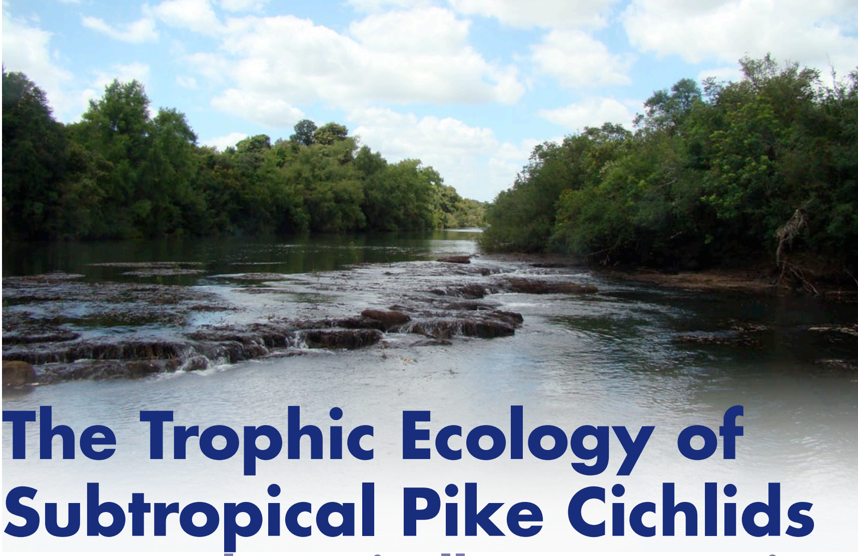

The Trophic Ecology of Subtropical Pike Cichlids

ACA Paul V. Loiselle Conservation Fund Grant Recipient

Upper Rio Cuareim, Uruguay (right) and Brazil (left).

Edward D. Burress
burressed@email.appstate.edu

Photographs by the author unless otherwise noted

It's a six hour drive from the airport in Montevideo to the Uruguay-Brazil border. Where pavement ends, it's another 90-minute drive on a patchy mixture of gravel, dirt, grass, and cacti to the headwaters of the Rio Cuareim. We get a private escort via the local gaucho, because there is no path or trail. He rides horseback and we follow in the truck. Otherwise, it'd be three hours instead of 90 minutes.

There's a well-developed riparian zone around what is certainly the central oasis for this area. Wildlife is everywhere. Rhea, burrowing owls, hawks, armadillo, and cattle watch as we make our way to the river. Most vegetation has some form of spine, thorn, or spear, so getting to the shore is often delicate. The banks are rocky, with patches of shrubs and rocky outcroppings. The water is clear and cool despite the scorching sun above.

Pairs of *Gymnogeophagus* and *Australoheros* species are scattered along the shore, tending eggs and fry, and schools of *Cyanocharax* dart away from my shadow. I watch them until they're swarmed by 50 startled *Corydoras* and my eyes lose focus. The water surface is calm between riffles and occasionally disturbed by small *Astyanax* as they break the surface in desperation, flinging themselves forward out of the river, re-submerge, dart a short distance and repeat. My heart rate picks up in anticipation. They flee and it's desperate. I never see their antagonist, but I know them.

Introduction

The Rio Cuareim is a major tributary to the middle Rio Uruguay. This basin supports many species of conservation concern (Soutullo et al., 2009), and supports a particularly high diversity of pike cichlids (*Crenicichla*) (Lucena and Kullander, 1992; Serra et al., 2011). For my master's thesis, I investigated diet partitioning and ontogenetic diet shifts in the six species of *Crenicichla* that co-occur in the upper Rio Cuareim, Uruguay. Kutty (2009) provides a detailed overview of these species and insight into their ecology and husbandry.

In the headwaters of the Rio Cuareim, *C. scottii*, *C.* cf. *lepidota*, *C. missioneira*, *C. minuano*, and *C. celidochilus* co-occur together. During fieldwork for this project, we were lucky enough to catch 11 *C. tendybaguassu*. The catch meant the first record in the middle Rio Uruguay and the first record in Uruguay. While the unique find was a pleasant surprise, it is not totally unexpected since they co-occur with many of the same species in tributaries of the upper Rio Uruguay in Brazil, 400 km (249 mi) to the north. Serra et al. (2011) officially document *C. tendybaguassu* in Uruguay. *Crenicichla vittata* occur in the lower portions of the Rio Cuareim, near its confluence with the Rio Uruguay, but are not included in the scope of this project.

Objectives

1) Provide evidence of resource-based competition.

