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Feeding habits of *Thoracocharax stellatus* (Characiformes: Gasteropelecidae) in the upper rio Tocantins, Brazil

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The silver hatchetfish *Thoracocharax stellatus* is one of the approximately 200 fish species recorded for the upper rio Tocantins, in the region where it was impounded by the Serra da Mesa hydroelectric dam. Analysis of the stomach contents of 88 specimens revealed a diet consisting almost entirely of insects (99.6%), most of which were terrestrial (87.6%). Ants, beetles, and mayflies were the main food items. Dawn and dusk seemed to be the periods of highest foraging activity for *T. stellatus*. As a specialist on terrestrial insects, this species has a close connection with the region near the river bank, where prey is provided from the associated riparian vegetation. Despite the impoundment and depletion of the land-water ecotone observed in later stages of reservoir formation, no significant changes in the diet of the few remnant specimens were recorded, which seems to indicate little feeding flexibility. Thus, feeding seemed to be an overriding factor for the displacement of this species after river impoundment.

O peixe borboleta *Thoracocharax stellatus* é uma entre quase 200 espécies que ocorrem no alto rio Tocantins, no trecho represado pela UHE Serra da Mesa. A análise do conteúdo estomacal de 88 espécimes revelou uma dieta composta quase totalmente de insetos (99,6%), sendo, a maioria desses, insetos terrestres (87,6%). Formigas, besouros e efemerópteros foram os principais itens alimentares. A aurora e o crepúsculo parecem ser os períodos de maior atividade de forrageamento de *T. stellatus*. Sendo especializada em insetos terrestres, esta espécie apresenta uma estreita relação com a área próxima às margens, onde presas são fornecidas pela vegetação ripária associada. Apesar do represamento e da depleção do ecótono terra-água observado em fases posteriores da formação do reservatório, não foram registradas mudanças significativas na dieta dos poucos espécimes remanescentes, o que parece indicar uma baixa flexibilidade alimentar. Desta forma, a alimentação parece ter sido um fator determinante para o deslocamento desta espécie após o represamento.

Key words: Hatchetfishes, Autoecology, Diet, Tocantins-Araguaia basin.

Introduction

The freshwater hatchetfishes, members of the Neotropical family Gasteropelecidae, constitute a small *incertae sedis* clade of the order Characiformes, apparently related to the family Characidae (Buckup, 1998). This family consists of three genera and nine species, distributed from Panama to the Paraná-Paraguay River drainage. Gasteropelecids are easily recognized by their highly modified body (Weitzman & Palmer, 2003). The most conspicuous modification is on the pectoral girdle, which forms a very developed keel, bearing strong muscles and long fin-rays (Géry, 1977; Weitzman, 1960; Weitzman & Palmer, 2003). This feature gives hatchetfishes the ability to perform long and high jumps out of the water (Weitzman & Palmer, 2003). The silver hatchetfish *Thoracocharax stellatus* (Kner, 1858) is one of the largest, and also the most widespread species of this family. It is known to occur in the Amazon, Orinoco, Paraguay and Tocantins-Araguaia basins (Weitzman, 1960).

This species was recorded for the upper rio Tocantins, in the stretch impounded by the Serra da Mesa hydroelectric dam in 1996. In the aftermath of the impoundment, the abundance of some species increased (*e.g.* Novaes *et al.* 2004), whereas the population of *T. stellatus*, as well as that of other

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species (*e.g.* Albrecht & Pellegrini-Caramaschi, 2003; Castro *et al*., 2003; Albrecht, 2005), was negatively affected. Fourteen months after the damming, *T. stellatus* was found only in the remaining upstream lotic areas, being no longer found in the recently formed reservoir (Netto-Ferreira *et al.*, unpublished manuscript).

Impoundments constitute a major disturbance in river ecosystems, being one of the main threats to freshwater fish (Lowe-McConnell, 1994). Survival, reproduction, and distribution of fish species are often conditioned to the availability of resources in the environment and species feeding ecology. Therefore, studies on the diet of fishes may provide valuable information on the responses of populations and assemblages after a disturbance. Furthermore, this knowledge can aid in the elaboration of management protocols and other conservation efforts.

