

Nymphal feeding habits of two *Anacroneuria* species (Plecoptera, Perlidae) from Sierra Nevada de Santa Marta, Colombia

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ABSTRACT

The knowledge of the diet of aquatic insects is important to assess the use of resources and overlap of trophic niche between species, as well as to understand their role in the food web of the freshwater ecosystems they inhabit. This is particularly necessary in tropical areas where information on this topic is scarce. The aim of the present work is to describe the feeding habits of the species *Anacroneuria marta* Zúñiga & Stark, 2002 and *A. caraca* Stark, 1995 in the middle section of the Río Gaira (Sierra Nevada de Santa Marta, Colombia). We sampled nymphs on three dates during the rainy and dry seasons in two major different microhabitats of the reach (leaf accumulations and gravel) in 2014. The nymphal diet of a total of 87 and 90 individuals of *A. caraca* and *A. marta*, respectively, was studied. With this information, niche breadth for each species and niche overlap between them in terms of trophic resources were calculated. The major trophic resource for both species in the dry and rainy season was the invertebrate animal matter. In the dry season, fine particulate organic matter was also important in the diet of *A. caraca*, and *A. marta* ingested a large quantity of coarse particulate organic matter in the rainy season. Larvae of Trichoptera were the most ingested prey in both species, followed by larvae of Chironomidae, Coleoptera Hydrophilidae, and nymphs of Ephemeroptera. No differences in diet between both species were detected, so this could favor niche overlap in terms of trophic resources and could lead to competition between them. The possible ecological scenarios are discussed.

INTRODUCTION

Stoneflies (Plecoptera) are important ecological components of fluvial biotas where they develop significant and diversified trophic roles (Stewart and Stark, 2002; Fochetti and Tierno de Figueroa, 2008; Stewart, 2009). In relation with this, it is outstanding the relatively few studies focused on this topic existing in South America, especially if we consider the great richness of species of this group of insects that it has (Stark *et al.*, 2009; Froehlich, 2010).

The Perlidae is the most diverse family among

stoneflies, both at a global scale and in South America (Fochetti and Tierno de Figueroa, 2008). They are considered as mainly predator from the functional feeding group point of view (Merritt and Cummins, 2006) and this is supported by many studies of various taxa from the Palearctic, Nearctic regions and, to a lesser concern, the Neotropical region (compiled, among others, in Hynes, 1976; Stewart and Stark, 2002; Monakov, 2003; Stark *et al.*, 2009). Nevertheless, as reported in most of these studies, it is known diets change with age or instars (being more detritivorous when younger and smaller). Moreover, differences in diet among coexistent species of this family have been reported, not only in relation to the ingested food but also in their digestive enzymatic capacity (López-Rodríguez *et al.*, 2012).

The genus *Anacroneuria* Klapálek, 1909, with 348 valid described species (plus other 20 taxa with informal designations and 27 considered as *nomen dubia*) and distributed from the South America (Argentina and Uruguay) to southwestern United States, is the most diverse stonefly genus in the Neotropics (Froehlich, 2010; DeWalt *et al.*, 2018). Although it can be found also in other habitats, species of this genus are more typically found at moderate elevations throughout the Andes and in many subtropical, large lowland rivers (Stark *et al.*, 2009). In Colombia, 61 species of *Anacroneuria* have been reported (Zúñiga *et al.*, 2013; Rúa García *et al.*, 2015).

The feeding habits of *Anacroneuria* nymphs in Central and South America have been studied in some localities, but data are usually reported only to the genus level and

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available information is generally scarce (most not published but reported in unpublished thesis). In a work at community level in southeastern Brazil, Oliveira and Froehlich (1997) studied the feeding habits of Ephemeroptera, Plecoptera and Trichoptera, but perlids (including *Anacroneuria*), considered as predators, were not analyzed. Fenoglio (2003) studying gut content of *Anacroneuria* nymphs from Central America found that this genus was a predator, feeding mainly on larval Diptera and nymphs of Ephemeroptera and even on other *Anacroneuria*, but diet was only detritus in smaller nymphs. Tomanova *et al.* (2006) studying the gut content of aquatic macroinvertebrates from rivers in the foothills of the Bolivian Andes pointed out that the diet of *Anacroneuria* was composed mainly of other macroinvertebrates, followed by microphytes, and fine particulate organic matter as well as some other minor food items. Gamboa *et al.* (2009) studied the nymphal feeding habits of four *Anacroneuria* species from Venezuela and found that the most consumed prey were mayflies of the family Baetidae followed by dipteran larvae of Simuliidae and Chironomidae. These authors also analyzed the diet breadth, which was different for the studied species and applying an electivity index they found that they had different choices; however, that diets were similar (Gamboa *et al.*, 2009). In a study on the macroinvertebrate feeding in Molino River (La Guajira, northern Colombia), Granados-Martínez *et al.* (2016) found that the diet of *Anacroneuria* was composed mainly by animal tissues (more than 85%) and fine particulate organic matter, while Villada-Bedolla *et al.* (2017) reported similar results in the Colombian Andean streams, where animal tissues was the dominant resource ingested by *Anacroneuria* nymphs followed by detritus and fine particulate organic matter and, to a considerable lesser concern, other items as coarse particulate organic matter and fungi.

