

Environmental correlates of diet in the swordtail characin (*Corynopoma riisei*, gill)

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Abstract In the sexually dimorphic swordtail characin (*Corynopoma riisei*, Gill), males are equipped with an opercular flag-ornament that has been suggested to function as a food-mimic since females bite at the ornament during courtship. However, virtually nothing is known about the diet in wild populations of this species. In this study, we first investigated composition of and variation in the diet of *C. riisei* across 18 different populations in Trinidad, using gut content analyses. We then related variation in gut content to habitat features of populations to investigate the potential link between environmental conditions and prey utilization. Our results showed that the dominating food type in the gut was various terrestrial invertebrates, both adults and larvae, but we also document substantial variation in prey types across populations. Furthermore, a canonical correlation analysis revealed a relationship between environmental characteristics and diet: populations from wider and more rapidly flowing streams with more canopy cover tended to have a diet based more on ants and mosquitoes while populations from narrow and slow flowing streams with little canopy cover tended to have a diet based more on springtails, mites and mayfly larvae. Our results add novel

information on the ecology of this interesting fish and suggest the possibility of local adaptation reflecting differences in prey availability across natural populations.

Keywords Sexual dimorphism · Gut content · Sensory exploitation · Sensory drive · Local adaptation · Habitat

Introduction

Fishes show large variation in feeding habits both between and within species (Helfman et al. 2009) and local adaptation to different food types has been suggested to be an important generator of diversity in this group. For instance, niche separation according to different food sources is considered an important factor behind the adaptive radiation of the East African cichlids (Clabaut et al. 2007; Gonzalez-Voyer et al. 2009). Ecological factors, for instance canopy coverage and stream velocity, can have strong effect on prey type availability in fish populations (Dussault and Kramer 1981; Grether et al. 2001). Therefore, identification and quantification of ecological factors and their relationships to food availability is an important step towards understanding the evolutionary mechanisms behind local adaptations and population diversity (Coyne and Orr 2004).

The swordtail characin (*Corynopoma riisei*) is a member of the large family of tetras (Characidae: subfamily Glandulocaudinae), and is endemic to

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rivers and streams in Trinidad and northern Venezuela (Weitzman and Menezes 1998). This species displays a remarkable and unique form of sexual dimorphism: males carry an opercular flag-shaped ornament on each side, which is normally held inconspicuously close to the body (Nelson 1964). Fertilization is internal in this subfamily and the male erects and displays this opercular flag during courtship in front of the female who bites at it prior to actual mating (Nelson 1964; Amcoff et al. 2009). Due to this peculiar behavior, Wickler (1968) hypothesized that the opercular flag is mimicking the natural prey of the female swordtail characin, which he believed to be aquatic invertebrates such as *Daphnia* or other “water fleas” (see Wickler 1968). If this ornament indeed is a functional food-mimick, this would support a mechanism of ‘sensory exploitation’. Under such a scenario, the opercular flag has evolved to exploit female tendencies to be attracted to objects that look like prey items (Arnqvist and Rowe 2005; Amcoff and Kolm in review). However, data on the actual diet of females across natural populations is clearly needed to shed light on whether there is scope for this ornament to have evolved as a mimick of *Daphnia* or some other food item in the natural diet of females.

Wickler’s (1968) hypothesis regarding the natural prey of *C. riisei* is concordant with a more recent general description of the Trinidadian tetras by Kenny (1995), which suggests they are “omnivorous or macrophagous, surface, mid-water or bottom feeders”. To date, however, there is unfortunately no detailed published information on the feeding ecology or diet of *C. riisei* and it is not known whether there is variation in available prey types or in food utilization across populations. In the present study, our aim was to investigate variation both in gut content of female *C. riisei* and in ecological variables (stream width, water depth, current velocity, level of canopy cover and water turbidity) across 18 natural populations in Trinidad. We then tested for a relationship between food types and environmental factors to investigate the potential for local adaptation to certain food types in this species.