Displacement and/ or diet shifts seem to be a common response of fish populations after disturbances such as river impoundments (*e.g.* Agostinho *et al.*, 1999). Because *T. stellatus* was relatively ubiquitous in the upper Tocantins system before the impoundment, we herein characterize the diet and feeding habits of this species under natural riverine conditions. As land flooding and changes in water dynamics are expected to alter the availability of resources (*e.g.* Hahn *et al.*, 1998; Albrecht, 2005), we also sought to determine potential differences on the diet related to reservoir formation. Since the population of *T. stellatus* has shown a demographic decrease after the damming (Netto-Ferreira *et al.*, unpublished manuscript), we hypothesized that this species has not profited from the newly available food resources. We document data on the diet of *T. stellatus*, relate it to environmental changes and diel period, and discuss briefly the feeding behavior of this species. Although sparse data on the diet (Weitzman & Palmer, 1996; Planquette *et al.*, 1996; Galvis *et al.*, 1997) and behavior (Wiest, 1995; Weitzman & Palmer, 1996) of some hatchetfish species are currently available, other features of the ecology of gasteropelecids remain unknown. The present paper constitutes the first study with an ecological approach for a species of the genus *Thoracocharax*.

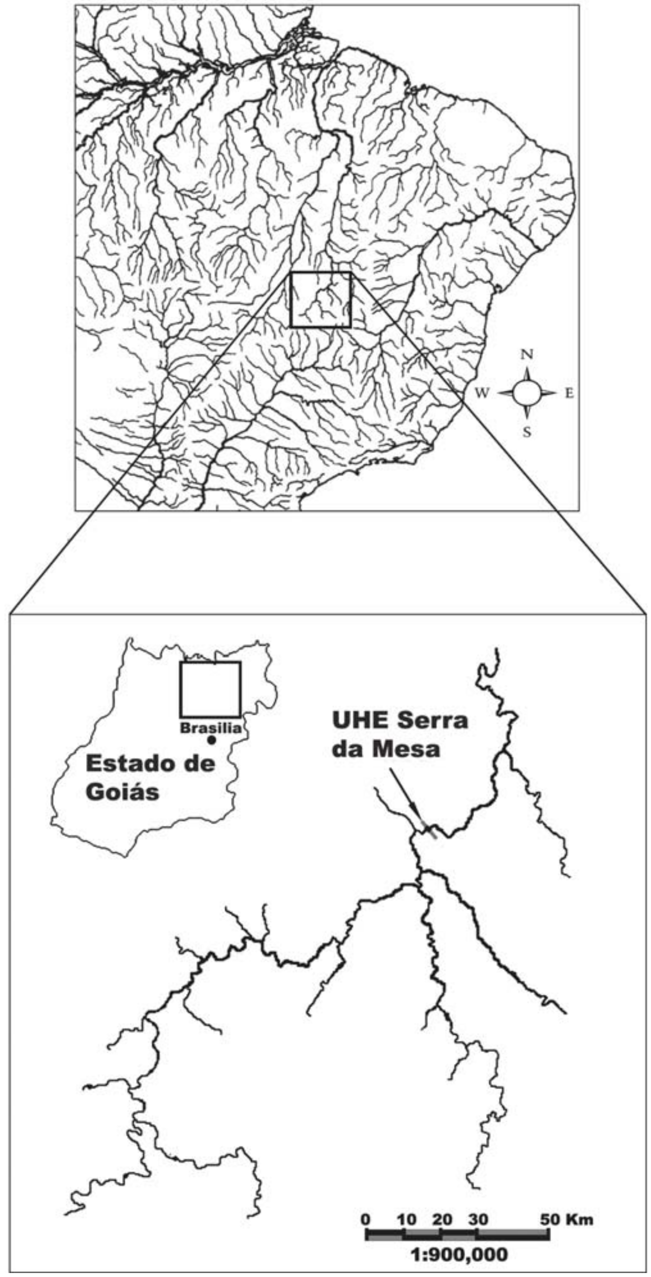

Fig. 1. Location of the study area, in the upper Rio Tocantins, where the Serra da Mesa Hydroelectric Dam was installed – Estado de Goiás, central Brazil.

Material and Methods

Study Area

The rio Tocantins forms in the Brazilian Pre-Cambrian Shield on the confluence of the Almas and Maranhão rivers. Our study area, in the upper stretch of this river, is situated between the geographical coordinates 13º-15º S 48º-49º 30'W (Fig. 1). The region has a well-defined hydrological regime, with high waters from November to April, and low waters from May to October. In October 1996 the upper stretch of the rio Tocantins was impounded by the Serra da Mesa hydroelectric dam. The reservoir has an area of approximately 1,700 km², and a volume of 54.4×10^9 m³, being the largest Brazilian reservoir in storage capacity (De Fillipo *et al.*, 1999). Before the impoundment, the affected portion of the river was a succession of waterfalls, riffles and pools within constrained reaches, surrounded by Cerrado vegetation, a type of wet seasonal savanna (Felfili & Silva, 1993).

