

Caudal Eyespots as Deterrents against Fin Predation in the Neotropical Cichlid *Astronotus ocellatus*

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Astronotus ocellatus and several other large cichlid fishes of South America exhibit bright ocelli, or eyespots, near the base of the caudal fin. *Astronotus ocellatus* sympatric with fin-nipping piranhas of the genus *Serrasalmus* shows less extensive fin damage that sympatric cichlids of similar size that lack distinct caudal ocelli. Ecological data and observed interspecific behavioral differences support the hypothesis that eyespots reduce piranha attacks by confounding visual recognition of the prey's caudal region. Dense scalation of the unpaired medial fins, especially the caudal fin, masks visual cues for fin recognition, further enhancing head mimicry by the caudal region. The hypothesis that caudal ocelli in *A. ocellatus*, and perhaps other large cichlid fishes, function primarily as eye mimics for defense against fin predators is more parsimonious than Zaret's earlier "inhibition of cannibalism" hypothesis.

FISH fins are a principal food resource for many characids of the South American genera *Serrasalmus* and *Pristobrycon* (Machado-Allison and Garcia, 1986; Northcote et al., 1986; Nico and Taphorn, 1988; Winemiller, 1989b). Fins provide a seemingly abundant, rapidly renewable food resource for these diverse piranhas. Fin-nipping is most prevalent among sub-adult and small adult size classes of most *Serrasalmus* spp. that have been investigated

closely (Sazima and Zamprogno, 1985; Nico and Taphorn, 1988; Winemiller, 1989b). Fishes captured from lowland aquatic habitats shared by *Serrasalmus* spp. commonly show extensive fin damage, particularly around the caudal region (Northcote et al., 1986; Nico and Taphorn, 1988; Winemiller, unpubl.).

Fin-nipping must have a serious negative impact on growth and survival of prey. For example, damaged fins of captive fishes are more

susceptible to bacterial and fungal infection (Reichenbach-Klinke and Elkan, 1965). Fin damage adversely affects swimming performance, which in turn hinders feeding and escape efficiency (Sazima and Pombal, 1988). In addition, fin damage impacts the fish's energy budget negatively, since matter and energy would be diverted away from gonadal development and overall somatic growth, and directed toward fin regeneration. Even the dominance status of individuals is affected by visual cues associated with fin morphology in some species, which in turn can influence mating success (Baerends and Baerends von Roon, 1950; Barlow, 1974; Baylis, 1974).

Large, slow-moving cichlids with broad medial fins are conspicuous and potentially vulnerable targets for fin-nipping piranhas. This report offers evidence that *Astronotus ocellatus* and perhaps several other large neotropical cichlids gain a measure of protection against fin predation via caudal mimicry of the head region. This head mimicry is achieved by three morphological features: 1) the caudal ocellus; 2) dense, opaque scalation of the medial fins; and 3) symmetry of the lateral profile. The caudal ocellus, or eyespot, of *A. ocellatus* consists of a bright orange ring of scales surrounding a black spot at the dorsolateral base of the caudal fin. Except for the conspicuous ocellus and orange iris of the eyes, the coloration of *A. ocellatus* is drab and cryptic. Depending on the fish's behavioral state and environment, body coloration can quickly change from uniform grey to a mottled pattern consisting of dark grey and light brown to grey patches. Less than half of 1% of wild *A. ocellatus* exhibit two or more ocelli, usually near the base of the dorsal fin or sides of the body (Winemiller, pers. obs., $n > 250$ over 5 yr period in Venezuelan llanos). These multiple ocelli are usually incomplete (sometimes consisting of only a black spot without the orange ring) and apparently anomalous. Except for the brilliant caudal ocellus, wild *A. ocellatus* from the Venezuelan llanos are very drab compared with selectively bred color varieties referred to as "oscar" in the international aquarium trade. Here I argue that most vertebrates probably perceive the caudal ocellus as an eye, much in the manner suggested for the ocellus of the eel-mimicking coral reef fish *Callopleysiops altivelis* (McCosker, 1977), marine butterfly fishes, *Chaetodon* spp. (Cott, 1957), and eyespots on the wings of certain moths and butterflies (Blest, 1957).

