



## Seasonal population and individual niche dynamics in a tetra fish in the Pantanal wetlands

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### ABSTRACT

In seasonal tropical regions, rainfall and/or temporary floods during the wet season generally increase the abundance and diversity of food resources to many consumers as compared to the dry season. Therefore, seasonality can affect intraspecific competition and ecological opportunity, which are two important ecological mechanisms underlying population and individual niche variations. Here, we took advantage of the strong seasonality in the Pantanal wetlands to investigate how within- and between-individual diet variations relate to seasonal population niche dynamics of the tetra fish *Astyanax lacustris*. We quantified dietary niche using gut contents and stable isotopes. Tetras had higher gut fullness and better body condition in the wet season, suggesting that competition is more intense in the dry season. The population niche was broader in the wet season due to an increase in diet divergence between individuals, in spite of potential stronger competition in the dry season. We posit that low ecological opportunity in the dry season limits the diversifying effect of intraspecific competition, constraining population niche expansion. Our results add new insights on how seasonality affects population and individual diets, indicating that intraspecific competition and ecological opportunity interact to determine temporal niche variations in seasonal environments.

Abstract in Portuguese is available with online material.

*Key words:* Floodplain; individual specialization; intraspecific variation; mixing models; resource fluctuation; trophic niche.

OPTIMAL FORAGING THEORY (OFT) HAS BEEN USED FOR OVER HALF A CENTURY TO PREDICT FORAGING DECISIONS THAT INDIVIDUALS MAKE IN HETEROGENEOUS HABITATS (MacArthur & Pianka 1966). In the classical view of OFT, when resources are abundant, all individuals should consume the most valuable prey, ignoring less profitable ones. When the preferred prey becomes depleted, individuals should begin to feed on alternative resources, increasing individual and, consequently, populational niche breadths (Schoener 1971). This prediction has the implicit assumption that all individuals have equal search and handling efficiencies, and as a consequence the same resource rank preferences (Stephens & Krebs 1986).

However, at odds with the assumption of individual ecological equivalence, it has become clear in the last decade that intraspecific niche variation is a widespread phenomenon in nature (Bolnick *et al.* 2003, Araújo *et al.* 2011). Empirical evidence in numerous taxa indicates that generalist populations can actually be composed of specialized individuals, whose niches are only subsets of the populational niche. This individual niche specialization has important ecological and evolutionary implications for natural populations, such as the facilitation of frequency-

dependent interactions that may increase population stability (Doebeli 1996) and cause disruptive selection (Dieckmann & Doebeli 1999, Svanbäck & Bolnick 2005).

This new perspective allows a better understanding of how niche dynamics at the individual level is translated into the population level (Bolnick *et al.* 2003). The niche of a population can become broader either because individuals become more generalist by including novel resources in their diets (within-individual niche expansion) or because they reduce diet overlap by exploiting different resources while remaining relatively specialized (increase in between-individual niche variation). Because these two mechanisms are non-exclusive, it is relevant to identify their relative importance to understand the temporal and spatial dynamics of the niches of natural populations (Bolnick *et al.* 2003, 2007).

Seasonality is recognized as an important factor affecting the niche dynamics of populations. Seasonal environments are subject to changes in temperature, water, and nutrient availability between different seasons. These environmental changes cause fluctuations in resource availability, often times characterized by a season with high-resource abundance (*e.g.*, rainy season) and a season with low-resource abundance (*e.g.*, dry season), affecting diverse aspects of the life history of organisms (Conover 1992, Merritt *et al.* 2001, Marshall & Burgess 2015). Particularly in the tropics,

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seasonality in rainfall generates a wet (rainy or monsoon) and a dry season. The former concentrates most of the rainfall and is characterized by higher productivity and resource abundance and diversity, while in the latter food can be scarce for some organisms, which is expected to affect the niche width of consumers (Karr 1976, Smith *et al.* 1978, Winemiller 1989).

Although it is intuitive that the niches of populations should respond to seasonal changes in resource abundance and diversity, there is still no clear understanding of how the seasonal dynamics of population and individual niches relate. Populations should generally expand their diets in the season in which resource abundance is low due to increased intraspecific competition for preferred resources (OFT), but they might as well become more generalized in the season in which resources are more abundant if for example they include energetically profitable resources that are only available at this moment (Schoener 1986). If individuals have the same rank preferences for resources (classic OFT), these changes in population niche breadth should not change the degree of interindividual diet variation. However, if individuals differ in rank preferences due to differences in morphology or experience that affect search and/or handling times, the degree of interindividual diet variation might either increase or decrease during changes in the population niche, depending on how rank preferences differ among individuals (Svanbäck & Bolnick 2005).

