BRIEF COMMUNICATION

Functional morphology of the tetra fish *Astyanax lacustris* differs between divergent habitats in the Pantanal wetlands

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This study investigated whether the body morphology of the tetra fish *Astyanax lacustris* (previously *Astyanax asuncionensis*) varied between populations inhabiting one lagoon (a lentic, shallow environment, with great habitat complexity created by aquatic macrophytes) and an adjacent river (a deeper, lotic environment where aquatic macrophytes are scarce) in a seasonally flooded wetland, despite population mixing during the wet season. Morphological differences matched *a priori* predictions of the theory relating functional body morphology and swimming performance in fishes between lagoon and river habitats. Observed morphological variation could have resulted from adaptive habitat choice by tetras, predation by piscivores and adaptive phenotypic plasticity during development.

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Key words: flood pulse; floodplain lagoon; phenotypic divergence.

Functional traits associated with fish swimming are usually correlated with ecological gradients, because survival, reproduction and feeding often depend on swimming performance (Domenici, 2010; Lauder, 2015). Fishes employ different swimming modes, the adaptive value of which varies along three main ecological gradients: water flow, environmental structural complexity and predation (Langerhans & Reznick, 2010). Two primary swimming modes, steady and unsteady, are expected to vary along such ecological gradients. The former is a constant-speed movement in a straight line, whereas the latter involves fast changes in direction and speed (Langerhans & Reznick, 2010). Steady swimming is employed in routine activities such as searching for food or mates, seeking favourable abiotic conditions or holding station in water currents (Langerhans, 2008; Yan *et al.*, 2013; Foster *et al.*, 2015). Unsteady swimming is normally employed in structurally complex environments or when evading a predator attack, as fast starts and rapid turns increase the ability to escape (Webb, 1986; Langerhans, 2009b; Langerhans & Makowicz, 2009). Available experimental

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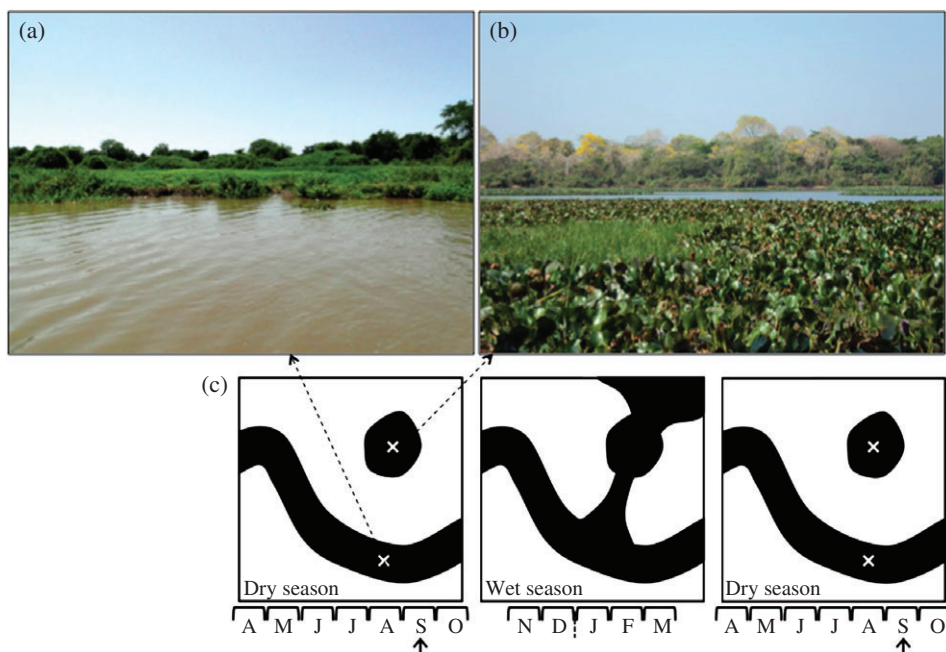
FIG. 1. The (a) Miranda River and (b) Medalha Lagoon in southern Pantanal, Brazil, during the dry season, showing the differences in habitat complexity and water flow. (c) A scheme representing the seasonal dynamics of connection and isolation between the Medalha Lagoon and the Miranda River. X⊡→, sampling locations; ↑, sampling season.

work indicates that steady swimming is facilitated by more streamlined bodies (deep anterior region with a relatively small caudal peduncle) because of associated drag, whereas body shapes with greater posterior body allocation (larger caudal peduncle and fin, and smaller anterior region) maximize thrust and stability, facilitating unsteady swimming performance (Blake, 2004; Langerhans & Reznick, 2010). Because these two primary swimming modes cannot be optimized simultaneously by a given fish design, fishes inhabiting contrasting environments are expected to have different body morphologies (Langerhans & Reznick, 2010; Yan *et al.*, 2013).

