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The almost invisible league: crypsis and association between minute fishes and shrimps as a possible defence against visually hunting predators

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Camouflage is one of the most widespread defence modes used by substrate-dwelling animals, whereas transparency is generally found in open-water organisms. Both these defence types are regarded as effective against visually guided predators. We present here three assemblages of similarly-sized freshwater fish and shrimp species which apparently rely on camouflage and transparency to evade some of their potential predators. In one of the associations, there is a transition from cryptic colours and translucency to transparency of the component species according to the position each of them occupies in the habitat. The likeness between the fishes and the shrimps is here regarded as a type of protective association similar to numerical or social mimicry. Additionally, we suggest that the assemblage may contain Batesian-like mimicry components.

Camuflagem é um dos tipos de defesa mais bem distribuídos entre os animais que vivem no substrato, sendo a transparência geralmente encontrada em organismos pelágicos. Ambos os tipos de defesa são considerados como eficientes contra predadores visualmente orientados. Apresentamos três conjuntos de espécies de peixes e camarões de tamanhos similares, que aparentemente dependem da camuflagem e transparência para escapar de potenciais predadores. Em uma das associações, há uma transição de coloração críptica ou translúcida para transparente, de acordo com a posição que cada espécie ocupa no habitat. A semelhança entre peixes e camarões é aqui considerada como um tipo de associação protetiva, similar a mimetismo numérico ou social. Além disso, sugerimos que o conjunto pode conter elementos similares ao mimetismo Batesiano.

Key words: Camouflage, Transparency, Defensive association, Mimicry, Freshwater fauna.

Introduction

Camouflage and disruptive coloration are among the most widespread defence modes used by substrate-dwelling animals, whereas transparency is generally found in open-water organisms, both crypsis types being regarded as effective against visually guided predators (Edmunds, 1974; McFall-Ngai, 1990). Different cryptic animals (*e.g.*, insects and frogs) dwelling in the same environment or habitat usually have similar shapes and colours, a remarkable instance of convergence (Cott, 1940; Edmunds, 1974). Moreover, similarly coloured animals may form protective associations. One such example is given by so called social or numerical mimicry (Moynihan, 1968; Vane-Wright, 1976). In this defence type the associated animals are similar in colour, size, shape, and behaviour, which likely hamper the predator's ability to sort them out. For fishes the best known examples came from studies on reef fishes (*e.g.* Dafni & Diamant, 1984; Randall & McCosker, 1993; Krajewski *et al*., 2004), whereas records of such associations in freshwater seem to be lacking. We present here three instances of crypsis and association between freshwater fishes and shrimps which apparently rely on camouflaging colour pattern and transparency to evade some of their potential predators. The view that these assemblages are instances of numerical mimicry is here advanced, and the possibility that the assemblage contain Batesian-like mimicry components is suggested.

Material and Methods

Field studies were conducted in several streamlets and rivers in North and Southeast Brazil. The northern study sites were located in the Amazon, where a markedly rainy season typically occurs between December and May, with a dry sea-

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son between June and November. Mean annual temperatures vary between 26º C and 27º C, with very small seasonal differences. The southeastern locality presents a more contrasting seasonal climate, including a dry season between May and September (monthly rainfall 80-160 mm) and a wet season from October to April (mean monthly rainfall 380 mm); mean annual temperature 21.9ºC (see Results for more details about study sites features).

Behavioural observations were conducted both in the field and under aquarium conditions. Part of the field observations was done above the water, since the shallow water and large amount of particulate material at the study sites impaired underwater observations on occasions. When water conditions were adequate, snorkelling was used for observations. "Focal animal" and "all occurrences" samplings (Lehner, 1979) were used in all observations, totalling about 21 h of behavioural records both at daytime and night. In the field, an underwater torchlight provided with a red plastic was used for night observations. Records of co-occurrence of fish and shrimp species were based on field observations and photographs, as well as on direct observation of catches with hand nets and sieves. During field observations we recorded the spatial distribution of fishes and shrimps and roughly assessed their relative abundances, as well as movement patterns and microhabitat characteristics. The proportion of fishes and shrimps in the catches were also recorded.