Materials and methods

In May, 2005, we collected samples of *C. riisei* from 18 different populations in 8 drainages (Fig. 1,

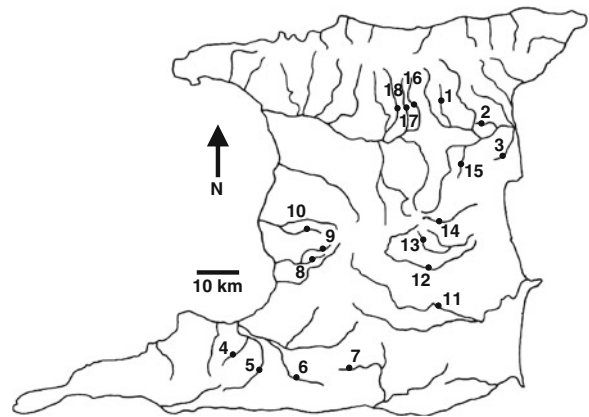


Fig. 1 Map over the major rivers and streams on Trinidad (after Kenny 1995). Filled and numbered circles represent the locations of the 18 populations sampled

Table 1) across the entire distribution of the species in Trinidad (Kenny 1995). Specimens were caught using a two-person push seine. Since *C. riisei* does not occur in mountain streams (Kenny 1995), the sites were located in the lowland or foothills and were chosen to represent a range of different habitat types. We aimed at collecting 10 sexually mature females at each site (note that for two populations we only managed to collect 9 females making the total sample $n=178$). Whole fish were immediately preserved in 95% alcohol for subsequent analyses of gut content. At each site, we also collected the following environmental variables: mean stream width, mean water depth, current velocity, the amount of canopy cover and water turbidity. Stream width and stream depth was measured in meters and the other variables were quantified independently by two observers, using a ranking system (Table 1).

The stomach content of 178 females from the 18 populations was carefully inspected under a stereo microscope, and all food/prey items were identified with appropriate taxonomic resolution (i.e. to the level of class, order, suborder or family) and counted. The diet was then analyzed using data on the numerical proportion of each prey type in each gut.

Statistical analyses

Due to the multitude of prey types recorded (i.e., variables), we used a combination of principal component analysis and canonical correlation analysis to maximize the power of the analyses while limiting

Table 1 Variation in environmental variables across populations. Current velocity was ranked on a scale from 1–3, canopy cover was ranked on a scale from 0–2 and turbidity was deemed either clear (0) or turbid (1)

Population: river	Width (m)	Depth (m)	Current velocity	Canopy cover	Turbidity
1: Turure River	8.0	0.5	3	2	0
2: Tributary of Oropuche River	1.5	1.0	1	0	1
3: Caigual River	2.0	1.0	2	1	1
4: Tributary of Cunapo River	1.5	1.0	2	2	1
5: Coora River	2.0	0.5	3	1	1
6: Curamata River	4.0	2.0	1	0	1
7: Tributary of Inniss River	1.5	0.5	1	0	1
8: Guaracara River	2.0	1.0	2	2	1
9: Tributary of Guaracara River	2.5	0.3	2	1	0
10: Savonetta River	1.5	0.5	1	2	0
11: Poole River	8.0	2.0	2	1	1
12: Navet River	2.0	0.3	2	1	1
13: Tributary of Bois Neuf River	1.5	0.3	2	0	0
14: Canque of Nariva River	4.0	2.0	2	1	0
15: Sangre Grande River	2.0	1.0	2	1	0
16: Aripo River	4.0	1.0	2	1	0
17: El Mano River	2.5	1.0	2	1	0
18: Guanapo River	3.0	1.5	2	1	0

the number of inferential tests performed (Quinn and Keough 2002). Firstly, we present descriptive data both on proportions of all food types from the gut-content analysis and on only the items that made up >1% of the diet across populations. We also tested for variation in food composition across populations using Manova with all food items that made up >1% of the diet as dependent variables and population as our factor. Secondly, for the analysis of covariation between mean diet and ecological variables across populations, it was necessary to first reduce both the environmental variables and the gut-content data (mean per population) using principal component analyses. For ecological variables, we retained the first two principal components, which were the only factors with eigenvalues larger than one (Jackson 1993). Together, these two factors accounted for 64% of the total variation in the environmental variables across populations. The loadings (i.e., the correlations with the original variables) were as follows (loadings on PC1 and PC2 within brackets): mean stream width (0.62, 0.67), mean water depth (−0.03, 0.92), current velocity (0.81, −0.15), canopy cover (0.72, −0.21) and water turbidity (−0.46, 0.22). This means that positive