The Pantanal wetland is one of the largest and most pristine wetlands in the world, covering around 140 000 km² in the centre of South America. Two particular aquatic environments in the Pantanal wetlands present a remarkable contrast in water flow and structural complexity. Floodplain lagoons are lentic and shallow environments, usually with high biomass of floating and submerged aquatic macrophytes (Junk *et al.*, 2011) (Fig. 1), which increases habitat complexity for small fishes (Súarez *et al.*, 2004; Milani *et al.*, 2010), whereas river channels are deeper lotic environments, where aquatic macrophytes are scarce (Junk *et al.*, 2011). River and lagoons are completely isolated during the dry season (from April to October), but connect during the wet season (from November to March) when the wetlands are flooded (Junk *et al.*, 1989, 2006) (Fig. 1), allowing the migration of many fish species from rivers to flooded areas, where they feed and reproduce before returning to their native habitat at the end of the wet season (Winemiller & Jepsen, 1998; Britski *et al.*, 1999).

Here, the tetra species *Astyanax lacustris* (Lütken 1875), the recently established senior synonym for *Astyanax asuncionensis* Géry 1972 (Lucena & Soares, 2016), a small-bodied ($\leq$12 cm) fish commonly found in the Pantanal wetlands (Fig. S1, Supporting Information), was used to investigate the relationship between functional morphology and divergent habitats in natural populations. This species is not only found in rivers, but also occurs in lagoons, at lower abundances (Heckman, 1998; Willink *et al.*, 2000). In the Pantanal wetlands, the reproductive period of *Astyanax* spp. and several other small fishes is synchronized with the wet season, when they migrate to lentic environments to reproduce (Heckman, 1998; da Silva *et al.*, 2010). Because of the contrast between river and lagoon environments, it is expected that individuals in rivers and lagoons differ in body morphology in line with predictions from swimming performance theory (Langerhans & Reznick, 2010). Specifically, individuals in rivers *v.* lagoons should have body morphologies that facilitate steady *v.* unsteady swimming, respectively. On the other hand, the mixture of individuals from these environments caused by seasonal migrations may constrain divergence in body morphology.

Populations of *A. lacustris* inhabiting the Miranda River and the nearby Medalha Lagoon (19° 34′ 34″ S; 57° 00′ 46″ W; Fig. 1) were studied. The Miranda River is a major (765 km long, 44 740 km^2 catchment) tributary of the Paraguay River. This meandering river has muddy and high-flow waters with low macrophyte density along its course [Fig. 1(a)]. It flows through an extensive plain in the Pantanal lowlands that is subject to seasonal flooding (Resende, 2000). During the wet season, the water level of the Miranda River increases progressively until it floods adjacent areas, connecting the Medalha and other lagoons to the river. The Medalha Lagoon is one of the many permanent water bodies in the Miranda River floodplain harbouring a population of *A. lacustris* and receiving reproductive migrants from the river during the wet season. This lagoon is *c.* 5·4 ha in area and is completely isolated from the Miranda River during the dry season (Costa-Pereira *et al.*, 2014). About 50% of its surface is covered by aquatic macrophytes, mainly *Eichhornia azurea* [Pontederiaceae; Fig. 1(b)], that constitute a microhabitat commonly used by small fishes (47 species of fishes, including *A. lacustris*) as feeding sites and refuge from predators (Severo-Neto *et al.*, 2015).

Samples were taken from the Miranda River (September 2011, $n = 21$ specimens, and 2013, $n = 44$) and the Medalha Lagoon (September 2009, $n = 13$, and 2011, $n = 39$) in the dry season, when the latter is isolated. Adult individuals of *A. lacustris* were collected using a cast net (mesh size: 30 mm; diameter: 2 m) in both habitats. Sampling was conducted around the perimeter of the Medalha Lagoon near macrophyte beds and along a stretch of *c.* 150 m on one of the margins of the Miranda River. Specimens were euthanized in eugenol and frozen until laboratory processing. Seven morphological traits were measured by the same person with a digital calliper ($\pm$0·01 mm), including: standard length (L_S), height of eye at horizontal through pupil, maximum head height, maximum body height, caudal peduncle length, maximum caudal peduncle height and maximum caudal peduncle width (Fig. S1, Supporting Information). To measure caudal-fin area, the caudal region of each individual was photographed using a Nikon D3200 (www.Nikon.com) placed 15 cm from the fish. The fin area was measured using ImageJ software (Schneider *et al.*, 2012).