After collection, specimens of fishes and shrimps of one of the associations were brought alive to the laboratory and maintained in an aquarium for detailed behavioural observations. The 140 l aquarium was provided with silica sand, leaf litter, and loose silt collected from the same or similar habitats. The aquarium was provided with an external canister filter, and kept at room temperature (26-33°C) and natural light. The fishes were fed *ad libitum* with zooplankton and *Artemia* sp. *nauplii*, and the shrimps foraged on litter organisms and debris. A 40 W red lamp was used above the aquarium at night time. The observations included the spatial distribution of fishes and shrimps over the aquarium bottom area, the vertical distribution (*i.e.*, use of the water column) by each species, daily activity rhythms, and possible agonistic interactions. In order to verify possible differences in the escape response for the fishes and shrimps, we intentionally disturbed (touched with a twig) about 10 individuals of each species, both in aquaria and in the field. Voucher specimens are deposited at the Instituto Nacional de Pesquisas da Amazônia Fish Collection (INPA 25243, 25244, 25245) as well as in the Crustacean Collection (INPA 1430, 1431, 1432, 1439), and the Museu de História Natural da Universidade Estadual de Campinas Fish Collection (ZUEC 5378, 6169, 6171, 6296, 6299).

Fig. 1. The studied igapó habitat in Amazonia (top left) with leaf-litter debris on the bottom; the eleotrid fish *Microphilypnus amazonicus* camouflaged on a decomposing leaf (17.5 mm SL, INPA 25244, top right), the characid fish *Priocharax ariel* hovering in the water column close to a dead leaf (14.3 mm SL, INPA 25243, bottom left), and the palaemonid shrimp *Palaemonetes carteri* crawling on a dead leaf (23. 7 mm TL, INPA 1432, bottom right). The cryptic effect of each species' colour pattern is lessened under artificial light (photographed in aquarium).

Fig. 2. Three members of the almost invisible league: *Priocharax ariel* (top centre), *Palaemonetes carteri* (bottom left), *Microphilypnus amazonicus* (bottom right) in aquarium under artificial light. Same specimens as in Fig. 1 except for *M. amazonicus* (17.8 mm SL, INPA 25244).

Results

One cryptic assemblage was recorded in an unnamed igapó stretch (Fig. 1) in the rio Negro basin (02º32'23''S, 60º47'41''W), Novo Airão, Amazonas State, Northern Brazil, during early dry season (August 2005). The assemblage was composed of two fish and three shrimp species. The shrimps outnumbered the fishes in the catches, the ratio being about 10:1. There was a transition from cryptic colours and translucency to transparency according to the position each species occupied in the habitat. Thus, the mostly bottom-dwelling eleotrid fish *Microphilypnus amazonicus* is mottled and partly translucent, merging with the heterogeneous debris-littered substrate it dwelled on. The bottom-dwelling and occasionally open-water swimming palaemonid shrimps *Palaemonetes carteri*, and *Pseudopalaemon amazonensis* and *P. chryseus* are transparent and bear disruptive golden to light-brown colour markings (see Melo, 2003), and the open-water characid fish *Priocharax ariel* is predominantly transparent (Figs. 1-2). Size ranges (standard length, SL) for *M.*