Sampling and analyses

Fishes were captured every month during 34 field trips, from December, 1995 to December, 2002, encompassing three temporal stages: December, 1995 to October, 1996 (pre-impoundment stage); December, 1996 to April, 1998 (filling stage, during the filling of the reservoir); and June, 1998 to December, 2002 (operation stage, when the power plant started operating for energy production). Fish were collected at five sites within the area that later became the reservoir, two sites downstream from the dam, and two sites upstream that remained lotic until the final months of reservoir formation. After impoundment, five sampling sites were added in order to survey the larger area formed by the reservoir. Collections were made with standardized arrays of gill nets with a mesh size varying from 15 to 150 mm, left for 24h at each sampling site, and monitored at 8h intervals (morning, afternoon and night). Non-standardized effort (seines and cast nets) was also employed for qualitative sampling purposes at three other sites located in side tributaries of the Tocantins main channel. Collecting permission was obtained from IBAMA/ MMA (process no. 03724/95-44 and 02001.001488/01-26). Voucher specimens of *T. stellatus* (Fig. 2) were deposited at the collection of the Setor de Ictiologia of Museu Nacional, Universidade Federal do Rio de Janeiro: MNRJ 12612, MNRJ 15255, and MNRJ-17659.

Captured specimens were measured (mm/SL), weighed (10^{-5} kg) and had their sex and gonad maturation development examined in the field laboratory. The digestive tracts that contained food were removed and fixed in 5% formaldehyde for later analysis. For dietary characterization regardless of spatial and temporal variation, the stomach contents of 88 specimens (48 females, 37 males and three of undetermined gender) with standard length ranging from 4.40 cm to 6.28 cm were analyzed. Food items were identified and each item was quantified (absolute volume) following the method described by Albrecht & Caramaschi (2003). In order to characterize the diet of *T. stellatus*, the volumetric and frequency of occurrence methods (Hynes, 1950; Hyslop, 1980) were combined to calculate the alimentary index (*I*Ai) proposed by Kawakami & Vazzoler (1980). Food items were considered as main items when *I*Ai values were greater than 1.00. These were the only items included in the graphic representation of the *I*Ai. Shannon's index of diversity was calculated as a measure of niche breadth (Krebs, 1989).

In order to represent spatial and temporal patterns of resource use by individuals of *T. stellatus*, a principal components analysis (PCA) (Ludwig & Reinolds, 1988) was performed using PC-Ord software v.3.00 (McCune & Mefford, 1997) with a non-parametric correlation matrix. Correlations among the values of the first axis of PCA and biological (standard length, weight, gender, gonadal development, gonad weight), spatial (sampling site, lotic or lentic sites) or temporal (rainy or dry season, stage related to impoundment, time of net checks) data were examined with Pearson's linear correlation test (Zar, 1984) using GraphPad InStat version 3.00 for Windows (GraphPad Software, San Diego California USA, www.graphpad.com).

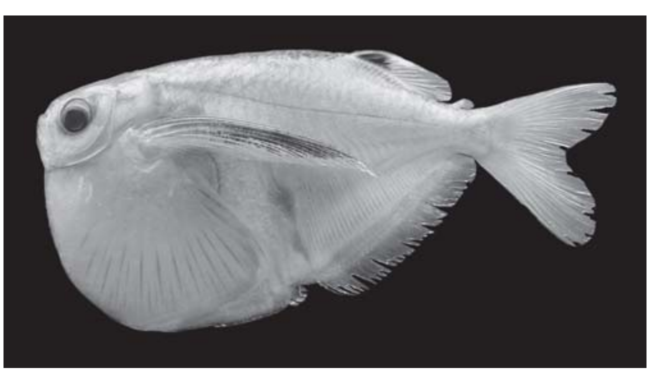

Fig. 2. Voucher specimen of *Thoracocharax stellatus* (5.54 cm in standard length) from the upper rio Tocantins (MNRJ 17659).