2) Determine if these six species are functionally redundant and elucidate the trophic role of subtropical *Crenicichla.*

3) Provide ecological data necessary for the understanding of life history characteristics that will be vital in conserving these species and the diverse ecosystems they inhabit.

Methods

I employed two methods to determine the trophic ecology of *Crenicichla*. First, traditional stomach content analysis. Items were dissected from preserved stomachs and identified to family. Stomach content analyses have long been used in ecology and present well-known limitations, such as discrepancies in digestion rates among prey items and the ambiguous identification of partially digested items. Additionally, stomach contents provide only a snapshot of what an organism ate in the immediate time preceding preservation. Thus, many individuals are needed to overcome these limitations. This isn't a great scenario for conservation-based research. Fortunately, there are other means to determine what an organism eats.

The second method I used was stable isotope analysis. Stable isotopes are more complex, but the concept is relatively simple: you are what you eat. A consumer assimilates prey into their own tissues and thus we can use $\delta^{13}C$ and $\delta^{15}N$ ratios to determine what an organism eats based on isotopic similarity. Generally, prey and consumer $\delta^{13}C$ signatures are very similar, and $\delta^{15}N$ ratios typically increase by stepwise intervals (about 2.5) from prey to consumer. Thus, $\delta^{15}N$ ratios are also useful in determining trophic levels. The advantage of stable isotopes is that they

Arroyo de la Invernada, Uruguay, a major headwater tributary to the Rio Cuareim.

are based on assimilation and thus reflect long-term dietary patterns. There are several statistical methods that allow researchers to estimate the contributions of multiple prey items to consumer diet. In combination, stomach contents and stable isotope analyses are powerful tools in trophic ecology.

The author (left) and Felipe Cantera (right) reflect on a long day of fieldwork.

Summary

The first thing I learned during this research is that in subtropical South America, you don't want to be a larval mayfly or characid, because everything eats you. Despite the accuracy of that broad statement, I found evidence for strict diet segregation among pike cichlids. For simplicity, I will overview my findings for each species in functional groups.

The Piscivores

It might surprise some that I will only discuss two species in this section, but overall piscivory isn't a good general descriptor of subtropical *Crenicichla*. I will forgo the old adage, 'save the best for last,' and start with my favorite species: *Crenicichla celidochilus*. *C. celidochilus* are particularly interesting because of their unique 'lip spots' and conspicuous coloration. Surprisingly, they display the most trophic specialization of any species by almost exclusively feeding upon one suite of prey. The unfortunate victims are characids (Characidae). *Astyanax* and *Bryconamericus* are common in much of the subtropics and are heavily exploited by *C. celidochilus*. Additionally, *C. celidochilus* display piscivorous tendencies by the modest size of 10 cm (3.9 in)!

Potentially the most abundant species, *Crenicichla missioneira* are generalist piscivores. They feed on roughly equal proportions of characids and cichlid young of year (YOY). Though the specific identity of the cichlid YOY was difficult to discern, most were assumed to be small *Gymnogeophagus*, which are common substrate sifters throughout the subtropics. It's rare to find large *C. missioneira* in shallow bank zones, so I further assume the cichlid prey to be

Female *Crenicichla celidochilus*.

Pedro Lasnier

Female *Crenicichla tendybaguassu* in breeding coloration.

G. gymnogenys, which will move into deeper waters than *G. meridionalis*. Interestingly, there's no obvious habitat segregation between *C. missioneira* and *C. celidochilus*. *C. celidochilus* simply do not appear to predate cichlids.

The Invertivores

This functional group also contains two species: *C. scottii* and *C.* cf. *lepidota*. *C. scottii* is a generalist carnivore, consuming fishes, larval invertebrates, and crustaceans. Their preferred prey items are two littoral crustaceans, *Aegla* and *Trichodactylus*. *C. scottii* is the only *Crenicichla* to consume notable quantities of either crustacean. *C. scottii* has a strong affinity to bank zones and likely finds these crustaceans to be abundant in those habitats and thus exploits them. However, both crustaceans are relatively large compared to other invertebrate taxa, so the large size of *C. scottii* probably further facilitates their exploitation.

C. cf. *lepidota* could also be considered a generalist carnivore. They display the most individual variation of any species by far, and are probably the most opportunistic species. They consume notable portions of characins and large littoral invertebrates, such as dragonfly larvae. However, they show a particular affinity for surface oriented prey such as terrestrial insects and even water striders. This is another unique behavioral pattern, as no other species consumes terrestrial-derived prey. *C.* cf. *lepidota* and *C. scottii* both display an affinity for bank zones; however, neither appear to consume cichlids, which generally occupy the same areas.