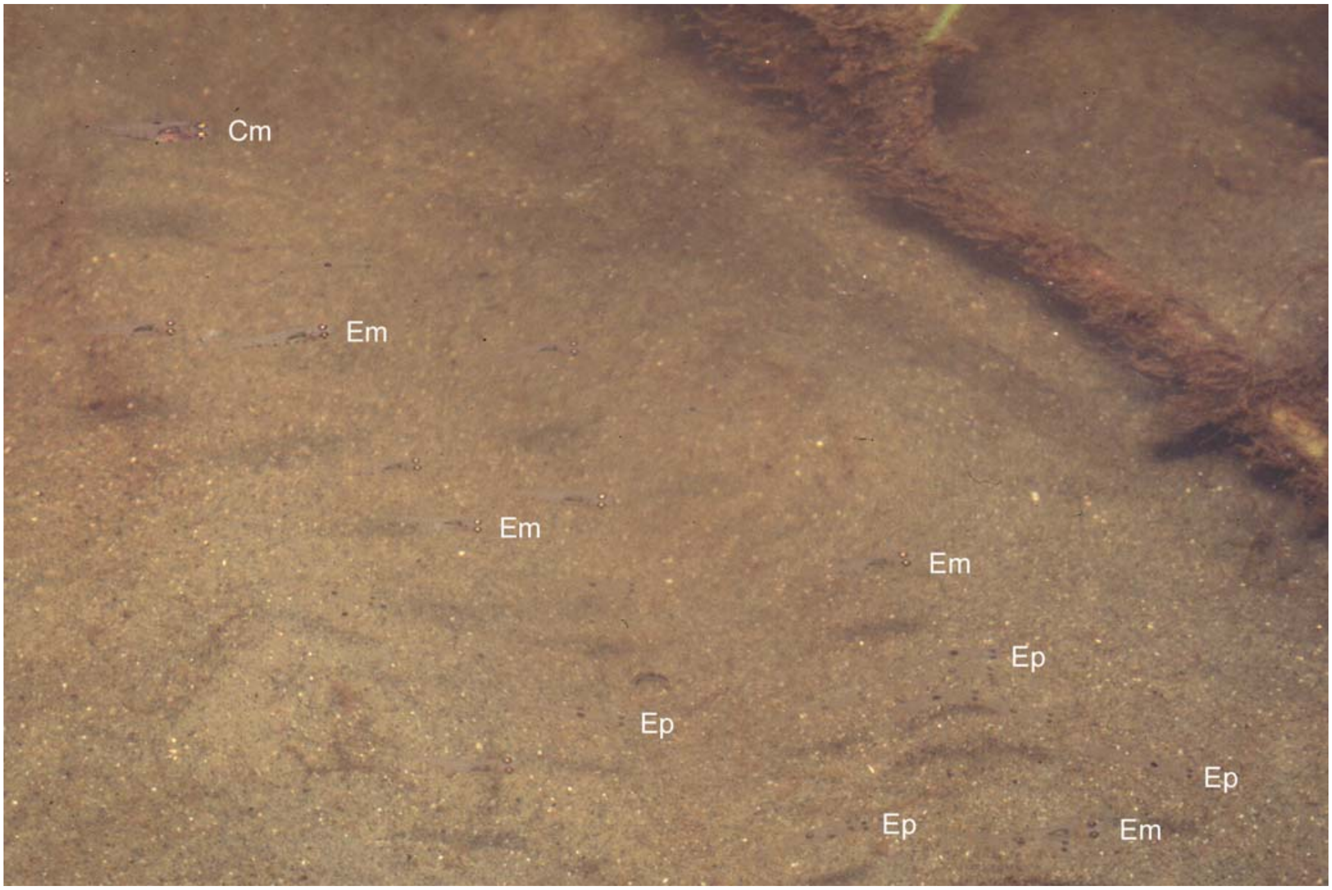

Fig. 3. A mixed column of larval eleotrid fish *Eleotris pisonis* and gerreid fish *Eucinostomus melanopterus*, associated with palaemonid shrimps *Palaemon pandaliformis*, moving upstream in the shallows of a coastal streamlet in Southeastern Brazil. The moving column is closely followed by larger larvae and juveniles of the predaceous centropomid fish *Centropomus mexicanus* in slightly deeper water. Some individuals marked in front of head to render them easier to spot (Cm= *C. mexicanus*, Em= *E. melanopterus*, Ep= *E. pisonis*); shrimps not visible against the background.