A particularly interesting system to explore these alternative scenarios is the Brazilian Pantanal, the world's largest continuous wetland, comprising more than 140,000 km<sup>2</sup> of a mosaic of seasonally flooded grasslands and savannas. About 80 percent of its area is seasonally flooded as a result of the runoff of rainfall waters from surrounding highlands toward wetlands, where the gently sloped topography allows the flooding of extensive floodplain areas (Junk *et al.* 2011). The strong seasonality in this system promotes drastic changes in productivity and resource availability between the dry and wet seasons (Alho 2008). In general, there is higher resource availability (both in abundance and diversity) for fishes during the wet season, when food items (*e.g.*, fruits, insects, mollusks) are more abundant and accessible than in the dry season (Pott & Pott 1994, Wantzen *et al.* 2002, Ragusa-Netto & Fecchio 2006).

Here, we took advantage of the annual flood pulse in the Pantanal wetlands to unravel the contribution of within- and between-individual diet variations as drivers of seasonal population niche dynamics of the tetra fish *Astyanax lacustris* (Lütken 1875). First, we describe the seasonality in diet of this tetra fish using stomach contents and stable isotopes. Then, we test the hypothesis that intraspecific competition is higher during the dry season due to the lower availability of resources (Resende 2000). Assuming this is true, there are three contrasting hypotheses regarding the responses of population and individual niches to seasonality. The first hypothesis, grounded in classic OFT, is that during the dry season, individuals begin to include the same alternative resources in their diet as competition decreases availability of the favorite ones, increasing within-individual diet variation and, accordingly, the population niche in relation to the wet season (Fig. 1B, scenario i). The second hypothesis is that during

the dry season, because of stronger intraspecific competition, there is a niche expansion via divergence in individuals' diets, increasing both population niche width and the degree of individual specialization (Fig. 1B, scenario ii). Third, in spite of the diversifying effect of intraspecific competition, the population niche becomes narrower in the dry season due to the reduction in the diversity of available resources (ecological opportunity) compared to the wet season (Fig. 1B, scenario iii).

## METHODS

**STUDY SYSTEM.**—The Pantanal wetlands are highly seasonal system, with two clearly contrasting seasons. During the dry season (from April to October in southern Pantanal), many fish species inhabit lagoons, feeding mainly on autochthonous resources (Resende 2000, Wantzen *et al.* 2002). In the wet season (from November to March), these fishes occupy floodplain habitats to feed on the abundant and diverse available food resources (Junk *et al.* 2011). For instance, many floodplain plant species fruit only during the wet season in the Pantanal (Pott & Pott 1994, Ragusa-Netto & Fecchio 2006), and fruits falling into the water are widely consumed by fishes (Costa-Pereira *et al.* 2011). In the wet season, a large amount and diversity of terrestrial soil invertebrates, which are hardly accessible to fish in the dry season, become available (Marques *et al.* 2006, Novakowski *et al.* 2008, Soares *et al.* 2013). Moreover, many invertebrates reproduce during the wet season, and aquatic larvae are abundant in floodplains and are commonly consumed by fish (Wantzen *et al.* 2002, 2011).

The tetra fish *A. lacustris* is a small trophic generalist species (up to 12 cm), commonly found in lagoons, river channels and seasonal flooded habitats in the Pantanal wetlands (Willink 2000). We studied a population of *A. lacustris* inhabiting the Medalha Lagoon (19°34'34" S, 57°00'46" W), a permanent floodplain lagoon with an area of 5.4 ha adjacent to the Miranda River. During the dry season, the Medalha lagoon is completely isolated from the Miranda River, and individuals of *A. lacustris* use the submerged roots of macrophytes (mainly *Eichhornia azurea*) to forage and as refuge from predators (Costa-Pereira *et al.* 2016). During the wet season, the increase in the water level of the Miranda River floods adjoining lowland areas, connecting the Medalha Lagoon to extensive floodplain habitats (Costa-Pereira *et al.* 2014). Many fish species, including *A. lacustris*, forage in the Miranda River floodplain during the wet season, feeding mainly on allochthonous resources, such as terrestrial invertebrates and fruits (Resende 2000, Costa-Pereira *et al.* 2011).

