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Intra and not interspecific competition drives intra-populational variation in resource use by a neotropical fish species

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Abstract Intra and interspecific competition may influence the strength of individual specialization in resource use. We evaluated how intra and interspecific competition affects the degree of individual specialization in food resource use within sub-populations of *Hoplerythrinus unitaeniatus*. To do so, we identified food items from fishes collected in the Pantanal wetland. We tested whether individual specialization was related to *H. unitaeniatus* density (a proxy of intraspecific competition) or to the density of a potential interspecific competitor (*Hoplias malabaricus*) using a multiple regression. Dietary variation was related to ontogeny. *Hoplerythrinus unitaeniatus* density, instead of *Hoplias malabaricus* density, had an effect on the specialization of *H. unitaeniatus* individuals. A greater the density of *H. unitaeniatus* leads to a greater individual specialization. Our results point to a lack of specialization in *H. unitaeniatus* individuals. In addition, intra and not interspecific competition affected the use of food resources. Individuals of denser populations may consume secondary resources, reducing the effects of intraspecific competition and becoming more specialists.

Keywords Intraspecific variation · Intrapopulation variation · Food resource · *Hoplerythrinus unitaeniatus*

Introduction

It has long been observed that individuals within a population may present variation in resource use (Van Valen 1965). Variation is the essence of evolution through natural selection. Consequently, this subject has received increasing attention from biologists interested in describing the forces that generate and maintain phenotypic variation within natural populations (Bolnick et al. 2007). With a growing body of publications since the last decade, a recent review pointed out that 189 of 202 species had some degree of interindividual variation in resource use (Araújo et al. 2011).

Individual specialization is an explanation for intrapopulation variation in resource use, and occurs when a subject's niche is substantially narrower than the population niche for reasons not attributed to sex, morphology and age (Bolnick et al. 2003). Thus, a generalist population may be composed of specialist individuals, and be ecologically heterogeneous (Bolnick et al. 2007; Pires et al. 2011). Individual specialization has important implications for ecological and evolutionary processes, and conservation programs (Bolnick et al. 2003).

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Individual variations within the population respond differently to selective pressures, which is important for natural selection. In addition, these variations also provide genetic diversity, which is essential for the adaptation to environmental changes to take place (Bolnick et al. 2003).

Ecological interactions influence specialization of individuals, which in turn, affects ecological dynamics (Araújo et al. 2011). Ecological interactions such as intra and interspecific competition may modify the strength of individual specialization (Araújo et al. 2011). Several observational and experimental studies indicate that individual specialization responds to population density in natural systems with limited resources (Bolnick 2001; Svanbäck and Bolnick 2005; Svanbäck and Bolnick 2007; Svanbäck et al. 2008; Bolnick et al. 2010; Araújo et al. 2011). Thus, increasing population density leads to increased intraspecific competition, where an increased competitive pressure may reduce per capita prey availability, and consequently increase individual specialization (Svanbäck and Bolnick 2005; Svanbäck and Bolnick 2007; Araújo et al. 2008; Araújo et al. 2011). This is because at low population densities individuals become specialized in the same preferred resource, ignoring all other resources; as population density increases this resource becomes scarce, and individuals add different secondary prey (Svanbäck and Bolnick 2005). This mechanism may therefore increase diet variation among individuals within a population (Svanbäck and Bolnick 2007), reducing intraspecific competition. However, interspecific competition may weaken or increase specialization depending on the competing species (Bolnick et al. 2010). The contrasting effects of interspecific competition on individual specialization, and how these effects differ depending on the strength of the interaction and the species involved, are still not fully understood (Bolnick et al. 2010).

Resource use may vary in several ways within a population, and individual specialization is one to the means among many that can lead to intrapopulation niche variation. The differential resource use between sexes (e.g., Martins et al. 2008), ontogenetic stages (Polis 1984; Zhao et al. 2014) or morphologically distinct subgroups within a population is also noteworthy (Binning and Chapman 2010; Mittelbach et al. 1992; Skúlason and Smith 1995; Mittelbach et al. 1999). Due to these factors, subgroups within a population may have different ecological roles in resource exploitation. An immediate consequence of differentiated resource use among these subgroups is the expansion of the population niche (Bolnick et al. 2003; Bolnick et al. 2007).