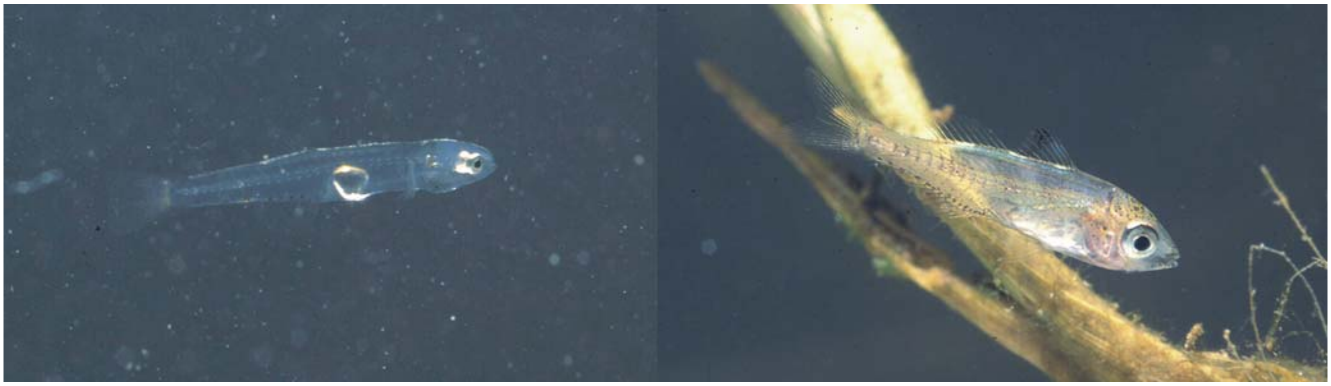

Fig. 4. A larval *Eleotris pisonis* (8.8 mm SL, ZUEC 6169, left) and a juvenile *Eucinostomus melanopterus* (11.3 mm SL, ZUEC 5378, right) photographed in field aquarium under artificial light.

amazonicus: 15.5-20.6 mm, for *P. ariel*: 12.6-16.1 mm, and for the three shrimp species (total length, TL): 10.1-20.6 mm.

Several individuals of *M. amazonicus* were also observed in their natural surroundings at the igarapé Tiotonho (02º51'19"S, 59º34'48"W), rio Preto da Eva drainage, Amazonas State, Northern Brazil, during the dry season (September 2005). The substrate was composed by silica sand, leaf litter and a mixture of loose silt and algae. The fish displayed a typical sit-and-wait foraging, and alternated short displacements with periods of apparent inactivity. During the day most of the individuals kept sheltered under dead leaves or partially buried in the substrate, occasionally lunging at small preys on the substrate or drifting in the current. At night time the individuals of *M. amazonicus* were found in the open, active and more dispersed on the substrate. When disturbed the fish buried in the substrate or hid among the leaf litter or loose sediment. Small shrimps (*Pseudopalaemon gouldingi*, Palaemonidae) were found foraging amidst the *M. amazonicus* individuals on the algae/loose silt patches close to the stream margin. Although not counted, the shrimps largely outnumbered the fish in those occasions.

In the aquarium most *M. amazonicus* individuals (n=15) hid under leaves and branches on the bottom at daytime, occasionally moving into the open to catch a prey on the bottom or ascending a little in the water column. After dark, they were scattered on the bottom and were more active, apparently searching for prey. *Priocharax ariel* (n=5) hovered in the water column at daytime and lunged at prey on surface, in mid-water, and near the bottom. After dark, it hovered almost stationary, 3-5 cm above the leaf litter, usually near a projection (twig, branch). The activity of the shrimps (~15 individuals) increased greatly after dark; they foraged crawling on the leaf-litter and occasionally ascended in the water column. When disturbed (*i.e.*, touched with a twig) the escape response was different for the fishes and the shrimps. *Microphilypnus amazonicus* darted to hide amidst the leaf-litter or buried in the sand, *P. ariel* changed its position, and the shrimps generally darted backwards with a quick bending and propulsion of the abdomen.

A second cryptic association was recorded in at least two occasions in Northern Brazil, at daytime (rio Côco , 09º38'46"S, 49 º59'27"W, rio Araguaia basin, Tocantins State, February 2001) and night time (Itapará stream, 00º16'51"S, 16º23'12"W, rio Branco basin, Roraima State, March 2005). Several individuals of the engraulid *Amazonsprattus scintilla* were found among swarms of the sergestid shrimp *Acetes paraguayensis* in a pelagic environment, both fish and shrimp with transparent body (see Whitehead *et al*., 1988; Melo, 2003). The small and slender shrimp congregates in huge numbers along the banks of clear and black water rivers, usually moving upstream at mid-water during early flooding season (Omori, 1975; J.Z., pers. obs.). The very small size (14.8-20.8 mm) and the transparency of the engraulid rendered it almost invisible among the similarly-sized shrimps (15.0- 20.9 mm) while swimming within the seine, and the fish came to view only when sorted among the catch.