**DATA COLLECTION.**—We sampled adult *A. lacustris* individuals in the Medalha Lagoon using a cast net (mesh size: 30 mm; diameter: 2 m) in two field campaigns at the peaks of the wet (March 2011,  $N = 42$ ) and the dry (September 2011,  $N = 44$ ) seasons. We euthanized specimens in Eugenol and froze them until laboratory work.

In the laboratory, we measured standard length with a digital caliper ( $\pm 0.01$  mm) and body mass (excluding gut and gonads mass) using a precision scale ( $\pm 0.01$  g). We dissected individuals for removal of guts, and analyzed gut contents under a

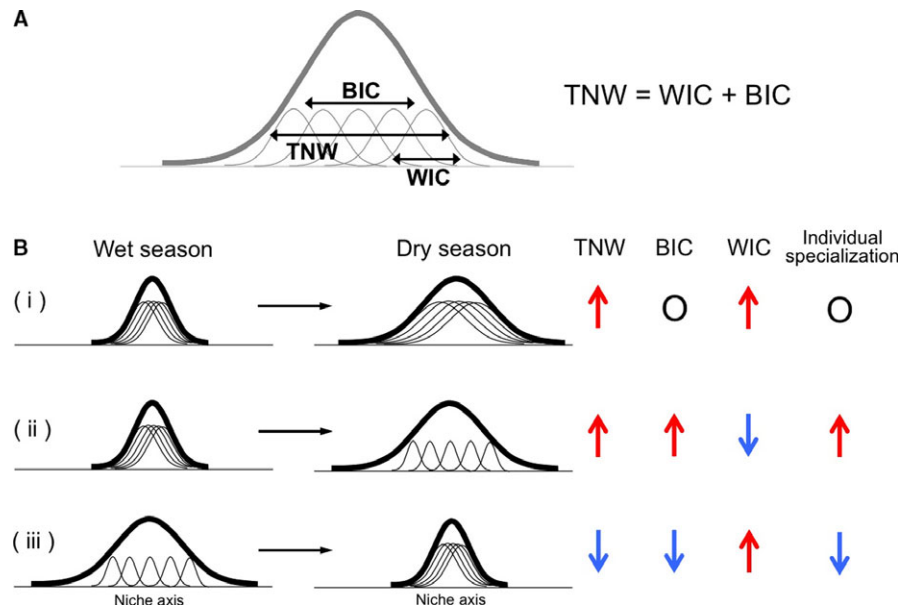


FIGURE 1. (A) Conceptual representation of Roughgarden's (1972) niche metrics (thick lines represents the population niche, thin ones the individuals). The total niche width (TNW) is the variance of total resource use of all individuals, the within-individual component (WIC) is the mean of individual niche widths, and the between-individuals component (BIC) is the variance in average resource use among individuals. In this view, as individuals' niche become more divergent (*i.e.*, high) and narrower (*i.e.*, low), the population niche expands and the degree of individual specialization increases (Bolnick *et al.* 2003). (B) Three theoretical scenarios of the response of individual and population niches to the transition between wet (high-resource availability) and dry season (low-resource) and the expected responses of Roughgarden's (1972) niche metrics and the degree of individual specialization to the transition between wet and dry seasons. In the wet season in the Pantanal wetlands, there is more abundance and diversity of resources to consumers than in the dry season.

stereomicroscope. We identified food items to the lowest feasible taxonomic level and weighed them ( $\pm 0.0001$  g). In addition, we used stable isotopes because they reflect long-term diet and have been used to measure interindividual diet variation (Layman *et al.* 2012). We quantified  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  isotope ratios from muscle tissue obtained from lateral muscle of each individual fish. We quantified stable isotopes of food items ingested by more than 10% of individuals, obtained from gut contents and field sites. Muscle and resource samples were rinsed in deionized water (Sweeting *et al.* 2004), oven-dried at  $60^\circ\text{C}$  (Magnusson *et al.* 1999), grounded to a fine powder, weighed (precision 0.00001 g) and encapsulated. Prey items were grouped by taxon (Order for invertebrates; Table S1) and dried and grounded together. Because the isotopic composition of resources can vary seasonally (Wantzen *et al.* 2002) samples from different seasons were processed separately. We analyzed the isotopes of 16 food resources in the wet season and 11 in the dry season. Stable isotope analysis was carried out at the Centro de Energia Nuclear na Agricultura (tetras from the wet season) and the UC Davis Stable Isotope Facility (tetras from the dry season and food resources). The isotope composition of samples is reported in conventional delta notation, showing differences between concentrations in the samples and those of Pee Dee Belemnite (carbon) and atmospheric air (nitrogen). The standard deviations of within-run organic references (bovine liver) were  $0.11\text{‰}$  for  $\delta^{13}\text{C}$  and  $0.05\text{‰}$  for  $\delta^{15}\text{N}$ . Unfortunately, we could not obtain enough mass to perform the isotope analysis of  $\text{C}_4$  grass seeds from gut contents and failed to collect

