

RESEARCH ARTICLE

Individual niche trajectories drive fitness variation

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Abstract

1. Variation in fitness across individuals is central to population growth, species co-existence and evolution by natural selection. Fitness variation associated with resource use is hugely consequential, but how this variation is generated and maintained within natural populations remains unclear. In particular, individual fitness may depend on many cumulative foraging decisions over time, but this hypothesis remains untested.
2. We used multi-tissue stable isotope analysis to determine isotopic niche trajectories within species, populations and sexes of thin-toed frogs and explored how this temporal dimension of diet affects individual reproductive investment, body condition and parasite load.
3. We found that individual frogs shifted their diets less than expected under a null model, likely due to functional trade-offs that limit the incorporation of new prey types over time. However, within the observed range of diet shifts, individuals that modified their diet to a greater degree exhibited higher fitness, although this effect was sex-dependent.
4. We suggest that these different relationships between isotopic niche trajectory length and fitness within thin-toed frogs are driven by variability in the resource environment, negative density dependence and allometric constraints. These strong fitness effects suggest that the temporal dimension of diet change is a potential target of natural selection and, therefore, could drive correlated evolution in phenotypic traits underlying diet flexibility. Our findings add a new level of complexity to the understanding of ecological and evolutionary consequences of niche variation by demonstrating that temporal variation in foraging consistency within populations leads to different fitness pay-offs.

KEYWORDS

body condition, individual specialization, *Leptodactylus*, parasites, reproductive investment, stable isotopes, trophic niche

1 | INTRODUCTION

Fitness and niche variation are key to ecological and evolutionary dynamics across biological scales. Particularly, community theory explores how species-level fitness and niche differences between

competitors affect species diversity and community stability (Chesson, 2000; Vellend, 2010). This *mean field* approach implicitly assumes that conspecific individuals are ecologically and demographically equivalent, an analytically tractable approximation (Bolnick et al., 2011; Clark et al., 2007). However, ecologists have

recently reconsidered this simplification because of the increasingly recognized relevance of intraspecific ecological variation. Mounting evidence across diverse taxa suggests that individuals *within* populations often differ in their resource use (Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2003), which may have important consequences for community structure (Bolnick et al., 2011; Costa-Pereira, Araújo, Souza, & Ingram, 2019; Costa-Pereira, Rudolf, Souza, & Araújo, 2018; Hart, Schreiber, & Levine, 2016; Violle et al., 2012).

Although niche theory has long assumed that individual niche variation leads to intrapopulation fitness differences (Schoener, 1971; Van Valen, 1965), we still know little about how these facets of individual variability are associated within natural populations (Cucherousset et al., 2011; Grémillet et al., 2008; Kernaléguen, Cherel, Guinet, & Arnould, 2016). Because resource uptake and the consequent allocation of energy and nutrients for reproduction and growth strongly influence fitness (Schoener, 1971, 1974), selection may act directly on individuals' ability to obtain resources (Bolnick & Araújo, 2011). Importantly, individual variation in fitness underpins selection and adaptation (Hallgrímsson & Hall, 2005), which may then feed back to affect ecological processes via eco-evolutionary dynamics (Hendry, 2016). Therefore, intraspecific variation in foraging strategies may constitute an important phenomenon shaping heterogeneity in the per capita contribution to population growth (Bolnick et al., 2011; Bolnick & Araújo, 2011).

Classic foraging theory compares the energetic and nutritional benefits of diet generalist versus diet specialist strategies (Schoener, 1971). Indeed, natural populations of diverse taxa are often a mixture of individual trophic specialists and generalists (Estes, Riedman, Staedler, Tinker, & Lyon, 2003; Golet, Kuletz, Roby, & Irons, 2000; Powell & Taylor, 2017; Werner, Mittelbach, & Hall, 1981). However, individuals do not necessarily have temporally consistent foraging strategies. For example, some individuals within a population may undergo diet shifts over time, while others may have relatively constant diets (Bearhop, Adams, Waldron, Fuller, & Macleod, 2004; Martínez del Río, Sabat, Anderson-Sprecher, & Gonzalez, 2009). Although this temporal dimension of individual foraging strategies is rarely considered in trophic studies (Novak & Tinker, 2015; Szigeti, Kőrösi, Harnos, & Kis, 2018; Warburton, Retif, & Hume, 1998), it may be particularly relevant in the context of individual fitness variation because reproductive and somatic allocation depends on multiple cumulative foraging events (Metcalf & Monaghan, 2001; Stephens, Boyd, McNamara, & Houston, 2009).

Foraging theory also predicts that the fitness consequences of temporally invariant versus temporally flexible diets depend on environmental context (Patrick & Weimerskirch, 2014). Because each food type presents specific costs and benefits, consumer individuals with a consistent diet may optimize their intake by repeatedly consuming persistent and profitable resources, such as prey types with lower handling time, higher digestibility or lower pathogen loads (Bolnick et al., 2003; Stephens & Krebs, 1986). In turn, temporally flexible diets come at the cost of the 'Jack of all trades-master of none' principle, which states that highly generalized individuals will necessarily perform poorly on specific resource types (MacArthur,

1972). However, these predictions only hold when resource availability is high and stable. Other ecological contexts, such as temporal fluctuations in prey availability and competition for highly profitable resources, may reduce the benefits of temporal diet consistency (Costa-Pereira, Tavares, Camargo, & Araújo, 2017; Svanbäck & Bolnick, 2005, 2007), and instead favour generalist foraging strategies that provide access to a wider range and quantity of resources (Roughgarden, 1972; Van Valen, 1965).