Particularly, in the Río Gaira (Sierra Nevada de Santa Marta, Colombia), Tamaris-Turizo *et al.* (2007) studied the diet of different morphospecies of *Anacroneuria*. Diet differences were not found among them and, although nymphs were mainly predators (feeding on Ephemeroptera and Diptera, particularly Chironomidae and Simuliidae, but also on leaves, detritus, fungi and algae), differences in feeding habits were found between younger nymphs and mature ones. Afterwards, Guzmán-Soto and Tamaris-Turizo (2014) in a more general article on the feeding habits of nymphs of Ephemeroptera and Plecoptera, and of larvae of Trichoptera also from Río Gaira, found that in the studied individuals of *Anacroneuria*, animal matter was the main component of the diet, followed by coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM) and, to a lesser concern, other minor items. Sierra-Labastidas *et*

al. (2017) reported similar results for this genus in the same river.

Although there is previous information about the feeding of this genus in the study area (see references above), the aim of our study is to provide an analysis at the species level that allows us to detect possible differences as well as the niche breadth for each species and the niche overlap between them. Particularly, in the present study we focused on two *Anacroneuria* species inhabiting the Río Gaira: *Anacroneuria marta* Zúñiga & Stark, 2002, endemic to Colombia, and *A. caraca* Stark, 1995, distributed in Venezuela, Colombia, and Ecuador (Zúñiga *et al.*, 2007). Additionally, the possible ontogenetic changes in nymphal feeding of both species are investigated, not only comparing big and small nymphs, but also analyzing diet shift as a continuum that allows us to statistically evaluate gradual changes. Finally, the possible influence of season (rainy period vs dry period) on the diet is also evaluated. All the obtained results are compared with that previously known for the *Anacroneuria* in Colombia and all the Neotropics.

METHODS

Samplings were carried out in the middle part of the Río Gaira, Magdalena Department, in the Hacienda La Victoria, Sierra Nevada de Santa Marta, northern Colombia. Sierra Nevada de Santa Marta is a mountain system with a total area of 10464.3 ha, located between 11°52'56" - 11°10'08" N, 74°46'22" - 74°01'07" W, with a total length of 32.53 km (Frayter *et al.*, 2000). The sampling station, Hacienda La Victoria (Sector Honduras), was at 900 m asl, coordinates 11°07'44.2" N, 74°05'35.8" W (Fig. 1). The basin is characterized by fast and low flows with different microhabitats and different biotas associated to them. In the section of the basin, coffee plantations are abundant (near of 300 ha); however, the riparian forest is in apparently good ecological conditions. The riparian vegetation included trees with canopy greater than 15 m, the most common taxa being *Ficus* spp., *Guarea guidonia* Sleumer 1956, *Zygia longifolia* Britton & Rose, 1928, *Myrsine costaricensis* Lundell, 1985, *Clusia* sp., which provided significant shade over the river. A more complete description of the study area can be found in Tamaris-Turizo *et al.* (2018).

In Río Gaira, a 100 m reach was sampled. With the objective to represent both climatic period, we sampled three times during the rainy season (2014 July, August and October) and three times during the dry season (2015 January, March and May). Two different microhabitats, leaf accumulations and gravel, were sampled. Six replicates in each microhabitat were taken on each sampling date. In leaf accumulations, approximately 500 g of leaves were collected manually for each sample. In

gravels, a Surber with 0.09 m² surface and 250 µm mesh size was employed. Collected macroinvertebrates were preserved in ethanol 96% and transported to the laboratory in plastic jars where individuals of *Anacroneria* were sorted and posteriorly identified. All nymphs considered for this study could be identified with reliability as *A. marta* Zúñiga & Stark, 2002 and *A. caraca* Stark, 1995. Nymphs of both species were associated previously to the adults and illustrated (Zúñiga *et al.*, 2007 for *A. marta*, Stark, 1995 for *A. caraca*). Moreover, some mature nymphs were additionally identified comparing its genitalia.

