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INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

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MORPHOLOGICAL AND BEHAVIORAL DETERMINANTS OF INDIVIDUAL TROPHIC NICHE VARIATION IN ANURANS

JORGE ARNALDO DIAZ PEREZ

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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia, Evolução e Biodiversidade.

Orientador: Dr. Márcio Silva Araújo.
Coorientador: Dr. Raul Costa Pereira.

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ORIENTADOR: MARCIO SILVA ARAUJO
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Departamento de Biodiversidade / UNESP / Câmpus de Rio Claro - IB

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Departamento de Biodiversidade / UNESP / Câmpus de Rio Claro - IB

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Abstract

Determining whether co-occurring organisms differ in their ecological niches, particularly in their trophic resource use, and what causes these differences has long been a central question in ecology. In recent years, the study of these topics using an individual-based approach has increased substantially and constitutes the focus of this thesis. The proximate causes of individual trophic niche variation may be morphological, behavioral, or physiological, or may arise from interactions among these factors. Despite advances in understanding these causes, the role of morphology as a prevalent factor driving individual niche variation across populations remains unclear, and studies often do not consider prey traits or apply an explicit functional mechanistic approach linking consumer morphology to trophic niche variation. In addition, the limited number of ecological systems studied and the historical disconnection between individual-based approaches to study ecological niche variation (i.e., individual specialization) and behavior (i.e., animal personality) have constrained the understanding of the behavioral causes of trophic niche variation within populations. To contribute to filling these knowledge gaps, this thesis integrates three chapters addressing the role of morphology (first chapter) and exploratory behavior (second and third chapters) in individual trophic niche variation, using anurans as a model system. Individual trophic niches were quantified using gut content and stable isotope analyses; feeding morphology (i.e., individual head shape) was characterized using geometric morphometrics; and individual exploratory levels were estimated through behavioral experimental assays. The main results of this thesis reveal that (i) morphology is an underlying cause of individual variation in consumed prey traits (size and mobility), and individual trophic niche specialization can be promoted by an increased strength of the relationship between morphology and diet; (ii) consistent individual differences in exploratory behavior drive variation in individual dietary niches but depending on sex and body size, and higher levels of exploration promote greater temporal variation in individual trophic niches; and (iii) predator proactivity in exploration-related behaviors drives interindividual differences in the mobility of consumed prey, with contrasting patterns between sexes. Together, these findings highlight the underappreciated role of morphology and the joint role of behavior and intrinsic factors (i.e., body size and sex) in shaping individual diets, contributing to the understanding of the proximate causes of trophic niche variation within natural populations.

Keywords: Niche variation, Individual specialization, Trophic niche, Animal personality, Functional morphology, Geometric morphometrics, Stable isotopes, Amphibia.