MATERIALS AND METHODS

Study sites.—Most specimens used in the present analysis came from Caño Maraca, a swamp/creek of the Rio Apure drainage of the llanos in the state of Portuguesa, Venezuela. Full descriptions of the Caño Maraca environment and methods of collection are given by Winemiller (1987, 1989a, 1989b). Fishes were collected monthly during 1984, preserved in 15% formalin, and later transferred to alcohol. Specimens were collected at less regular intervals during 1984 from Caño Maporal, a broad shallow creek of the low llanos of Apure state ($7^{\circ}27'00''N$, $69^{\circ}32'00''W$), and preserved in the same manner. Additional collections were made at each site during Jan. 1988 and 1989. Both Caño Maraca and Caño Maporal exhibit dramatic changes in response to seasonal rainfall (Winemiller, 1989a, 1989b). During the dry season, there is little significant discharge, and water at each site is confined to the main channel. Fish densities are highest at both sites during the dry period (Oct.–April). Heavy rains from May–Sept. cause extensive flooding of broad, low-lying floodplains. Aquatic macrophyte and periphyton production is high and many fishes spawn during this period. Caño Maraca has four piranha species: *Pygocentrus notatus*, *S. irritans*, *S. medini*, and *S. rhombeus* (Winemiller, 1987, 1989b; see below). Caño Maporal has at least eight piranha species: *Catopristion mento*, *Pristobrycon* sp., *S. altuvei*, *S. elongatus*, plus the four species at Maraca (Nico and Taphorn, 1988). Specimens were deposited in the TNHC and MCNG (institutional abbreviations are as listed in Leviton et al., 1985).

Measurements.—Diets of all fish species collected at Caño Maraca were quantified by volumetric stomach-contents analysis. Fish prey were identified to species whenever possible. Identifications were performed using a dissecting microscope. Fishes were measured (all reported lengths are SL) and fins were examined for recent piranha nips. Fins damaged by narrow-bodied serrasalmin piranhas show distinct characteristics. First, the distal fin margin within the damage area is usually crescent or rectangular in shape. Fins damaged by larger red-belly piranhas, *Pygocentrus notatus*, are much broader in relation to the depth of the nip than fins nipped by *Serrasalmus* spp. Nips from large *P. notatus* were extremely rare compared to *Serrasalmus* nips. Presumably, large *P. notatus* nips result

