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Gape size influences seasonal patterns of piscivore diets in three Neotropical rivers

Carmen G. Montaña¹, Craig A. Layman² and Kirk O. Winemiller¹

We examined diets of four piscivores, two in the order Perciformes (*Cichla temensis* and *C. orinocensis*) and two in the order Characiformes (*Boulengerella cuvieri* and *B. lucius*), from the Cinaruco, La Guardia, and Ventuari rivers in Venezuela throughout the wet-dry seasonal cycle. The four piscivores consumed a phylogenetically and morphologically diverse group of fishes, reflecting the overall diversity of fish species in these rivers. At the start of the falling-water period, *Cichla* consumed large prey, especially the abundant, migratory, fish of the genus *Semaprochilodus*. As these relatively large prey became depleted during the dry season, *Cichla* tended to consume smaller prey. For *Boulengerella*, gape limitation precluded consumption of larger, seasonally abundant, fishes, and so prey sizes were more consistent throughout the seasonal cycle. Our findings show how prey abundance and gape limitations interact to influence seasonal patterns of predator-prey interactions.

Foram examinadas as dietas de quatro espécies de peixes piscívoros, duas da ordem Perciformes (*Cichla temensis* and *C. orinocensis*) e duas da ordem Characiformes (*Boulengerella cuvieri* and *B. lucius*), coletadas durante os ciclos de cheia e seca nos rios Cinaruco, La Guardia e Ventari, Venezuela. Os quatro piscívoros consumiram grupos de peixes filogenética e morfologicamente diversos, o que reflete a ampla diversidade de peixes nos rios estudados. No início da vazante, *Cichla* consumiu presas grandes, especialmente *Semaprochilodus*, um peixe migrador muito abundante. Com a diminuição das presas maiores durante a estação seca, *Cichla* tendeu a se alimentar de presas menores. Para *Boulengerella*, a limitação da abertura bucal impediu o consumo de peixes grandes e sazonalmente abundantes e, deste modo, o tamanho de suas presas foi menos variável ao longo do ciclo sazonal. Nossos resultados mostram como a abundância das presas e a limitação na abertura bucal interagem, influenciando os padrões de interação predador-presa.

Key words: Floodplain river, Food web, Optimal foraging theory, Predator-prey interaction, Venezuela.

Introduction

Predatory fishes affect prey diversity and abundance in aquatic ecosystems, and thus can influence community structure and ecosystem function (Zaret, 1980). Predator-prey interactions are determined by morphological constraints such as predator and prey body size (Paine, 1976) and gape limitation (Hambright, 1991), which affect the efficiency of prey capture (Gill, 2003) and handling time (Hoyle & Keast, 1987). As such, body size is an important predictor of the maximum potential prey size that a given predator can consume. For example, Mittelbach & Persson (1989) found that sizes of prey consumed by 34 freshwater piscivores were largely determined by differences in piscivore body size. Similarly, Hambright *et al.* (1991) found that largemouth bass,

Micropterus salmoides, never ingested prey that were greater than their mouth width, but did take prey that were as large as their own body depth. In general, a prey item can be captured and eaten if the prey/predator body size ratio is within a specific range, *i.e.*, the 'predation window' (Claessen *et al.*, 2002).

Environmental conditions are also primary determinants of predator-prey dynamics (Navarrete & Manzur, 2008), and can moderate the relative importance of body-size based mechanisms in determining prey selection (Jennings & Warr, 2003). In tropical floodplain rivers, a distinct seasonal hydrological cycle provides the context in which predator-prey dynamics are set (Jepsen *et al.*, 1997; Rodríguez & Lewis, 1997; Layman *et al.*, 2005). During high water, fish and other aquatic organisms are widely dispersed (Lowe-McConnell,

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1987). As water levels fall, prey densities increase, biotic interactions become more intense, and predation may drive many community-and-ecosystem-level processes (Layman & Winemiller, 2004). During the falling-water, piscivore feeding rates and growth may increase (Jepsen *et al.*, 1999) as prey are forced from the flooded forests and savannas into the main river channel. Changing water levels are also associated with spawning migrations of benthivorous prochilodontid fish, some of which provide important energy subsidies to predators in relatively nutrient-poor systems (Winemiller & Jepsen, 1998; Hoeninghaus *et al.*, 2006).

