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UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

THERMAL AND HYDRIC PHYSIOLOGY DETERMINE HABITAT OCCUPANCY IN A GROUP OF NEOTROPICAL FROGS AND INFLUENCE THEIR VULNERABILITY TO CLIMATE CHANGE

LUIS MIGUEL SENZANO CASTRO

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ABSTRACT

Amphibians balance their thermal and water budgets depending on their physiological state and the physical environment to avoid detrimental consequences in organismal performance. Most mechanistic assessments emphasize thermal over water constraints, potentially overlooking important aspects of the amphibian's particular morpho-physiological attributes. Herein, we evaluated the influence of thermal and hydric constraints, combined and separately, on the activity budget across the geographic distribution of ground-dwelling Neotropical frogs belonging to the *Leptodactylus* genus (*L. fuscus*, *L. mystacinus*, *L. macrosternum* and *L. luctator*). Based on laboratory and field data, we integrated species-specific functional attributes with their ground-level microclimate through a mechanistic modeling procedure. We inferred environmental suitability using principles of heat and mass balances, while allowing for interactive behavioral responses of sheltering during restrictive conditions. Our results show that hydric-related restrictions in activity are influenced by body size and may become an impediment even under conditions considered thermally adequate. We also found that the consideration of shelters as thermal and hydric refugia improved the resilience capacity of frogs to stressful climatic conditions. More strikingly, thermal-induced restrictions in activity were linked to low temperatures rather than warmer conditions, indicating a trade-off in diel activity driven by upper and lower thermal bounds. These findings provide a broader picture of climatic constraints on anuran activity and offer new insights into how species may respond to changing climatic conditions in tropical regions.

Keywords: Amphibians, Climate change, Mechanistic niche modeling, Thermal and water balance, Ontogeny.

RESUMO

Os anfíbios equilibram a manutenção do seu balanço hídrico e térmico dependendo do seu estado fisiológico e do ambiente físico para evitar consequências deletérias no desempenho do organismo. A maioria das avaliações mecanicistas enfatiza as restrições térmicas sobre as hídricas, potencialmente negligenciando aspectos importantes dos atributos morfo-fisiológicos específicos dos anfíbios. Aqui, avaliamos a influência das restrições hídricas e térmicas, combinada e separadamente, no tempo de atividade em toda a distribuição geográfica de rãs neotropicais terrestres pertencentes ao gênero *Leptodactylus* (*L. fuscus, L. mystacinus, L. macrosternum* e *L. luctador*). Com base em dados de laboratório e de campo, integramos atributos funcionais específicos das espécies com seu microclima ao nível do solo usando um procedimento de modelagem mecanicista. Inferimos a adequabilidade ambiental usando princípios de equilíbrio de calor e massa, ao mesmo tempo que permitimos respostas comportamentais interativas de procura de abrigo durante condições restritivas. Nossos resultados mostram que as restrições hídricas na atividade são influenciadas pelo tamanho corporal e podem se tornar um impedimento mesmo em condições consideradas termicamente adequadas. Encontramos também que a inclusão dos abrigos como refúgios térmicos e hídricos melhorou a capacidade de resiliência das rãs a condições climáticas estressantes. Importante, as restrições na atividade induzidas pela troca de calor estavam ligadas a baixas temperaturas e não as condições mais quentes, indicando um compromisso na atividade diária impulsionado pelos limites térmicos superiores e inferiores. Estas descobertas fornecem uma imagem mais ampla das restrições climáticas à atividade dos anuros e oferecem novos insights sobre como as espécies podem responder às mudanças nas condições climáticas nas regiões tropicais.

Palavras-Chave: Anfíbios, Mudanças climáticas, Modelagem mecanicista, Balanço hídrico, Ontogenia.

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GENERAL INTRODUCTION

As most organisms, amphibians are not randomly distributed in space. Rather the observed distribution corresponds to a variety of ecological, behavioral, and physiological processes that, in conjunction with environmental factors, shape their geographic distribution and dispersal abilities (Griffiths et al. 2010, Dabés et al. 2012). The limitations imposed by thermal and hydric constraints are particularly acute because, as ectotherms, their body temperature is highly influenced by the thermal environment and, as moist skinned organisms, cutaneous evaporative water loss expose them to the constant risk of dehydration (Hillman et al. 2009). As such, anuran's survival and fitness are dependent on the selection of microhabitats that provide favourable thermal and moist conditions that allows for activity while minimizing the risks of incurring in excessive water loss (Seebacher and Alford 2002).

Thermal and hydric attributes of microhabitats are usually associated to thermal and hydric physiology variations in anurans (Wells 2007, Pittman et al. 2014). Species occurring in thermally variable environments, for example, generally exhibit both broader thermal tolerances and thermal preferred ranges than species from more stable areas (Calosi et al. 2008, Deutsch et al. 2008). Likewise, species from hotter areas and usually low humidity are more likely to withstand higher rates of evaporative water loss (Cruz-Piedrahita et al. 2018). A remarkable tolerance to dehydration and a rapid water uptake capacity through the pelvic patch may act as adaptive responses to withstand prolonged periods in habitats with water-limiting conditions (Hillman et al. 2000, Titon et al. 2010). Additionally, morphological variations on body size also lead to interspecific differences by effects on the surface-to-volume ratio, a key factor in determining size-dependent rate processes like water loss and uptake (Titon and Gomes 2015) and heat gain/loss balance (Amado et al. 2018).