A third cryptic assemblage was recorded in a coastal streamlet under tidal influence at Picinguaba (23º22'30"S, 44º52'30"W), Ubatuba, São Paulo State, Southeastern Brazil, in April and November 2002, and March 2003. This association was observed *in situ* and was composed of larvae and juvenile fishes and shrimps travelling upstream in the shal-

Fig. 5. A juvenile *Centropomus mexicanus* (12.9 mm SL, ZUEC 6171) gorged with eleotrid fish prey, photographed in field aquarium under artificial light.

lows (Fig. 3). The eleotrid fish *Eleotris pisonis* is transparent (Fig. 4), whereas the gerreid fish *Eucinostomus melanopterus* is nearly transparent with light-brown to light-grey sheen on the back (Figs. 3-4). The palaemonid shrimp *Palaemon pandaliformis* is transparent with few light-brown markings. Size ranges for *E. pisonis*: 8.8-9.3 mm SL, for *E. melanopterus*: 8.1-11.6 mm SL, and for *P. pandaliformis*: 8.3-9.8 mm TL. Larval and juvenile predaceous centropomid fish *Centropomus mexicanus* (12.9-21.1 mm SL) moved with the assemblage in slightly deeper water (Fig. 3) and occasionally lunged at the stragglers from the moving mixed group. The centropomid (Figs. 3, 5) seemed to have a higher predatory success on straggled fishes than on shrimps (5 successful lunges out of 13 preying attempts on fishes, and 1 successful lunge out of 6 attempts on shrimps).

Discussion

As far as we know, this is the first record of a protective association involving minute fishes and shrimps, especially in freshwater. From the three associations presented here, the one of the igapó leaf-litter habitat may be regarded as temporally stable, as all its components may be found there year-round (Henderson & Walker, 1990). The disruptive, mottled and translucent colours of *M. amazonicus* may be related to the stability of the association, as this pattern renders this fish well camouflaged against the heterogeneous and sun flecked background. Thus, from its transparent larval phase, this paedomorphic, mottled and translucent fish may keep the association with the remainder, transparent fishes and shrimps with disruptive colour markings (see Figs. 1 and 2).

On the other hand, the other two associations are transitory. The upstream movement of eleotrid and gerreid fish larvae and juveniles along with the shrimps is a seasonal recruitment mostly during the wet season (*e.g.*, Perrone & Vieira, 1990; Teixeira, 1994; I.S., pers. obs.) and its occurrence is ephemeral, *i.e.*, lasts for a short time during the day (I.S., pers. obs.). Not by coincidence, all of its component species are transparent or at least translucent. The pelagic engraulid fish and sergestid shrimp association likely falls in a similar category, *i.e.*, a migratory movement even if on a larger scale.

The three cryptic associations described here have at least two features in common: 1) similarly-sized fish larvae and juveniles, or paedomorphic species; 2) one or more shrimp species outnumbering the fishes. Miniature or paedomorphic fish species are commonly found in nutrient-poor environments (Weitzman & Vari, 1987; 1988), and their transparency favours their association with small and transparent shrimps. In the fish life cycle the larval stage is the most vulnerable to predation (*e.g.*, Helfman *et al*., 1997), as also indicated by our observations in situ. Transparency and/or camouflage are regarded as one viable and economical defence against visually guided predators (Edmunds, 1974; McFall-Ngai, 1990), and the association with the morphologically and behaviourally similar and abundant shrimps possibly enhances the effectiveness of these defence strategies and increase survivorship of larval and juvenile fishes.