In this study, we examined dietary patterns of four piscivores, two belonging to the family Cichlidae (*Cichla temensis* and *C. orinocensis*) and two in the family Ctenoluciidae (*Boulengerella cuvieri* and *B. lucius*) in three Neotropical rivers that have a distinct wet-dry seasonal hydrology. We examined prey size in relation to predator gape width, and explored how gape limitations may mediate seasonal patterns of predator-prey dynamics

Materials and Methods

Study site

The study was conducted in three floodplain rivers with similar seasonal hydrology: Cinaruco, La Guardia, and Ventuari (Fig. 1). The Cinaruco and La Guardia rivers are moderate blackwater rivers within Venezuelan's Santo Lizardo National Park, in Apure State. Blackwater rivers in this region are characterized by low nutrient concentrations, low pH, sandy bottoms, and scattered floodplain lagoons (Montoya *et al.*, 2006). Fish diversity (>300 species) is high, and fishes display a wide range of ecological attributes and life history strategies (Layman *et al.*, 2005). These two rivers are characterized by a strongly seasonal hydrology with water levels typically fluctuating >5 m during an annual hydrological cycle (Arrington & Winemiller, 2006; Layman *et al.*, 2010). The Ventuari River is a tributary of the Orinoco River in Venezuela's Amazonas State characterized by clear water, low pH, and high fish diversity (> 400 fish species, Montaña *et al.*, 2005). In each river, during the wet season (May to October) the riparian forests and adjacent savannas are flooded and organisms are dispersed widely throughout the floodplain. Water begins receding during November, with lowest water levels occurring in February and March (Arrington & Winemiller, 2006; Winemiller *et al.*, 2006, Montaña & Winemiller, 2009). As water levels fall, aquatic organisms are forced into the main channels and associated littoral habitats, which exposes them to high risk of predation (Layman & Winemiller, 2004).

Piscivore species

Two species of large piscivorous cichlids in the order Perciformes (*Cichla temensis* Humboldt, 1821 and *Cichla orinocensis* Humboldt, 1821) and two species of large piscivorous pike characins in the order Characiformes (*Boulengerella cuvieri* Spix & Agassiz, 1829 and *B. lucius*

Cuvier, 1816) were examined. *Cichla* species have large, wide, gapes, and an elongate and laterally compressed body (Fig. 2). *Boulengerella* has an elongate body, elongated-narrow snout, and relatively small gape (Fig. 2).

Fish Sampling

For all three rivers, sampling was conducted in both lagoons and the main channel from October to May 2002-2005. Sampling included three important periods of the annual hydrological cycle: the descending limb (October-December), low water period (February-March) and ascending limb (April-May) (for more detail on this seasonal hydrology, see Arrington & Winemiller, 2006; Montoya *et al.* 2006, Winemiller *et al.*, 2006). Sampling effort and frequency were not equal among rivers and varied among years and months due to logistical considerations. *Cichla* and *Boulengerella* were collected with gill nets, cast nets, and by angling with artificial lures. Stomach contents of *Cichla* were removed by pressing down the posterior region of the tongue and pushing gently on the fish's stomach while holding the fish in a head-down position (Layman *et al.*, 2005). Specimens of *Boulengerella* were euthanized, preserved in 10% formalin, and transported to the laboratory at the Museo de Ciencias Naturales Guanare (MCNG) where the stomachs were removed for examination. Predator and prey fishes were measured to the nearest 1.0 mm standard length (SL). Stomach contents were identified to the lowest feasible taxonomic level and quantified volumetrically following Winemiller's (1990) method. Voucher specimens are archived in the Museo de Ciencias Naturales at UNELLEZ, Guanare, Venezuela, and the Texas Cooperative Wildlife Collection, College Station, Texas, USA (*Boulengerella cuvieri*: MCNG 3095, 3277, 9659, 13458, 17268, 17268, 20153, 30895, 31208, 34692, 38721, 39167, 39202, 39667, 39736, 41667, 43824, 43989, 44269, 44453, 45068, 47071, 52482, 53069, 54853, 54960, 54960, 55073, 55181 and *B. lucius*: MCNG 17966, 21790, 26502, 29497, 31007, 35406, 35492, 35835, 39688,

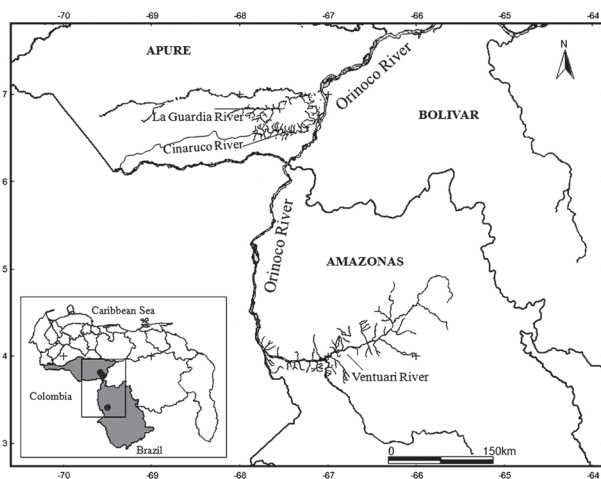


Fig. 1. Map of Venezuela showing the locations of the three tributaries of the Orinoco River considered in this study: La Guardia, Cinaruco, and Ventuari Rivers.

