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Original Article

Trophic relationships among three species of ornamental fish from the region of Lake Amanã, Amazon

Relações tróficas entre três espécies de peixes ornamentais da região do lago de Amanã, Amazonas

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Abstract

The present study objectified to evaluate the trophic relationships and the possible aggressive mimicry involving *Carnegiella strigata*, *Carnegiella marthae* and *Gnathocharax steindachneri*, in lowland forest streams. Samplings occurred in November 2002, March and August 2003 in Amanã Sustainable Development Reserve (ASDR). The total of 943 fish was caught, being 79.43% of *C. marthae,* 3.18% of *C. strigata* and 17.39% of *G. steindachneri*. Stomach contents, degree of stomach repletion, relative volume and frequency of occurrence of food items were evaluated. Thirteen food items were identified, and the presence of terrestrial and aquatic insects indicates the high dependence of these species and the flooded forest. Low feeding overlap was observed between *Carnegiella strigata* and *C. marthae* compared to *Gnathocharax steindachneri*. However, the overlap between the two *Carnegiella* species was relatively high, which could explain the low frequency of syntopic occurrence among these species, suggesting a possible case of competitive exclusion.

Keywords: food, freshwater fish, mimic, diet.

Resumo

Este estudo teve como objetivo analisar as relações tróficas e a possível existência de uma relação de mimetismo agressivo envolvendo *Carnegiella strigata*, *Carnegiella marthae* e *Gnathocharax steindachneri*, em igarapés de terra firme. As coletas ocorreram em novembro de 2002, março e agosto de 2003 e foram realizadas na Reserva de Desenvolvimento Sustentável de Amanã (RDSA). Foram capturados 943 peixes, onde *C. marthae* representou 79,43%, *C. strigata* 3,18% e *G. steindachneri* 17,39%. Foram analisados os conteúdos estomacais e verificados grau de repleção, volume relativo e frequência de ocorrência dos alimentos. Foram identificados 13 itens alimentares, onde insetos terrestres e aquáticos denotaram alto grau de dependência destas espécies em relação à floresta alagada. Ocorreu baixa sobreposição alimentar das espécies *Carnegiella strigata* e *C. marthae* em relação a *Gnathocharax steindachneri*. Entretanto, a sobreposição entre as duas espécies de *Carnegiella* foi relativamente alta, o que poderia explicar a baixa frequência de ocorrência sintópica entre essas espécies, sugerindo um possível caso de exclusão competitiva.

Palavras-chave: alimentação, peixe de água doce, mímico, dieta.

1. Introduction

In the Amazon ichthyofauna, the species of the Gasteropelecidae family, *Carnegiella strigata* (Günther, 1864) and *Carnegiella marthae* (Myers, 1927), which are popularly known as butterfly fish, stand out due to the distinctive body shape and are normally commercialized as ornamental (Anjos et al., 2009; Ladislau et al., 2019). This species abundant especially in flooded areas in rivers of dark and white water of Amazon, including lowland forest streams of Central Amazon (Barros et al., 2011; Queiroz et al., 2013). They have as main characteristics, the small body (are small) and the narrow ventral region and an expanded, fan-shaped pectoral waist, consisting of fused and expanded coracoids, pectoral fin elongated and positioned to the top and the side. Such modifications allow small jumps above the water surface (Wiest, 1995; Weitzman and Palmer, 1996). The geographic distribution of *C. marthae* comprises Venezuela and Brazil and *C. strigata*

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naturally occurs in Colombia, Guyana, Peru, Surinam and Brazil (Weitzman and Palmer, 2003).

Another species that is confused and also traded with butterfly fish is the species *Gnathocharax steindachneri* (Fowler, 1913) from Characidae family, with occurrence restricted to northern South America including Brazil, Guyana and Venezuela, also occurs in lowland forest streams and in rivers of white water (Barros et al., 2011; Queiroz et al., 2013) and dark water (Montag et al., 2008). This species presents morphological characteristics similar to the species of the genus *Carnegiella*, with expanded pectoral waist and long pectoral fins, although not as modified as in butterfly fish (Weitzman and Palmer, 1996). *G. steindachneri* are found and captured together the shoals of *Carnegiella* spp and are usually erroneously sold as butterfly fish in the national and international market of ornamental fish due to their morphological similarities.