Resumo

Determinar se organismos que coexistem diferem em seus nichos ecológicos, particularmente no uso de recursos tróficos, e quais são as causas dessas diferenças tem sido, há muito tempo, uma questão central na ecologia. Nos últimos anos, o estudo desses temas por meio de uma abordagem baseada no indivíduo aumentou substancialmente e constitui o foco desta tese. As causas proximais da variação individual no nicho trófico podem ser morfológicas, comportamentais ou fisiológicas, ou podem surgir de interações entre esses fatores. Apesar dos avanços na compreensão dessas causas, o papel da morfologia como um fator prevalente que determina a variação individual do nicho nas populações permanece incerto, e os estudos frequentemente não consideram as características das presas nem implementam uma abordagem funcional mecanicista explícita que vincule a morfologia do consumidor à variação do nicho trófico. Além disso, o número limitado de sistemas ecológicos estudados e a desconexão histórica entre abordagens baseadas no indivíduo para o estudo da variação do nicho ecológico (i.e., especialização individual) e do comportamento (i.e., personalidade animal) têm restringido a compreensão das causas comportamentais da variação do nicho trófico dentro das populações. Para contribuir para o preenchimento dessas lacunas de conhecimento, esta tese integra três capítulos que abordam o papel da morfologia (primeiro capítulo) e do comportamento exploratório (segundo e terceiro capítulos) na variação individual do nicho trófico, utilizando anuros como sistema modelo. O nicho trófico dos indivíduos foi quantificado por meio de análises de conteúdo estomacal e de isótopos estáveis; a morfologia alimentar (i.e., o formato da cabeça dos indivíduos) foi caracterizada utilizando morfometria geométrica; e os níveis individuais de exploração foram estimados por meio de ensaios comportamentais experimentais. Os principais resultados desta tese revelam que (i) a morfologia é uma causa subjacente da variação individual nas características das presas consumidas (tamanho e mobilidade), e que a especialização individual do nicho trófico pode ser promovida por um aumento na força da relação entre morfologia e dieta; (ii) diferenças individuais consistentes no comportamento exploratório determinam a variação nos nichos alimentares individuais, mas de maneira dependente do sexo e do tamanho corporal, e níveis mais elevados de exploração promovem maior variação temporal nos nichos tróficos individuais; e (iii) a proatividade do predador em comportamentos relacionados à exploração determina diferenças interindividuais na mobilidade das presas consumidas, com padrões contrastantes entre os sexos. Em conjunto, esses achados destacam o papel subestimado da morfologia e o papel conjunto do comportamento e de fatores intrínsecos (i.e., tamanho corporal e sexo) na determinação das dietas individuais, contribuindo para a compreensão das causas proximais da variação do nicho trófico em populações naturais.

Palavras-chave: Variação de nicho, Especialização individual, Nicho trófico, Personalidade animal, Morfologia funcional, Morfometria geométrica, Isótopos estáveis, Amphibia.

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General introduction

The *ecological niche* is a core concept in ecology and evolution and can be defined as the set of resources and environmental conditions required for a species to maintain a persistent population over time (Hutchinson 1957; Holt 2009; Takola & Schielzeth 2022). Although most of the ecological theory have traditionally treated the ecological niche as an attribute of species, this concept also applies to individuals within the same species (Bolnick *et al.* 2003; Takola & Schielzeth 2022). A central question in ecology is whether co-occurring organisms differ in their ecological niches and what explains such differences (Pianka 1974; Buche *et al.* 2022; Reyes-Puig *et al.* 2025). Although this has historically been assessed in an interspecific context, interest in individual niche differences, as well as their causes and consequences, has increased dramatically over the past two decades (Bolnick *et al.* 2003; Martin & Pfennig 2009; Knudsen *et al.* 2010; Araújo *et al.* 2011).

Individuals within populations often differ in their ecological niches. Such within-population variation arises from both discrete and continuous phenotypic differences among individuals. *Individual specialization* is a population-level attribute defined as the degree to which individuals' niches are restricted relative to that of the population. It represents a continuum, ranging from low specialization—when each individual's niche width approaches that of the population—to high specialization—when individuals exploit only a small subset of the resources used by the population (Bolnick *et al.* 2003; Costa-Pereira & Araujo 2024). Natural populations may consist of specialist individuals, generalist individuals, or a mixture of both. Consequently, populations predominantly composed of specialist individuals exhibit higher levels of individual specialization.

Although individual specialization can be examined in relation to any resource or environmental condition, most theoretical and empirical research has focused on trophic resource use (e.g., Araújo *et al.* 2014; Cloyed & Eason 2016; Costa-Pereira *et al.* 2018; Balme *et al.* 2019). Organisms must allocate energy to both growth and reproduction and the acquisition of food resources constitutes a fundamental process influencing multiple aspects of their biology, including habitat use, predation risk, and intra- and interspecific competition, all of which ultimately affect individual fitness (Svanbäck & Bolnick 2019). Patterns of trophic resource use have also been identified as key drivers of the evolution of several phenotypic traits (Schluter 1995; Svanbäck & Schluter 2012) and of ecological processes such as nutrient cycling and ecosystem functioning (Evangelista *et al.* 2017). Moreover, variation in resource use has the potential to shape species coexistence and biodiversity patterns (Hart *et al.* 2016)—topics whose underlying mechanisms are central to ecology and can be effectively explored through the study of individual specialization.