40942, 40956, 42376, 43432, 46291, 46544, 46614, 46955, 47160, 47176, 51610, 51689, 52477, 52481).

Gape width was measured in a subset of *Cichla* (*C. temensis* = 47 individuals, *C. orinocensis* = 37 individuals) and *Boulengerella* (*B. cuvieri* = 36 individuals, *B. lucius* = 35 individuals) with calipers to the nearest 0.1 mm. These data were used to create a regression between predator SL and gape width, which was then used to estimate gape sizes for additional field caught specimens based on their measured standard lengths.

Prey availability

To provide one example of potential seasonal patterns in prey availability (logistical constraints prevented us from sampling all systems), we surveyed fishes on 7 sandbanks in the main channel and along the shoreline of 8 lagoons in the Cinaruco River from November 2002 (start of falling water levels) to April 2003 (end of the dry season). For each collection, a seine (6.4 m x 1.8 m with 4 mm mesh) was oriented parallel to shore. The seine hauls were initiated from a depth up to ~1.5 m depth, and the haul was terminated at the shoreline. At each site, three non-overlapping seine hauls comprised a sample. All fishes were identified to species, enumerated, and measured to the nearest 1.0 mm SL. Fish sizes were used to construct a frequency histogram of prey

fishes collected in the main channel and lagoons.

Statistical analysis

Prey identified from stomach contents were used to examine seasonal patterns of prey-predator body size ratios. Univariate regressions were conducted with Sigma Stat (1997) to test for variability in prey/predator body sizes across hydrological seasons. One-way ANOVA was performed with SPSS 16.0 (2007) to test whether predators SL, predator's gape width and prey consumed SL differ significantly between genera. To examine prey fish composition in the littoral zone, we measured the body length (SL) of fish collected in lagoons and main channel. Samples were pooled according to habitat type for each month. Frequency histograms of prey fishes were performed and compared between hydrological seasons. Analysis of similarity (ANOSIM, Clarke & Warwick, 1994) was used to test for differences of fish composition in lagoons and main-channel sand banks for this data set.

Results

We analyzed 4,761 individual stomachs of *Cichla* and *Boulengerella*, and identified 8 orders, 24 families, 53 genera, and 73 species of prey fish (Appendix 1). The number of prey fish consumed varied between piscivore genera: 69 prey taxa were identified in stomachs of *Cichla* and 21 in *Boulengerella*. Characids (e.g., genera *Bryconops*, *Hemigrammus*, *Moenkhausia*), hemiodontids, and the prochilodontid *Semaprochilodus kneri* were the most common prey consumed by *Cichla*. *Semaprochilodus kneri* (a relatively deep bodied fish) was found only in *Cichla* stomachs, whereas small characids (< 40 mm) were the most common prey of *Boulengerella* (Appendix 1).

Predator standard length and gape width were strongly related (*C. temensis*: $\text{Gape} = 0.15\text{SL} - 1.01$ [$R^2 = 0.90$], *C.*



Fig. 2. Photographs of representative individuals of the focal species in this study (not preserved). From top: **a)** *Boulengerella cuvieri* (SL= 320 mm), **b)** *Boulengerella lucius* (SL= 420 mm), **c)** *Cichla temensis* (SL= 360 mm), **d)** *Cichla orinocensis* (SL= 305 mm).

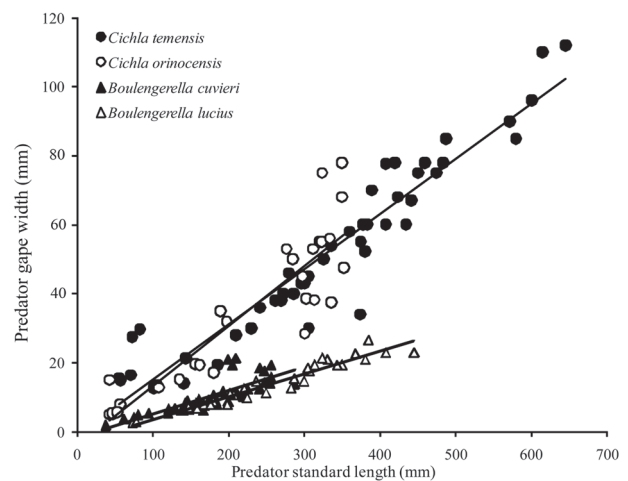


Fig. 3. Relationship between standard length and gape width for the four predator species.