To analyse body shape variation, all morphological traits were $\log_{10}$ transformed and then size standardized by taking the residuals from a regression of trait values on L_S (Sokal & Rohlf, 1981). All residual trait values were normally distributed (Shapiro−Wilk test, all *P*-values > 0.05). There was no difference in morphology

within habitats between sampling years (PERMANOVA, lagoon 2009 *v.* 2011: $P > 0.05$; river 2011 *v.* 2013: $P > 0.05$), so that all fish from the same location were pooled in the following analysis.

Morphological differences between individuals inhabiting the Medalha Lagoon and the Miranda River were investigated using PERMANOVA (Anderson, 2006). In order to identify what specific functional traits differed between environments, the residuals of each trait were compared between river and lagoon habitats using ANOVA (including false-discovery rate test to control type I error for multiple tests). As a further description of morphological variation, a principal component analysis (PCA) was performed using residuals of the functional traits that significantly differed among environments. Statistical analyses were performed in R 3.1.1 (R Development Core Team; www.r-project.org) using the package vegan (Oksanen *et al.*, 2013). A model including year nested within habitat as a random effect was also tested but results did not change qualitatively (Table SI, Supporting Information).

Specimens from the river and the lagoon significantly differ in overall morphology (PERMANOVA, $r^2 = 0.35$, $F_{1,115} = 59.77$, $P < 0.01$). When analysed individually, all traits except maximum body height and caudal peduncle height differ between environments (Fig. 2 and Table SII, Supporting Information). The first PC captured 41·6% of the variance in the data (Table SIII, Supporting Information), with negative scores associated with longer caudal peduncles and larger fin areas and positive scores with increased peduncle width (Fig. 3). Consistent with previous results, individuals in the river have more positive scores and those in the lagoon more negative scores.

The observed morphological divergence between river and lagoon habitats matches *a priori* predictions of swimming performance theory (Langerhans & Reznick, 2010). The Medalha Lagoon is a lentic, structurally complex environment where unsteady swimming is expected to be favoured. In line with these expectations, *A. lacustris* in this habitat exhibit relatively larger caudal regions and shallower heads. The Miranda River in turn is a high-flow, less structurally complex environment, where steady swimming should be more advantageous. As expected, *A. lacustris* in the river exhibited a more fusiform body shape, with smaller caudal regions and deeper heads.