Besides the defensive value of crypsis by transparency and disruptive pattern, we regard the three instances described here as a type of protective association similar to social or numerical mimicry (Moynihan, 1968; Vane-Wright, 1976; Randall & McCosker, 1993). In this mimicry type the associated animals are similar in shape, size, colour, and behaviour, which likely hamper the predator's ability to sort them out. The degree of cohesiveness of the fishes and shrimps groups varied among the three cases studied, being less evident in the *Microphilypnus-Priocharax*-palaemonid shrimps association and stronger between the engraulid *A. scintilla* and the sergestid *A. paraguayensis*. The upstream moving *Eleotris-Eucinostomus*-palaemonid shrimp association in the tidal creek, even if ephemeral, seems strong as well. Apart from the differences in group cohesiveness, the three assemblages we present here seem to fit the general requirements of the social mimicry concept (Moynihan, 1968; Dafni & Diamant, 1984).

The litter bank assemblage (*Microphilypnus*, *Priocharax* and palaemonid shrimps) shows a gradient of cryptic colours, and the transparency and disruptive markings of the behaviourally versatile shrimps make a convenient transition between the mottled and translucent bottom-dwelling *Microphilypnus* and the transparent, more open-water *Priocharax* (Weitzman & Vari, 1987). Additionally, the evasive responses of these three components of the litter assemblage are different, which may enhance the confusion effect. This combination of characteristics may represent an effective defensive tactic against visually oriented diurnal predators that are commonly found in the litter banks, such as small to medium sized cichlids (*e.g.* small pike cichlids, such as *Crenicichla notophthalmus*, and the larger *Astronotus ocellatus* and *Aequidens pallidus*, our pers. obs.). The defensive value of this and the other associations presented here may be tested with use of enclosures in the habitat (or in aquaria reproducing the natural habitat) in presence of potential predator fishes.

The association between the shrimp *A. paraguayensis* and the engraulid *A. scintilla* arguably represents convincing evidence in favour of the social mimicry hypothesis. The combination of a large number of individuals (sometimes thousands) with small size and almost transparent bodies may constitute an effective defence against fish predators in the pelagic environment of clear water rivers (McFall-Ngai, 1990). Several shrimp-eating predators are known to chase and engulf shrimps in Amazonian rivers, such as the pristigasterids *Pellona flavipinnis*, *P. castelnaeana* and *Ilisha amazonica*; the pelagic and wide-mouthed auchenipterid catfishes of the genus *Ageneiosus*; and the freshwater drums of the genus *Plagioscion* (Goulding & Ferreira, 1984; J.Z., pers. obs.).

Other potential predators on the studied associations would be wading birds, as two of the studied habitats are too shallow for kingfishers or terns (the exception is the open habitat of *Amazonsprattus*). In the Amazon, the most likely avian predator would be the small green-backed heron (*Butorides striatus*), a sit-and-wait and dexterous hunter of small animals including insects and fishes (Sick, 1997). The only potential predator we recorded at the tidal creek in the Southeast was the snowy egret (*Egretta thula*), which preyed on small fishes such as mugilids and poeciliids. However, the larval and juvenile fishes and shrimps in the studied association are minute and, thus, likely not important prey if preyed on at all. The same would apply to kingfishers and terns in the open habitat of *Amazonsprattus*.

An alternative and non-exclusive view is that this association type functions similarly to the principle which operates in Batesian mimicry, *i.e.*, that it contains a model which the predator perceives as disadvantageous (Edmunds, 2000). In this mimicry type, when the model is not aposematic the mimic may be poor, because the predator perceives that to pursue such a prey would render low reward due to the escape ability of the potential prey (Pinheiro, 1996; Edmunds, 2000). If this is the case indeed, the most likely candidate to the model are the shrimps, as they: 1) outnumber the fishes; 2) move both on the bottom and in the water column; 3) display a somewhat unpredictable and quick escape response; 4) the centropomid apparently has a higher predatory success on fishes than on shrimps in the third assemblage, even if the shrimps outnumbered the fishes. Additionally, in the aquarium observations, shrimps used effectively their pincers to repel fish predators such as the syntopic cichlid *Aequidens pallidus* (our pers. obs.). All these features seem to render the shrimps a hard-to-catch prey and a suitable model for the remainder species of the assemblage (Edmunds, 2000). Cryptic and/or mimetic defensive association between minute fishes and shrimps swarms is likely widespread both in freshwater and the sea and additional instances will be recorded with further field, natural history oriented studies.

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