In organisms with seasonal reproduction, temporal patterns of resource intake prior to reproductive bouts are crucial in determining individual fecundity and growth. In wetland thin-toed frogs (*Leptodactylus* spp.), the beginning of the rainy season triggers an intense foraging period after months of low activity and metabolic rates during the dry season. During this temporal window, frogs must accumulate lipid and energy to ensure successful reproduction a few months later (Uetanabaro, Prado, Rodrigues, Gordo, & Campos, 2008), that is, capital breeding (Stephens et al., 2009). Environmental resource availability (i.e. prey community composition) shifts gradually over this time (Junk, Silva, Nunes da Cunha, & Wantzen, 2011; Wantzen et al., 2011), and thin-toed frogs consume a wide spectrum of prey types (~70 invertebrate families, fish, anurans), though not without considerable individual specialization (Costa-Pereira, Rudolf, et al., 2018). Here, we used multi-tissue stable isotopes to evaluate whether the consistency of individuals' trophic niches over this key foraging period is predictive of fitness outcomes.

Stable isotopes are powerful tools to characterize trophic niches because they allow inference of resource use by organisms over distinct temporal scales (Dalerum & Angerbjörn, 2005; Newsome, Martínez del Río, Bearhop, & Phillips, 2007). This application is particularly useful when stable isotopes from the same organism are measured in body tissues that differ in the rate at which they incorporate new materials, that is, turnover rate (Martínez del Río et al., 2009; Schmidt, Olden, Solomon, & Zanden, 2007). By comparing isotope values of body tissues with distinct turnover rates, it is possible to quantify the temporal consistency of individual diet through isotopic niche trajectories (Figure 1), because individuals with temporally consistent diets have more similar isotope values across tissues than individuals with temporally variable diets (Bond, Jardine, & Hobson, 2016; Martínez del Río et al., 2009).

Here, we quantified the extent and direction of trophic niche trajectories across individuals, sexes and species in two species of thin-toed frogs. Specifically, we asked whether individual niche trajectories are smaller (i.e. more consistent diets) or larger (i.e. more temporally variable diets) than expected by chance. Then, to understand temporal diet shift congruence across individuals, we asked whether niche trajectories in isotopic niche space show trends in directionality towards specific regions of isotopic space. Finally, we investigated how variation in the magnitude of niche trajectories affects three components of individual fitness: reproductive investment, body condition and parasite load. Because thin-toed frogs inhabit dynamic environments, we expected that individuals with larger niche trajectories (more flexible diets) should exhibit

increased reproductive investment, better body condition and lower parasite load. Accordingly, individuals should exhibit niche trajectories larger than expected by chance. Regarding niche directionality, we expected that individuals' diets should converge towards certain profitable resources throughout the foraging season, resulting in directional niche trajectories in the isotopic space.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied thin-toed frog populations in the Pantanal wetlands, the largest and most pristine continental wetland on Earth (Junk et al., 2011). The Pantanal is a seasonal system with a characteristic annual flood regime that influences the life history of native anurans. During the dry season (usually from April to late September in southern Pantanal), many frog species reduce their activity and metabolism to

avoid hot and dry conditions (Uetanabaro et al., 2008). By the end of the summer (between late November and early January), however, run-off from rainfall in the surrounding highlands floods ~80% of the Pantanal's area (Junk et al., 2011). Because predatory fish and aquatic insects (mainly Hemiptera and Odonata larvae) are highly abundant in these floodplains, most frog species breed in ponds and lagoons before the beginning of the flood season to avoid predation on their eggs and larvae (Prado & Haddad, 2005; Prado, Uetanabaro, & Haddad, 2005). Therefore, the annual alternation of dry and flood seasons, both of which present challenges for reproduction, forces anurans to concentrate their reproductive activities in the ~3 month temporal window between the peaks of these contrasting periods (Prado et al., 2005; Uetanabaro et al., 2008). Here, we aim to understand how foraging consistency within this temporal window affects subsequent reproduction.

We investigated niche and fitness variation in two congeneric species of thin-toed frogs, *Leptodactylus chaquensis* and *Leptodactylus podicipinus*. Within the Pantanal, these syntopic species are particularly abundant and exhibit high but variable diet overlap (Costa-Pereira, Rudolf, et al., 2018; Piatti & Souza, 2011). Both species forage on the ground and in low vegetation at night, feeding on a large variety of invertebrate and small vertebrate prey (Costa-Pereira, Araújo, Olivier, Souza, & Rudolf, 2018; Costa-Pereira, Rudolf, et al., 2018; Costa-Pereira et al., 2015). However, because *L. podicipinus* is smaller (max size: ~50 mm), this species tends to consume smaller-sized and less diverse prey types when compared to *L. chaquensis* (max size: ~100 mm) (Costa-Pereira, Rudolf, et al., 2018). Helminth parasites of *Leptodactylus* spp. often exploit trophic transmission (Campião et al., 2014). Despite some differences in their reproductive behaviour, both species deposit eggs in foam nests in water-filled depressions at the edges of water bodies in which exotrophic tadpoles develop (Prado et al., 2005).