orinocensis: Gape=0.17SL - 4.31 ($R^2=0.83$), *B. lucius*: Gape=0.06SL - 3.01 [$R^2=0.93$], and *B. cuvieri*: Gape=0.06SL - 1.70 [$R^2=0.65$]. Both *Cichla* species had a larger gape than *Boulengerella* species at a given standard length (ANOVA, $F_{3,154}=46.2$, $P=0.0001$; Fig. 3). Similarly, there were statistically significant differences in fishes of prey consumed by *Cichla* and *Boulengerella* ($F_{3,320}=16.09$, $P=0.0001$). *Cichla temensis* fed on larger prey (range 2-255 mm, mean \pm S.D., 60.6 \pm 40.6) than its congener *C. orinocensis* (1.5-125 mm, 38.7 \pm 29.6). *Boulengerella lucius* and *B. cuvieri* consumed smaller prey, ranging from 15-85 mm (30.6 \pm 15.1) in *B. lucius* and 3-95 mm (27.8 \pm 15.1) in *B. cuvieri* (Fig. 4).

Variation in prey-predator body size ratios was observed through the hydrological cycle. *Cichla* (*C. temensis*, $r^2=0.2$, $p<0.001$; *C. orinocensis*, $r^2=0.1$, $p<0.07$, Fig. 5). Ratios tended to be higher during the early falling water phase and lower during the low-water phase (Jan/Apr). Seasonal variation in

ratios was not significant for *Boulengerella* (for both species, $p>0.2$).

Monthly seine haul samples from the Cinaruco River yielded a total of 13,846 fishes of 58 species; the mean value of the largest 5% of fish (calculated across all species) tended to decline as the water level fell during the dry season. This trend was significant for lagoons ($F_{1,5}=17.0$, $P=0.015$, $r^2=0.81$) but not for the main channel ($F_{1,4}=2.6$, $P=0.20$, $r^2=0.46$) (Fig. 5). Assemblage composition in the main-channel differed significantly among months (ANOSIM, $R=0.29$, $P<0.001$). This difference was due to fewer individuals of relatively large species (e.g., *Bryconops* spp. and *Hemiodus* spp.) as water levels fell. Additionally, a few juvenile fishes appeared in samples just before the onset of the wet season (Apr/May). Lagoon assemblages were characterized by a similar, although non-significant, trend (ANOSIM, $R=0.02$, $P=0.37$).

Discussion

Piscivores examined in this study were found to consume phylogenetically and morphologically diverse fish taxa that reflect the overall diversity of fishes in these floodplain rivers. Even within individual piscivore species, prey varied broadly in terms of body size and other phenotypic traits, with body size likely a primary determinant of emergent trends. Based on gape width, there was a tendency for *Cichla* to consume a large size range of prey, including migratory hemiodontids and semaprochilodontids (Appendix 1) that are abundant during the falling-water cycle (Layman & Winemiller, 2005). In contrast, *Boulengerella* consumed primarily small-bodied characids throughout the seasonal cycle, likely because of gape constraints.

Seasonal shifts in prey availability appear to drive the seasonal decline in the size of prey consumed by *Cichla*. For example, larger prey were more abundant as waters began to fall (Fig. 5a), but they became less abundant through the dry season likely due to predator-induced mortality. Piscivores encounter large prey relatively less frequently during the low-water period, resulting in the seasonal shift in prey/predator body size ratios for *Cichla* species.

In South American rivers, the annual flood pulse is associated with fish migrations (Lowe-McConnell, 1987). During the falling-water period, large predators apparently increase foraging activities with preference for large prey, many of which are those migrating from the Orinoco River into tributaries (Winemiller & Jepsen, 1998). In the Cinaruco River, the diet of *Cichla temensis* contains about 50% *Semaprochilodus* (>40 mm SL) by volume during the falling water period (Jepsen *et al.*, 1997). Similarly, dietary and isotope analyses support the conclusion that *Cichla* species have greater body condition during the falling-water period (Hoeinghaus *et al.*, 2006).

Prey selection may arise through either active or passive processes (Turesson *et al.*, 2002). Predators that primarily feed on mobile prey may show little or no active choice among prey taxa (Juanes & Conover, 1994; Christensen, 1996; Scharf