There is extensive evidence of individual specialization in trophic resource use across a wide range of taxa, in both terrestrial and aquatic ecosystems and in tropical, subtropical, and temperate regions, indicating that this phenomenon is widespread in nature (Costa-Pereira & Araújo 2024). The causes of this phenomenon have traditionally been classified into two broad categories: proximate causes and ecological causes (Bolnick *et al.* 2003; Araújo *et al.* 2011). Proximate causes refer to intrinsic morphological, behavioral, and physiological traits of individuals that influence resource use, whereas ecological causes involve ecological interactions, such as intraspecific competition, interspecific competition, and predation, as well as resource diversity. The present thesis focuses on proximate causes, specifically morphological and behavioral traits.

A useful general framework for understanding why individuals exploit only a subset of the resources used by the population as a whole (i.e., individual specialization) is *optimal foraging theory* (OFT) (Pyke 1984; Sih & Christensen 2001). One core prediction of OFT is that individuals tend to maximize energetic gain per unit of search and handling time for prey (Stephens & Krebs 1986). Accordingly, individuals rank prey items to maximize energetic gain per unit of search and handling time. In this sense, OFT incorporates a behavioral component shaping foraging decisions, including, for example, the amount of movement or distance an individual covers to feed and the decision to attack prey once encountered. However, the realized outcome of foraging decisions depends on multiple interacting factors associated with both prey (e.g., energy content, prey size, prey escape strategies, and prey abundance) and predator traits (e.g., experience, handling behavior, morphology, and physiology) (Schmitz *et al.* 2017).

Regarding predator traits, functional *trade-offs* represent an important mechanism underlying individual niche variation. Such trade-offs imply that an individual with a given phenotype is efficient at using one type of resource but necessarily inefficient at using alternative resources (Svanbäck & Bolnick 2019). The occurrence of these trade-offs has been documented in several phenotypic traits, including morphological and behavioral traits. For example, predator head shape can influence both the force and the velocity of jaw opening and closing (Adams & Rohlf 2000). A head shape conferring high force necessarily results in lower jaw-opening and -closing speed, and vice versa; therefore, when prey exhibits distinct escape tactics (e.g., differences in prey velocity), interindividual variation in head shape can lead to interindividual trophic niche variation. With respect to behavior, when profitable resources are concentrated in risky habitats, trade-offs can arise between resource quality and predation risk (Darimont *et al.* 2007). For instance, an individual with a bolder phenotype (i.e., a higher propensity to take risks) might tend to forage in habitats with high-quality resources where predation risk is higher. Conversely, a shyer individual (i.e., with a lower propensity to take risks) might forage in safer habitats, where predation risk is lower, and consumes a lower-quality diet. Together, these examples illustrate how individual niches are constrained by phenotypic traits, which prevent individuals from efficiently using all resources within populations, thereby promoting individual specialization.

Despite substantial advances in understanding the proximate causes of individual specialization, knowledge of how the functional traits of resources relate to the phenotypic traits of consumers to shape patterns of individual specialization within and among populations remains limited. In addition, several studies have failed to detect an association between morphology and individual specialization, creating uncertainty about the importance and general prevalence of morphology as a proximate cause of individual specialization (Araújo *et al.* 2007, 2009; Carvalho-Rocha *et al.* 2018; Atencia-Gándara *et al.* 2021). This gap exists in part because individual specialization has often been assessed using taxonomic classifications of resources or stable isotopes. However, prey belonging to different taxonomic categories (e.g., orders or families) do not always differ in their functional traits (e.g., size or mobility) and therefore do not necessarily differ in their vulnerability to predation. Consequently, predation success does not necessarily depend on taxonomic identity but rather on functional prey traits and the predator's ability to capture prey, which may involve morphological and behavioral traits. Accordingly, adopting a functional approach that considers both predator and prey traits may be useful for understanding the proximate causes of individual specialization (Ferry-Graham *et al.* 2002), although this approach has rarely been implemented.