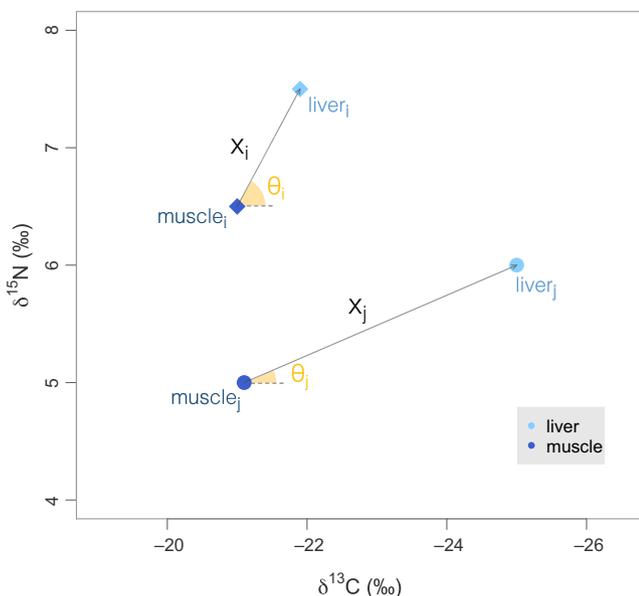


FIGURE 1 Schematic representation of niche trajectory length and angle of change for two hypothetical individuals *i* and *j* in the isotopic δ -niche space (see Figure 2). A niche trajectory is defined as the vector between stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) from muscle and liver, respectively, from a given individual. Because muscle isotope values reflect dietary carbon and nitrogen intake over several months and liver reflects intake along the last few weeks (Dalerum & Angerbjörn, 2005), niche trajectories (represented by arrows in the plot) measure temporal change of individuals' diets. We used vector arithmetic to calculate two properties of niche trajectories: length (i.e. magnitude of change) and direction (i.e. angle of change). Trajectory length (X_i) increases as the diet of an individual is less consistent over time. In turn, variation in angle of change (θ_i) indicates the direction in which individuals' diets temporally shift regarding prey trophic level ($\delta^{15}\text{N}$, vertical shift) and prey position in food webs ($\delta^{13}\text{C}$, horizontal shift; e.g. C4 vs. C4 food chains). In this hypothetical example, both individuals feed on prey at increasingly higher trophic (vertical change) and towards higher $\delta^{13}\text{C}$ values (i.e. C4 food chain, horizontal change) positions over time

2.2 | Field and laboratory data collection

We sampled 15 populations of *L. chaquensis* and 12 populations of *L. podicipinus* around a total of 21 grassland lagoons in an extensive area of the Pantanal between mid-November 2014 and early January 2015. In each sampled site, we established six 10 × 10 m plots and hand-captured all individuals of *L. chaquensis* and *L. podicipinus* (see details in Costa-Pereira, Rudolf, et al., 2018). Frogs were euthanized with an overdose of lidocaine and then stored in a -20°C freezer until laboratory processing. Collection and euthanasia procedures were carried out in accordance with Universidade Estadual Paulista guidelines for the care of vertebrate animals (UNESP-Animal Care and Use Committee 03120501).

In the laboratory, we measured snout-vent length (0.01 mm) and body mass (0.001 g) of each adult specimen of *L. chaquensis* ($n = 296$) and *L. podicipinus* ($n = 267$). We then dissected adult frogs to obtain gonads and weighed testes (Figure S1c) or mature ovaries and eggs (only mature females with fully developed eggs were analysed) using a precision scale (0.00001 g). During dissection, we inspected each frog's body cavity, digestive tract, kidneys, liver, urinary bladder,

lungs and musculature for helminth parasites (Figure S1). Due to challenges in identifying Neotropical anuran parasites to precise taxonomic scales (e.g. genus, species; Campião et al., 2014), we counted the total number of helminth parasites found in each individual frog and used it as a measure of aggregate helminth abundance. Aggregate helminth abundance is a strong predictor of the negative effects of parasites on anuran growth and survival (Goater & Ward, 1992).

To quantify stable isotopes of carbon and nitrogen, we removed pieces (~1 cm³) of muscle and liver from each individual and rinsed them in deionized water. We then oven-dried samples for 48 hr at 60°C and placed ground and weighed samples (~0.5 mg) into tin capsules. Because C:N ratios were generally low (<4), we did not extract lipids from our samples or mathematically correct for lipid content (Post et al., 2007). The abundances of ¹³C/¹²C and ¹⁵N/¹⁴N were quantified at the Washington State University Stable Isotope Core Laboratory using an Elemental Combustion System 4010 elemental analyzer (Costech Analytical) and a Delta Plus XP continuous flow isotope ratio mass spectrometer (Thermo Finnigan). We report isotope compositions using conventional delta notation ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), showing differences between the measured isotope ratios and that of Pee Dee Belemnite for carbon and atmospheric N₂ for nitrogen. The standard deviation of replicates of the internal reference material (Nylon) was 0.03‰ for $\delta^{13}\text{C}$ and 0.06‰ for $\delta^{15}\text{N}$.

2.3 | Using stable isotopes to quantify individual niche trajectories

Multi-tissue stable isotope analyses are particularly useful to investigate temporal changes in individual trophic niches. By comparing the isotopic values of body tissues deposited during different lengths of time, it is possible to distinguish individuals that shift their diet over time from individuals with relatively constant diets (Martínez del Río et al., 2009). We used liver and muscle to capture diet at different temporal scales: liver has a higher turnover rate and its isotopic values integrate dietary inputs over a few weeks, while muscle has a lower turnover rate and its isotope values reflect dietary carbon and nitrogen intake over several months (Dalerum & Angerbjörn, 2005; Tieszen, Boutton, Tesdahl, & Slade, 1983).

We compared isotope values of liver and muscle to quantify the temporal consistency of individual diets, that is, individual isotopic niche trajectories. Vector arithmetic is used to calculate two key properties of niche trajectories in the bivariate isotopic δ -space: length (i.e. magnitude of change, X_i) and direction (i.e. angle of change, θ_i ; Martínez del Río et al., 2009; Schmidt et al., 2007; Figure 1). The utility of these properties to quantify temporal niche variation hinges on the idea that individuals with temporally consistent diets have more similar liver and muscle isotope values than individuals with temporally variable diets (Martínez del Río et al., 2009). We acknowledge that this approach has two potential caveats. First, muscle and liver isotope values are not independent measures because part of the dietary information integrated into liver isotopes is also integrated in muscle. Second, differences in liver and

muscle stable isotope values may emerge not necessarily due to diet variation but via temporal variation in environmental baselines and/or differential isotopic routing. However, because these potential biases should be homogeneous across individuals within populations, we do not expect them to bias our results.

First, we determined the vector representing the niche trajectory between muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (starting point) and liver $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (endpoint) for each individual (Figure 1). Then, we quantified the length of each individual niche trajectory (X_i) as the Euclidean distance between muscle and liver $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values:

$$X_i = \sqrt{(\text{liver}_i\delta^{13}\text{C} - \text{muscle}_i\delta^{13}\text{C})^2 + (\text{liver}_i\delta^{15}\text{N} - \text{muscle}_i\delta^{15}\text{N})^2}$$

To quantify the angle of change θ_i (Figure 1), we measured the counter clockwise angle between the positive x-axis and the vector representing niche trajectories, which may result in values from a circular distribution ranging from 0 to 360° (or 0 to 2π radians). In biological terms, differences in the angle of change indicate whether and in which direction individuals' isotopic values shift vertically ($\delta^{15}\text{N}$, trophic level shift) and/or horizontally over time ($\delta^{13}\text{C}$, ultimate carbon sources; e.g. C3 vs. C4 food chains, aquatic vs. terrestrial primary production; Dalerum & Angerbjörn, 2005; Newsome et al., 2007).