Morphological differences between fish populations inhabiting lentic and lotic habitats have been documented in several species (Langerhans *et al.*, 2003; Foster *et al.*, 2015; Gaston & Lauer, 2015). In the case of *A. lacustris*, this divergence is maintained in the presence of seasonal migrations between these contrasting habitats, which should have a homogenizing effect. Different mechanisms might be responsible for the observed divergence in morphology. First, divergence between habitats can be facilitated if river migrants are able to return to their native habitat at the end of the wet season. In many species, including fishes, individuals can actively select habitats where their phenotypes are expected to be optimal, a behaviour called adaptive habitat choice (Chapman *et al.*, 2012, 2015; Edelaar & Bolnick, 2012). For example, in a mark–transplant–recapture experiment using phenotypically distinct lake and stream populations of three-spined stickleback *Gasterosteus aculeatus* L. 1758, 90% of individuals returned to their native habitat (Bolnick *et al.*, 2009). In the Pantanal wetlands, fishes migrate to the floodplains during the wet season, where they take advantage of the abundance of food resources and reproduction sites and return to rivers at the end of the wet season (Junk *et al.*, 2011). If *A. lacustris* with steady-swimmer phenotypes comprise most of those leaving the Medalha Lagoon towards the Miranda River, morphological differentiation would be maintained despite
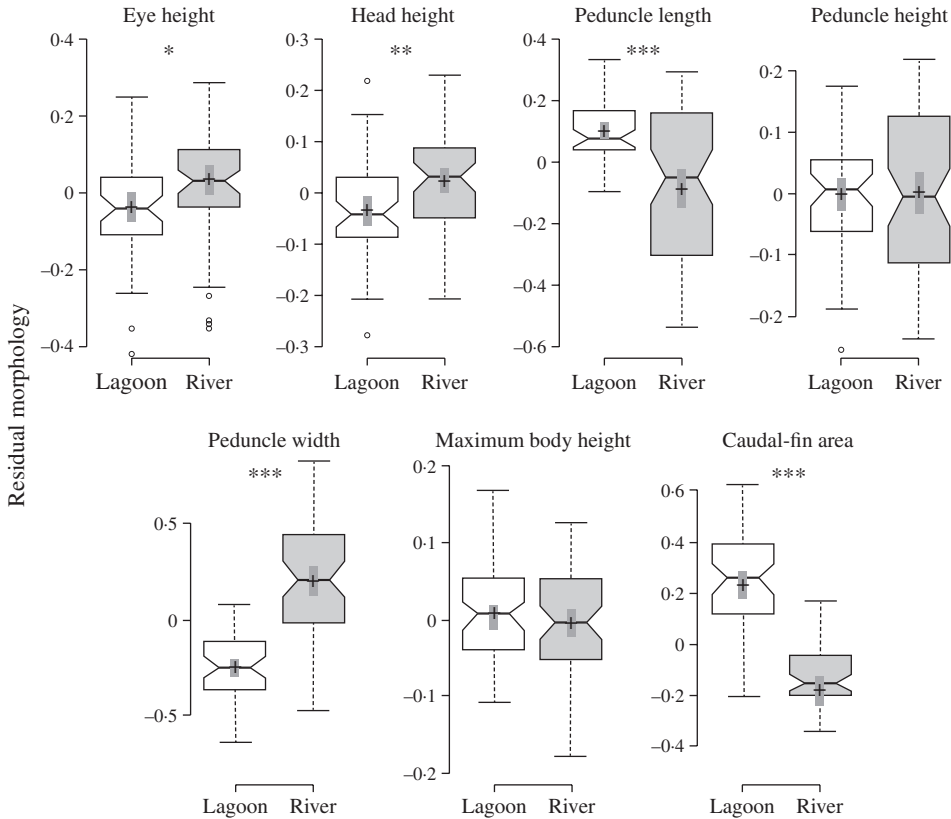
FIG. 2. Boxplots comparing the residual morphology of the tetra *Astyanax lacustris* between the (□) Medalha Lagoon and (▨) the Miranda River. Centre lines represent the medians, box limits indicate the interquartile range (IQR) from the 25th and 75th percentiles and whiskers indicate data range. ○, outliers; +, sample means; ▪, 95% C.I. around the means. Notches represent $\pm 1.58 \times \text{IQR}(\sqrt{n})^{-1}$, which gives roughly 95% C.I. around medians. Significant differences in means: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

seasonal migrations. Capture–mark–recapture techniques could be used in the future in order to test this idea.