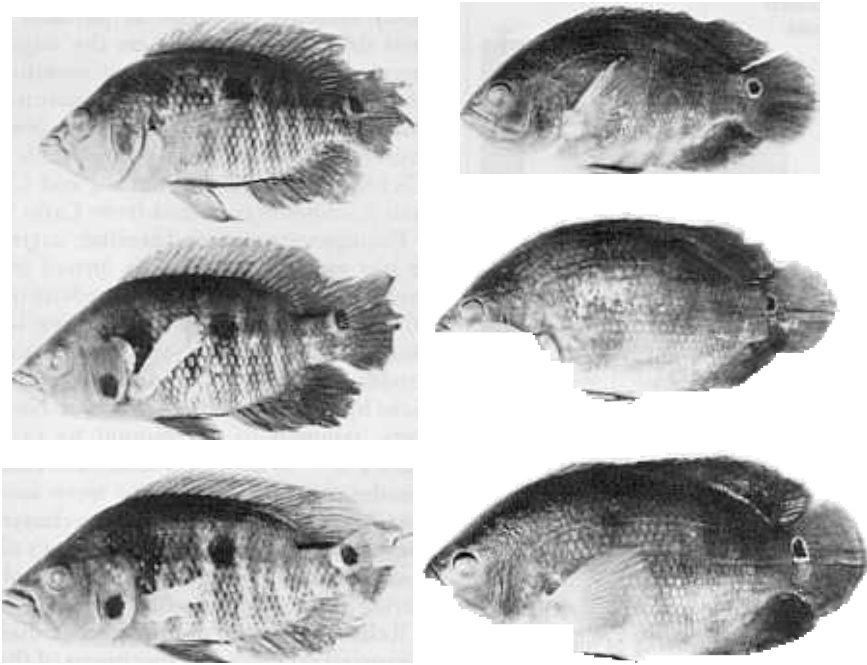


Fig. 1. *Caquetia kraussii* (left; 170–180 mm) and *Astronotus ocellatus* (right; 170–210 mm) collected on the same date from the same habitat in the Venezuelan llanos. Extensive damage from fin-nipping piranhas is evident on *C. kraussii*, whereas *A. ocellatus* suffered only minimal damage to its dorsal and anal fins. Interspecific differences in patterns of caudal ocelli are apparent even in preserved museum specimens.

from failed attempts at tearing out pieces of flesh rather than fins alone. However, some evidence suggests that juvenile *P. notatus* may attack fins rather than flesh (Machado-Allison and Garcia, 1986; Nico and Taphorn, 1988). Some specimens captured by hook and line were damaged by *P. notatus* before they could be removed from the water (evident from large bleeding wounds).

Second, *Serrasalmus* spp. produce clean, abrupt tears at the edge of damaged fins. Aquarium observations revealed that three species (*S. irritans*, *S. medini*, and *S. rhombeus*) can instantly clip off pieces of fin tissue with their razor sharp teeth. Tight occlusion of the teeth apparently facilitates abrupt tearing of fins (some juvenile *Serrasalmus* used a jerking motion to dislodge fin fragments).

Regenerating fins retain unambiguous visible evidence of the initial extent of fin damage. Newly regenerated fin tissue is usually more

transparent and frequently exhibits abrupt discontinuity with previous soft-ray formations. Fins damaged by other agents, such as intraspecific aggressive encounters among cichlids or failed attacks by grasping predators show ragged borders rather than smooth edges.

Recent fin nips were counted on all fins of *A. ocellatus* and *Caquetia kraussii*, another large cichlid found at Caño Maraca. Both species have a caudal ocellus, but that of *A. ocellatus* is far more symmetrical and brightly contrasting with the fish's background coloration than that of *C. kraussii* (Fig. 1). Specimens smaller than 40.0 mm were not included in the analysis. *Astronotus ocellatus* is widespread throughout lowland aquatic habitats of the Orinoco and Amazon drainage basins. As a result it usually coexists sympatrically with several fin-nipping *Serrasalmus* spp.

Caquetia kraussii ranges from the Lake Maracaibo and coastal drainages of Venezuela into