2.4 | Are niche trajectories random walks in isotope space?

We constructed null models to test whether (a) the length of observed niche trajectories is larger or smaller than expected by chance, and (b) the angles of niche trajectories show signs of directionality or assume a uniform circular distribution. First, for each subset of individual trajectories from a given sex from a given species (i.e. *L. chaquensis* females, *L. chaquensis* males, *L. podicipinus* females, *L. podicipinus* males), we computed the observed mean niche trajectory length (\bar{X}_i) and the Rao's spacing statistic (U). Rao's spacing statistic measures the uniformity of circular data by aggregating the deviations between consecutive angular observations, resulting in larger U values as directionality increases (i.e. less deviation in angles of change between individuals' trajectories; Jammalamadaka & Sengupta, 2001). We calculated all circular statistics in the R package *circular* (Agostinelli & Lund, 2013).

Then, we carried out a randomization process to produce stochastic individual niche trajectories in the isotopic space. For each individual, we held constant the observed isotopic starting point (muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) and then assigned the isotopic endpoint by drawing randomly a pair of liver $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the distribution of observed liver isotope values within the group of the focal individual. Thus, the endpoint of random trajectories can assume isotope values observed in the conspecific individuals, from the same sex, and that were captured in the same local site. We did not account for differences in trophic enrichment factors between liver and muscle because we do not have specific values for the studied species. Additionally, because the effect on the length and direction of niche trajectories would be homogeneous across individuals, uncertainty in trophic enrichment factors should not bias the results.

Finally, we generated the null distributions of mean niche trajectory length and Rao's spacing statistic for each species and sex. We used 10,000 replicates in Monte Carlo bootstrap simulations to obtain p -values for these metrics.

2.5 | Fitness proxies

Lifetime fecundity and survivorship are very difficult to measure in most of natural populations of vertebrates. Therefore, we quantified three widely used proxies for these fitness components: reproductive investment, body condition and parasite load. Reproductive investment was quantified as the percentage of mass of mature ovaries and eggs (for females) or testis (for males) relative to total body mass (Prado & Haddad, 2005). We calculated a metric of parasite load by dividing the aggregate helminth abundance found in each individual by its somatic body mass. Finally, to quantify individual body condition we used the scaled mass index, which is body size independent and can readily be used to compare different populations (Peig & Green, 2010):

$$\widehat{M}_i = M_i \left(\frac{L_0}{L_i} \right)^e$$

where \widehat{M}_i is the scaled body condition index, M_i and L_i are, respectively, body mass and snout-vent length of the individual i , e is the scaling exponent estimated by the standardized major axis linear regression of $\ln(\text{body mass})$ on $\ln(\text{snout-vent length})$, and L_0 is the arithmetic mean value of L for the study population.

2.6 | Effects of niche trajectories on individual fitness

For each sex, we tested how individual-level fitness components respond to variation in niche trajectories using linear mixed-effects with beta distributions in the package glmmTMB (Bates, Maechler, Bolker, & Walker, 2014). Because fitness components were not strongly correlated (see Results3), we constructed separate models for each fitness component. We included reproductive investment, body condition or parasite load as the response variable (scaled to vary between 0 [minimum fitness proxy value observed within each population] and 1 [maximum value within each population]), site identity as the random effect, and three predictors interacting with species identity: (a) niche trajectory length X_p , (b) sine and (c) cosine of the trajectory angle of change θ_p . Because θ_p is a circular variable (i.e. the