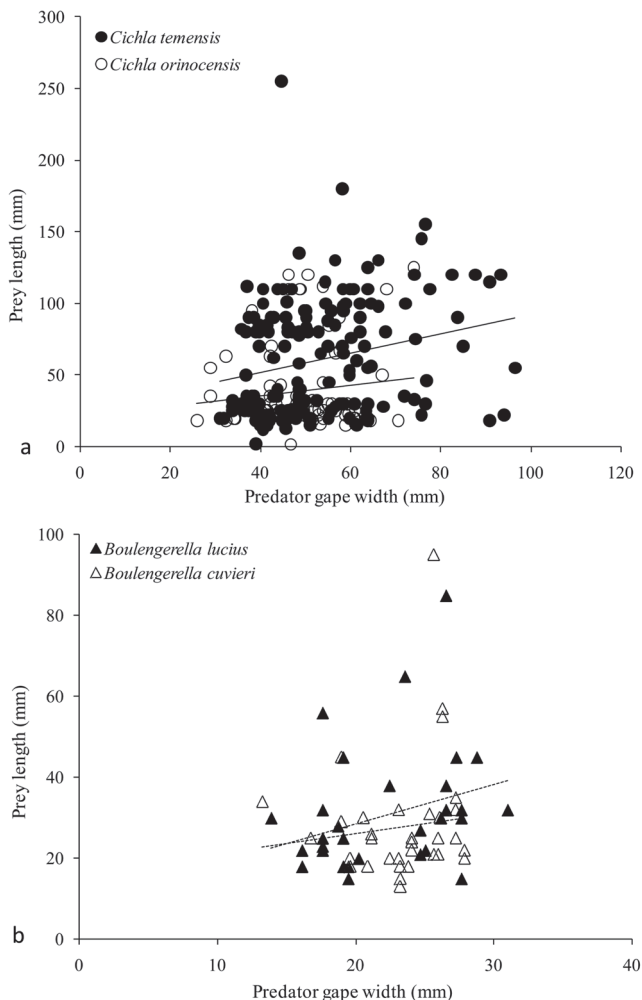


Fig. 4. Relationship between estimated predator gape width (from Fig. 3) and measured prey length size. Significant relationships are represented by solid lines and non-significant relationships with dotted lines. **a)** *C. temensis* and *C. orinocensis*; **b)** *B. lucius* and *B. cuvieri*.