For the dietary analysis, we identified the gut contents of a minimum of twenty individuals of each species from each season (dry and rainy). Total length of each individual was measured with a software ZEN (V. 2.1, Zeiss) of the Axiocam ERc5s camera adjusted to a CARL ZEISS stereomicroscope Discovery V8, with the objective to study the correlation between nymphal size and feeding habits. For the study of the contents of the alimentary canal, we followed the methodology employed in studies of the Perlidae nymphal feeding (Bo *et al.*, 2008; López-Rodríguez *et al.*, 2012; Rúa *et al.*, 2014; Tierno de Figueroa *et al.*, 2015). For small nymphs, the gut contents were analyzed following the transparency method proposed by Bello and Cabrera (1999), *i.e.*, each

nymph was placed in a vial with Herwitsgs' liquid for 24 h at 65°C, and afterwards, cleared individuals were placed in Herwitsgs' liquid on a glass slide with a cover slip. For large individuals, guts were dissected and placed in Herwitsgs' liquid on a glass slide with a cover slip, and afterwards analyzed. As previously observed, no differences resulted using both methods (Bo *et al.*, 2008). In both cases, food items were identified under a ZEISS Primo Star microscope. Also the microscope equipped with an ocular micrometer was employed for estimating the percentage absolute gut content (at 40x as % total area occupied by the contents in the digestive tract) and the relative abundances of food items in the gut content (at 400x as % area occupied by each component of the total gut contents). Five food categories were initially considered: FPOM, CPOM, algae (ALG), fungi (FUN), animal matter (AM, when possible, identified at order, family or subfamily level), and non-identified animal matter (NIAM).

Mean, standard deviation, minimum and maximum were calculated for each species in each season. A Spearman correlation was carried out between the total length of the nymphs of each species and their gut contents. To compare the diet of each species in each season, a permutational multivariate analysis of variance (PERMANOVA) with Bray-Curtis distance matrices was



Fig. 1. Río Gaira basin showing the study area, La Victoria estate - Sector Honduras, Sierra Nevada de Santa Marta, Colombia.

used applying 9999 permutations. This analysis was done using the `adonis2` function from the `vegan` package in R (Oksanen *et al.*, 2018; R Core Team, 2018). Finally, a study of the trophic niche was performed calculating the niche breadth with the standardized Levins index and the niche overlap with the simplified Morisita index (Krebs, 1999).

RESULTS

A total of 87 individuals of *A. caraca* and 90 of *A. marta* were examined, of which 52 and 57 individuals, respectively, had some gut contents. The main trophic resource of *A. caraca*, both in the dry and rainy season, was the animal matter (Tab. 1). In the dry season, FPOM was also important in the diet, though in the rainy season, CPOM was the second more important resource. In the case of *A. marta*, a similar pattern was detected: it fed mainly on prey in both seasons and also ingested a great quantity of CPOM in the rainy season. Of the prey that could be identified in the gut of the studied nymphs in each season, larvae of Trichoptera were the most ingested (Tab. 1). Overall, Chironomidae were also frequent in the diet of both species; except in the diet of *A. caraca* during the dry season in which Coleoptera, Hydrophilidae, and nymphs of Ephemeroptera were more abundant.

The nymphal size of both species ranged from 1.5 to 13.5 mm in *A. caraca* and from 1.5 to 14.1 mm in *A. marta*. Only positive correlation was found between the size of *A. caraca* and the quantity of Chironomidae in the gut (Spearman $r=0.43$, $P<0.05$), while for *A. marta*, a positive correlation was found between size and non-identified animal matter (Spearman $r=0.44$, $P<0.05$) and a negative correlation, although only marginally

significant, between size and Trichoptera in the gut (Spearman $r=-0.27$, $P<0.05$).

The PERMANOVA analysis only showed significant effect of the season on the diet, but with a very low R^2 ($F_{1,105}=4.719$, $R^2=0.04$, $P<0.05$). No differences were detected between both species neither an interactive effect of the season and the species factors.