Additionally, the historical lack of integration between individual-based research on ecological niches (i.e., individual specialization) and on behavior (i.e., animal personality) has limited our understanding of how behavioral differences drive trophic niche variation within populations (Toscano *et al.* 2016). To date, most empirical evidence on the role of behavior in individual trophic niche variation comes from a small number of study systems, often based on experimental studies conducted under non-natural conditions, and only a few studies have linked individual behavior with resource use in natural settings (e.g., Gharnit *et al.* 2022; Herath *et al.* 2021). This context highlights the need to evaluate the general prevalence of individual variation in behavior as a driver of individual trophic specialization in natural populations.

An important challenge in studying the behavioral causes of individual specialization is the need to assess individual consistency in both resource use and behavior (Toscano *et al.* 2016). For trophic resource use, the application of complementary methods, such as gut content analysis and stable isotope analysis of multiple tissues, is recommended to evaluate long-term dietary preferences (i.e., trophic niche consistency) (Araújo *et al.* 2011). However, obtaining repeated measures of behavior under natural conditions can be logistically more challenging. Fortunately, foraging-related behaviors, such as exploration measured under laboratory conditions, have been shown to reflect behavior in nature (e.g., Edwards *et al.* 2018; Garcia-Loor *et al.* 2025). This provides a reliable alternative for obtaining repeated measures of behavior and for assessing behavioral consistency when repeated measurements in the wild are not feasible.

This thesis was developed to contribute to understanding the role of morphology (first chapter) and exploratory behavior (second and third chapters) in individual trophic niche variation using anurans as a model system. The thesis is composed of three chapters. In the first chapter, I evaluated whether individual variation in head morphology explains variation in the size and mobility of consumed prey and whether the degree of individual specialization is shaped by the strength of morphology–prey trait relationships across several populations of two co-occurring species. In the second chapter, I assessed whether exploratory behavior influences individual trophic (isotopic) niches and their temporal niche consistency within populations of two species. In the third chapter, I tested whether individual variation in proactivity behaviors, used as proxies for foraging activity, drives differences in the mobility of consumed prey in a population of a generalist terrestrial frog.

References

Adams, D.C. & Rohlf, F.J. (2000) Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphometric study. *Proceedings of the National Academy of Sciences*, 97(8), 4106–4111.

Araújo, M.S., Dos Reis, S.F., Giaretta, A.A., Machado, G. & Bolnick, D.I. (2007) Intrapopulation diet variation in four frogs (Leptodactylidae) of the Brazilian savannah. *Copeia*, 2007, 855–865.

Araújo, M.S., Bolnick, D.I. & Layman, C.A. (2011) The ecological causes of individual specialisation. *Ecology Letters*, 14(9), 948-958.

Araújo, M.S., Langerhans, R.B., Giery, S.T. & Layman, C.A. (2014) Ecosystem fragmentation drives increased diet variation in an endemic livebearing fish of the Bahamas. *Ecology and Evolution*, 4(16), 3298-3308.

Araújo, M.S., Bolnick, D.I., Martinelli, L.A., Giaretta, A.A. & Dos Reis, S.F. (2009) Individual-level diet variation in four species of Brazilian frogs. *Journal of Animal Ecology*, 78, 848–856.

Atencia-Gándara, P.L., Torres, R.A. & Diaz-Perez, J.A. (2021) Seasonal and intra-populational diet variation in the Colombian swamp frog *Pseudopaludicola pusilla* (Anura Leptodactylidae). *Ethology Ecology and Evolution*, 33, 611–627.