The morphological similarity between the species described, besides the fact they are usually found and collected together, indicate that the association of these species should not be fortuitous, but may be related to the occupation of similar trophic niches. The top mouth of *Carnegiella* spp. and the powerful pectoral fins should probably provide fast and efficient capture of feed that fall on the water surface, from the riparian forest (Sabino and Zuanon, 1998) and can be associated to a non-piscivorous diet, while *G. steindachneri* have upward largemouth used to prey insects on the water surface (Queiroz et al., 2013).

Study by Pereira et al., (2011) reported the possibility of protective mimicry involving species of the genus *Haemulon* with similar morphology forming a single shoal, and this grouping has a protective function. However, Sazima et al., (2005) reported an aggressive mimicry between two species (*Cephalopholis fulva* and *Chromis multilineata*) with similarly sized and coloured that associated is able to approach unaware prey which made the disguise successful.

The reasons that generate associations among fish species study are unknown, but may represent factors such as interspecific feeding associations, partial sharing of habitats (Pacheco and da Silva, 2009) and trophic relationships (Novakowski et al., 2007; Oliveira et al., 2020), however it is common fish species presenting similar feeding behavior and living in the same space, however, these usually have different foraging methods, suggesting that behavioral differences are essential to species coexistence (Mise et al., 2013). However, aggressive interactions are common among fish of the same guild and individuals of each species can obtain advantages in feed efficiency over other individuals from other species of the same trophic guild (Menegatti et al., 2003).

The studied species are economically important a ornamental species, being collected for the subsistence of riverside dwellers in the region of the middle Rio Negro (Chao, 1998, 2001; Ladislau et al., 2019), and are representative (1-4%) in the collections of these piabeiros. The morphological similarity between *Gnathocharax* and *Carnegiella*, associated with the fact that they are observed and collected together in nature, indicates that the association of these species should not be casual, but associated with the occupation of similar trophic niches or intraspecific interactions. According to the principle of competitive exclusion, two populations of different species living sympathetically cannot occupy exactly the same ecological niche (Zaret and Rand, 1971; Giacomini, 2007). Under these conditions, and in the presence of a limiting resource, there may be an overlap of niches and one of the populations will be excluded or ecologically displaced (Zaret and Rand, 1971).

In fish communities, from the ecological point of view and from the knowledge that a species feeds, we can obtain information on the trophic relationships that are established in the aquatic ecosystem, including the biological mechanisms of intra and interspecific interactions (Hérran, 1988). However, there is no scientific information detailing aspects of ecology, food and reproductive biology of the species described in this article. Thus, this article aimed to analyze the diets of the species and analyze their possible trophic relationships in nature.

2. Material and Methods

Samplings were accomplished in the Amanã Sustainable Development Reserve (ASDR) located between the black water of Negro river and white water of the rivers Japurá and Solimões .Three streams were selected, two with black water (Baré: 02º 17'S and 64º 40'W and Juá Grande: 02º 29'S and 64º 48' W); and one with white water (Kalafate: 02º 37'S and 64º 34'W). Two samplings were carried out one in November 2002 (dry season) and the other in August 2003 (rainy season). Specimens were collected through standardized experimental fishing using hand nets and small trawl nets, in streams with free, shallow environments, in small meanders arranged along the streams' path and along the marginal flooded vegetation (Mendonça et al., 2005).

The collected material was fixed in a solution of 10% formalin and stored in plastic bags. After washing in running water, the samples were transferred to flasks with 70% ethanol and stored. For data analysis we used relationships among species only sampling events were considered, where at least two of the three species were captured together, i.e. caught in the same fishing equipment in the same location, date and time.

2.1. Diet composition

To determine the composition of the diets, the selected specimens were measured (standard length-SL, millimeters-mm) opened through an incision in the ventral region and the digestive tracts were removed and stored in 70% alcohol. Thereafter, each stomach was dissected and examined under a stereomicroscope, and the food items were sorted and identified to the most precise taxonomic level possible, following the recommendations of McCafferty (1981), Borror et al. (1981), and Merrit and Cummins (1996).

The degree of stomach repletion of each specimen was evaluated in a proportional scale: 1. Empty (0%); 2. Little full (25%); 3. Frequent (50%); 4. Full (75%);

5. Distended (100%) (Yabe and Bennemann, 1994). Relative volume (RV) (defined as the percentage in volume of each item in relation to the total food in the stomach) was calculated for each type of food identified and due to small size of the stomachs of the fish, we used petri dishes for the indirect estimation, with the items estimated by visual evaluation, generating comparison with blocks of known volumes (Larimore, 1957; Teixeira and Gurgel, 2002).