Initial studies on individual specialization only tested the null hypothesis that resource was equally consumed by individuals of the same population (shared the same resource dimension of the niche), while few have quantified variation among individuals (Bolnick et al. 2002). Over time, studies have transcended the limitation of documenting only specialization and have hypothesized how individual specialization varies among ecological contexts (Araújo et al. 2011). Hence interactions with different ecological mechanisms such as intraspecific competition (Araújo et al. 2008; Bolnick et al. 2011; Evangelista et al. 2014; Newsome et al. 2015; Cloyed and Eason 2016; Mateus et al. 2016), ecological opportunity (Evangelista et al. 2014; Cloyed and Eason 2016) and interactions with more than one species (e.g. interspecific competition; Bolnick et al. 2010; Bolnick et al. 2011; Cloyed and Eason 2016;) and predation (Eklöv and Svanbäck 2006) were addressed to clarify how individual specialization responds to such mechanisms. Individual specialization has been documented primarily on fish, among the groups for which specialization was studied (Araújo et al. 2011).

It is reasonable to expect that phylogenetically close or morphologically similar species compete for resources (Krebs 1994). *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829) and *Hoplias malabaricus* (Bloch, 1794) are two erythrinids distributed throughout South and Central America (Reis and Kullander 2003), commonly found in lentic environments. In addition, they exhibit similar morphology and use of food resources (Carvalho et al. 2002); both are piscivorous, and *H. unitaeniatus* tends towards omnivory (Godoi 2004).

In this study we investigated the pattern of food resource use within sub-populations of *H. unitaeniatus*. We first investigated whether the use of food resource varies according to intrapopulation factors (sex, ontogeny or morphology), or could be attributed to individual specialization. We also evaluated how intra and interspecific competition (i.e., *H. malabaricus* density) affect the individual specialization level. Individual specialization is common in fish (Bolnick et al. 2003). Therefore, we expect that variation in the use of food resources among *H. unitaeniatus* individuals is caused by individual specialization. There is no evidence of sexual dimorphism or slight variations in morphology, nor any indication of ontogenetic variations in how *H. unitaeniatus* use food resources. However, these factors must be tested to ensure that individual specialization is responsible for variations in resource use. Finally, we evaluate possible mechanisms that may influence individual specialization in these populations. To do this we tested the hypothesis that individual specialization is affected by competition (inter and intra-specific). We tested this hypothesis by predicting that the magnitude of individual specialization increases with *H. unitaeniatus* abundance, and reduces when the abundance of a potential competitor (*H. malabaricus*) increases.

Materials and methods

Study area

The Pantanal wetland is one of the largest wetlands on the planet and covers an area of approximately 160,000 km^2 (Junk et al. 2011) encompassing Brazil, Paraguay and Bolivia in the central part of South America (Mourão et al. 2002; Signor and Fernandes 2010). The region is characterized by an annual flood cycle (which may vary from year to year), local differences in the hydrological regime combined with variations in topography, soil that provides a mosaic of rarely, periodically and permanently flooded areas, and areas that do not flood (Signor and Fernandes 2010). This study was carried out at the Pantanal LongTerm Sampling Sites (PLTSS), which takes place at three private properties in the northern Pantanal (Fernandes et al. 2014). The PLTSS consists of 30 sampling plots of 250 m, systematically distributed within 25 km^2 (16°19′ - 16°22’ S; 56°21′ - 56°18’ W: Fig. 1), located 1 km apart from each other (Magnusson et al. 2005). This is a region of low altitude (112 to 116 ma.m.s.l.), without active sedimentation. The soil is composed mainly of sandy deposits of riverbeds from the Quaternary period. Flooding occurs annually between December and May, with a dry season between June and November. The annual amplitude (maximum water depth) varies from 20 to 40 cm, and lasts 65 to 130 days, providing a low amplitude and long lasting flood system (Lários et al. 2017). The area studied comprises a highly heterogeneous landscape with many types of vegetation cover (Fernandes et al. 2015).