Balme, G.A., Le Roex, N., Rogan, M.S. & Hunter, L.T. (2020) Ecological opportunity drives individual dietary specialization in leopards. *Journal of Animal Ecology*, 89(2), 589-600.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, 161(1), 1-28.

Buche, L., Spaak, J.W., Jarillo, J. & De Laender, F. (2022) Niche differences, not fitness differences, explain predicted coexistence across ecological groups. *Journal of Ecology*, 110(11), 2785-2796.

Carvalho‐Rocha, V., Lopes, B.C. & Neckel‐Oliveira, S. (2018) Interindividual patterns of resource use in three subtropical Atlantic Forest frogs. *Austral Ecology*.

Cloyed, C.S. & Eason, P.K. (2016) Different ecological conditions support individual specialization in closely related, ecologically similar species. *Evolutionary Ecology*, 30(3), 379-400.

Costa‐Pereira, R., Rudolf, V.H.W., Souza, F.L. & Araújo, M.S. (2018) Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology*, 87, 1452–1464.

Costa-Pereira, R. & Araújo, M. (2024) Individual Specialization. In: Scheiner, S.M., editor. *Encyclopedia of Biodiversity*, 3rd edn, vol. 6, pp. 1–14. Elsevier.

Darimont, C.T., Paquet, P.C. & Reimchen, T.E. (2007) Stable isotopic niche predicts fitness of prey in a wolf–deer system. *Biological Journal of the Linnean Society*, 90(1), 125-137.

Edwards, D.D., Rapin, K.E. & Moore, P.A. (2018) Linking phenotypic correlations from a diverse set of laboratory tests to field behaviors in the crayfish, *Orconectes virilis*. *Ethology*, 124(5), 311-330.

Evangelista, C., Lecerf, A., Britton, J.R. & Cucherousset, J. (2017) Resource composition mediates the effects of intraspecific variability in nutrient recycling on ecosystem processes. *Oikos*, 126(10), 1439-1450.

Ferry-Graham, L.A., Bolnick, D.I. & Wainwright, P.C. (2002) Using functional morphology to examine the ecology and evolution of specialization. *Integrative and Comparative Biology*, 42(2), 265-277.

García-Loor, J., Katsis, A.C., Common, L.K. & Kleindorfer, S. (2025) Exploration Behavior Is Consistent and Associated With Foraging Behavior in Island Songbirds. *Biotropica*, 57(4), e70057.

Gharnit, E., Dammhahn, M., Garant, D. & Réale, D. (2022) Resource availability, sex, and individual differences in exploration drive individual diet specialization. *The American Naturalist*, 200, 1–16.

Hart, S.P., Schreiber, S.J. & Levine, J.M. (2016) How variation between individuals affects species coexistence. *Ecology Letters*, 19(8), 825-838.

Herath, A.P., Wat, K.K., Banks, P.B. & McArthur, C. (2021) Animal personality drives individual dietary specialisation across multiple dimensions in a mammalian herbivore. *Functional Ecology*, 35(10), 2253-2265.

Holt, R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, 106(supplement_2), 19659-19665.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427.

Knudsen, R., Primicerio, R., Amundsen, P.A. & Klemetsen, A. (2010) Temporal stability of individual feeding specialization may promote speciation. *Journal of Animal Ecology*, 79(1), 161-168.

Martin, R.A. & Pfennig, D.W. (2009) Disruptive selection in natural populations: the roles of ecological specialization and resource competition. *The American Naturalist*, 174(2), 268-281.

Pianka, E.R. (1974) Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*, 71(5), 2141-2145.

Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, 15, 523-575.

Reyes-Puig, C., Enriquez-Urzelai, U., Sillero, N. & Kaliontzopoulou, A. (2025) Niche differences in coexisting species: ecological insights into the role of activity patterns, space use, and environmental preferences. *Ecology and Evolution*, 15(8), e71802.