it in the field. We, thus, obtained isotope values of  $\text{C}_4$  grasses in Neotropical savannahs, including the Pantanal wetlands, from the literature (Magnusson *et al.* 1999, Medina *et al.* 1999, Wantzen *et al.* 2002, Bustamante *et al.* 2004). We obtained a mean isotopic value of  $\delta^{13}\text{C} = -12.86\text{‰}$  (SD =  $\pm 0.80$ ) and  $\delta^{15}\text{N} = 2.2\text{‰}$  ( $\pm 0.28$ ), and used these values in our analysis.

**DATA ANALYSIS.**—To compare the magnitude of intraspecific competition during wet vs. dry seasons, we used body condition (Jakob *et al.* 1996) and gut fullness as indirect measurements (Svanbäck & Bolnick 2007). We investigated differences in body condition between individuals collected in different seasons comparing the residuals of the regression of the natural logarithm of body mass (subtracting gut contents and gonads mass) on the natural logarithm of standard length. We compared the calculated residuals between seasons using an ANOVA. Similarly, to test differences in gut fullness between wet and dry seasons, we did the same procedure, but using the residuals of the regression between the natural logarithms of gut-content mass vs. body mass (Svanbäck & Bolnick 2007).

For dietary analyses, we grouped food items found in gut contents into six trophic categories: terrestrial invertebrates, aquatic invertebrates, fruits and seeds, macrophytes, filamentous algae, and detritus (Table S1). This classification considers the taxonomic identity of the resource and the microhabitat where it is available (*e.g.*, bottom, water surface). We averaged the isotope values of all food items within each trophic category and used

these values (and the respective standard deviations) in the analysis. We treated grass seeds as a distinct trophic category in this analysis (in the other analyses, it is included among fruits and seeds) because  $C_4$  plants have a very different carbon isotopic composition from  $C_3$  plants (Fry 2006).

We estimated the contribution of each of the resource categories to the population diet in each season using a Bayesian stable isotope mixing model in the package SIAR (Parnell *et al.* 2010). We used Dirichlet distributions (the generalized multivariate equivalent of the Beta distribution) as priors (Parnell *et al.* 2010), treating each food source independently, but necessarily the diet proportions sum to 1. Models were fitted using Markov chain Monte Carlo (MCMC) to estimate parameters based on both the data and the prior distribution, which allowed us to generate probabilistic density distributions of resource contributions to population diet. SIAR also incorporates a residual error term (*i.e.*, consider unknown sources of error in the observed data) (Parnell *et al.* 2010).

We calculated Roughgarden's (1979) niche metrics using the relative mass of trophic categories found in gut contents. We measured the total niche width (TNW) of populations applying the Shannon index of diversity to the population's distribution of resource use (Roughgarden's 1979). We partitioned TNW into the within-individual component of niche width (WIC), which is the average individual niche width, and the between-individual component of niche width (BIC), which is the variation between individuals' niche positions, such that  $TNW = WIC + BIC$  (Roughgarden 1972).

Complementarily, we calculated the proportional similarity index of each individual ( $PS_i$ ), which quantifies the overlap between individual  $i$ 's niche and the population niche. We averaged the  $PS_i$  values in each season to obtain the individual specialization index (IS), which is the average overlap between individuals' niches and the population niche (Bolnick *et al.* 2002). When all individuals' niches overlap totally with the population niche (all  $PS_i$  values equal 1), the IS index equals 1, assuming lower decimal values as

the degree of individual specialization increases. We opted to use a more intuitive measure of individual specialization,  $V = 1 - IS$ , so that  $V$  assumes higher values as individuals become more specialized (Bolnick *et al.* 2007). To test if the degree of individual specialization varies between the wet and dry seasons, we transformed the  $PS_i$  values by the arcsine of the square root and compared them between seasons using a  $t$ -test.