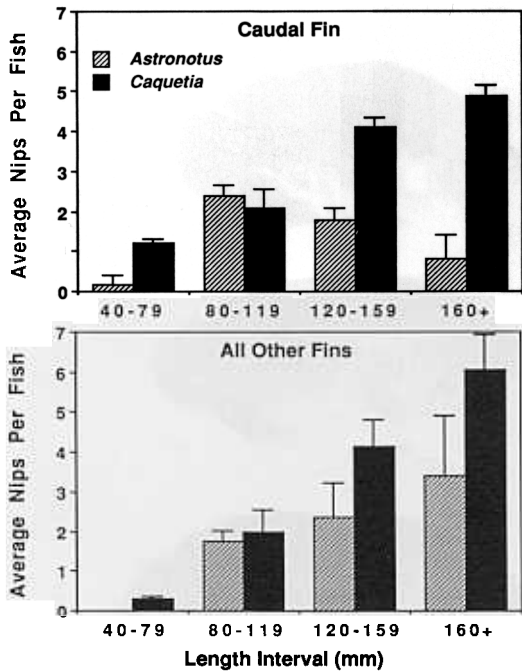


Fig. 2. Differences in frequency of nips to caudal fins (top) and all other fins (bottom) between *Astronotus ocellatus* ($n = 76$) and *Caquetia kraussii* ($n = 123$) collected from the Venezuelan llanos with piranhas. Vertical lines represent ± 1 SE. Nip frequencies in top graph showed significant main effects of species (two-way ANOVA; $F_{1,192} = 47.8$; $P < 0.0001$), size interval ($F_{3,192} = 28.4$; $P < 0.0001$), and interaction effect of species with size ($F_{3,192} = 23.2$; $P < 0.0001$). Nip frequencies in bottom graph showed significant main effects of species ($F_{1,192} = 11.0$; $P < 0.01$) and size interval ($F_{3,192} = 38.2$; $P < 0.0001$), but no interaction effect of species with size ($F_{3,192} = 2.3$; $P = 0.073$). Differences between species (ANCOVA with size interval as the covariate) were significant in both comparisons ($F_{1,192} = 35.7, 29.2$; $P < 0.0001$).

northern tributaries of the Río Orinoco in the western llanos; it is not currently found in the low llanos (Apure state) and may be a relatively recent invader of the high llanos, where it is sometimes a dominant species of local fish assemblages (D. C. Taphorn, pers. comm.). This cichlid was formerly listed as *Petenia kraussii* (Mago-Leccia, 1980), but was more recently considered a separate genus endemic to South America (Kullander, 1982).

The depth of fin nips was measured (nearest 0.1 mm) on adult size classes of *A. ocellatus* and *C. kraussii* (> 120 mm). Nip depth was measured as the distance from the most proximal edge of the damaged area to a line running between

undamaged distal tissue on either side of the nip. Nips were not measured if bordered by other recently damaged or partially regenerated tissue. Nips located on the edge of rectangular fin margins were not measured when undamaged distal tissue only remained on one side of the nip. Fin nips were also measured on preserved specimens of *Crenicichla saxatilis* (Cichlidae) from Caño Maraca and *Cichla ocellaris* (Cichlidae) collected from Caño Maporal.

Fin nips were classified as either narrow (depth of nip greater than width), broad (nip width greater than depth), or intermediate (nip depth and width roughly equal, resulting in a semi-circular notch). Based on piranha jaw shapes, broad nips were assumed to correspond to attacks by *P. notatus* at Caño Maraca. Narrow nips were assumed to correspond to various size classes of *S. irritans* plus small size classes of *S. rhombeus*. Intermediate nips were assumed to correspond to *S. medini* almost exclusively, since the other possibility, adult size classes of *S. rhombeus*, was rare at Caño Maraca (sample $n = 1$ during spawning period).

Relative scalation of unpaired medial fins was measured on two adult specimens of the following cichlids collected from the two sites: *A. ocellatus*, *C. kraussii*, *C. ocellaris*, *Crenicichla saxatilis*, *C. lugubris* (Caño Maporal), *Geophagus surinamensis* (Caño Maporal), *G. jurupari* (Caño Maporal), *Aequidens pulcher* (Caño Maraca), and *Cichlasoma orinocense* (Caño Maraca). Relative fin scalation was defined as the ratio of the length of the scaled portion of the longest fin ray divided by the total length of the ray (nearest 0.1 mm). Long filaments on dorsal and anal fins were not used for this measure.

RESULTS AND DISCUSSION

Three species of fin-nipping *Serrasalmus* (*S. irritans*, *S. rhombeus*, and *S. medini*) and the red-belly piranha, *P. notatus*, were collected during the high-water period at Caño Maraca (June-Dec.). Fins were prevalent in stomachs of all three *Serrasalmus* spp., whereas both whole fishes and fish fragments dominated diets of larger *P. notatus* (Winemiller, 1989b). *Astronotus ocellatus* and another large cichlid, *Caquetia kraussii*, were collected year-round at Caño Maraca (1984 total sample $n = 111$ and 588, respectively).