values on PC1 describes shallow, fast flowing, clear streams with substantial canopy cover while PC2 describes broad, deep, slow flowing, more turbid streams with less canopy cover. For diet, we retained the first six principal components from a PCA based on the covariance matrix, which together accounted for >95% of the variation in gut contents (see Table 2 for the loadings of these principal components on the original variables). In the final step of the analysis, we used canonical correlation analyses to test for a relationship between the two principal components of the ecological variables and the five principal components describing variation in diet. All analyses were run using Statistica 8.0 (StatSoft, Inc 2008).

Results

Each stomach contained on average 13.1 (SE=0.9) distinct food items. Our data thus provides a reasonably rich foundation for a description of the diet of *C. riisei*. We found in total 41 different food types in the gut content across populations (see Table 3). When we only considered food types that

Table 2 Correlations (factor loadings) between principal components of gut content (proportional data on the 15 most common items) and the original variables. Correlations >0.6 are highlighted in bold

Variable	PC1	PC2	PC3	PC4	PC5	PC6
<i>Trichoptera (larvae)</i>	-0.19	0.19	-0.35	0.20	-0.36	-0.40
<i>Ephemeroptera (larvae)</i>	0.04	0.10	-0.14	-0.23	-0.76	-0.43
<i>Nematocera (larvae)</i>	-0.32	-0.81	0.47	0.03	0.10	-0.08
<i>Nematocera (pupae)</i>	-0.40	-0.24	-0.35	-0.19	0.43	-0.23
<i>Coleoptera (larvae)</i>	-0.55	-0.30	-0.32	0.11	-0.06	0.42
<i>Fish eggs</i>	0.17	-0.16	0.10	0.04	-0.50	0.02
<i>Acari</i>	-0.65	-0.02	0.01	0.14	-0.02	0.57
<i>Collembola</i>	-0.65	-0.04	-0.67	0.29	0.16	-0.13
<i>Formicidae</i>	0.99	-0.03	-0.03	0.08	0.05	-0.01
<i>Hymenoptera</i>	-0.06	0.15	-0.14	-0.01	-0.27	0.09
<i>Nematocera (adults)</i>	-0.33	0.65	0.61	0.29	0.08	-0.06
<i>Homoptera</i>	0.11	-0.10	-0.17	-0.09	0.04	0.17
<i>Heteroptera</i>	-0.05	0.13	-0.29	-0.58	0.19	0.05
<i>Coleoptera (adults)</i>	-0.04	0.47	-0.00	-0.76	0.41	-0.09
<i>Plant seeds</i>	0.11	0.15	0.07	-0.38	-0.50	-0.27

made up >1% of the average proportion of gut content across populations, 15 remained. Out of these, Formicidae (ants) strongly dominated the gut content (>45%, Table 3) while Nematoceran larvae (a Dipteran suborder, including mosquitoes and midges), Coleoptera (beetles) and Collembola (springtails) all contributed with >5% of the average gut content across populations (Table 3). Other invertebrates and their juvenile life stages (e.g., aquatic larvae and pupae), but also unidentified plant seeds and fish eggs, made up the remainder of the diet among these 15 most common food types (Table 3). We found substantial variation in food composition across populations (Fig. 2) (Manova, Wilk's $\lambda=0.003$, $p<0.001$). Out of the invertebrates found in the gut, terrestrial invertebrates dominated the diet (mean% of gut content (\pm SE): terrestrial groups: 77% (± 0.03); aquatic groups: 23% (± 0.03); t -test of the null hypothesis of a mean proportion of 50%: $t=8.7$, $n=18$, $p<0.0001$).