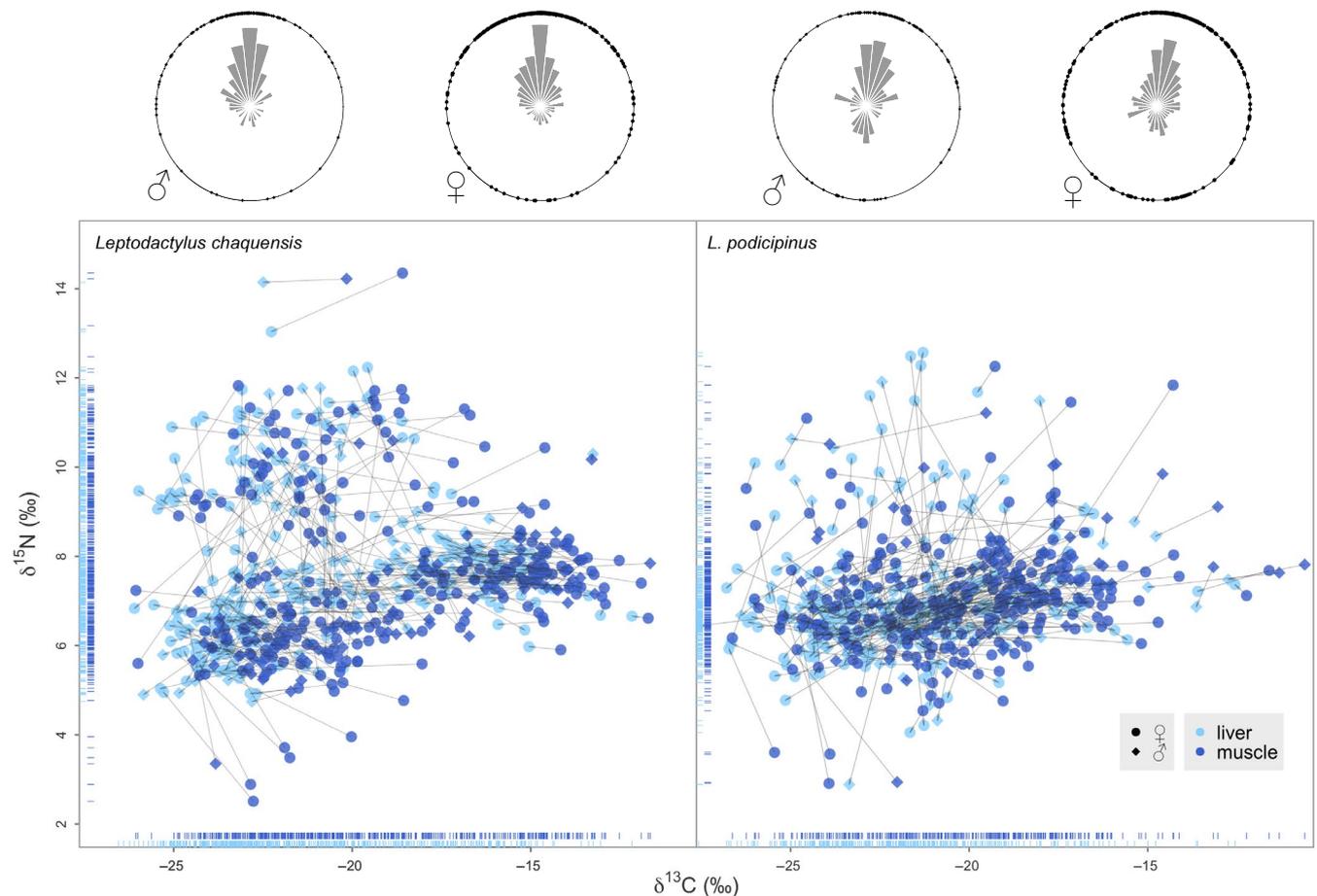


FIGURE 2 Niche trajectories, that is, vector between muscle (dark blue symbols) and liver (light blue symbols) isotope values, respectively, for all individual *Leptodactylus chaquensis* (left) and *Leptodactylus podicipinus* (right). Female niche trajectories are indicated by circular points while male niche trajectories are indicated by diamond-shaped points. Upper circles represent the observed circular frequency of angles of change in niche trajectories for each sex

beginning of the scale is the same as the end, $0^\circ = 360^\circ$), it is problematic to directly use it as a predictor of a linear model. Therefore, we decomposed θ_i into its sine and cosine and used these as predictors in our model (Cox, 2006) representing, respectively, vertical ($\delta^{15}\text{N}$) and horizontal ($\delta^{13}\text{C}$) components of niche direction. p -Values were obtained using the Wald chi-squared test. We performed all statistical analyses in R 3.5.1 (R Development Core Team, 2017).

3 | RESULTS

3.1 | Variation in individual niche trajectories

Thin-toed frogs were widely dispersed in isotopic niche space (Figure 2). The length of isotopic niche trajectories varied across individuals within populations up to 83-fold for *L. podicipinus* and 55-fold for *L. chaquensis* (Figure 2). In biological terms, this means that individuals vary strikingly in the consistency of their feeding strategies during the foraging period that precedes reproduction. While some individuals presented very similar isotope values in their liver and muscle, indicating a temporally consistent diet (a short isotopic niche trajectory), others presented remarkably distinct isotopic variation across tissues, revealing sizable temporal diet change (a long isotopic niche trajectory; Figure 2). Despite the high degree of niche variation observed for some individuals, null models revealed that observed mean niche trajectory length was smaller than expected by chance for both sexes in *L. podicipinus* ($p_{\text{females}} = 0.006$, $p_{\text{males}} = 0.002$) and for females in *L. chaquensis* ($p_{\text{females}} = 0.002$, $p_{\text{males}} = 0.26$; Figure 3, left panels).

Individual frogs also varied substantially in the direction of their niche trajectories in isotopic niche space. However, turning angles showed a significant directionality towards larger $\delta^{15}\text{N}$ values ($U = 179.95$, $p = 0.03$), meaning that most individuals are shifting to relatively higher trophic levels (Figure 2). Interestingly, species differed in the degree of directionality in their niche trajectories. While for *L. chaquensis* both males ($p < 0.001$) and females ($p < 0.001$) exhibited turning angles significantly more directional (towards higher trophic positions) than expected by chance, *L. podicipinus* females had turning angles more uniform than expected by chance ($p < 0.001$) and males' turning angles indicated a random distribution ($p = 0.82$; Figure 3, right panels).

3.2 | Effects of niche trajectories on individual fitness

Individual fitness components varied substantially between and within sexes and species (Figure S2). For instance, some *L. chaquensis* females invested little in reproduction, while others had more than 30% of their body mass allocated to reproductive tissues. Similarly, most frogs had between zero and 20 helminth parasites, but we observed individuals hosting more than 300 parasites. Body condition also varied considerably, particularly within males of *L. chaquensis* (Figure S2). Fitness components were only weakly correlated: individuals with better body condition had slightly higher reproductive investment ($r = 0.21$, $p = 0.01$) and less parasites ($r = -0.28$, $p = 0.01$). Reproductive investment and parasite load were not correlated ($r = 0.03$, $p = 0.39$).