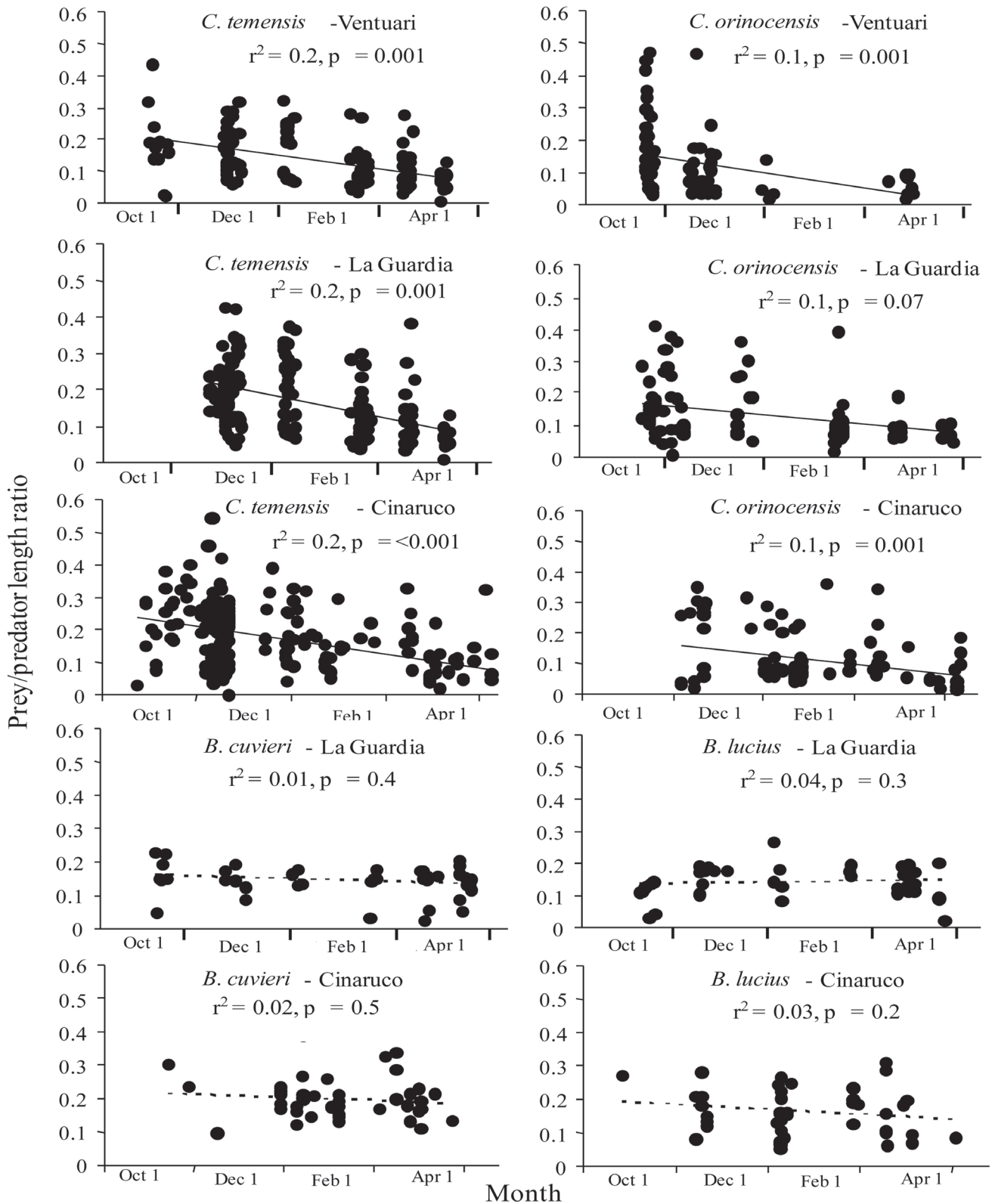


Fig. 5. Prey/predator body length ratios for four predator species. Relationships are presented from falling water (October) to rising water (May) period. Significant relationships are represented by a solid line and non-significant relationships with dotted lines. Number of stomach contents examined during the study period: Ventuari: *C. temensis* = 408, *C. orinocensis* = 698; Cinaruco: *C. temensis* = 1365, *C. orinocensis* = 755, *B. cuvieri* = 292, *B. lucius* = 411; La Guardia: *C. temensis* = 444, *C. orinocensis* = 228, *B. cuvieri* = 93, *B. lucius* = 67.

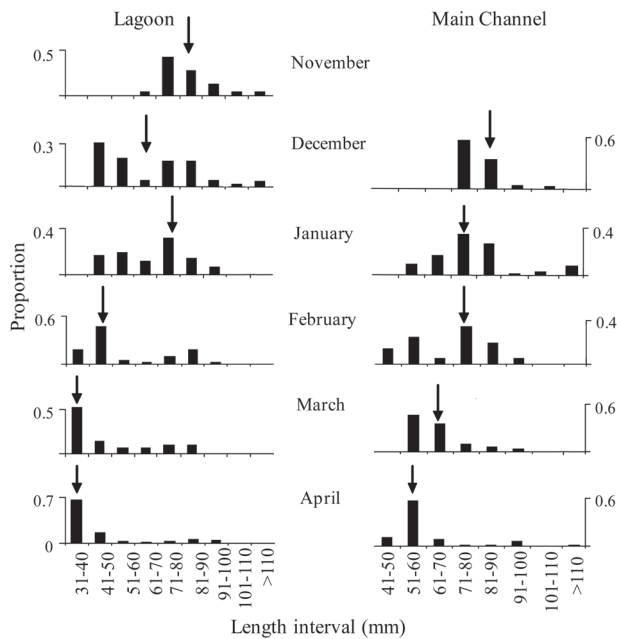


Fig. 6. Frequency histogram of the largest (SL) 5% of individuals collected each month in seine hauls. Larger individuals became increasingly rare from November to April as water levels fall. Arrows indicate the median size for each month.

et al., 1998), and thus prey selection may be driven largely by differences in prey encounter rates (partially a function of prey availability) and capture probabilities. The range of prey species consumed by piscivores in this study is consistent with the idea that prey selection is largely passive in this system, especially in periods when the large hemiodontids and migratory semiprochilodontids are not abundant.

Predation mortality is very high in tropical floodplain systems (Rodríguez & Lewis, 1997), and thus predators likely induce changes in the fish community (Jepsen *et al.*, 1997; Jepsen & Winemiller, 1999; Hoeninghaus *et al.*, 2006), which in turn results in a shift in predator-prey interactions (Winemiller, 1989; Gratwicke & Marshal, 2001). Although prey selection by piscivores is a function of many factors, including species-specific traits and spatial variability (*e.g.*, differential predator and prey densities in patchy habitats), there nonetheless are general patterns of predation that provide a foundation for predicting predator-prey dynamics in species-rich tropical food webs. Our study highlights the importance of size relationships between piscivores and their prey over a seasonal hydrological cycle, which may help to predict prey-predator interactions.

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Appendix 1. List of fish species indentified in the stomach contents of four focal species. Items are reported as percent (%) diet composition based on dietary volumetric proportions. Unidentified fish and crustaceans were excluded from family level quantification. Name abbreviations: *Cichla temensis* (*C.tem*), *Cichla orinocensis* (*C.orin*), *Boulengerella cuvieri* (*B.cuv*), and *Boulengerella lucius* (*B.luc*).