Moreover, the frequency of occurrence (FO%) of ingested items was calculated): FO%= 100 x Fi/n, where: Fi is the number of stomachs containing a particular prey taxon; n is the total number of stomachs with any prey.

2.2. Feeding strategies

The results of both methods were combined in the Feeding Index (IAi, Kawakami and Vazzoler, 1980), expressed as a percentage. This index assesses the degree of importance of each food item in the fish diet, where: = IAi = feeding index; i = 1,2, ... n = particular food item; Fi=FO% of item *i;* and Vi%= volume of item *i.* According to the expression: IAi = Fi x Vi (Σni=1(Fi x Vi))$^{-1}$. Feeding strategies of the species were evaluated using the graphic method of Costello (1990), modified by Amundsen et al. (1996), that infers about feeding ecology through the estimate of the specific abundance of the prey (Pi) and its frequency of occurrence, according to the expression Pi = (Si/Sti) X 100, where Si = number of stomach containing the prey *i*; Sti = total number of stomachs in which the prey *i* occurs.

2.3. Similarity of diets

Similarity between the diets of *Carnegiella marthae*, *C. strigata* and *Gnathocharax steindachneri* was calculated using the simplified index of Morisita-Horn (Krebs, 1998), applied to combinations of pairs of species (*C. marthae* and *C. strigata*; *C. marthae* and *G. steindachneri*; *C. strigata* and *G. steindachneri*). This index uses the frequency of occurrence of the items ingested by each species. Uses a scale from 0 (zero), indicating absence of the use of the same source (absence of similarity diets) to 1 (one) indicating complete similarity of diets. According to the expression: CH=2ΣniPijPik (ΣniP^{2}ij+ΣniP^{2}ik)$^{-1}$, where CH = Simplified Index of overlap between species j and species k; Pij= proportion of the food i in the total food of the species j; Pik = proportion of food i in total food of the species k; n = total number of food (i: 1,2,3,4, ..., n).

3. Results

A total number of 943 specimens was caught, being 79.4% of *C. marthae* (749), collected only in black water. *C. strigata* represented 3.2% (30 specimens) and *G. steindachneri* 17.4% (164 specimens), collected in both environments, with black and white water. The pattern of occurrence in the region showed the occurrence of the three species in the Baré stream (black water). In Juá Grande (black water) only *C. marthae* and *G. steindachneri* were found. In Kalafate stream (white water) *C. strigata* and *G. steindachneri* were present.

The pattern of occurrence revealed that in the Baré stream (black waters) the three species investigated in the present study occurred. In the Juá Grande stream (black waters), only the species *C. marthae* and *G. steindachneri* occurred. In the Kalafate stream, which has clear waters, the species *C. strigata* and *G. steindachneri* occurred. The co-occurrence of *G. steindachneri* and *C. marthae*, and *C. marthae* and *C. strigata* was restricted to the black water environment (Baré stream). The occurrences of the species *C. strigata* and *G. steindachneri* together, were restricted to environments of clear water (igarapé Kalafate).

In the Baré stream the co-occurrence of *C. marthae* and *C. strigata* was observed with 81 specimens caught in the same sample event, at the 3:1 proportion, respectively. For *C. marthae* and *G. steindachneri* the proportion observed was 5:1. In Kalafate, the proportion of *C. strigata* and *G. steindachneri* was approximately 1:1 and narrow co-occurrence (i.e., in the same sampling event) was not observed between the species in Juá Grande.

3.1. Diet composition

Of the total species captured, only 92 stomachs of the three species were evaluated (32 of *C. marthae*, 30 of *C. strigata* and 30 of *G. steindachneri*) for meeting the criteria for the analysis of co-occurrence patterns (species captured in the same equipment) fishing, location, date and time). Regarding empty stomach, *C. marthae* presented 68% (22), *C. strigata* 41% (13) and *G. steindachneri* 3% (one stomach). Considering the degree of repletion, only *C. strigata* presented one specimen with full stomach and another with distended stomach.