Fin damage.—No fin damage was observed in a sample of 93 specimens of *A. ocellatus* and *C. kraussii* taken during 4 mo of the harsh dry season when fin-nipping piranhas were absent

from Caño Maraca (Winemiller, 1989a). During the remainder of the year, both the frequency and magnitude of fin nips was much greater for *C. kraussii* than *A. ocellatus* (Figs. 1–2). *Astronotus ocellatus* had significantly fewer caudal-fin nips than *C. kraussii* for the 40–79 mm size interval (2-tailed t-test = 4.5, df = 31, $P < 0.0001$), the 120–159 mm interval ($t = 4.6$, df = 4, $P < 0.025$), the 160+ mm interval ($t = 4.6$, df = 4, $P < 0.01$), but not the 80–119 mm interval. Except for the 40–79 mm size interval ($t = 2.9$, df = 31, $P < 0.01$), lower nip frequencies for *A. ocellatus* on fins other than the caudal were not statistically significant (Fig. 2, lower panel). The average depth of fin nips was significantly greater for *C. kraussii* ($\bar{x} = 12.6$ mm, SD = 5.3) than *A. ocellatus* ($\bar{x} = 5.4$ mm, SD = 2.1; t-test = 8.59, $P < 0.0001$).

Larger cichlids tended to suffer greater damage from fin predators than smaller conspecifics, and interspecific differences in nip frequencies appeared most pronounced in the largest size intervals (Fig. 2). Size interval 40–79 mm *A. ocellatus* had significantly fewer nips to both the caudal and other fins than 80–119 mm ($t = 6.1$, 5.2; df = 21; $P < 0.0001$) and 120–159 mm conspecifics ($t = 2.8$, 3.1; df = 13, $P < 0.025$). The largest *A. ocellatus* size class actually averaged fewer caudal nips than intermediate conspecific size intervals; however, statistics were not significant due to small sample for the 160+ mm group ($n = 5$). Size 40–79 mm *C. kraussii* had significantly fewer nips to both caudal and other fins than 120–159 mm ($t = 6.3$, 5.7; df = 28; $P < 0.0001$) and 160+ mm conspecifics ($t = 7.9$, 5.8; df = 13; $P < 0.0001$). Size 80–119 mm *C. kraussii* had significantly fewer caudal nips than size 120–159 mm ($t = 2.3$, df = 13, $P < 0.05$) and 160+ mm conspecifics ($t = 3.7$, df = 13, $P < 0.01$). Size 160+ mm *C. kraussii* had significantly more nips to fins other than the caudal compared with intervals 80–119 mm ($t = 4.4$, df = 12, $P < 0.01$), 120–159 mm ($t = 4.0$, df = 13, $P < 0.01$), in addition to 40–79 mm conspecifics mentioned above.

Approximately half of all fin damage was to the caudal fin for both cichlids (Table 1). Paired fins received little damage relative to unpaired fins in each case. The two cichlids did not differ significantly in the proportion of nips to various fins or shapes of fin nips (Table 1). Both species were attacked most frequently by narrow-snouted piranhas (*S. irritans* and small *S. rhombeus*), followed by round-snouted *S. medini*, and only rarely by broad-snouted *P. notatus*. The ratio of total narrow nips to total intermediate nips on

TABLE 1. PERCENTAGE OF NIPS OF THREE SHAPES DELIVERED TO VARIOUS FINS OF *Astronotus ocellatus* (180 NIPS) AND *Caquetia kraussii* (530 NIPS). Chi square tests for association between cichlid species with frequencies of different nips, and cichlid species with frequencies of fins nipped were not significant ($P > 0.05$, for all cichlid size classes combined).