	Cinaruco				La Guardia				Ventuari			
	<i>C.tem</i>	<i>C.orin</i>	<i>B.cuv</i>	<i>B.luc</i>	<i>C.tem</i>	<i>C.orin</i>	<i>B.cuv</i>	<i>B.luc</i>	<i>C.tem</i>	<i>C.orin</i>	<i>B.cuv</i>	<i>B.luc</i>
Order Clupeiformes												
Family Clupeidae												
<i>Amazonsprattus scintilla</i>										0.5		
Family Engraulidae												
<i>Anchoviella</i> sp.	1.9	1.0	3.8	1.2	1.0		3.7		2.2	1.6		3.4
Order Characiformes												
Family Anostomidae												
<i>Anostomus anostomus</i>										0.5		
<i>Laemolyta taeniatus</i>	0.8		1.3			0.5						
<i>Leporinus</i> sp. A	0.4	0.5			0.5	0.5			0.6	0.5		1.1
<i>Leporinus</i> sp. B	1.1								0.5	1.8		1.1
<i>Pseudanos gracilis</i>	3.8	4.0			0.5							1.1
Family Characidae												
<i>Acestrorhynchus microlepis</i>	0.8				0.5				1.1			
<i>Acestrorhynchus minimus</i>	1.5	1.0		1.2	1.4				1.7	1.1	3.6	1.1
<i>Brycon falcatus</i>	0.8	0.5			1.4				1.1	1.1		
<i>Brycon pesu</i>	1.9	1.5							1.7	0.5		
<i>Bryconamericus</i> sp.		1.0	2.5			1.0			0.6	1.1	3.6	3.4
<i>Bryconops alburnoides</i>	1.5	0.5	2.5	2.3	1.4	1.0			1.7	1.6	1.8	2.3
<i>Bryconops caudomaculatus</i>	1.5	2.0			2.4	0.5	2.5	1.7	1.7	0.5		
<i>Bryconops giacopinii</i>	0.4				0.5				0.6	0.5		
<i>Chalceus macrolepidotus</i>		0.5			1.9		1.2					
<i>Creagrutus phasma</i>	1.5								1.1			
<i>Hemigrammus analis</i>	1.5	2.5	8.9	9.3	2.4	2.4	6.2	11.7	5.1	5.5	12.7	5.7
<i>Hemigrammus barrigonae</i>	0.4		1.3		0.5							
<i>Hemigrammus elegans</i>	1.1	3.0	7.6	7.0	1.9	5.3	12.3	23.3	1.1	1.6	5.5	3.4
<i>Hemigrammus micropterus</i>	0.8	2.0		1.2		3.4				1.1	1.8	1.1
<i>Hemigrammus rhodostomus</i>				1.2		1.9	2.5					
<i>Hemigrammus schmardae</i>	1.1	3.0	6.3	3.5	2.4	3.4			1.7	2.7	5.5	2.3
<i>Hemigrammus stictus</i>		0.5		1.2		1.4			0.0	0.5		2.3
<i>Hemigrammus vorderwinkleri</i>		1.5	12.7	10.5	4.8	5.3	3.7	5.0	5.6	9.3	10.9	10.2
<i>Hemigrammus</i> sp. A	3.4	10.0	13.9	9.3	1.9	4.8	1.2			1.1		
<i>Metynnys hypsauchen</i>	0.8				0.5					0.5		
<i>Microschemobrycon callops</i>	2.3	3.0		5.8	2.4	3.8	6.2	3.3		2.7	5.5	3.4
<i>Microschemobrycon casiquiare</i>	1.5	2.0	2.5	1.2	1.9	1.4	1.2	1.7	1.7	1.6	5.5	6.8
<i>Moenkhausia copei</i>	1.1	2.0	5.1	4.7	4.8	7.7	9.9	13.3	5.6	4.9	10.9	5.7
<i>Moenkhausia lepidura</i>	3.0	3.5	1.3	2.3	1.4	1.0	3.7	3.3	2.2	2.2	3.6	3.4
<i>Moenkhausia</i> sp. A	1.1	1.5	5.1	4.7	1.0	0.5	1.2			1.1	7.3	4.5
<i>Serrasalmus manueli</i>	0.8					0.5			0.6			
<i>Serrabrycon magoi</i>	1.1	1.0			1.0	1.4				1.1		
Family Crenuchidae												
<i>Characidium</i> sp. F	1.5	1.0	3.8	2.3	1.4	1.4	4.9	1.7	1.1	1.6	1.8	4.5
<i>Characidium</i> sp.	0.4	1.0			1.9	3.8	6.2	3.3	1.1	1.1		3.4
Family Chilodontidae												
<i>Caenotropus labyrinthicus</i>	1.5											
Family Curimatidae												
<i>Curimata incompta</i>	1.1	0.5		1.2		1.0				0.5		
<i>Cyphocharax oenas</i>	1.9	2.5	2.5	1.2		7.2	14.8	15.0	6.2	4.9	7.3	6.8
Family Erythrinidae												
<i>Hoplerythrinus unitaeniatus</i>					0.5	0.5				0.5		
<i>Hoplias malabaricus</i>	0.4				0.5				0.6			
Family Hemiodontidae												
<i>Argonectes longiceps</i>	1.5											
<i>Bivibranchia fowleri</i>	1.5	1.5	6.3	8.1					1.1	1.6		4.5
<i>Hemiodus gracilis</i>	1.9	1.0	6.3	9.3	5.7	6.3	4.9	3.3	5.6	2.7		
<i>Hemiodus immaculatus</i>	2.3	2.0			5.3	2.4			1.1	0.5		
<i>Hemiodus semitaeniatus</i>	0.8				2.4	1.0			1.1	0.5		
<i>Hemiodus unimaculatus</i>	1.5	1.5			12.0	2.9			3.9	2.2	1.8	1.1
Family Lebiasinidae												
<i>Copella metae</i>	0.4	1.0		1.2	1.0	1.0	1.2	3.3	1.7	4.4		
<i>Nannostomus unifasciatus</i>	0.4	0.5	2.5	2.3	1.0	1.4			1.7	3.3		
<i>Pyrrhulina lugubris</i>	0.8									0.5		3.4
Family Prochilodontidae												
<i>Semaprochilodus kneri</i>	11.3	12.5			12.0	7.7			11.2	6.6		