Thirteen types food items were found in the diet of the three evaluated species, mainly insects as Collembola, Homoptera (nymphs), Lepidoptera (larvae), Ephemenoptera (nymphs), Hemiptera (Gerridae: nymphs + adults), Diptera (larvae + adults); Chironomide (larvae); Chaoboridae (larvae), Coleoptera (adult). Fragments of insects and plants were found in the stomach contents, but the precise identification was not possible due to the advanced stage of digestion. Food items were grouped into the categories of order or family (Table 1).

Seven food items were found in the stomachs of *C. marthae*, in the same frequency: Ephemenoptera (nymph), Diptera (adult + larva), Chironomidae (larva), Coleoptera (adult), fish scales. In the stomachs of *C. strigata* eight food items were verified, plant fragments in higher frequency (31%), followed by Coleoptera (27%) and adult Hymenoptera (16%), this constituted by several species of ants. The most important food items were Coleoptera (46%) and Hymenoptera (adult) 25%. Although plant fragments occurred at a higher frequency, its feeding importance was very low (Table 1). *G. steindachneri* ingested 11 food items (Table 1). The mostly frequent food items were Gerridae (nymph + adult) accounting for 28% and presenting feeding importance of 48%, followed by Chaoboridae with frequency of occurrence of 20% and feeding importance 31%.

Table 1. Frequency of occurrence (FO%), relative volume (RV), feed rate (IAi) and the specific abundance of prey (AE), expressed as percentages of food items found in the stomachs of studied species (n = number of stomachs with food, L = larva, N = nymph, A = adult).

Food Items	*C. marthae* (n=10)				*C. strigata* (n=19)				*G. steindachneri* (n=29)			
	FO%	RV%	IAi%	AE%	FO%	RV%	IAi%	AE%	FO%	RV%	IAi%	AE%
Collembola									2.0	1.0	1.0	1.0
Homoptera (N)									2.0	2.0	1.0	1.0
Lepidoptera (L)					4.0	2.0	1.0	6.0	2.0	2.0	1.0	1.0
Ephemeroptera (N)	11.0	10.0	8.0	10.0	4.0	14.0	9.0	6.0				
Hemiptera												
Gerridae (N + A)					4.0	4.0	1.0	3.0	28.0	26.0	48.0	30.0
Hymenoptera (A)					16.0	21.0	25.0	29.0	9.0	8.0	5.0	4.0
Diptera (L + A)	11.0	10.0	17.0	10.0					8.0	11.0	3.0	4.0
Chironomidade (L)	11.0	10.0	8.0	10.0	4.0	4.0	1.0	3.0				
Chaoboridae (L)									20.0	24.0	31.0	43.0
Coleoptera (A)	11.0	10.0	17.0	10.0	27.0	22.0	46.0	26.0	4.0	5.0	1.0	2.0
Fish scales	11.0	10.0	8.0	20.0					9.0	3.0	2.0	5.0
Insects fragments	22.0	30.0	25.0	20.0	4.0	30.0	9.0	23.0	11.0	13.0	4.0	5.0
Planto of fragments	22.0	20.0	17.0	20.0	31.0	4.0	8.0	3.0	4.0	4.0	3.0	2.0

3.2. Feeding strategies

The feeding strategies of the species are presented in Figure 1A, B and C. Small amounts of some food items were observed in stomachs of *C. marthae*, i.e. low specific abundance, and a high rate of empty stomachs. Based on frequency and abundance of the ingested food items, the population of *C. marthae* presented a generalist feeding strategy, with the points representing preys (food items) distributed in the lower left corner of the graph (Figure 1A). The *C. strigata* population presented a generalist feeding strategy, similar to C. *marthae* with low values of occurrence frequency and specific abundance of preys, but with presence of Hymenoptera, Coleoptera and fragments of insects (Figure 1B). *G. steindachneri* also showed a generalist feeding strategy, with most of the prey points in the lower left corner of the graph (Figure 1C). However, a greater importance of two of the food items was observed, Chaoboridae (L) and Gerridae (L + A).

3.3. Similarity of diets

Diet similarity was calculated for each species. The pairs *Carnegiella strigata* and *G. steindachneri*; *Carnegiella marthae* and *G. steindachneri* presented different diets with CH= 0.34 indicating low similarity in feeding behavior. *C. strigata* and *C. marthae* showed a much higher similarity index, CH = 0.61.

4. Discussion

The *C. marthae*, *C. strigata* and *G. steindachneri* feed basically on both terrestrial and aquatic insects. Thus, insects are an important food source for fish populations, especially in the streams of Amazon.