The periods of highest feeding activity of *T. stellatus* were estimated by the comparison of the mean volumes of ingested food among the three times the nets were monitored throughout the diel period (morning, afternoon and night). A one-way ANOVA with Tukey's *post hoc* test was used to test for significance (Zar, 1984). Data were first log-transfomed, as the requirement of homogeneity of variances were not met (Levene's test). Prey volumes before and after impoundment (regardless of spatial variation, *i.e.*, lotic or lentic sites) were compared using a t-test to determine if the feeding activity of *T. stellatus* was affected by the reservoir filling process. Analyses were performed using Statistica 6.0 software (StatSoft, Inc. 2001).

Results

Thirty one food items were identified in the diet of *T. stellatus* (Table 1). Shannon's index for niche breadth was H'=1.216 bits.ind^{-1}. Insects comprised 99.6% of the diet, when considering data of volume and frequency of consumption combined in the alimentary index (IAi). Terrestrial insects were more important (87.6%) than those of autochthonous origin (12.0%). Ants, beetles, and mayflies were the main resource items in the diet of *T. stellatus* (Fig. 3). Prey size varied from small mites and springtails (both smaller than 0.01 mm³) to coleopterans (Elateridae) and hymenopterans (Pompillidae and Vespidae), about 35 mm³ and 32 mm³ in volume, respectively. There was no evidence that proportionally larger prey were consumed as fish individuals grew larger. A high percentage (39.6%) of the insects found in the stomach content was too damaged to allow proper identification. These fragments were classified as "insect remains", and therefore excluded from further data analyses.

The eigenvalues of the first two axes of principal components analysis (PCA) were 0.376 and 0.235, respectively, explaining 61.1% of the total variation. The first axis was positively associated with Coleoptera and negatively associated with Formicidae. Chironomidae pupae, Coleoptera, Formicidae and Ephemeroptera had the most extreme values for the formation of the second axis. Eigenvectors for principal components axes 1 and 2 are presented in Table 2. Specimens that consumed mainly coleopterans clustered on the upper right quadrant whereas those that consumed mainly ants clustered on the upper left corner of the PCA plot. The lower right corner of PCA was occupied by specimens feeding mainly on chironomids and ephemeropterans. Individuals that had a more diversified diet assembled closer to the axis origins (Fig. 4). No significant correlation was observed between the scores of first PCA axis and any of the factors examined in the present study.

Table 1. Alimentary index (IAi) calculated for each food item in the diet of *Thoracocharax stellatus* in the upper rio Tocantins. Items with IAi > 1.00 were considered main items.

Food Items	IAi
Formicidae	31.70
Ephemeroptera (Adults)	29.95
Coleoptera (Adults)	18.24
Chironomidae (Pupae)	10.41
Hymenoptera	2.64
Heteroptera	2.33
Diptera	1.89
Diptera (Larvae)	1.01
Auchenorrhyncha	0.36
Sediment	0.21
Trichoptera (Adult)	0.20
Organic Material	0.17
Isoptera	0.17
Odonata (Adult)	0.15
Ceratopogonidae (Larvae)	0.14
Lepidoptera	0.13
Invertebrate eggs	0.08
Araneae	0.07
Lepidoptera (Larvae)	0.04
Dermaptera	0.02
Thysanoptera	0.02
Blattaria	0.01
Ephemeroptera (Nymph)	0.01
Vegetal Material	0.01
Feather	<0.01
Trichoptera (Pupae)	<0.01
Psocoptera	<0.01
Scales	<0.01
Collembola	<0.01
Acari	<0.01
Coleoptera (Larvae)	<0.01

Table 2. PCA axis 1 and axis 2 eigenvectors for dietary data (eight main items) of individuals of *Thoracocharax stellatus* from the upper rio Tocantins.

	Eigenvectors	
Itens	1	2
Chironomidae	0.0837	-0.2934
Coleoptera	0.5705	0.6625
Diptera adult	0.0098	-0.0069
Diptera larvae	0.0063	-0.0186
Ephemeroptera	0.1133	-0.5841
Formicidae	-0.8080	0.3505
Heteroptera	-0.0140	-0.0076
Hymenoptera	0.0383	-0.1025

Of 342 specimens collected with standardized methods, 159 (46.5 %) individuals were collected in the morning, 75 (22.0 %) in the afternoon, and 108 (31.5 %) at night. The specimens collected in the morning check ingested the highest mean volume of food (117.43 mm^3), followed by the night check (112.01 mm^3). Specimens collected in the afternoon consumed a markedly lower volume of prey (45.93 mm^3). Overall, mean volumes were significantly different (ANOVA; $F=3.456$; $p=0.037$). Mean volume of consumed food was significantly lower in the afternoon check related to the morning ($p=0.03$) and evening ($p=0.05$) checks.