	Narrow	Inter- mediate	Broad	Total
<i>Astronotus ocellatus</i>				
Caudal	27.8	22.8	0	50.6
Dorsal	9.4	12.2	1.1	22.7
Anal	8.3	7.8	0.5	16.6
Pectoral	6.7	1.1	0	7.8
Pelvic	1.7	0.5	0	2.2
Total	53.9	44.4	1.6	100
<i>Caquetia kraussii</i>				
Caudal	34.3	18.7	1.5	54.5
Dorsal	8.5	6.6	0.5	15.6
Anal	11.1	4.5	0.5	16.1
Pectoral	10.4	2.1	0	12.5
Pelvic	1.3	0.4	0	1.7
Total	65.6	32.3	2.5	100

cichlids was 445:251 (1.8:1). The ratio of *S. irritans* and small *S. rhombeus* to *S. medini* collected in seine samples at Caño Maraca was $n = 126$:68 (1.8:1), which suggests equivalent feeding rates of each type of fin-nipping piranha on cichlids.

Fin predation/head mimicry hypothesis—Based on observations of piranha feeding behavior (Nico and Taphorn, 1988; Winemiller, 1989b), cichlid swimming performance, and cichlid diet data from the field (Winemiller, 1987, 1989b), *A. ocellatus* should be more exposed to predation by fin-nipping piranhas than *C. kraussii*. *Astronotus ocellatus* swims slowly with smooth, seemingly uninterrupted movement as it examines roots of floating aquatic macrophytes for cryptic insects and fishes. This foraging behavior is easily observed in aquaria containing water hyacinths or other floating plants. *Astronotus ocellatus* ($n = 176$, range 40–210 mm) consumed 19% fishes, 28% aquatic insects, 30% terrestrial insects, and 3% crustacea at Caño Maraca. The fishes consumed were all highly cryptic, relatively sedentary catfishes. Three of these small catfishes (*Bunocephalus amauros*, *Rineloricaria caracasensis*, and *Ochmacanthus alternus*) were commonly captured from the roots of floating aquatic plants of Caño Maraca. Presumably, the large bulging eyes of *A. ocellatus* permit good visual discrim-

ination of fine-scale structural features of the environment during foraging for cryptic fishes and invertebrates.

Caquetia kraussii, on the other hand, is primarily a sit-and-wait, rapid-pursuit predator of small midwater fishes; it ($n = 370$, range 40–180 mm) consumed 43% fishes, 26% aquatic insects, 15% terrestrial insects, and 6% crustacea. Small, midwater-dwelling characids (*Asytanax bimaculatus*, *Odontostilbe pulcher*, *Ctenopoma spilurus*, and *Hemigrammus* sp.) were the dominant fishes consumed (Winemiller, 1989b). Aquarium-housed *Caquetia kraussii* were frequently observed to ambush small moving prey. The pointed conical teeth and highly protrusible jaw apparatus of *C. kraussii* are used to suck in and grasp small prey organisms.

As a sit-and-wait forager, *C. kraussii* may have more opportunities to detect and avoid approaching fin-nipping piranhas than *Astronotus ocellatus*, the latter frequently being positioned with its snout amid floating vegetation and its caudal region exposed in the water column beneath. As a consequence, the caudal region of *A. ocellatus* is probably more exposed to fin-nippers than that of *C. kraussii*.

The distinct caudal ocellus of *A. ocellatus* probably functions as an eye mimic (Blest, 1957; Wickler, 1968). Ocelli of living specimens closely match both the size and color of the iris of the true eye. In addition, the position of the ocellus closely matches the relative height of the eye in lateral profile (Fig. 1). The combination of near complete scalation of the unpaired medial fins (producing an opaque, dull gray coloration that matches the head and body) with smooth-margined, overlapping dorsal, caudal, and anal fins results in symmetry of the fish's lateral profile (Fig. 1). Caudal mimicry of the head region is probably most effective under twilight conditions, a period when fin-nipping piranhas are particularly active. In addition to enhancing head mimicry, dense scalation of fins probably eliminates many visual cues used by fin-nipping piranhas for recognition of appropriate food resources (e.g., transparency, fin rays, a discrete border separating fin from body).