4.1. Feeding strategies

We can infer that these studied species are predominantly insectivorous generalists, that is, they belong to the same trophic guild, and still describe that the morphological adaptations of the collected species enabling efficient catches of insects and other items that fall into the surface of streams, resulting in a generalist or opportunistic feeding diet (Abelha et al., 2001). The differences observed in the structure of mouth and teeth of the species indicate the possibility of different origins for insect fragments in the stomach contents (Abelha et al., 2001). On the other hand, cuspidate teeth are efficient for mastication and processing of preys (Langler et al., 1977), which may have generated the fragments of insects found in the stomachs. In contrast, the big mouth and conical teeth of *G. steindachneri*, usually found in predatory fish (Bemvenuti and Fischer, 2010), could explain the low proportion of fragments of insects in the composition of its diet.

Only one food item was found per stomach of *C. marthae*, which can indicate a specialized feeding strategy (Abelha et al., 2001). According to the studies of Amundsen et al. (1996) and Bolnick et al. (2003), when the population presents different individuals specialized in different food sources, possibly it presents a high inter-individual phenotypic component (IPC), indicating some individual specialization for the food strategy. The *C. marthae* and *G. steindachneri* presented up to three types of food items per stomach, indicating a more opportunistic feeding strategy. This indicates a population with a high intra-individual phenotypic component (IFC), that is, most of the individuals use several types of resources simultaneously (Amundsen et al., 1996; Bolnick et al., 2003).

Some fish scales were found in stomachs of *C. strigata* and *G. steindachneri*, which may have four possible origins

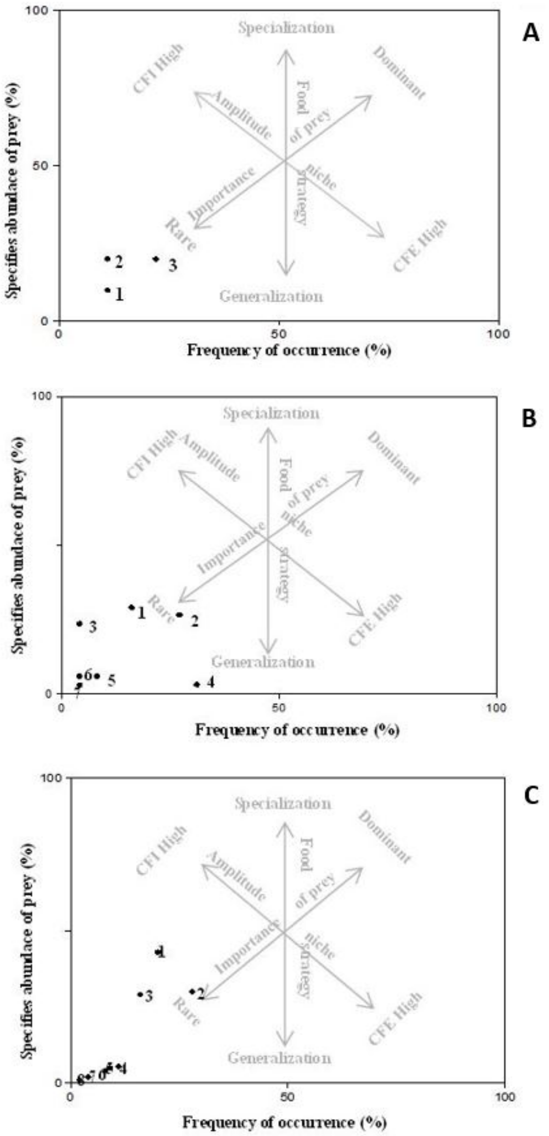

Figure 1. (A) Feed Strategy *Carnegiella marthae*. (1) Ephemenoptera (N), Diptera (L + A), Chironomidae (L) and Coleoptera (A); (2) Scales of fish; (3) Fragments of plants and insects. Points over an item indicates that they are overlapped; (B) Feed Strategy *Carnegiella strigata*. (1) Hymenoptera (A); (2) Coleoptera (A); (3) insect fragments; (4) fragments of plants; (5) Ephemenoptera (N); (6) Lepidoptera (L); (7) Chironomidae (L) and Gerridae (A + L). The points-arrested over an item indicates that they are overlapping; (C) Feed Strategy *Gnathocharax steindachneri.* (1) Chaoboridae (A); (2) Gerridae (N + A); (3) Hymenoptera (A); (4) fragments of insects; (5) fish scales; (6) Diptera (larvae + adults); (7) Coleoptera (A) and vegetable fragments; (8) Collembola, Homoptera (L) and Lepidoptera (L). Points over an item indicates that they are overlapped.