Schluter, D. (1995) Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology*, 76(1), 82-90.

Schmitz, O.J. (2017) Predator and prey functional traits: understanding the adaptive machinery driving predator–prey interactions. *F1000Research*, 6, 1767.

Sih, A. & Christensen, B. (2001) Optimal diet theory: when does it work, and when and why does it fail? *Animal Behaviour*, 61(2), 379-390.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging theory*. Princeton University Press.

Svanbäck, R. & Schluter, D. (2012) Niche specialization influences adaptive phenotypic plasticity in the threespine stickleback. *The American Naturalist*, 180(1), 50-59.

Svanbäck, R. & Bolnick, D.I. (2019) Behavioral Ecology: Food Specialization. In: Fath, B., editor. *Encyclopedia of Ecology*, 2nd edn, pp. 204–211. Elsevier.

Takola, E. & Schielzeth, H. (2022) Hutchinson's ecological niche for individuals. *Biology & Philosophy*, 37(4), 25.

Toscano, B.J., Gownaris, N.J., Heerhartz, S.M. & Monaco, C.J. (2016) Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia*, 182(1), 55-69.

Trappes, R., Nematipour, B., Kaiser, M.I., Krohs, U., Van Benthem, K.J., Ernst, U.R. & Takola, E. (2022) How individualized niches arise: defining mechanisms of niche construction, niche choice, and niche conformance. *BioScience*, 72(6), 538-548.

Final considerations

Understanding of the proximate causes of individual niche variation has increased substantially in recent years. Despite these advances, because of the diversity of ecological systems found in nature and the highly context-dependent nature of ecological variation within populations, several aspects related to the role of phenotypic variation in niche differences among individuals within the same population and its relevance for shaping patterns of individual specialization across multiple populations remain unclear. This thesis aimed to contribute to the understanding of how phenotypic variation, specifically morphology and behavior, is associated with individual trophic niche variation within populations and how these intrinsic factors, specifically functional morphology, promote variation in individual niche specialization across different populations. Although this study focused on anurans, its findings have broader implications for understanding the mechanisms underlying individual specialization in general. Additionally, most of the results are novel for these organisms.

In the first chapter (Diaz-Perez *et al.* 2025), I showed that individuals specialized in prey size and mobility, revealing new dimensions of ecological niche specialization within populations, in addition to the widely documented specialization in prey taxa and isotopic niches. Feeding morphology proved to be an important factor associated with individual variation in prey traits, and the nature of this association has a functional basis. Morphology–function predictions proposed to explain differences in prey traits among species were also supported within individuals of the same species. However, our findings showed that these relationships depended on species identity, individual head size, and individual prey trait preferences. Despite the observed association between functional morphology and prey mobility, functional morphology did not appear to be an important underlying cause of individual specialization in prey mobility in one of the study species, suggesting a role for other phenotypic traits, such as behavior. Most importantly, the finding that individual specialization was promoted by an increase in the strength of the relationship between functional morphology and prey size highlights individual feeding morphology as an important, previously underappreciated phenotypic driver of individual specialization. Additionally, it highlights the potential role of individual niche specialization in maintaining morphological diversity in natural populations.

In the second chapter, I showed that consistent individual differences in exploratory behavior constitute an important underlying factor driving individual niche (isotopic) variation within populations of generalist anurans. However, the emergence of this association depended on body size. These findings highlight a state dependence in the effect of behavior on individual trophic niches, in which body size emerged as an important, underappreciated mediator of dietary outcomes across sexes and species of generalist predators. Furthermore, individual exploratory behavior was an important factor associated with the temporal consistency of individual trophic niches, with more exploratory individuals exhibiting more variable diets over time. These results have potential ecological implications for population dynamics in changing environments. When more exploratory individuals maintain more variable (i.e., more flexible) diets over time, populations composed of more exploratory individuals may be better able to cope with temporal changes in resource diversity, thereby enhancing individual survival and promoting greater population stability in changing environments (Moran *et al.* 2017).