In contrast, the caudal ocellus of *C. kraussii* is asymmetrical and matches the golden background color of the body more closely than the iris, which can change between gold and crimson. The most distinctive feature of the caudal marking of *C. kraussii* is the large black spot, rather than the bright ring of scales surrounding the spot in *A. ocellatus*. The unpaired medial fins of *C. kraussii* are largely unpigmented and

incompletely sheathed with tiny transparent scales. If the mode of foraging of *C. kraussii* (i.e., scanning the environment for midwater fishes) facilitates visual detection and thus avoidance of fin predators, then selection may be acting more weakly on the caudal spot as an eye mimic. Also, *C. kraussii* may have a relatively short history of ecological association with piranhas if, as postulated, it is a recent invader of the llanos.

While data to support the hypothesis of recent association are not presently available, the detection/avoidance hypothesis can be tested by comparing fins and ocelli of cichlids of different sizes. Smaller, deeper-bodied fishes should have greater abilities for performing evasive darting maneuvers along acute angles or for concealment in dense vegetation. The relative degree of caudal-fin scalation is generally greater for larger llanos cichlids (Fig. 3). Moreover, highly symmetrical yellow, orange, or red caudal ocelli are found only in four of the longest cichlids. As already noted, *C. kraussii* has a rather weakly developed caudal ocellus, while the smaller *Geophagus* spp., *Aequidens pulcher*, and *Cichlasoma orinocense* have small, dark caudal spots and no ocellus. Two deep-bodied, highly maneuverable dwarf cichlids (*Apistogramma hoignei* and *Microgeophagus ramirezi*) commonly collected from dense vegetation in the llanos have small, asymmetrical caudal spots but no ocellus. The dark caudal spots of small diurnal fishes of numerous other freshwater families may serve a variety of adaptive functions: 1) confusion or deflection of predator attacks by drawing attention away from the head; and 2) intraspecific communication (Barlow, 1972; Lagler et al., 1977; Lowe-McConnell, 1987).

If a simple caudal spot enhances survival by reducing the success rate of predatory strikes, the addition of conspicuous color in the form of an ocellus would only reduce survival by increasing the rate of detection by predators. Alternatively, caudal mimicry of the head region could reduce the rate of predation, if more conventional, whole-fish swallows sometimes incorrectly anticipate the path of escape to be taken by a motionless prey organism (Cott, 1957). In addition to concealing vulnerable fin tissues, the false head of large piscivorous cichlids would yield the appearance of a predation threat to small fin-nipping piranhas, thus discouraging many exploratory approaches. Experimental work on captive fishes could shed light on these alternative possibilities.

Other possibilities exist for lower incidence of fin-nips on *Astronotus ocellatus* in addition to

the head-mimicry hypothesis. For example, the fins of *A. ocellatus* may contain distasteful substances that discourage attacks following initial sampling and learning by piranhas. In addition, the abundant scales on fins may increase the piranha's energetic foraging cost by hindering removal of fin fragments. Because some individual *A. ocellatus* had multiple nips and nips were generally as abrupt and smooth-edged as nips on other llanos cichlids, these explanations seem unlikely. Alternatively, *A. ocellatus* could be more adept than *Caquetia kraussii* at protecting their caudal regions. As described previously, foraging behavior of captive cichlids suggests just the opposite for situations in which piranhas remain undetected. Upon detection of an approaching piranha, both cichlid species appeared capable of effectively repelling attacks with frontal displays (see description from experimental trial below).