The Molluscivore

Another specialist, the diminutive *Crenicichla minuano* is the only species that consumes insignificant proportions of fish. The miniscule proportion of fish that they do consume is cichlids, which probably indicates an opportunistic exploitation of fry. However, the staples of *C. minuano* diet are bivalves and snails. They're the only species to eat bivalves and one of two species to eat snails. Bivalves actually constitute half their diet! They crush the shells and swallow the mangled remnants whole. They also prey upon the classic larval insects such as caddisflies and mayflies, and generally seem to target small prey items. They also consume small quantities of vegetal material, most of which is associated with caddisfly retreats.

The Grazer

Crenicichla tendybaguassu feeds on similar items as *C. minuano*, but it forages completely differently. *C. minuano* picks items, whether they are snails, bivalves, or

The author samples invertebrates in a riffle.

caddisfly cases, crushes them and consumes all the associated material whole. In contrast, *C. tendybaguassu* grazes and thus consumes primarily mayflies and caddisflies, but also considerable amounts of vegetal material and even algae. I was fortunate enough to observe them scraping the dorsal surface and margins of rocks.

I assume that despite their omnivorous diet, they graze for invertebrates and that plant material is merely consumed inadvertently. However, it does seem as though the plant material is assimilated. Their hypertrophied lips likely facilitate this foraging mode. Similar morphologies are shared by *Gymnogeophagus gymnogenys* and *G. labiatus*, which are considered omnivorous. Thus, it's entirely possible that *C. tendybaguassu* is truly omnivorous and intentionally consuming plant material.

Discussion

My expectation was that cichlid young of year would be widely preyed upon by *Crenicichla*. In fact, they are barely consumed at all. In most species they would barely be considered a tertiary prey item and only *C. missioneira* consumes notable quantities of cichlids. Characids are the only widely consumed prey item, which was also unexpected. Though it wasn't possible to identify the prey fishes to genus, a pharyngeal tooth plate was the only indication of another *Crenicichla* being consumed (by *C. celidochilus*). Interestingly, very small proportions of catfishes (less than 1% of diet) of the families Loricariidae, Auchenipteridae, and Pimelodidae were consumed by *C. celicochilus*, *C. missioneira*, and *C. scottii*.

The second part of my research was investigating the food web structure of the Rio Cuareim. I analyzed stable isotope ratios of 23 species, including representatives from all theoretical trophic levels/guilds. Where do *Crenicichla* stack up among the community? *C. minuano*, *C.* cf. *lepidota*, *C. scottii*, and *C. tendybaguassu* occupy an intermediate trophic level. Their relative trophic position could be described as the top of the invertivore trophic level, which consists of most fish species (*Gymnogeophagus*, *Australoheros*, *Astyanax*, *Leporinus*, etc.). *C. missioneira* and *C. celidochilus* occupy the next trophic level, along with *Oligsarcus robustus* and *Serrasalmus spilopleura*, which constitutes the primary piscivores. Yet another trophic level that consists of secondary piscovores (that consume other predators) includes three *Hoplias* species: *H. lacerdae*, *H. australis*, and *H. malabaricus*.

Conservation

Possibly the most important finding of my research is that these species each occupy distinct trophic roles within the community, which has profound conservation implications. Despite the co-occurrence of six *Crenicichla*, there appears to be very little functional redundancy among them. This suggests that each species has its own

***Astyanax* are common characids throughout subtropical South America and widely consumed by *Crenicichla*.**

ecological identity and should be considered important to ecosystem function. Loss of species that lack functional redundancy can have dramatic ecosystem implications (see Taylor et al., 2006).

Furthermore, predatory species often structure communities. The Rio Cuareim supports many species of conservation concern and is considered a high diversity area for fishes (Zarucki et al., 2010; Soutullo et al., 2010). My research demonstrates that conservation at the functional-level often means conservation at the species-level. However, due to the close proximity of all six species, preservation of the upper Rio Cuareim basin should benefit all species in this high diversity area.

Conclusions and Future Research

Crenicichla are diverse mesopredators that possess surprising trophic specialization. They are without a doubt important predators in South American drainages and they likely exert trophic pressures that shape those communities. My future research will further investigate the food web structure of subtropical rivers, niche shifts among mesopredatory fishes, predator-prey interactions, and species-specific impacts on ecosystem function.

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The contrasting jaw morphology of *Crenicichla missioneira* (left) and *C. minuano* (right).

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