Data collection

The data were collected in April 2009, March 2010 and 2011 during the aquatic phase in the flooded plots. Some of the 30 plots were not flooded. Therefore, we collected 21 plots in 2009, 18 in 2010 and 22 in 2011. Each of these fish samples collected at each year and site consist of a sampling unit of *H. unitaeniatus* and its potential competitor *H. malabaricus*. Fish were collected using selection of gillnets and throw trap. Nets with 20 m width and 1.5 m height were distributed throughout the plots (mesh sizes of 12, 15, 18, 20, 25, 30 and 50 mm). Nets were deployed between 4:00 and 5:00 p.m. and removed between 8:00 and 9:00 a.m. of the following day. The throw trap consists of a metal frame with nylon covered sides (1.5 mm mesh opening), measuring 1 m^3. This sampling apparatus is placed and pressed quickly against the substrate, where fish that become trapped and are then removed with a hand-held net. We used the throw trap systematically, conducting six ‘throws’ every 50 m in each plot (see details in Fernandes et al. 2014).

The fish collected were fixed in a 10% formalin solution and transferred to 70% alcohol. We collected a total of 354 *H. unitaeniatus* individuals (107 in 2009, 102 in 2010 and 145 in 2011) and 167 *H. malabaricus* individuals (65 in 2009, 50 in 2010 and 52 in 2011). In the laboratory, we measured morphological features directly or indirectly associated with the food exploitation from each of the *H. unitaeniatus* individuals (except those that had been deposited in the collection or that had damaged morphological structures) (Table S1; Dumay et al. 2004). Measurements were taken in a straight line using a digital pachymeter (0.01 mm accuracy). Subsequently, the stomachs and the gonads of individuals were removed, and sex determined. The food items present in the stomach of each individual were identified to the lowest possible taxonomic level according to specialized literature, using a stereomicroscope (McCafferty 1981; Britski et al. 2007), and the diet was quantified numerically (abundance of each food resource in the diet of each individual). This research was conducted under SISBIO Collection of Species Permit number 11729–1 issued by Brazilian Environmental Agency (ICMBio). Voucher specimens were kept in the Vertebrate Collection of the Institute of Biosciences, Federal University of Mato Grosso.

Data analysis

The database was divided into two databases for analyses. The first database was analyzed only with the individuals that had food items in their stomach and sex determined (a total of 45 *H. unitaeniatus* in 2009,