The *t*- test revealed a significantly higher prey ingestion during the post-impoundment periods ($p=0.006$).

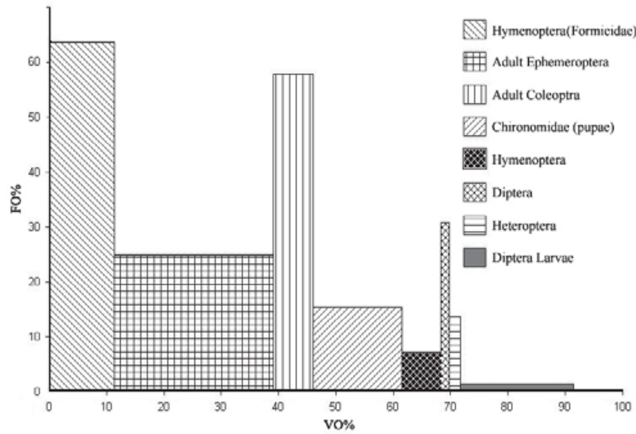

Fig. 3. Representation of the alimentary index (IAi), associating relative frequency (FO%), and relative volume (VO%) of the main items in the diet of *Thoracocharax stellatus* of the upper rio Tocantins.

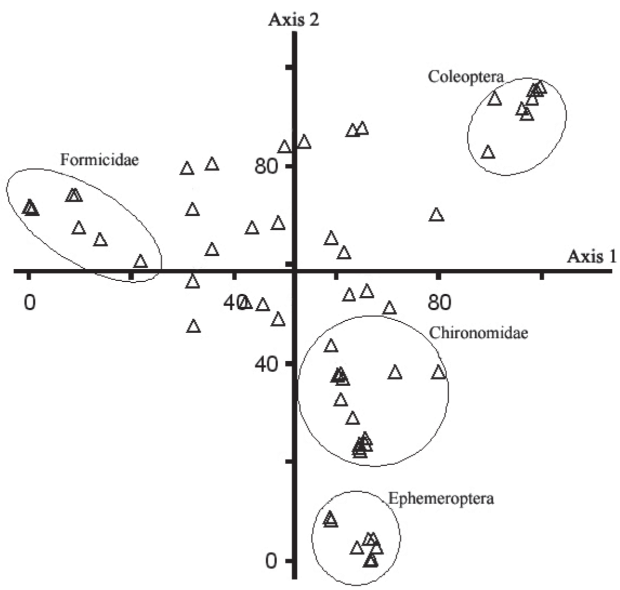

Fig. 4. Principal Components Analysis plot, based on the volumetric proportions of food items consumed by individuals of *Thoracocharax stellatus* in the upper rio Tocantins.

Discussion

Thoracocharax stellatus is an insectivorous species, along with its relatives *Carnegiella marthae* Myers (Weitzman & Palmer, 1996), *C. strigata* (Günther), *Gasteropelecus sternicla* (Linnaeus) (Planquette *et al.*, 1996) and *G. maculatus* Steindachner (Galvis *et al.*, 1997). Allochthonous insects are regular items in its diet, and belong mainly to groups that inhabit the riparian vegetation (*e.g.* beetles, leafhoppers and some ants) or perform seasonal reproductive flights (*e.g.* winged ants and mayflies). The highly modified body of *T. stellatus* and other gasteropelecids allows these fish to maintain position very close to the water surface (Weitzman, 1960; Weitzman

& Palmer, 2003), where feeding on fallen terrestrial insects is facilitated by their upturned upper mouth (Weitzman & Palmer, 1996), flattened pre-dorsal area, and powerful, long pectoral fins (Weitzman & Palmer, 2003).

Thoracocharax stellatus seems to be selective for live insects that fall, or that seem to have fallen into the water, but within the array of this prey category, there is no apparent selection of specific taxa by the fish. The high frequency of ants and coleopterans in the stomach contents must be carefully interpreted, since these insects possess a thick, hardened exoskeleton, whose digestion is much slower than that of other insects that bear more fragile exoskeletons, such as mayflies and caddisflies. These differences in digestibility may lead to an overestimation of the contribution of insects with thickened exoskeletons to fish diets. The high frequency and amount of unidentifiable fragments of insects in the stomach contents is probably due to damage caused by the multicuspidate teeth of *T. stellatus* during prey handling, or to advanced stages of prey digestion, and is unlikely to indicate a necrophagous behavior. This supposition is justified by the above-mentioned habits and derived morphology of the gasteropelecids. Furthermore, if *T. stellatus* were a necrophagous species, autochthonous items would possibly be more common in its diet. In fact, most of the aquatic insects consumed were midge pupae with ruptured integument, which indicates that these pupae were about to emerge as adults near the surface. The movements made by the pupae to breathe or emerge as adults possibly stimulated the hatchetfish to capture them.