The sampled populations displayed substantial variation in environmental features, ranging from turbid, slow flowing, and narrow streams with little canopy cover to clear, fast flowing, and wide streams with a well developed canopy cover (Table 1; Fig. 3). As shown in the ordination plot of the relationship between PC1 and PC2 of the environmental variables (Fig. 3), there was some grouping of populations into three clusters along

PC1 but a more continuous variation among populations along PC2. Based on the factor loadings, populations 2, 6 and 7 were from slow flowing, narrow streams with little canopy cover while population 1 were from a rapid flowing, wide stream with plenty of canopy cover. The remaining majority of populations were all relatively intermediate in terms of PC1 but more variable in PC2 (the latter being related primarily to stream depth).

The canonical correlation analysis between the set of six principal components of gut content variation and the two principal components of environmental variation showed a significant correlation between food types and environment across populations (canonical $r=0.90$, $\chi^2=24.7$, $d.f.=12$, $p=0.016$). This relationship was caused by the first pair (i.e. the first root) of canonical variables since its removal produced a non-significant model (canonical correlation with first pair of canonical variables removed: canonical $r=0.54$, $\chi^2=4.4$, $d.f.=5$, $p=0.50$). Inspection of the canonical loadings on this first pair of canonical variables revealed that this pattern of covariation was mainly the result of females from rapid flowing, wide streams with more canopy cover having a diet more dominated by Formicidae (ants) and adult Nematocera (mosquitos and midges) but with relatively few Acari (mites), Collembola (springtails) and Ephemeroptera larvae (mayflies). Hence, females from wider streams with stronger currents

Table 3 Diet composition and the environmental origin of food items (aquatic or terrestrial) across the surveyed 18 populations

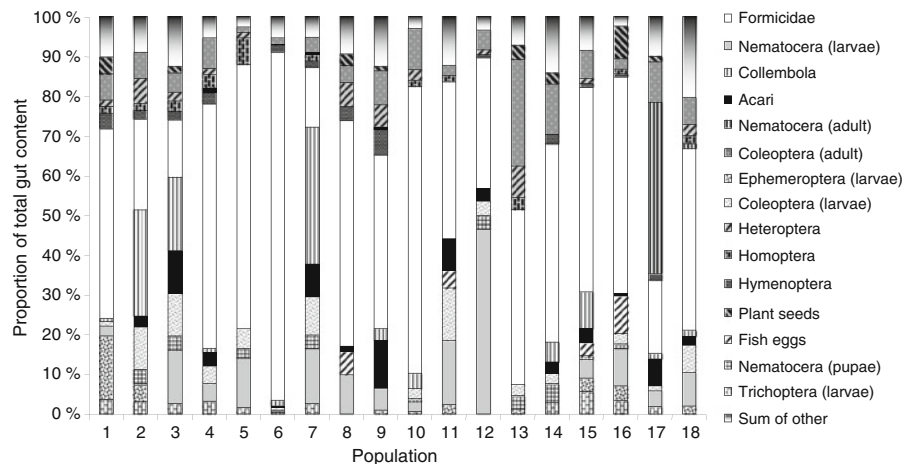
Food type	Average proportion (%)	Environmental origin
<i>Formicidae</i>	45.7	Terrestrial
<i>Nematocera (larvae)</i>	8.7	Aquatic
<i>Coleoptera (adult)</i>	7.1	Terrestrial
<i>Collembola</i>	6.0	Terrestrial
<i>Coleoptera (larvae)</i>	4.4	Aquatic
<i>Acari</i>	3.7	Aquatic
<i>Heteroptera</i>	2.3	Terrestrial
<i>Nematocera (adult)</i>	2.3	Terrestrial
<i>Ephemeroptera (larvae)</i>	2.0	Aquatic
<i>Hymenoptera</i>	1.7	Terrestrial
<i>Trichoptera (larvae)</i>	1.7	Aquatic
<i>Homoptera</i>	1.6	Terrestrial
<i>Nematocera (pupae)</i>	1.5	Aquatic
<i>Plant seeds</i>	1.4	–
<i>Fish eggs</i>	1.3	Aquatic
<i>Brachycera/Cyclorrhapha (adult)</i>	0.8	Terrestrial
<i>Brachycera/Cyclorrhapha (larvae)</i>	0.8	Terrestrial
<i>Coleoptera (larvae)</i>	0.8	Terrestrial
<i>Thysanoptera</i>	0.7	Terrestrial
<i>Araneae</i>	0.7	Terrestrial
<i>Psocoptera</i>	0.6	Terrestrial
<i>Mallophaga</i>	0.5	Terrestrial
<i>Isopoda</i>	0.5	Aquatic
<i>Neuroptera (larvae)</i>	0.4	Aquatic
<i>Gastropoda</i>	0.4	Aquatic
<i>Simuliidae (larvae)</i>	0.4	Aquatic
<i>Pseudoscorpionida</i>	0.2	Terrestrial
<i>Copepoda</i>	0.2	Aquatic
<i>Eggs (indeterminate)</i>	0.2	–
<i>Brachycera/Cyclorrhapha (larvae)</i>	0.2	Aquatic
<i>Chilopoda</i>	0.2	Terrestrial
<i>Coleoptera (adult)</i>	0.1	Aquatic
<i>Odonata (larvae)</i>	0.1	Aquatic
<i>Lepidoptera (larvae)</i>	0.1	Terrestrial
<i>Ostracoda</i>	0.1	Aquatic
<i>Lepidoptera (adult)</i>	0.1	Terrestrial
<i>Corixidae</i>	0.1	Aquatic
<i>Orthoptera</i>	0.1	Terrestrial
<i>Dermaptera</i>	0.1	Terrestrial
<i>Isoptera</i>	<0.1	Terrestrial
<i>Trichoptera (adult)</i>	<0.1	Terrestrial