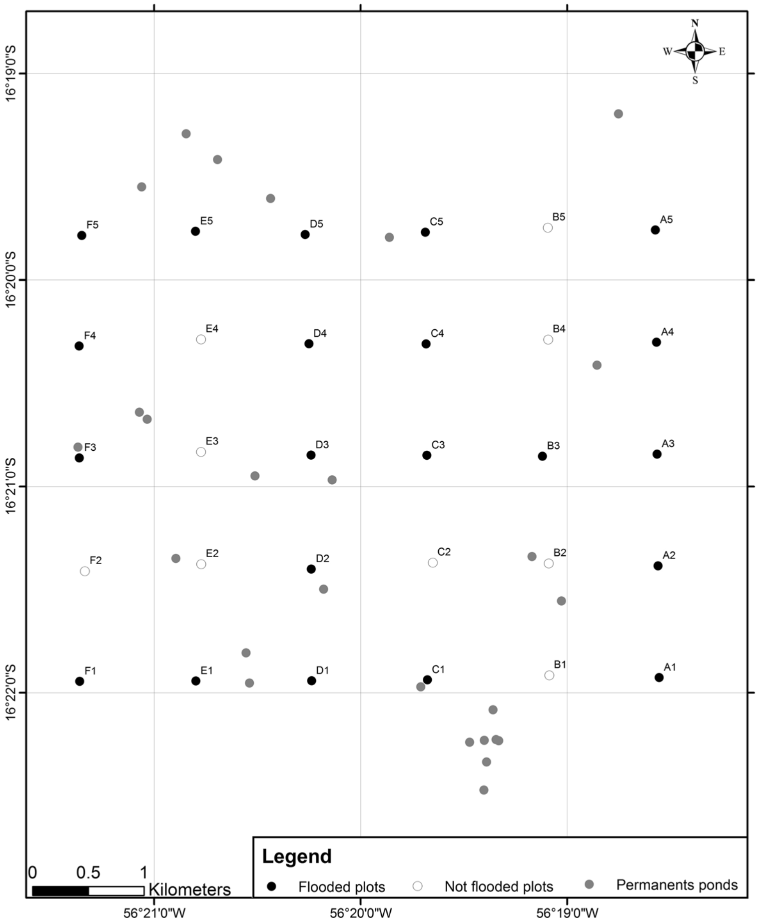

Fig. 1 Map of the PLTSS in Pantanal wetlands. Filled and white circles represent plots that were flooded and not flooded, respectively, in 2009, 2010 and 2011.Grey circles represent the permanent ponds inside and around the PLTSS

52 in 2010 and 48 in 2011). This was used to calculate the resource use variation in the population. The second database excluded the individuals that had not eaten any food (63 *H. unitaeniatus* in 2009, 68 in 2010 and 63 in 2011), and was used to calculate the effect of competitive interactions. A conceptual model was constructed to explain the pattern of individual variation in the diet. In our model the individual variation in the use of food resources results from the difference between sex (male and female), ontogeny (here we use standard length as a proxy of ontogeny), and morphological differences unrelated to age (morphological variation). When this variation is not a result of any of these factors, we assume that it is an effect of individual specialization and may be affected by differences in co-specific density (intraspecific competition) and differences in the density of a hypothetical interspecific competitor (*H. malabaricus*). In turn, sex, age and shape can lead to differences in the biological pattern of resource use. Meanwhile, density (both conspecifics and competitor) causes ecological differences, which is the focus of our interest. However, before evaluating the density effects we have to assess the contribution of fish biology to the resource use pattern in the population (considering all samples), once biology could mask the patterns generated by ecological interactions.

To do this, we determined the standard length as a proxy of ontogeny. We choose not to divide individuals into age classes because diet changes occurs continuously among individuals, and they are able to use new resources as they grow. We summarized the morphological measurements taken from each individual using a principal component analysis (PCA) with a covariance matrix to verify if there were morphological groups, or if morphological variation was continuous within the population. A covariance matrix was used to remove correlations between morphological variables and standard length. Most of the morphological variation among individuals is associated with body size due to allometric relations (Peres-Neto 1995). Therefore, we scaled the morphological measurements by dividing it by standard length. We retained the first two axes of the PCA to interpret morphology patterns.

We conducted a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001) to evaluate whether dietary use differed between sexes, ontogeny, or if diet composition was affected by continuous morphological variations within these populations. PERMANOVA is a non-parametric method based on permutation tests, which can be based on any dissimilarity measure (Bray-Curtis distance matrix). A PERMANOVA was performed between the food items matrix as response variable and sex, standard length, and scores of the PCA as predictor variables. This model was tested using 1000 permutations.

To test the hypothesis of individual specialization within the sub-population, we calculated the proportional similarity index (PS_i; Schoener 1968; Bolnick et al. 2002) separately in each sample unit (separately between sites and years), so that individuals would have the same resource use ability (e.g., differentiated exploitation between sexes and/or ontogeny), only using samples with over three individuals. The PS_i is based on the average overlap of the individual's niche relative to that of the population:

$$PS_i = 1{-}0.5\sum_j p_{ij}{-}q_j\vee$$

where p_{ij} is the frequency of resource j in the individual's diet i, and qj is the proportion of resource j in the population as a whole.