We also obtained  $V$  values in the wet and the dry seasons based on the isotope variances using an adaptation of the method proposed by Araújo *et al.* (2007b). In other words, this method allows converting the observed population isotope variances into a simulated  $V$  index of individual specialization (originally designed by Araújo *et al.* 2007b, to WIC/TNW index), which can be compared to a gut-content based  $V$  value. Comparing these two  $V$  values, it is possible to infer if gut-content data is a reliable measure of diet variation in the studied population. Based on the observed population size, diet, and prey masses and isotope values, this method simulates populations with different degrees of individual specialization and variance in individuals' isotope values ( $Var\delta_i$ ), allowing us to estimate a  $V$ -value based on the empirical  $Var\delta_r$ . We compared gut-content diet variation ( $V$ ) with isotope-derived diet variation ( $V_\delta$ ) (Araújo *et al.* 2007b). We performed statistical analysis in R version 3.1.1 (R Core Team 2014) using the package RInSp (Zaccarelli *et al.* 2013), and we ran simulations to quantitate the  $V$  index based on isotope data using the program VarIso1.0 (Araújo *et al.* 2007b).

## RESULTS

Tetra fish consumed a higher diversity of resources in the wet season (26 food items) than in the dry season (14 items); 14 food items were exclusively consumed in the wet season (Table S1). Gut contents analyses indicated that fruits and seeds were the most consumed resources in the wet season, and filamentous algae in the dry season (Fig. 2). The isotopic probability

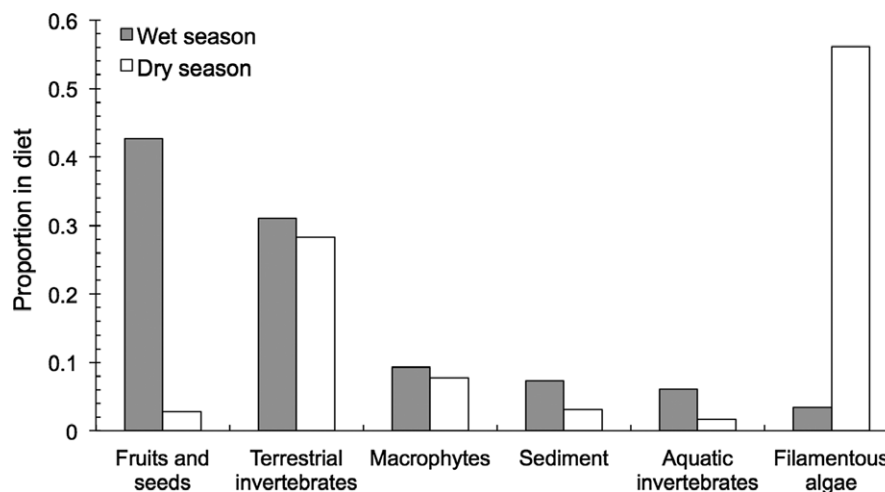


FIGURE 2. Proportions of the mass of resources in the diet of the tetra fish *Ashtyanax lacustris* in the wet (grey bars) and dry (white) seasons in the Pantanal wetlands.

distributions of resource contributions to population diet partly agreed with gut-content data. Tetra fish assimilated carbon and nitrogen mainly from macrophytes and filamentous algae during the dry season, and mostly from invertebrates (terrestrial and aquatic) in the wet season (Fig. 3; Table S2).

Tetra fish presented significantly better body condition ( $F_{1,84} = 153.25$ ,  $P < 0.001$ ) and higher gut fullness ( $F_{1,84} = 135.84$ ,  $P < 0.001$ ) during the wet season (Fig. 4), suggesting that they experienced higher competition during the dry season. Population niche was wider in the wet than in the dry season

(Table 1). During the transition between the wet and dry seasons, individuals became slightly more generalized (increase in WIC) and converged in resource use (decrease in BIC). Because the decrease in BIC was higher in magnitude than the increase in WIC, the population niche narrowed (decrease in TNW; Table 1), indicating that population niche contraction in the dry season was driven by decreased between-individual diet variation, corroborating the scenario (iii) of the Fig. 1B. Indeed, the degree of individual specialization (calculated from gut-content data) was higher in the wet than in the dry season ( $t = 2.35$ ,  $df = 84$ ,  $P = 0.01$ , Table 1).  $V$  values