In this chapter, the use of stable isotopes allowed us to identify how individual behavior is related to consistent individual differences in trophic niches and their temporal variation, as planned to address the specific research questions for which the study was designed. However, this methodology necessarily leaves us blind to which types of prey (e.g., taxa) and their functional characteristics (e.g., mobility) were consumed by the frogs. This prevents a deeper mechanistic understanding of the causes of individual specialization; specifically, how individual behavior interacts with prey functional characteristics to generate individual specialization. While stable isotopes can be used to roughly infer the taxonomic identity of prey by assessing the isotopic composition of prey available in the environment, this approach would not be very accurate in the studied system. Leptodactylid frogs consume a broad range of prey from different taxonomic groups that often share similar isotopic values (Costa-Pereira *et al.* 2018), which prevents precise discrimination among taxa and makes it difficult to classify prey according to their functional characteristics, such as mobility. Consequently, the most direct and suitable method for evaluating how predator behavior and prey traits influence the degree of individual dietary specialization is through the analysis of gut contents, which was the focus of the following chapter.

In the third chapter, I showed that individual variation in proactivity-related behaviors emerged as an important driver of the mobility of consumed prey, highlighting the functional role of intraspecific behavioral variation in ecological niche variation within populations. The fact that prey mobility was associated with predator proactivity behaviors constitutes a mechanistic explanation to understand how behavior shapes niche variation in the long term, as observed in the second chapter of the thesis, although using another species as a model for study. Whereas more proactive males consumed less mobile prey, consistent with the predator–prey locomotor hypothesis (Huey and Pianka 1981), the contrasting pattern observed in females, in which more proactive individuals consumed more mobile prey, indicates that the relationship between predator proactivity and prey mobility does not necessarily follow a uniform trajectory within populations. Furthermore, although the locomotor-crossover hypothesis can be considered a starting point for understanding the outcomes of predator–prey interactions, the findings reported here indicate that it is not sufficient to explain the complexity of within-population ecological variation in prey mobility. Indeed, morphology and alternative behaviors, once prey is encountered, are documented as potential mechanisms explaining variation in the mobility of consumed prey, calling for further investigation to explain intersexual differences in prey mobility consumption.

By adopting an explicit mechanistic functional approach linking individual predator morphology and behavior to prey traits (Ferry-Graham *et al.* 2002; Schmitz 2017), this study highlights the underappreciated role of functional morphology and the previously unknown role of behavior in individual trophic niche specialization in anuran amphibians. The dependence of dietary outcomes on additional intrinsic individual traits, such as body size and sex, underscores the complex set of interacting factors driving intraspecific ecological niche diversity within natural populations and suggests that these traits should be incorporated into models aimed at understanding the proximate causes of individual specialization.

References

Huey, R. B., & Pianka, E. R. (1981). Ecological consequences of foraging mode. Ecology, 62(4), 991-999.

Diaz-Perez, J. A., Araújo, M. S., & Costa-Pereira, R. (2025). Head morphology predicts prey traits and drives individual dietary specialization in generalist anurans. *Proceedings of the Royal Society B: Biological Sciences*, *292*(2061).

Moran, N. P., Wong, B. B., & Thompson, R. M. (2017). Weaving animal temperament into food webs: implications for biodiversity. Oikos, 126(7), 917-930.

Costa-Pereira, R., Rudolf, V. H., Souza, F. L., & Araújo, M. S. (2018). Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology*, *87*(5), 1452-1464.

Ferry-Graham, L. A., Bolnick, D. I., & Wainwright, P. C. (2002). Using functional morphology to examine the ecology and evolution of specialization. Integrative and Comparative Biology, 42(2), 265-277.

Schmitz, O. (2017). Predator and prey functional traits: understanding the adaptive machinery driving predator–prey interactions. F1000Research, 6, 1767.