From the mean of the PS_i values, the prevalence of individual specialization (*IS*) in the sample unit is then measured. This measure corresponds to the average similarity between the diet of the individual and the diet of the population (Bolnick et al. 2002). The *IS* ranges from 0 to 1, where 1 indicates that the estimated individual's niche is the same as that of the population (consequently, lower values indicate individual specialization within the population; Bolnick et al. 2002). The statistical significance of IS values observed were tested using Monte Carlo resampling procedure (Zaccarelli et al. 2013). After defining the number of items used by each individual (i.e., observed diet), food items were randomly reassignment to each individual, keeping the observed number of food items used by each individual. This resampling routine was conducted 999 times to generate the null distribution.

Finally, we performed a multiple linear regression to test whether individual specialization was affected by intra and interspecific competition, using *H. unitaeniatus* abundance as a probable intraspecific competition effect (the values are related to the individuals collected in each plot, and the competition was analyzed for juveniles and adults separately) and *H. malabaricus* abundance as a possible interspecific competition effect. The response variable (*IS*) was a proportion. Therefore, we log transformed *IS* values (natural log) to perform the regression. Before conducting the regression analysis, we checked for multicollinearity between predictor variables using Pearson correlations.

All analyses were performed with R 3.0.1 software (R Core Team 2019). The RInSp package (Zaccarelli et al. 2013) was used to calculate individual specialization and to test for significance. We used the vegan package (Oksanen et al. 2017) for the principal components analyses and PERMANOVA, and the psych package (Revelle 2013) for the correlation analysis. The results were considered significant at a $\alpha = 0.05$ significance level.

Results

The standard length (SL) of *H. unitaeniatus* individuals captured ranged from 27.62 mm to 234.12 mm (113.99 ± 38 mm; mean ± standard deviation). The stomach contents of 194 specimens were analyzed, and 56 of the 194 specimens were identified as male (SL ranging from 49.02 to 200.22 mm, mean ± standard deviation: 113.76 ± 38.28), and 89 as female (SL ranging from 64.13 and 204.50 mm, mean ± standard deviation: 110.3 ± 31.9 mm) and 40 could not be identified.

Food items were ranked into 22 categories: Characiforms, Siluriforms, Perciforms unidentified fish, anuran, insects, Odonata (nymphs and adults), Hemiptera, Hymenoptera, Coleoptera (larvae and adults), Orthoptera, Diptera, Lepidoptera, Diplopoda, Araneae, Brachyura, Gastropods, plants, fruit and organic matter. The first two PCA axes on morphological characteristics comprised approximately 61% of the morphological variability (Table 1). Axis 1 was positively related to eye diameter and caudal peduncle width. Axis 2 was negatively related to the gape (mouth opening).

Males and females did not differ in the composition of resources used (PERMANOVA: $F_{1,140} = 1.59$; $p = 0.08$). However, diet composition varied

Table 1 Principal component analysis of the morphological traits of *Hoplerythrinus unitaeniatus* individuals collected in the Pantanal wetland. The eigenvalues of each variable in the axes, the eigenvalues and the percentage of variance of each axis are presented

Variables	Axis 1	Axis 2
Body Height	0.01	0.02
Body Width	−0.02	0.07
Head Length	0.0323	−0.29
Head Width	−0.0127	−0.003
Eye Diameter	0.85	−0.03
Mouth Width	−0.22	−0.03
Mouth Height	−0.01	−0.92
Caudal Peduncle Length	0.001	−0.04
Caudal Peduncle Width	0.51	0.06
Caudal Peduncle Height	0.01	−0.01
Pelvic Fin Length	0.03	−0.16
Pelvic Fin Width	−0.01	0.04
Pectoral Fin Length	0.01	−0.11
Pectoral Fin Width	0.03	0.06
Eigenvalue	0.06	0.0411
Percentage of variance (%)	42.26	19.53

ontogenetically (PERMANOVA: $F_{1,140} = 5.76$; $p < 0.01$). We found no relationship between dietary variation and morphology, compared to diet composition (PERMANOVA: axis 1, $F_{1,140} = 1.07$, $p = 0.36$; axis 2, $F_{1,140} = 1.34$, $p = 0.18$).

