, SSP 370, and SSP 585 scenarios for the years 2050 and 2090. Blue areas indicate regions currently unsuitable for the species, while red areas represent areas projected to have climatic suitability.

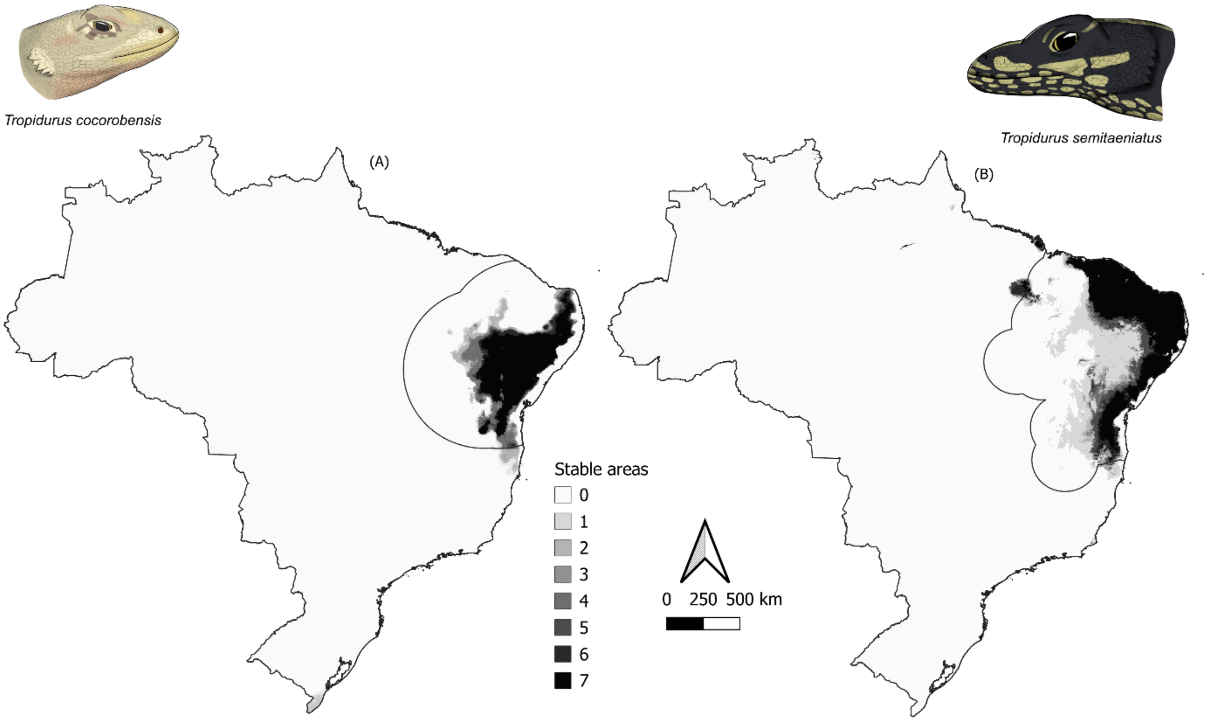

Figure 5. Stable climatically suitable areas for A) *Tropidurus cocorobensis* and B) *T. semitaeniatus* across all future climate scenarios and time periods (SSP 245, 370, and 585 for 2050 and 2090).

Table 1. Mean and standard deviation of body temperature at capture and preferred body temperature of *Tropidurus cocorobensis* and *Tropidurus semitaeniatus* individuals.

	Body temperature at capture (N=117)		**Preferred body temperature (N=20)**	
Specie	Mean	SD	Mean	SD
Tropidurus cocorobensis	33.97	2.62	33.37	2.57
Tropidurus semitaeniatus	30.33	3.13	32.34	4.72

Table 2. Projected changes in climatically suitable areas (in km² and %) for *Tropidurus cocorobensis* and *Tropidurus semitaeniatus* under current conditions and future climate scenarios (SSP 245, SSP 370, and SSP 585) for the years 2050 and 2090. Values represent the total area classified as suitable for each species under each scenario and time point. Percentage changes indicate the proportional increase or decrease relative to current suitable area.