Appendix 1 (cont.). List of fish species identified in the stomach contents of four focal species. Items are reported as percent (%) diet composition based on dietary volumetric proportions. Unidentified fish and crustaceans were excluded from family level quantification. Name abbreviations: *Cichla temensis* (*C.tem*), *Cichla orinocensis* (*C.orin*), *Boulengerella cuvieri* (*B.cuv*), and *Boulengerella lucius* (*B.luc*).

	Cinaruco				La Guardia				Ventuari			
	<i>C.tem</i>	<i>C.orin</i>	<i>B.cuv</i>	<i>B.luc</i>	<i>C.tem</i>	<i>C.orin</i>	<i>B.cuv</i>	<i>B.luc</i>	<i>C.tem</i>	<i>C.orin</i>	<i>B.cuv</i>	<i>B.luc</i>
Order Gymnotiformes												
Family Rhamphichthyidae												
<i>Gymnorhamphichthys rondoni</i>	1.5	0.5			1.0				2.2	1.1		
Family Sternopygidae												
<i>Eigenmannia virescens</i>	1.1	0.5		1.2	0.5	0.5			3.4	2.2		
Order Siluriformes												
Family Auchenipteridae												
<i>Centromochlus concolor</i>	1.1			2.3		0.5						
Family Cetopsidae												
<i>Pseudocetopsis</i> sp.	0.4					0.5				0.5		
Family Doradidae												
<i>Leptodoras</i> sp.	0.8											
<i>Scorpiodoras heckelii</i>	1.9	3.0			1.0	1.0			1.1	0.5		
Family Loricariidae												
Unidentified Loricariidae	1.1	2.0							1.1	1.6		
Family Heptapteridae												
<i>Imparfinis</i> sp.	1.5	1.0			1.9	1.4	2.5	1.7		0.5	1.8	1.1
<i>Pimelodella</i> sp.	2.3	2.0							0.6	0.5		1.1
Family Pseudopimelodidae												
<i>Microglanis iheringi</i>	0.8								0.6	0.5		
Family Trichomycteridae												
<i>Ochmacanthus alternus</i>	0.8	1.0				0.5				0.5		
Order Beloniformes												
Family Belonidae												
<i>Belonion</i> sp.	0.8									0.5		
Order Synbranchiformes												
Family Synbranchidae												
<i>Synbranchus marmoratus</i>	0.4	0.5			0.5	0.5			0.6	1.1		
Order Perciformes												
Family Cichlidae												
<i>Apistogramma</i> sp.	1.1	2.5	2.5	1.2	2.4	2.9	3.7	5.0	1.7	2.7		4.5
<i>Biotoecus dicentrarchus</i>						1.0			1.1	0.5		2.3
<i>Biotodoma wavrini</i>	1.5	3.0	1.3	1.2	1.9	1.4	1.2		1.7	1.1	3.6	2.3
<i>Crenicichla</i> aff. <i>wallacii</i>	1.9	1.5			2.9	2.4	3.7	3.3	2.8	2.2		
<i>Cichla</i> sp. (juveniles)	3.8	3.5			2.9	1.4			3.4	1.6		
<i>Dicrossus filamentosus</i>	1.9				1.9				2.2	1.1		
<i>Geophagus</i> sp. (juveniles)	7.5	6.0		2.3	1.4	1.4			3.4	2.7	3.6	2.3
<i>Mesonauta insignis</i>	1.5					0.5				0.5		
Family Eleotridae												
<i>Microphilypnus ternetzi</i>							1.2					