Diet composition differed ontogenetically. Therefore, individual specialization (Ps*i*) standard length was included in our model, to remove the effect of ontogeny. In general, IS ranged from 0.22 to 0.59 among *H. unitaeniatus* populations, with none of the expected values being different from the randomly expected, rejecting our hypothesis of individual specialization (Table 2).

The IS varied as a function of competition. The general model comprised approximately 65% of the variation in IS ($F_{3,19} = 14.59$; $r^2_{adjusted} = 0.649$; $p <$ 0.001 0.026). The degree of individual specialization of this population was not affected by the abundance of *H. malabaricus* ($t = -1.810.32$; $p = 0.0875$) but was negatively affected by the abundance ($t = -3.01$; $p = 0.007$; Fig. 2a) and standard length of *H. unitaeniatus* ($t = -3.38$; $p < 0.001$; Fig. 2b). As the density of *H. unitaeniatus* increases, the more specialized the population becomes (i.e., the lower the IS).

Table 2 Prevalence of individual specialization (IS), in different sites and years in *H. unitaeniatus*, separated by age groups, in the Pantanal wetland. N: number of individuals in the analysis

Year	Sites	N	IS	*P*
2009	A1	6	0.26	0.05
	A2	7	0.30	0.09
	A3	6	0.30	0.07
	A5	4	0.54	0.5
	B3	8	0.27	0.11
	C5	5	0.33	0.05
	D3	6	0.31	0.1
	F3	5	0.39	0.23
2010	A1	19	0.22	0.32
	A2	8	0.40	0.37
	B1	7	0.39	0.24
	B3	5	0.42	0.23
	D1	5	0.40	0.21
	E1	4	0.39	0.11
	F2	7	0.50	0.71
2011	A4	4	0.60	0.65
	A5	5	0.58	0.73
	B1	12	0.36	0.58
	C3	5	0.56	0.61
	D1	6	0.38	0.25
	E5	5	0.34	0.31
	F4	5	0.36	0.15
	F5	5	0.49	0.51

Discussion

Intraspecific competition, rather than interspecific competition, had an effect on individual niche width within *H. unitaeniatus* populations. Empirical evidence reveals that intra and interspecific competition may cause resource limitation, which in turn leads to individual variation (Svanbäck and Bolnick 2007; Araújo et al. 2008; Araújo et al. 2011). Intraspecific competition is widely recognized as the main driver of individual variation (Araújo et al. 2011). Svanback et al. (2008) provided evidence that intraspecific competition is more important than interspecific competition in determining the morphological patterns of two potential competitor fish species – Eurasian perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in Swedish lakes.

Two hypotheses may complement the results found in this study. The optimal foraging theory predicts that the individuals of the population use the preferred resource