Alternatively, some river migrant *A. lacustris* may stay in the Medalha Lagoon after it disconnects from the river in the dry season, so that the lagoon population is partly renewed by immigrants every year. In fact, data on helminth parasites of *A. lacustris* support this proposition, because the parasite community found in the fish in the lagoon in any given dry season is more similar to that in the previous wet season (R. Costa-Pereira, unpubl. data). Because the Medalha Lagoon was sampled at the peak of the dry season (September; Fig. 1), the observed phenotypic distribution might also reflect the effect of predation in the previous months. Floodplain lagoons in the Pantanal wetlands harbour piscivores [*e.g.* the trahira *Hoplias malabaricus* (Bloch 1794) at densities of $500 \, \text{kg ha}^{-1}$; Resende *et al.*, 1996]. Assuming that predation rates are high in the lagoon in the dry season due to the combined effects of abundant piscivores and decreased water volume (Resende *et al.*, 1996), preferential predation on steady swimmers, which are less capable of evading a predator (Langerhans, 2009*a*),
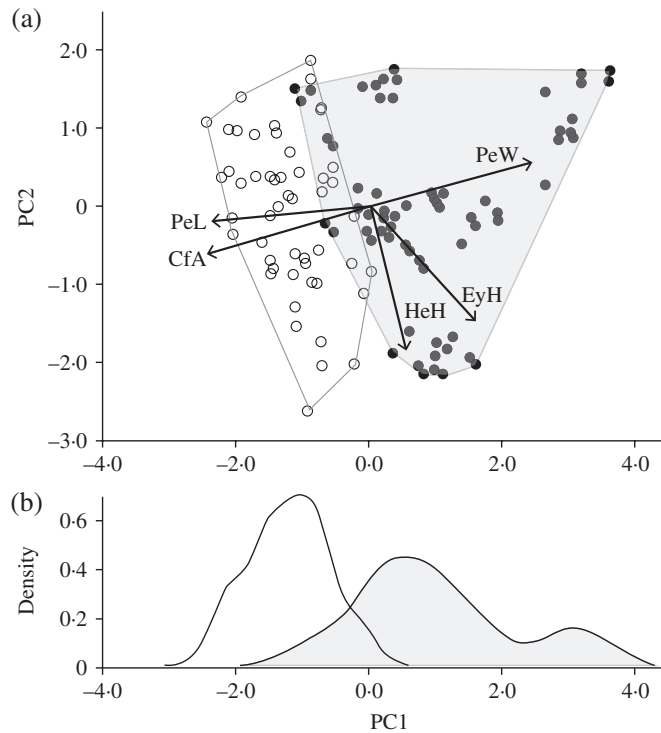
FIG. 3. (a) Biplot of a principal component (PC) analysis (variance explained $= 67 \cdot 9\%$) on residual morphology of *Astyanax lacustris* in the (○) Medalha Lagoon and in the (●) Miranda River. EyH, height of eye at horizontal through pupil; HeH, head height; PeW, peduncle width; PeL, peduncle length; CFA, caudal-fin area. (b) Density plot of the scores of the PC1 axis showing the difference in morphology between habitats: (□) Medalha Lagoon and (▨) the Miranda River.

would be predicted to remove this phenotype from the population. An additional line of evidence suggests that predation is intense in the Medalha Lagoon. Eye position is displaced downwards in the fish found in the Medalha Lagoon (Fig. 3). A lower eye position improves the detection of benthic predators, such as *H. malabaricus*, and has been interpreted as an adaptation to strong predation pressure (Langerhans & DeWitt, 2004).

Finally, the observed phenotypic divergence may be generated by adaptive phenotypic plasticity during development (McLaughlin & Grant, 1994; Imre *et al.*, 2002). During the wet season, when *A. lacustris* reproduce in the floodplain, their larvae develop within macrophyte beds (Milani *et al.*, 2010; Tondato *et al.*, 2010) and disperse passively as macrophyte beds drift through the floodplain (Bulla *et al.*, 2011). When water levels begin to decrease, most of the floating macrophytes are carried to the Miranda River (Pott *et al.*, 2011). A small portion of macrophyte beds, however, remains in floodplain lagoons, where larvae develop. Depending on the degree of developmental plasticity in body morphology, which can be high in fishes (Svanbäck & Eklöv, 2006), individuals that develop in the lagoon might develop into adults with unsteady-swimmer phenotypes, whereas those carried to the river would develop into steady swimmers.

In conclusion, the different habitats of the Miranda River and the Medalha Lagoon are associated with divergence in the body morphology of *A. lacustris*, in line with *a priori* predictions from swimming performance theory. This divergence could have resulted from combinations of adaptive habitat choice, predation and adaptive phenotypic plasticity, suggesting that these mechanisms can maintain phenotypic variation in organisms inhabiting environmental gradients, even in the presence of migration.

Supporting Information

Supporting Information may be found in the online version of this paper:

Fig. S1. Morphological traits measured in the tetra *Astyanax lacustris*: standard length (L_S); EyH, height of eye at horizontal through pupil; HeH, maximum head height; MBH, maximum body height; PeL, caudal peduncle length; PeH, maximum caudal peduncle height; PeW, maximum caudal peduncle width; CFA, caudal-fin area. Image adapted from Britski *et al.* (1999).

Table SI. Results of a nested MANOVA testing the differences in overall morphology of the tetra *Astyanax lacustris* between the Medalha Lagoon and the Miranda River (habitat) including the year of collection (year) nested within habitat as a random effect

Table SII. ANOVA results testing the differences in morphological traits in the tetra *Astyanax lacustris* between the Medalha Lagoon and the Miranda River.

Table SIII. Loadings and variance explained by PC axes of a PCA on five size-standardized morphological traits of the tetra fish *Astyanax asuncionensis*

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