and greater canopy cover tended to eat more adult terrestrial insects while females from slower flowing, deeper and narrow streams with less canopy cover tended to eat more juvenile and aquatic invertebrates.

Discussion

Our study is the first detailed account of the diet of *C. riisei*, and it is clear from our results that terrestrial

Fig. 2 Visual representation of variation in gut content of food types that contributed individually to >1% of the total average gut content across the sampled populations. The sum of the remaining food types are represented as ‘sum of other’. See Table 1 for description of the names and ecological characteristics of each population



insects, particularly ants, dominate the diet of this interesting fish. We also found substantial variation in environmental variables as well as a clear link between environmental variables and mean diet across populations.

The aquatic invertebrates that dominate the fauna of these streams, such as non-biting midges (Chironomidae) and mayflies (Ephemeroptera) (e.g., Turner et al. 2008), did not dominate the diet of *C. riisei*.

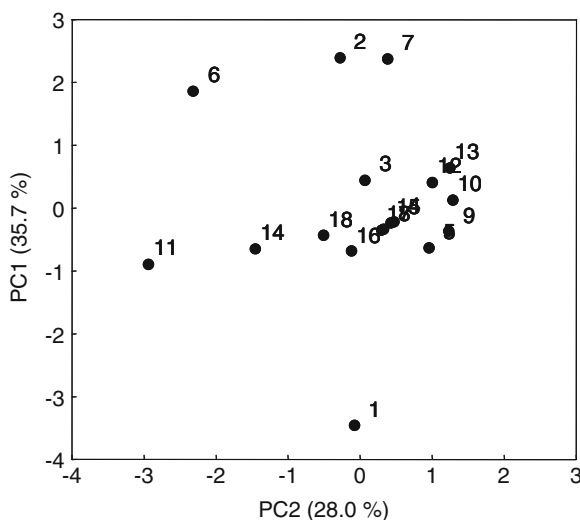


Fig. 3 Ordination plot of correlation between PC1 and PC2 of environmental variables. Populations group in three different clusters along PC1 while they form a more continuous distribution along PC2. Positive values on PC1 describes shallow, fast flowing and clear streams with substantial canopy cover while PC2 describes broad, deep, slow flowing and more turbid streams with less canopy cover (see text for details). Values within brackets represent the proportion of total variation among the environmental variables described by each principal component

Instead, terrestrial insects formed the majority of the gut content and there was little support for Wickler's (1968) hypothesis that aquatic invertebrates such as *Daphnia* or other water fleas are important food sources in this species. This is in fact unsurprising, since *C. riisei* rarely if ever occurs in stagnant waters (Kenny 1995; Table 1) where cladocerans are common (Viroux 2002). Together with the limited representation of aquatic invertebrates in the diet, this shows that *C. riisei* is mainly a surface-feeder. This is further supported by a recent analysis of body morphology in *C. riisei* which showed this species share many of the characteristics normally associated with surface feeding (e.g. an upwards pointing mouth) although substantial variation in body morphology was also found among populations (Arnqvist and Kolm 2010).