(excluding the possibility of contamination of the samples at the time of removal of the digestive tract for analysis): 1) the scales could be intentionally detached from fish of other species, characterizing a lepidophage behavior; 2) the scales could have been removed from conspecifics during agonistic encounters; 3) the scales could have been obtained on the environment from various sources; and 4) the scales could be the remains of the digestion of small fish consumed by *C. marthae* and *C. strigata.* The most possible hypothesis is that these scales could have been taken of the environment as they were ingested in small amounts and have very low importance in the diet of the species. Furthermore, these species have no obvious morphological adaptations for lepidophagy, and there are no known published records of aggressive agonistic behavior. Finally, this item should not have been derived from digestion of whole fish, because no fish remains were observed in the stomachs of specimens analyzed (such as bones, muscles).

In the present study, the similarity of diets does not mean complete overlap of trophic niches, probably due to the great diversity of insects available in the environment. Specialized techniques of food capture, for example, can cause segregation of niches and allow the coexistence of the species (Peroni and Hernández, 2011; Chivambo et al., 2019). On the other hand, Motta (1989) reported that teeth morphology and some characteristics of the skull anatomy can indicate a feeding specialization based on the efficiency of exploitation of certain types of food. This author, studying butterfly fish (Chaetodontidae, Perciformes) verified that relatively simple morphological changes in some points of head structure resulted in a diversity of feeding strategies among species. Values of indexes of similarity between *C. strigata* and *G. steindachneri* and between *C. marthae* and *G. steindachneri* indicate that was no overlap occurred among these species, which can be due to the high diversity of potential preys available in the Amazon environment, particularly for fish species with opportunistic feeding strategy. A similarity value was observed for *C. marthae* and *C. strigata*, indicating that these species could be competing for food.

The Gerridae and Chaoboridae showed a feeding importance in the diet of *G. steindachneri*, but not for the other two species of *Carnegiella* sp. The high ingestion of insects of the Gerridae family, which live in the water surface of streams, showed the possibility of occurrence of a different form of aggressive mimicry. The gerrids are lurking hunters that feed on carrion and mainly on terrestrial insects that fall on the surface of the streams (Andersen, 1979) and may potentially compete for food with butterfly fish of the genus *Carnegiella*. Preys that fall in the water surface or remain drifting would be shared by gerrids and butterfly fish, a situation where the morphological adaptations of these fish would be important (powerful fins, mouth facing upwards). It is possible that individuals of *G. steindachneri* take advantage in situations of competition for food between gerrids and butterfly fish in the water surface, and eventually collected together. In this sense, the superficial similarity of form and habits between *G. steindachneri* and *Carnegiella* spp. would be sufficient to ensure the effectiveness of the aggressive mimicry involving these species.

The apparent association observed among these species in nature may also represent a case of numerical mimicry, since it is possible to assume the existence of a lower individual risk of death by predation for fish that aggregate in shoals. According to the studies of Keenleyside (1979) and Milinski (1993), fish are easier detected by a predator when dispersed (Bozza and Hahn, 2010). Machado (2003), studying fish of the Pantanal, reported the occurrence of numerical mimicry and described that mimic in a multispecies shoal integrates with the largest number of individuals of other species, thereby reducing the risk of predation. In the present study, the occurrence of numerical mimicry may be more probable between *G. steindachneri* and *C. marthae*, compared to *C. strigata*.

5. Conclusion

According to the results, we can affirm that the species presented insectivorous eating habits, characterizing dependence in relation to the resources coming from the flooded forest. These species presented a generalist feeding strategy, that is, a wide range of the trophic niche.

Regarding the individual food strategy, only C. Marthae showed a tendency towards specialization, whereas C. Strigata and G. Steindachneri demonstrated a generalist individual food strategy, that is, food based on the opportunistic consumption of items available in the environment.

There was low food overlap between Carnegiella species over Gnathocharax steindachneri, however, among Carnegiellas, the overlap was suggestible which may explain the low frequency of syntopic occurrence between them (possible case of competitive exclusion).

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