We also suggest that *T. stellatus* does not use its jumping ability to capture prey out of the water, refuting one of the previous hypotheses to explain the function of the long jumps of the gasteropelecids (Géry, 1977). Some individuals of this species were observed while feeding on allochthonous insects and water striders in the rio Solimões, and no individual was springing out of the water to capture its prey (J. Zuanon and J. L. Nessimian, pers. obs.). Furthermore, experiments showed that frightening stimuli, such as live predators, predator models, or sudden approaches near the aquarium, were the only stimuli proved to be effective in eliciting out-of-water excursions in gasteropelecids (Wiest, 1995; Weitzman & Palmer, 1996).

Sunrise and sunset are the most active feeding periods for *T. stellatus*, as indicated by the higher abundance of captured individuals, and by the higher volume of food ingested at these periods. The large percentage of nocturnal insects consumed (winged ants and adult mayflies) lend support to this finding. In spite of the large eyes, which suggest visual predation, *T. stellatus* probably relies on mechanical cues to detect prey. Furthermore, at twilight these bright fish become less visible, probably minimizing predation risk.

The ordination of specimens in the diet space suggests that *T. stellatus* has a generalized rather than a specialized diet. A species' broad niche may be the result of an individual preference for distinct prey, or of a truly generalist behavior of each specimen of the population (Crespin de Billy *et al.*, 2000; Bearhop *et al.*, 2004). The examination of stomach contents and PCA ordination suggest that *T. stellatus* fits both patterns, as exemplified also by other animal taxa (Bolnick *et al.*, 2003). The four discrete clusters in the ordination analysis were formed by groups of individuals that consumed greater volumes of either formicids, coleopterans, ephemeropterans or midge pupae. On the other hand, the ingestion of rare or many different items led to specimens clustering near the origin of the first and second axes of PCA. The ingestion of rare items also led to a low niche breadth value, since the index used is maximized both by many diet categories and equal utilization of each (Magurran, 1988).

Contrary to *T. stellatus*, many individuals of other small omnivores and/ or insectivores invaded the recently formed lentic area, which provided abundant resources (Albrecht, 2005). Although higher amounts of food were consumed, no significant changes in the diet composition of *T. stellatus* related to the environmental alteration were recorded, which seems to indicate little feeding flexibility. Trophic specialization is reported to be rather uncommon in tropical environments, as seasonal hydrologic cycles change the availability of resources (Lowe-McConnell, 1987; Winemiller, 1990). Other insectivorous species from the upper rio Tocantins have shown diet shifts in different phases of reservoir development. *Auchenipterus nuchalis* (Spix & Agassiz) fed mainly on ephemeropterans in the pre-impoundment stage, and changed diet to capitalize on aquatic items, which were mainly dipteran larvae and pupae during reservoir filling, and microcrustaceans, both planktonic and benthic, during the operation stage (Albrecht, 2005). *Triportheus albus* (Cope) has shown a similar response (Gama & Caramaschi, 2001), albeit less pronounced. *Bryconops* cf. *melanurus*, whose diet in the riverine environment is very similar to that of *T. stellatus*, has shown a remarkable diet shift about 12 months after the damming, when it starts consuming autochthonous insects, mainly heteropterans (water striders, water boatmen and back swimmers), and chironomid larvae (unpublished data). Such diet shifts may indicate a reduction in the availability of allochthonous food after complete filling of the reservoir.

Thoracocharax stellatus is a specialist on terrestrial insects, and thus has a close connection with the region near the river bank, where prey are provided from the associated riparian vegetation. Despite the depletion of the land-water ecotone observed in later stages of reservoir formation (pers. obs.), no significant changes in the diet of the few remnant specimens were recorded, and the population decreased in the area. We conclude that the feeding habit was an overriding factor for the displacement, or even local extirpation of the population of *T. stellatus*. Unlike other insectivores, it was not able to profit from the resources made available in the novel environment after the impoundment of the upper rio Tocantins.

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