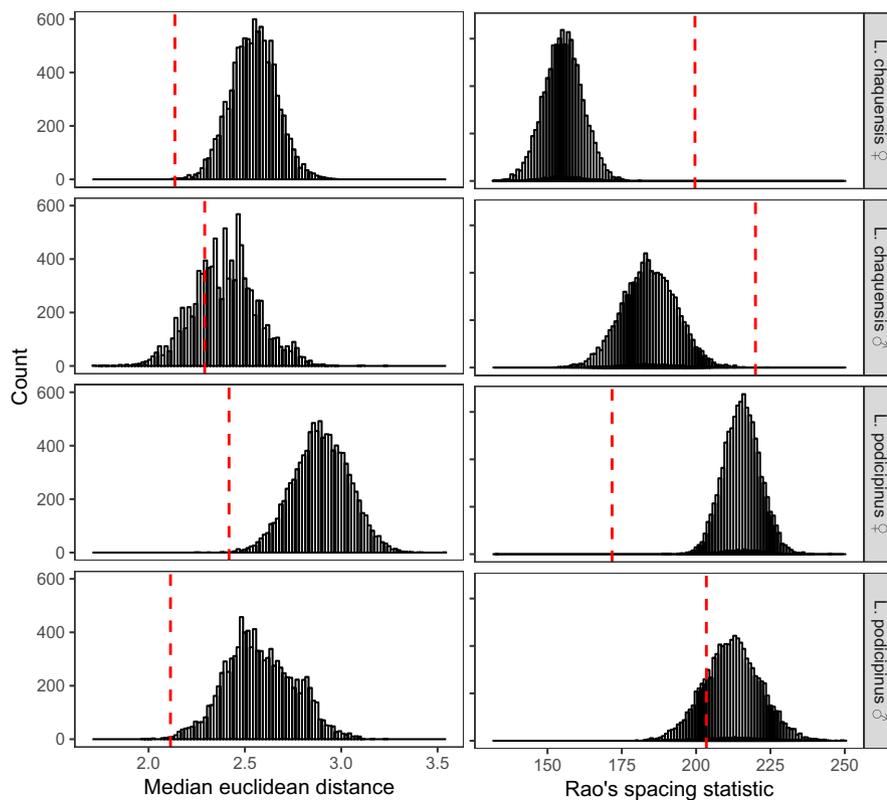


FIGURE 3 Null distributions of niche trajectory length (left panels), quantified as the mean Euclidean distance between muscle and liver stable isotope values from a given individual), and Rao's spacing statistic (right panels), which quantifies the degree of directionality in niche trajectories angle of change. Null distributions were obtained from null models simulating random trajectories in niche space (see details in the Methods2). Red vertical lines indicate observed values

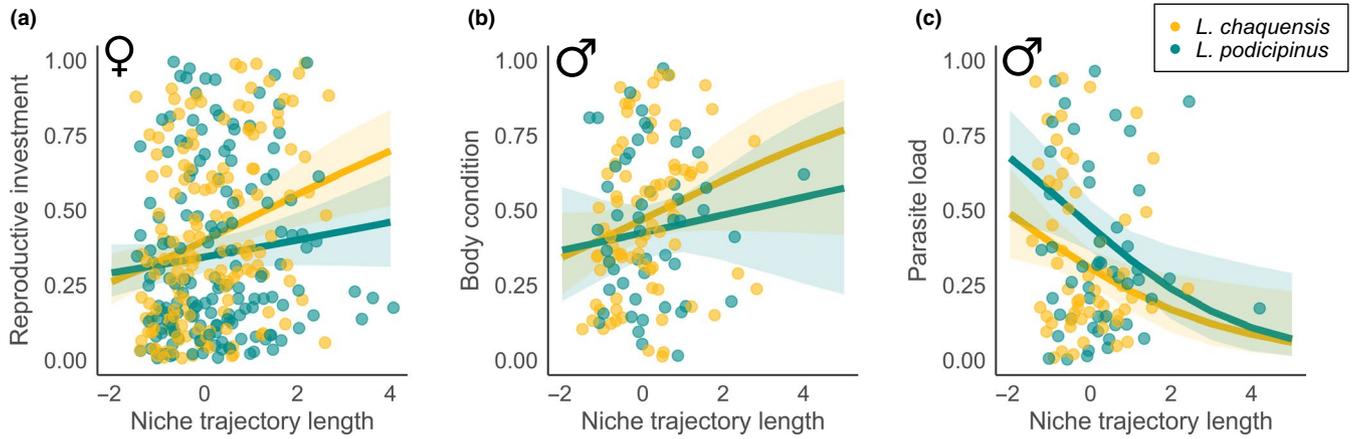


FIGURE 4 Effects of individual variation in niche trajectory length on three fitness components: (a) reproductive investment, (b) body condition and (c) parasite load. Fitness components are scaled (between 0 and 1) within each frog population. Each dot represents one frog individual, and species (*Leptodactylus chaquensis* or *Leptodactylus podicipinus*) are represented by different colours. Panels show the predicted responses estimated from the mixed-models [package sjPlot (Lüdtke, 2018)]

TABLE 1 Effects of individual variation in niche trajectory length and direction (sine and cosine) on three fitness components (reproductive investment, body condition and parasite load) of thin-toed frogs (*Leptodactylus chaquensis* and *Leptodactylus podicipinus*) in the Pantanal wetlands, Brazil

Predictors	Reproductive investment			Body condition			Parasite load		
	β	χ^2	p	β	χ^2	p	β	χ^2	p
♀									
Niche trajectory length	0.31	10.55	<0.001	-0.16	1.13	0.29	-0.06	0.70	0.40
Species identity (Spp)	-0.25	3.86	0.05	-0.21	1.78	0.18	-0.14	1.30	0.25
Sine (turning angle)	0.03	0.33	0.56	0.11	0.01	0.94	0.03	2.57	0.11
Cosine (turning angle)	-0.03	1.37	0.24	-0.02	0.56	0.45	0.04	0.20	0.65
Trajectory length * Spp	-0.19	2.34	0.13	0.16	1.96	0.16	0.02	0.04	0.85
Sine * Spp	-0.12	0.81	0.37	-0.18	2.11	0.15	-0.21	2.87	0.09
Cosine * Spp	0.23	2.90	0.09	-0.07	0.33	0.56	-0.14	1.31	0.25
♂									
Niche trajectory length	0.05	0.58	0.45	0.09	5.87	0.01	-0.39	13.04	<0.001
Species identity (Spp)	0.12	0.03	0.86	-0.06	0.99	0.32	0.44	7.05	0.01
Sine (turning angle)	-0.05	0.80	0.37	-0.03	0.50	0.48	-0.38	0.20	0.65
Cosine (turning angle)	0.21	0.65	0.42	0.02	1.43	0.23	-0.25	6.68	0.01
Trajectory length * Spp	0.09	0.14	0.70	-0.04	0.60	0.53	-0.09	0.14	0.71
Sine * Spp	-0.14	0.32	0.57	0.02	0.11	0.74	0.63	5.54	0.02
Cosine * Spp	-0.27	0.97	0.32	0.03	0.27	0.60	-0.29	1.01	0.31

The magnitude of niche trajectories was a major predictor of fitness variation across individuals. In both frog species, females with larger niche trajectories invested more in reproduction ($R^2 = 0.4$,

Figure 4a). In turn, males with larger niche trajectories had lower parasite load ($R^2 = 0.18$) and better body condition ($R^2 = 0.08$; Table 1, Figure 4b,c). Overall, the direction of niche change, represented in

our models by the sine and cosine of the angular change, had no significant explanatory power on fitness variation across individuals. The only exception was the effect of cosine of angular change on parasite load observed in males (Table 1).