Under the current global warming scenario, there has been a growing interest on how species fitness will response to rising temperatures, and species' ability to buffer against the detrimental effects associated to higher thermal conditions (Calosi et al. 2008, Sinervo et al. 2010, Scheffers et al. 2013). Amphibian populations are declining globally (Duarte et al. 2012), and species with a narrow thermal and desiccation tolerance, higher rates of dehydration or a lower rehydration capacity might be at special risk of extinction (Huey et al. 2012), unless they are able to find cooler microsites that provide sufficient moisture to rehydrate and prevent excessive water loss (Seebacher and Alford 2002). Most studies on species' vulnerability to climate change correlate georeferenced occurrence records of species to climatic variables to identify climatically suitable areas (the correlative ecological niche modeling; see Peterson et al. 2011). Although correlative approaches provide insightful information on species' environmental suitability, they do not capture causal aspects relating intrinsic functional properties of organisms and their environment. In this way, species that today occupy similar environmental conditions may not response equally under novel climatic events, which certainly will play a key role in shaping and setting future species distributions (Evans et al. 2015, Elith and Leathwick 2009). Additionally, most correlative studies are based on above-ground coarse macroclimates, which may fail to capture the thermal and hydric conditions at the microhabitat where the organisms thrive (Nadeau et al. 2016), thereby misleading correlations and predictions (Scheffers et al. 2013, Jiménez et al. 2019).

There is a growing consensus on the benefits of considering additional functional parameters when approaching species distribution patterns (Kearney et al. 2010), and mechanistic models incorporating physiological traits of organisms have shown to be a good alternative to this end (Mitchell et al. 2013, Evans et al. 2015). In essence, mechanistic models integrate organismal functional attributes as metrics to set critical environmental constraints and use the outcomes to infer whether an organism can sustain positive balances of mass and/or energy at a given place (reviewed by Briscoe et al. 2023). This approach has been adopted successfully in studies aiming to evaluate reptile vulnerability to climate change (e.g., Huey et al. 2009, Sinervo et al. 2010, Clusella-Trullas and Chown 2014, Ceia-Hasse et al. 2014), with most of them primarily focusing on organismal thermal traits (Evans et al. 2015).

Besides temperature, water balance sensitivity is an equally important and comparatively less explored aspect of organismal response to climate warming. In wet-skinned organisms like amphibians, mechanistic modeling must consider not only heat, but also water relationships when trying to establish a linkage between the physical properties of the environment and organismal functional attributes (Amado et al. 2018). Phenological activities, such as activity time and reproduction, are markedly tied to the availability of water in anurans. As such, drastic changes in rainfall regimes (e.g., droughts) may hamper anurans' ability to regulate their water balance, causing anurans to reduce their activity time or even cease reproduction to avoid desiccation risk. This must be particularly true in species-rich regions like the south American Neotropics, where declining species events has been related to droughts (Stewart 1995, Walls et al. 2013), tied to heat events (Tuff et al. 2016) which are both expected to become more variable in duration, frequency, and magnitude under a climate change scenario (Nuñez et al. 2009, Stillman 2019). However, there is a paucity of functional trait-based studies assessing climate change risks on amphibians, and even less well-founded studies rooted simultaneously in their thermal and hydric eco-physiological relationships, with mechanistic-based modeling assessments virtually absent for Neotropical anuran species.

In tropical and subtropical regions, daytime temperatures are much higher and variable than at night (Muñoz and Bodensteiner 2019), but most amphibians in these regions are strictly nocturnal (Anderson and Wiens 2017). The thermal consequences of nocturnality have important implications from a thermoregulatory perspective. For example, thermally permissive conditions at night reduce the risk of overheating but also lower thermoregulatory opportunities (Hitchcock and McBrayer 2006, Rock and Cree 2008), which may have important consequences on amphibian physiological performance. Likewise, because of their moist and highly permeable skin, water loss is still an ongoing process that can constraint activity even under conditions considered thermally suitable.

In this thesis work, we aimed to enhance our understanding of the potential interactions between thermal and hydric constraints on anuran activity at the organismal scale (microclimate) and then scale them up to broad-scale distributional patterns to infer environmental suitability. Bridging these fine-scale mechanisms to broad geographical scales allows us to account for a broader spectrum of processes influencing species' distributions, which might improve our ability to predict species' response to climate change. For such a purpose, we employ thermal, hydric, and performance organismal traits from *Leptodactylys* frogs (*L. fuscus*, *L. mystacinus*, *L. macrosternum* and *L. luctator*), and from this, we provide a mechanistic assessment rooted on principles of heat and mass balance to infer environmental optimality under current and future microclimates. Species of this genus are traditionally associated to water bodies (Haddad et al. 2013), although the extent of dependency to moist conditions greatly vary among species. This turns them a good taxon model, as they inhabit a variety of habitats varying in moist and thermal conditions. The strategy of this thesis was to develop three chapters under three-fold approaches. In chapter 1, we measured thermal and water organismal traits that are thought to limit anuran activity and we also explored their interspecific ecological implications. In chapter 2, we gathered this organismal trait information, and linked them to the hourly ground-level microclimate via a mechanistic modeling approach to infer environmental suitability and predict potential species distribution.

Finally, in chapter 3, we decouple the thermal and water sensitivity in a model species (*L. macrosternum*) between young and adult individuals and integrate them to ground-level conditions for present-day and future microclimates to mechanistically forecast the potential consequences of climate change.

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