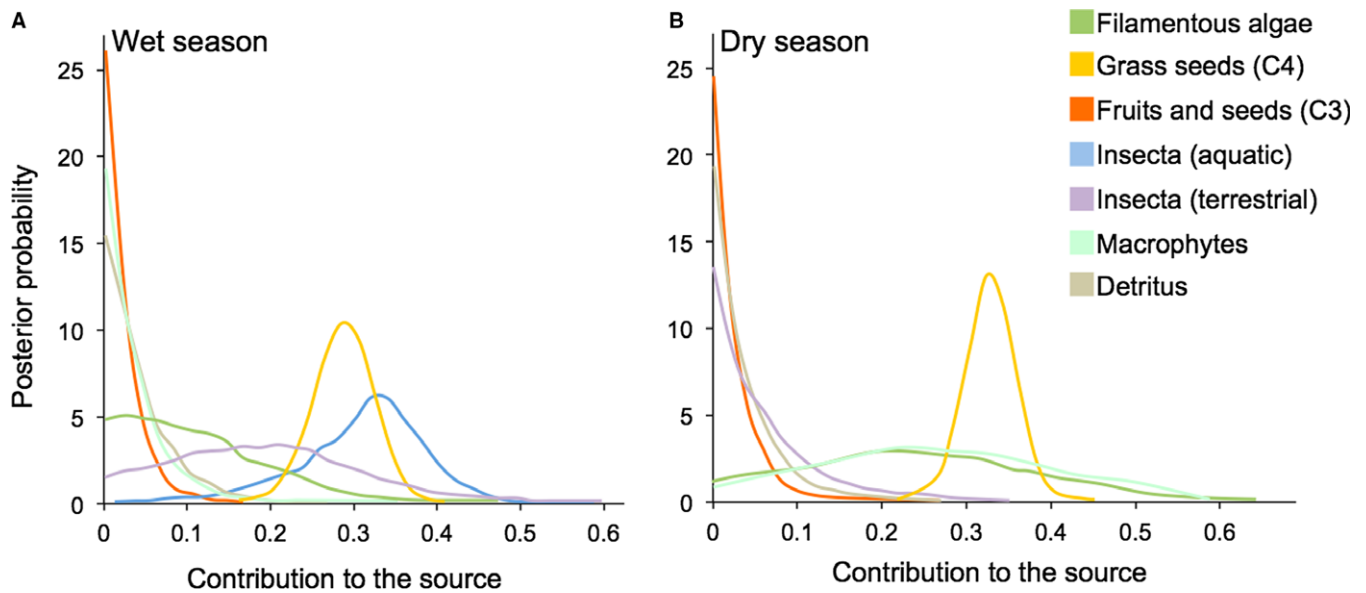


FIGURE 3. Distribution of the solutions of a SIAR mixing model for contribution of resources to the diet of the tetra fish *Astyanax lacustris* during the wet (A) and dry (B) seasons in the Pantanal wetlands. See Table S2 for Bayesian confidence intervals (95%) and mode of each distribution.