4 | DISCUSSION

Our study explored relationships between individual trophic consistency over the foraging period preceding reproduction (represented as isotopic niche trajectories) and three fitness proxies in tropical thin-toed frogs. We found that individual frogs adopting a more flexible feeding strategy (i.e. larger niche trajectories) had higher fitness due to larger reproductive investment, improved body condition and, overall, lower parasite load. Yet despite this fitness advantage of generalists, null models indicate that individual frogs shifted their diets less than expected by chance, suggesting the presence of trade-offs in prey acquisition that constrain individuals' diets. Together, these findings emphasize the fitness advantages of trophic flexibility within populations, which may bring new insight into the role of niche variation in shaping life-history strategies in dynamic environments.

4.1 | Variation in individual niche trajectories

We used multi-tissue isotopes to elucidate the under-explored consequences of individual variation in trophic strategies over time. Recent evidence based on gut contents and single-tissue (liver) isotope analysis suggests that while thin-toed frogs are considered trophic generalists as a species, individuals actually function as specialists within relatively short periods of time (Costa-Pereira, Rudolf, et al., 2018). However, by analysing diet consistency along the foraging window preceding reproduction, our findings suggest that thin-toed frog foraging strategies observed at any one time may not be consistent over months (i.e. variation in niche trajectories or the temporal consistency of diet). As recent theory indicates that the degree of individual niche variation impacts how species interact in local communities (Bolnick et al., 2011; Costa-Pereira, Rudolf, et al., 2018; Hart et al., 2016; Hausch, Vamosi, & Fox, 2018), our results emphasize the importance of additionally considering the temporal dimension of individual niche variation.

Despite some individuals changing their diets much more than others, we found that, on average, thin-toed frogs exhibit smaller niche trajectories than expected by chance (except for males of *L. chaquensis*). This finding suggests that, despite the fitness benefits of relatively larger niche trajectories (see *Effects of niche trajectories on fitness*), diet shifts over time are somehow constrained. Allometric constraints provide one potential mechanism. Because thin-toed frogs swallow their prey whole, gape size constrains the potential size spectrum of prey available to any individual (Costa-Pereira, Rudolf, et al., 2018). Thus, small-bodied and more gape-limited individuals would have access to a narrower range of prey types with less scope for temporal diet change. These allometric constraints could

explain why only males in *L. chaquensis* (mean snout-vent length: 64.04 ± 9.83), which are often larger than conspecific females (SVL: 58.19 ± 13.58) and *L. podicipinus* (mean SVL: $33.7 \text{ mm} \pm 4.48$), did not exhibit niche trajectories smaller than expected by chance. We tested this hypothesis a posteriori by correlating individual snout-vent length with niche trajectory length, but found no significant relationship ($r = -0.03$, $p = 0.39$). An alternative explanation with wide theoretical and empirical support is that functional trade-offs prevent individuals from changing their diets over time. For example, adding a novel resource might require cognitive skills and/or biomechanical and physiological features that are not possible for a given individual (Bolnick, Svanbäck, Araújo, & Persson, 2007; Robinson, Wilson, & Shea, 1996). Previous evidence suggests that trade-offs in thin-toed frogs do not arise from morphology (Araújo, Reis, Giaretta, Machado, & Bolnick, 2007). Thus, we speculate that behavioural plasticity (e.g. propensity for risky behaviours, or ability to recognize different prey types; Toscano, Gownaris, Heerhartz, & Monaco, 2016) and/or differences in digestive performance between individuals (Hooker, Van Leeuwen, & Adams, 2017) may play an important role in constraining individuals' diets. Unravelling whether and how functional trade-offs shape individual niches, and ultimately fitness variation, is an important step for future studies.

Thin-toed frogs also varied widely in the direction of their trajectories, although this variation did not affect individual fitness (see *Effects of niche trajectories on fitness*), suggesting that there is no single optimal direction of niche change for all individuals. In practical terms, variation in niche trajectory direction indicates that individuals change their trophic positions ($\delta^{15}\text{N}$, vertical shift) and/or ultimate sources of carbon that might be associated with different food chains ($\delta^{13}\text{C}$, horizontal shift; Dalerum & Angerbjörn, 2005; Newsome et al., 2007). Despite individual variation in the direction of trajectories, we observed some species-specific patterns. Males and females of *L. chaquensis* shifted their niches towards higher trophic levels. Conversely, niche trajectories of *L. podicipinus* females showed a uniform circular distribution, suggesting that individuals diversified their diets rather than converging on specific prey types. These distinct patterns of niche directionality may be associated with two complementary and non-mutually exclusive mechanisms. First, because *L. chaquensis* are larger than *L. podicipinus*, the latter should be more gape constrained to capture and ingest large-sized prey, which tend to occupy relatively higher positions in food webs (e.g. centipedes, large spiders, small vertebrates; Costa-Pereira, Araújo, et al., 2018; Costa-Pereira, Rudolf, et al., 2018). Thus, *L. podicipinus* could be biomechanically limited in their ability to move to higher positions in isotopic niche space. Larger prey may constitute a competitive refuge for *L. chaquensis*, explaining the orientation of their niche trajectories. Additionally, because both *L. podicipinus* and *L. chaquensis* share small-sized prey (Costa-Pereira, Araújo, et al., 2018), competition might prevent diet convergence of *L. podicipinus* individuals, resulting in the observed pattern of circular dispersion across niche trajectories. Indeed, individual trophic specialization is predicted to arise via negative density dependence (Bolnick et al., 2011; Costa-Pereira et al., 2017; Tinker et al., 2012). Altogether,

these findings indicate that the dispersion of individual trajectories in niche space may reveal patterns of trophic variation that are not captured by niche trajectory length, which may bring new insights on how processes operating at the scale of individuals and interspecific differences may interact to determine niche variation.