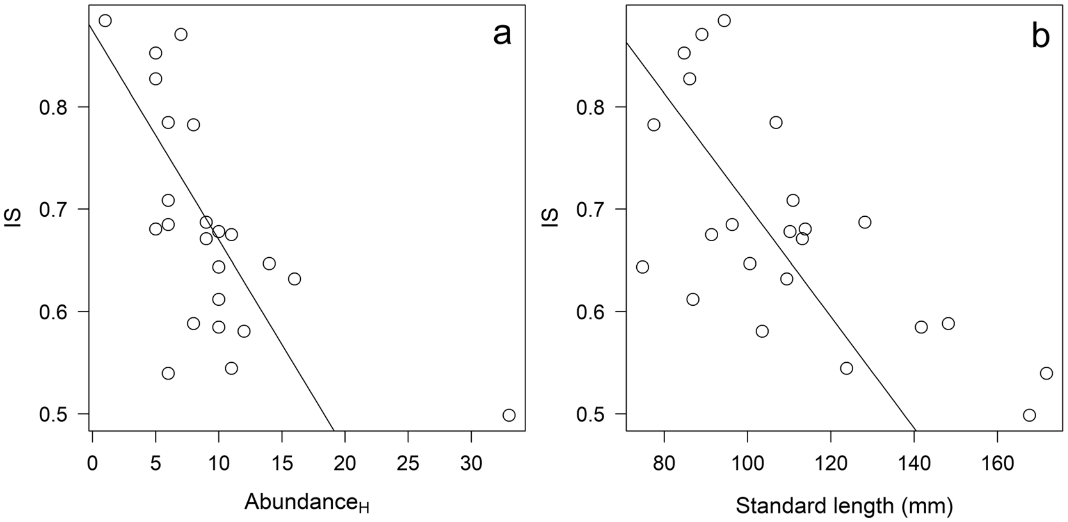

Fig. 2 Relationship between **(a)** the abundance of *Hoplerythrinus unitaeniatus* and the individual specialization index value (IS) in the populations and **(b)** average Standard Length (mm) of individuals and IS

that is more abundant, allowing for population become more specialized. When the preferred resource is scarce, individuals are expected to broaden the diet of the population (Perry and Pianka 1997). If we couple resource limitation with intraspecific competition, we can see that the strategy used to mitigate competition is resource partitioning. The niche partitioning is an efficient mechanism through which competing species or competing individuals may coexist (Jensen et al. 2017).

Different from previous studies, this study was conducted in a temporary habitat subjected to an annual flood. Evidences show that *H. unitaeniatus* hunt in groups (Oliveira 2013), have aerial respiration, and presents group territorialism (Lima Filho et al. 2012). This collective behavior can favor aspects of individual ecology, such as food capture, making them stronger competitors.

Individual specialization is not necessarily a general phenomenon in fish populations (Araújo et al. 2011). The scarcity of negative results, where populations are composed only of generalist individuals, is mainly associated with the effect that the lack of significant results is not considered publication worthy (Bolnick et al. 2003). This lack of publications can overestimate the strength of individual specialization in natural populations (Araújo et al. 2011). According to a recent review, an additional 12 species presented low or nonexistent individual specialization (Araújo et al. 2011).

In this study, the increased density of individuals led to greater specialization in *H. unitaeniatus*. Optimal diet theory (ODT) seeks to understand why an organism chooses a particular resource among the wide range of possibilities available (Schoener 1971; Sih and Christensen 2001). In addition to energy requirements and capture costs, we cannot disregard that individuals differ in their ability to find, handle and capture their prey (Svanbäck and Bolnick 2005). Intraspecific competition tends to increase difference among the resources used by individuals within a population. According to the shared preference hypothesis, all individuals of a population have the same preferred resource, which becomes limited in high densities. Individuals need to add secondary resources to their food supply by increasing variation between individuals and consequently individual specialization (Svanbäck and Bolnick 2005).

Gender was not exert an important influence in resource use for this population, pointing to a lack of sexual dimorphism regarding resource exploitation. Diet composition differed between juveniles and adults and was influenced by morphological variations. The growth of individuals in natural populations is continuous (from larvae to death), factor which is often responsible for the structuring of populations (Werner and Gilliam 1984; Winemiller 1991). Size directly influences the individual's energy demand and resource exploitation potential (Werner and Gilliam 1984). Thus, individuals can choose their food as to maximize the amount of energy gained from catching prey, taking into account the energy spent in foraging (MacArthur and Pianka 1966). The individuals were not divided into morphotypes in this study.

In summary, *Hoplerythrinus unitaeniatus* of the Pantanal wetland tended towards intraspecific variation in resource use explained by ontogeny and also by morphological variations within the population. This variation may represent a strategy to reduce intraspecific competition within the population (Araújo et al. 2010; Bolnick et al. 2010; Araújo et al. 2011).

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