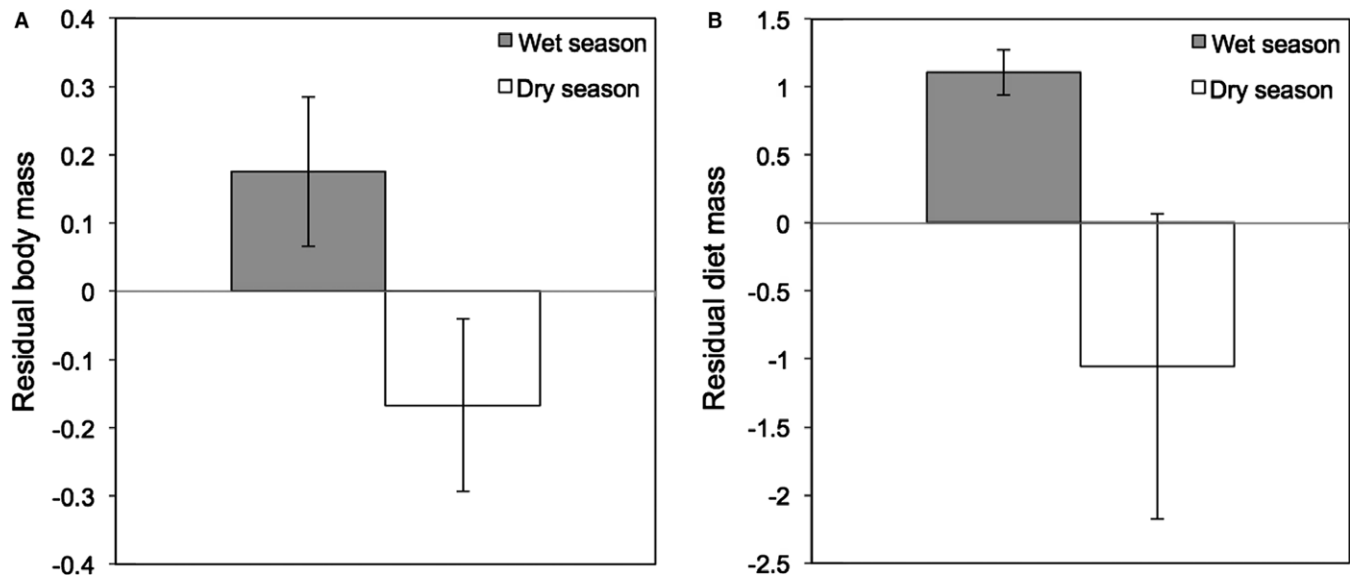


FIGURE 4. (A) Residual body mass and (B) gut fullness of the tetra fish *Astyanax lacustris* in the wet (grey bars) and dry (white) seasons in the Pantanal wetlands.



calculated using stable isotopes were similar to those calculated using gut-content data both in the wet and dry seasons (Fig. 5).

## DISCUSSION

Our main results can be summarized as follows: *A. lacustris* had a clear seasonal change in diet, presenting lower body condition and gut fullness in the dry season, suggesting the possibility that intraspecific competition is stronger in this season as compared to the wet season, when there is a higher abundance and diversity of available resources. Population dietary niche was narrower in the dry season, when ecological opportunity is reduced. Between-individual diet divergences accounted for most of the variation associated with the population niche contraction in the dry season. Overall, during the wet season the population as a whole was more generalist, but individuals were slightly more specialized and overlapped less in their diets than in the dry season. Taken

together, these results indicate that ecological opportunity is an important driver of population and individual niche dynamics, in line with previous empirical studies in seasonal environments (Araújo *et al.* 2007b, Martins *et al.* 2008, Camargo *et al.* 2014). Furthermore, our results suggest that the low scope for diet variation during the dry season may constrain the diversifying effect of intraspecific competition.

Our interpretation of the results relies on the assumption that ecological opportunity is higher in the wet season and intraspecific competition is stronger in the dry season. The former assumption is in line with the well-documented input of allochthonous resources in aquatic habitats during the wet season in the Pantanal (Resende 2000, Wantzen *et al.* 2002, Ragusa-Netto & Fecchio 2006), which were widely consumed by *A. lacustris* in this season. The latter assumption is strongly supported by our results on gut fullness and body condition, which were lower in the dry season, when tetras were constrained to forage in the Medalha lagoon, consuming mostly filamentous algae and macrophyte roots. We also acknowledge that we studied only one of the many floodplain lagoons in the Pantanal wetlands and the study only included a single year of data. Future studies should replicate the dry-wet season comparison both spatially and temporally (*e.g.*, inter-annually) to establish the generality of the observed patterns.

Our results indicate that ecological opportunity favors population niche expansion in the wet season as a result of an increase of interindividual dietary variations, because the additional abundance and diversity of resources available in this season (*e.g.*, seeds, fruits, terrestrial invertebrates) expand individuals' foraging possibilities and allow their niches to diverge. This was confirmed by the higher degree of individual

TABLE 1. Degree of individual specialization based on gut contents ( $V$ ) and empirical isotope variance ( $V_{\delta}$ ) and Roughgarden's (1979) TNW (total niche width), WIC (within-individual component), and BIC (between-individual component) of *Astyanax lacustris* in wet and dry seasons in the Pantanal.

	Wet season	Dry season
TNW	1.45	1.12
WIC	0.42	0.46
BIC	1.03	0.66
$V$	0.56	0.45
$V_{\delta}$	0.64	0.46