The niche breadth calculated with the standardized Levins index was reduced in the four studied cases (both species in both seasons: 0.325 for *A. caraca* in the dry season, 0.368 for *A. caraca* in the rainy season, 0.344 for *A. marta* in the dry season and 0.375 for *A. marta* in the rainy season). On the other hand, the simplified Morisita index showed a great niche overlap between both species in the dry and in the rainy season (0.942 and 0.976, respectively).

DISCUSSION

According with the obtained results, the studied nymphs of both species seem to be omnivores behaving almost equally as predators than as detritivores, feeding in this last case both on FPOM and CPOM. Part of the large amount of non-animal resources found in their guts could come from the prey gut contents as have been reported previously in other typically predator stoneflies (López-Rodríguez *et al.*, 2009), though this would not explain such a high content of these resources in the studied guts. This omnivorous character has been previously noted by other authors as a common feature of most Neotropical freshwater macroinvertebrate taxa (Tomanova *et al.*, 2006), though the nymphs of *Anacroneria* have been classified as mainly predators (Oliveira and Froehlich,

Tab. 1. Gut contents of nymphs of *A. caraca* and *A. marta* in each season.

	<i>Anacroneria caraca</i>										<i>Anacroneria marta</i>									
	Dry					Rainy					Dry					Rainy				
	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
FPOM	20	32.7	36.2	0.0	100.0	32	20.3	22.9	0.0	95.0	27	20.3	29.2	0.0	100.0	30	12.9	10.7	0.0	43.0
CPOM	20	8.0	10.3	0.0	30.0	32	28.1	22.1	0.0	79.9	27	14.7	15.5	0.0	50.0	30	29.0	21.4	0.0	74.8
Fungi	20	0.0	0.0	0.0	0.1	32	0.3	0.7	0.0	4.0	27	0.7	2.9	0.0	15.0	30	1.4	2.7	0.0	10.0
Algae	20	1.2	3.0	0.0	10.0	32	1.6	3.2	0.0	15.0	27	6.8	19.1	0.0	90.0	30	4.6	12.1	0.0	60.0
NIAM	20	43.0	41.0	0.0	100.0	32	37.3	26.6	0.0	100.0	27	40.6	37.3	0.0	90.0	30	33.5	29.4	0.0	99.0
Leptophlebiidae	20	0.0	0.0	0.0	0.0	32	0.0	0.0	0.0	0.0	27	0.1	0.6	0.0	3.2	30	0.0	0.0	0.0	0.0
Other Ephemeroptera	20	4.1	18.1	0.0	81.0	32	0.0	0.0	0.0	0.0	27	0.0	0.0	0.0	0.0	30	0.0	0.0	0.0	0.0
Coleoptera	20	5.0	22.4	0.0	100.0	32	0.0	0.0	0.0	0.0	27	0.0	0.0	0.0	0.0	30	0.4	2.3	0.0	12.8
Trichoptera	20	5.0	22.4	0.0	100.0	32	3.6	17.7	0.0	100.0	27	9.0	24.1	0.0	100.0	30	9.4	26.5	0.0	100.0
Tanypodinae	20	0.0	0.0	0.0	0.0	32	0.0	0.0	0.0	0.0	27	2.1	7.6	0.0	30.0	30	0.6	2.1	0.0	10.5
Other Chironomidae	20	1.1	3.3	0.0	12.0	32	4.2	9.2	0.0	32.0	27	5.5	20.4	0.0	100.0	30	6.3	9.1	0.0	40.0
Simuliidae	20	0.0	0.0	0.0	0.0	32	1.6	5.7	0.0	28.5	27	0.1	0.6	0.0	3.2	30	2.0	6.7	0.0	35.6

FPOM, fine particulate organic matter; CPOM, coarse particulate organic matter; NIAM, not identified animal matter.