We note that gut content analysis, as a basis for the estimation of diet, can suffer from biases (Hyslop 1980). Most importantly, evacuation times of different food items can vary substantially and be affected by the amount of other food items (Rindorf and Lewy 2004). Our chosen method of gut content analysis, the numerical method, has been suggested to be suitable when food items are of similar size and when food items occur in discrete units (Hyslop 1980). These preconditions are fulfilled in *C. riisei*. Moreover, sampling during the period of peak feeding has been suggested to minimize bias since even prey items with short evacuation times will thus remain present in the gut content (Hyslop 1980). We sampled only during day-time and since *C. riisei* is a diurnal feeder (Nelson 1964) it is unlikely that any particular food items were consistently left undetected. Finally, to test

whether the documented differences in diet across different populations were caused simply by differences in the relative evacuation times of the utilized prey, we correlated the average number of food items per stomach to the mean scores of the principal components of proportional gut content variation across populations. However, these quantitative and qualitative measures of gut content were not significantly correlated (Pearson correlations: $p > 0.24$ in all cases).

Even though this study forms only a snap-shot of the diet during a limited temporal period, several differences are apparent between *C. riisei* and other species that occur in similar habitats in Trinidad. For instance, the well studied tetra, *Astyanax bimaculatus*, is omnivorous, feeding on terrestrial invertebrates, aquatic invertebrates (including zooplankton) but also on plant material and algae (Esteves 1996). Further, the guppy, *Poecilia reticulata*, feeds mainly on benthic algae and aquatic insect larvae (Dussault and Kramer 1981). The diets of these species thus contrast with the diet of *C. riisei*, which was dominated by terrestrial and aquatic insects while it contained virtually no vegetable matter, algae or zooplankton. Hence, in comparison to these other common species in similar environments in Trinidad, *C. riisei* appears to occupy a partly distinct food niche.

Environmental features varied across the sampled populations, suggesting that the habitat requirements of *C. riisei* are not narrow (Fig. 3). Our results thus support previous views of *C. riisei* being common throughout Trinidad except for more brackish waters and mountain streams with high velocity (Nelson 1964; Kenny 1995). The observed patterns of more terrestrial insects, mainly ants, in populations with more canopy cover and stronger currents and more larvae-shaped invertebrates in slower flowing streams with less canopy cover, point towards ecological differences that could set the stage for local adaptation to habitat-specific prey-types in *C. riisei* (Loreau 2000). We note that canopy-dwelling ants frequently jump or fall from branches and leaves (Yanoviak and Dudley 2006), resulting in a substantial “terrestrial drift” of ants in neotropical environments (Longino and Colwell 1997; Yanoviak et al. 2005). Apparently, *C. riisei* has capitalized on this fact.

In light of these results we can make some interesting inferences regarding the evolution of the

remarkable sexual dimorphism and courtship behaviors in *C. riisei*. Firstly, we reject the hypothesis that the male opercular flag ornament is a water flea mimic (Wickler 1968), since cladocerans are exceedingly rare both in the typical lotic environment of *C. riisei* and in the actual diet. Instead, our data suggests that the strong feeding response of females towards the opercular flag during courtship (Amcoff et al. 2009) occurs because the ornament is mimicking either an ant or some more larval-shaped invertebrate. Secondly, the environmental influence of diet in female *C. riisei* suggests, in addition to the possibility of local adaptation to food types, that there is also opportunity for the shape of the opercular flag ornament to evolve to match the population-specific diets of females. If female diet is temporally stable, population-specific feeding preferences could cause divergence among populations in male ornament characteristics and even lead to speciation. This is an important avenue for future research on this fascinating fish.

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