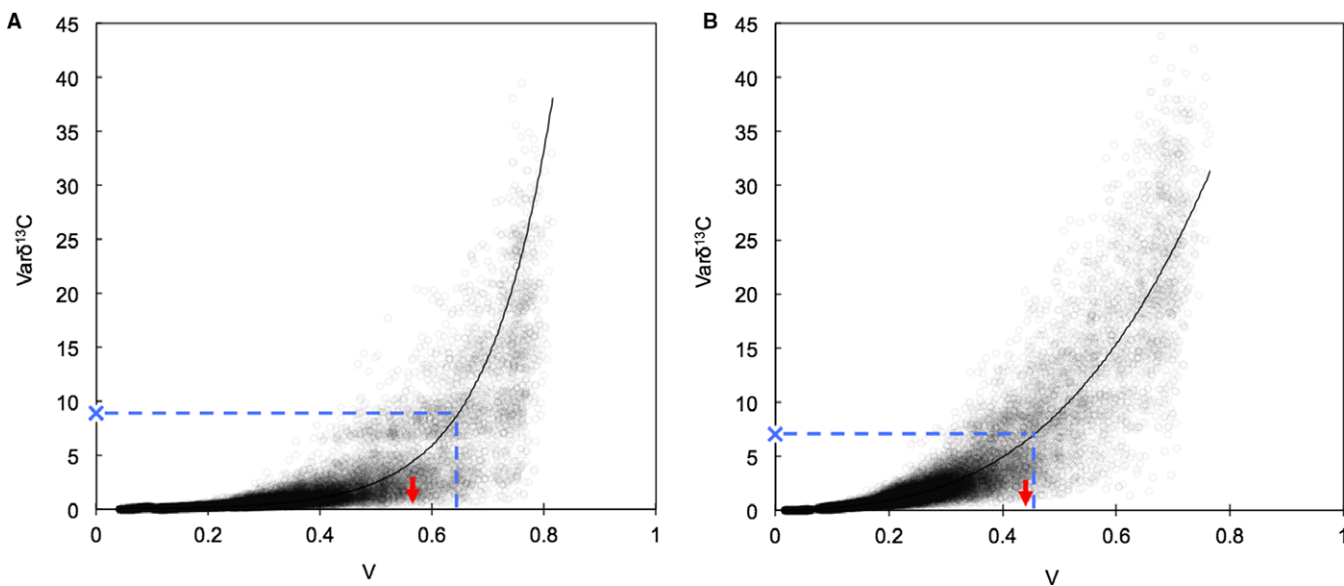


FIGURE 5. Estimation of  $V$  values from  $\delta^{13}\text{C}$  isotope variances of the tetra fish *Astyanax lacustris* in the (A) wet and (B) dry seasons in the Pantanal wetlands. Black curves indicate quadratic fitted regressions. The blue 'x' indicates the empirical isotopic variance and the vertical-dashed line represents the expected  $V$  value. The red arrow indicates the  $V$  value based on gut contents.

specialization observed in the population of *A. lacustris* in the wet season. Although the positive effect of ecological opportunity on niche expansion and interindividual variation has been demonstrated by several studies (Layman *et al.* 2007, Murray & Wolf 2013, Robertson *et al.* 2015), most of them focus on spatial gradients of ecological opportunity. Our results highlight the fact that the degree of individual specialization can also vary over time, which still is an overlooked dimension of intraspecific diet variation. Resource pulses are common across ecosystems worldwide (Yang *et al.* 2008), so that temporal changes in individual and population niches may be more common than currently appreciated.

Intraspecific competition has received wide support as a major driver of interindividual niche differences (Araújo *et al.* 2011). However, the theory on the effects of intraspecific competition on individual and population niche variations implicitly assumes constant diversity of available resources (Svanbäck & Bolnick 2005). Our results suggest that the effect of intraspecific competition in determining population and individual niche dynamics depends on its interaction with ecological opportunity. During the dry season, although tetra fish likely experienced stronger intraspecific competition, there were fewer resources available (*i.e.*, lower ecological opportunity), which constrained the diversifying effect of competition. In line with this idea, the habitat type used by sea otters (*Enhydra lutris*), which is related to a spatial gradient in functional diversity of prey, affects the strength with which intraspecific competition influences individual specialization (Newsome *et al.* 2015). Other ecological mechanisms associated with the occurrence of diet variation (*e.g.*, predation, interspecific competition) may also interact with ecological opportunity over space and time (Layman *et al.* 2015). The consequences of these potential interactions on population and individual niches remain to be determined.

In conclusion, our study adds to the small but growing list of examples showing that (1) environmental seasonality in resource diversity can affect population niche by changing the degree in which individuals' diet diverge; and (2) ecological opportunity favors increased diet divergence between individuals. In addition, our study suggests that low ecological opportunity can constrain the expected positive effect of intraspecific competition in promoting diet variation. Our results therefore emphasize the importance of a more integrative understanding of how ecological interactions, which might change seasonally, interact to determine the population and individual niche breadths in natural populations, particularly in seasonal ecosystems.

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## DATA AVAILABILITY

Data deposited in the Dryad Repository: <https://doi.org/10.5061/dryad.kn0v7> (Costa-Pereira *et al.* 2017).

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. Food items and respective trophic categories consumed by the tetra fish *Astyanax lacustris* in the Pantanal wetlands during the wet and dry seasons.

TABLE S2. Confidence intervals and modes of source contribution distributions to the isotopic composition of the tetra fish *Astyanax lacustris* in the wet and dry seasons in the Pantanal wetlands.

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