1997; Fenoglio, 2003; Gamboa *et al.*, 2009; Guzmán-Soto and Tamaris-Turizo, 2014; Granados-Martínez *et al.*, 2016; Vidalla-Bedolla *et al.*, 2017). Most of the prey found in the gut of the studied nymphs could not be identified at a taxonomic level lower than order due to occurrence of only small fragments, but exceptions are the mayfly family Leptophlebiidae and the midge Tanypodinae. The latter are usually predators, so the ingestion of these larvae by *A. marta* indicates that this species is in the medium to top trophic levels of the macroinvertebrate food web, though probably does not act as a top predator given the size of their nymphs (Tamaris-Turizo *et al.*, 2018). In many other species of predaceous stoneflies, an ontogenetic shift in diet has been detected (Stewart and Stark, 2002; López-Rodríguez *et al.*, 2009), with smaller nymphs feeding more on detritus and algae, and bigger nymphs on prey, and even changes in the size of prey that those nymphs ingest have been recorded. In fact, a previous study carried out also in the Río Gaira on the feeding habits of *Anacroneturia* sp. detected variations in the items consumed by young and mature nymphs (Tamaris-Turizo *et al.*, 2007). In our study, only a slight positive correlation was found between the size of the nymphs of *A. caraca* and the quantity of Chironomidae non-Tanypodinae in their guts, indicating that bigger nymphs ingest more larvae of these organisms. In contrast, larger *A. marta* nymphs, fed less on Trichoptera and had more NIAM in their guts. The first fact is curious, as Trichoptera are, generally large prey, difficult to ingest, but a relatively large number of caddisflies has also been recorded as prey in other Perlidae species (Bo *et al.*, 2008), even case-building taxa. In our study, some remains of Trichoptera were larvae of the genus *Smicridea* (Hydropsychidae), which are net-spinning, not case-building, caddisflies. The second fact, a correlation between nymphal size and NIAM is probably an artifact of the data, as in this category are included many different taxa that we could not identify and separate as different categories of prey. Nonetheless, the abundance of NIAM in general in both species also points out that these nymphs chew their prey, opposite to many other perlid species that act as engulfers and use to swallow their prey almost intact or part of them (Sheldon, 1969; Wallace and Webster, 1996; Merritt and Cummins, 2006). In relation to this, handling time in predator stoneflies appears to increase with prey size due to limitations of the predator for swallowing large prey (Peckarsky, 1982) and the difficulty of subduing them (Molles and Pietruszka, 1987).

The analysis to detect differences in diet between both species and between both seasons, only found a significant effect for the season, what could indicate that between the dry and the rainy seasons the availability of trophic resources change importantly. Similar results were reported in the Río Gaira in three sections of the basin along an altitudinal gradient during two seasons (Tamaris-Turizo *et*

al., 2018). However, changes in the food composition of stonefly nymphs across seasons have been previously reported and those differences often depend on the species environment in a particular period (Monakov, 2003). Nevertheless, in our study this conclusion should be taken with caution as the R^2 of 0.04 makes this result meaningless. The absence of differences in diet between both species (coinciding with that found by Tamaris-Turizo *et al.* in 2007 for different morphospecies of *Anacroneturia* in the high part of the Río Gaira), combined with their reduced niche breadth, favors the niche overlap in terms of trophic resources, and so could lead to competition between them.

These results support previous analyses carried out on four *Anacroneturia* species from Venezuela (Gamboa *et al.*, 2009), in which the authors found also a high overlap in the diet of the studied species. Although interspecific competition depends on many factors (such as the previous existence of intraspecific competition, the limitation of resources, *etc.*) a great niche overlap, as the one detected in this study, is a first step to it. Particularly in stable or homogenous environments (mainly in terms of temperature), such as those present in some parts of the tropics, populations of organisms that are under favorable conditions can reach their carrying capacity, leading the intraspecific competition necessary for further interspecific competition (Begon *et al.*, 2006). In relation to this, the Río Gaira is in apparently satisfactory environmental condition (principally by the riparian vegetation and substrata heterogeneous), so this should result in constant input of CPOM of allochthonous source in the system during dry and rainy seasons (Collantes *et al.*, 2014). Besides, the rectangular form of the basin permit that during the rainy season the discharge on the principal streambed is fast and the current velocity returns speedily to the “normal conditions” that favors the repopulation to the communities of aquatic insects. Thus, these punctual, high flow events, would not probably affect greatly to the populations of the studied species of *Anacroneturia* (Tamaris-Turizo *et al.*, 2007). In this framework, it is possible that both species are in an imminent competition process, if the shared trophic resources would be limiting, but further observational and experimental studies are required to confirm this hypothesis.

CONCLUSIONS

In conclusion, this study shows the great overlap in diet of the two *Anacroneturia* species studied by us. Considering their reduced trophic niche breadth and their high trophic niche overlap, a competitive interaction among them would be probable, but this would only occur if their populations would have reached their carrying capacity and the shared trophic resources are limiting, what does not seem to be the case in the Río Gaira.

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