Specie	**Current**	**SSP 245**		**SSP 370**		**SSP 585**	
		2050	**2090**	**2050**	**2090**	**2050**	**2090**
Tropidurus cocorobensis	269326.2	305760.5	325094.4	444648.9	479192.9	429265.5	488241.7
Change in area (%)		13.52	20.7	65.09	77.92	59.38	81.28
Tropidurus semitaeniatus	889967.8	593872.8	531079.2	549903	437505.5	533736.4	407821.2
Change in area (%)		-33.27	-40.32	-38.21	-50.84	-40.02	-54.17

Suplementary Material 1. Variables of WorldClim with the highest ecological relevance for the species.

Specie	Variables
Tropidurus cocorobensis	BIO1 = Annual Mean Temperature
Tropidurus cocorobensis	BIO7 = Temperature Annual Range (BIO5-BIO6)
Tropidurus cocorobensis	BIO15 = Precipitation Seasonality (Coefficient of Variation)
Tropidurus cocorobensis	BIO16 = Precipitation of Wettest Quarter
Tropidurus cocorobensis	BIO18 = Precipitation of Warmest Quarter
Tropidurus cocorobensis	BIO19 = Precipitation of Coldest Quarter
Tropidurus semitaeniatus	BIO3 = Isothermality (BIO2/BIO7) (×100)
Tropidurus semitaeniatus	BIO7 = Temperature Annual Range (BIO5-BIO6)
Tropidurus semitaeniatus	BIO10 = Mean Temperature of Warmest Quarter
Tropidurus semitaeniatus	BIO12 = Annual Precipitation
Tropidurus semitaeniatus	BIO14 = Precipitation of Driest Month
Tropidurus semitaeniatus	BIO15 = Precipitation Seasonality (Coefficient of Variation)
Tropidurus semitaeniatus	BIO18 = Precipitation of Warmest Quarter

CONCLUSÃO

Através os resultados apresentados nos três capítulos dessa tese concluímos que os aspectos ecofisiológicos relacionados ao estado hídrico e à ecologia térmica dos lagartos da Caatinga estão profundamente relacionados com as condições ambientais e com os traços ecológicos específicos de cada espécie. As análises demonstraram que a hidratação dos lagartos pode estar fortemente entrelaçada com a ocupação de microhabitats, comportamento de forrageio e com a sazonalidade climática da região semiárida. No primeiro capítulo, verificou-se que espécies mais ativas e expostas à radiação solar, como *Ameivula ocellifera*, apresentaram maior desidratação em campo e, consequentemente, maior absorção de água em experimentos, destacando a importância das estratégias comportamentais na manutenção do balanço hídrico. Em contraste, *Tropidurus semitaeniatus*, com hábitos saxícolas, exibiu menor desidratação, o que sugere que ambientes rochosos podem oferecer microclimas mais favoráveis à conservação hídrica. O segundo capítulo revelou um dado contraintuitivo: a ingestão de alimentos por indivíduos desidratados não contribuiu positivamente para sua reidratação e, em alguns casos, acentuou o déficit hídrico. Este resultado reforça a ideia de que, sob estresse hídrico, os custos fisiológicos da digestão podem se sobrepor aos benefícios da ingestão alimentar, impondo um trade-off entre nutrição e hidratação. No terceiro capítulo, observou-se que as preferências térmicas das espécies, associadas à sua tolerância ao calor, têm implicações diretas sobre sua distribuição geográfica atual e futura. A modelagem de nicho ecológico indicou que as mudanças climáticas podem reduzir drasticamente as áreas adequadas para *T. semitaeniatus*, possivelmente por conta de sua restrição de microhabitat. Isso alerta para possíveis restrições futuras à persistência dessas populações frente ao aumento da aridez e das temperaturas extremas. Em conjunto, os três capítulos demonstram que a ecologia térmica e a fisiologia hídrica são fatores determinantes na distribuição, no comportamento e na sobrevivência dos lagartos da Caatinga. As interações entre desidratação, temperatura corporal, alimentação e uso do habitat revelam a complexidade das respostas adaptativas desses organismos às pressões ambientais. Esses conhecimentos são, portanto, fundamentais para antecipar os efeitos das mudanças climáticas sobre a diversidade de espécies de lagartos do semiárido e subsidiar estratégias de conservação que considerem as particularidades ecológicas e fisiológicas das espécies.

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