4.2 | Effects of niche trajectories on fitness

Our results indicate that higher trophic flexibility resulted in higher fitness than consistent diets over the time period of the study. However, individual diets were significantly less flexible than random. While these results may appear counterintuitive at first glance, they are consistent with two major lines of theory aiming to explain individual niche variation. Theory and empirical work indicates that a constant and more specialized diet is advantageous because individuals that shift diets or foraging behaviours often incur costs resulting from functional trade-offs in prey capture or digestion (see *Variation in individual niche trajectories*; Bolnick et al., 2003; Hooker et al., 2017; MacArthur, 1972; Patrick & Weimerskirch, 2014). In line with this expectation, our null models indicate that large trophic flexibility is restricted in thin-toed frogs. Conversely, because generalist individuals have access to a broader variety of resources and, consequently, a greater amount of prey, classic foraging theory predicts that individuals' niche should fluctuate to include the whole set of resources used by the population, particularly in variable environments (Roughgarden, 1972; Taper & Case, 1985). Therefore, our results seem to reconcile these two apparently conflicting bodies of theory by suggesting that, within the potential foraging limitations imposed by functional trade-offs, individuals that managed to vary their diets more over time exhibit higher fitness.

The overall positive relationship between niche trajectory length and individual-level fitness could be due to the higher feeding rate of predators when environmental prey availability fluctuates. Indeed, our study system is dynamic and gradual changes in temperature, humidity and vegetation structure over the summer lead to shifts in the presence and abundance of important invertebrate prey for frogs (Battitola, Batistella, Rosado-Neto, Brescovit, & Marques, 2016; Santos-Silva, Pinheiro, Chagas-Jr, Marques, & Battitola, 2018; Soares et al., 2013). Therefore, these temporal changes in prey availability may provide the scope for temporal niche variation, favouring individuals that can plastically adjust their diets to the best foraging options at a given time. For example, depending on their learning and foraging skills, individuals tend to adjust their diets to more abundant, more nutritive and/or less risky resources (e.g. lower infection rates; Lee, Cory, Wilson, Raubenheimer, & Simpson, 2006; Senior, Nakagawa, Lihoreau, Simpson, & Raubenheimer, 2015; Werner & Hall, 1974).

Male and female frogs exhibited different fitness responses to variation in niche trajectories, which might be related to their different reproductive roles. For example, variation in reproductive investment was much higher and was explained by niche trajectory length for females. This is expected because the egg production and development is much more energetically costly than sperm

production in a broad variety of organisms (Hayward & Gillooly, 2011). In turn, body condition and parasite load responded to niche trajectory length only for males, also emphasizing the benefits of diet flexibility. In many *Leptodactylus* species, males compete physically for females (Heyer, 1969) and larger forelimbs and better body condition may confer intrasexual reproductive advantages by enhancing resistance to fatigue (Camurugi et al., 2017; Navas & James, 2007). In addition to better body condition, males with larger niche trajectories had relatively less parasites, which suggests that diet consistency may lead to increased infection rates, therefore favouring prey shifts over time. Accordingly, while we present evidence that temporally flexible diets result in higher fitness in both sexes of thin-toed frogs, the generality of this pattern should depend on system-specific sexual differences regarding behaviour, nutritional requirements and foraging priorities (Patrick & Weimerskirch, 2014).

Given this evidence for fitness consequences of individual variation in foraging strategies, a naturally following question is how these consequences scale to population-level processes. This is a relevant problem because most of community and population theory considers the effect of mean population demography rather than fitness variation among individuals. Therefore, if temporal prey switching brings fitness advantages to individuals, populations composed of individuals with more flexible diets should present higher mean fitness, favouring population stability and persistence (May & Arthur, 1972). More specifically, subtle effects may arise if population-level fitness depends nonlinearly on individual diet niche consistency, so that populations with identical niche variation means but different variances (e.g. variation in niche trajectories lengths across individuals) will have distinct mean fitness (Jensen's inequality), which may have important consequences for demographic rates and community dynamics (Bolnick et al., 2011; Hart et al., 2016; Ingram, Costa-Pereira, & Araújo, 2018). Therefore, determining the potentially nonlinear relationship between the temporal dimension of diet change and population fitness (e.g. growth rates) is a key direction for future studies.

Our findings add a new level of complexity to the understanding of ecological and evolutionary consequences of niche variation by demonstrating that temporal variation in foraging consistency within populations leads to different fitness pay-offs. This mechanistic link between diet consistency and key fitness components within and across populations may bring new insights to species interaction studies that have traditionally overlooked niche and fitness variation within populations. We suggest that an important next step is to clarify whether and how functional trade-offs determine shifts in individuals' niches and, consequently, individuals' contribution to population fitness. Specifically, experimental studies should test whether foraging variation over time is correlated with behavioural, morphological and/or physiological traits. Determining whether such variation in foraging consistency arises as a simple consequence of plasticity or heritable variation in thin-toed frogs and other taxa may open new avenues to understand the potential eco-evolutionary implications of population adaptation and species interactions.

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AUTHOR'S CONTRIBUTIONS

R.C.-P., M.S.A. and B.T. conceived the ideas; R.C.-P., M.S.A. and F.L.S. designed the methodology; R.C.-P. and F.L.S. conducted the field work; R.C.-P. processed the samples; R.C.-P. analysed the data; R.C.-P. led the writing of the manuscript; and all authors contributed to revisions.

DATA AVAILABILITY STATEMENT

Data supporting results are archived in the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.6qh7n6k> (Costa-Pereira, Toscano, Araújo Márcio, Souza Franco, & Ingram, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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