Additionally, *A. ocellatus* might detect fin-predators more effectively than *C. kraussii* via social cooperation. Both cichlids form pair bonds during reproductive bouts and brood protection that may last several weeks (Winemiller, 1989c). A dense school consisting of over 300 juvenile *A. ocellatus* measuring 35–55 mm was captured at Caño Maraca during Aug. 1984. The relatively large size of these schooling juveniles, which were assumed to be siblings, indicates a 2–3 mo period of parental care. By comparison, *C. kraussii* pairs were never captured with offspring larger than 15 mm. Captive groups of *A. ocellatus* as large as 130 mm exhibited tight schooling behavior when disturbed by human observers. Yet, the same individuals showed little hesitation in confronting solitary *S. irritans* with frontal displays. Although social facilitation remains a viable possibility for defense against fin-predators, it appears somewhat unlikely pending further evidence.

Other neotropical cichlids with caudal ocelli.—The head-mimicry hypothesis probably applies to the large piscivore *Cichla ocellaris* and *Crenicichla* spp. as well. Based primarily on data taken from a recently established population outside the natural range of the species (Zaret and Paine, 1973), Zaret (1977; Schroder and Zaret, 1979) postulated that cannibalism in *Cichla ocellaris* is inhibited via the ocellus, which functions as a signal for species recognition. This evolutionary hypothesis relies on the assumption that *C. ocellaris* encounters its own offspring as potential prey at frequencies sufficiently high in relation to encounters with unrelated individuals, such

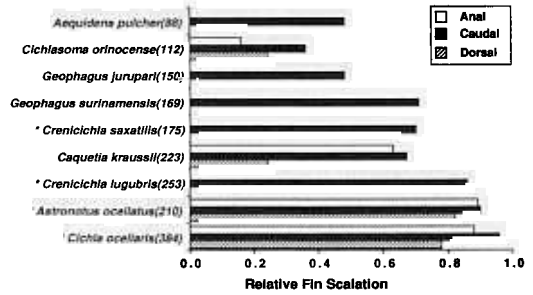


Fig. 3. Relative scalation of anal, caudal, and dorsal fins for cichlid fishes collected from two sites in the Venezuelan llanos inhabited by fin-nipping piranhas. Relative fin scalation was measured as the ratio of the length of the scaled portion divided by the total length of the longest fin ray. Asterisks denote species with a distinct, brightly colored caudal ocellus. Values in parenthesis are maximum standard lengths among material examined.

that indiscriminate predation on conspecifics reduces lifetime fitness. This assumption relies on the additional assumption that offspring remain within the home range of their parents following the period of brood defense. Moreover, inhibition of cannibalism implies that reduced mortality from cannibalism more than offsets the increase in mortality caused by higher rates of detection by other diurnal piscivores caused by the conspicuous ocellus. This is unlikely in native environments in the Amazon and Orinoco river basins, where other species of diurnal piscivores far outnumber *C. ocellaris* (Goulding, 1980; Taphorn and Lileystrom, 1985; Winemiller, 1987).

In addition to the questionable validity of these assumptions, the primary assumption that *C. ocellaris* never exhibits cannibalism is based almost entirely on data from two populations located outside of its native range. I know of no other large, freshwater piscivore for which a similar scenario has been proposed. Zaret (1977) presented data that indicated a lower integrity of the caudal ocellus pattern in *C. ocellaris* from an exotic Panamanian population compared with native Amazonian populations. The difference was hypothesized to be a result of relaxed selection on inhibition of cannibalism during the initial phase of explosive population expansion (Zaret, 1977). Following the fin-predation hypothesis, the same data can be attributed to relaxed selection on the ocellus as an eye mimic in the absence of fin-nipping piranhas in the exotic setting.

Zaret (1977) theorized that *A. ocellatus* and

TABLE 2. PREY ITEMS TAKEN FROM STOMACHS OF *Cichla ocellaris* FROM THE LOW LLANOS OF ESTADO APURE, VENEZUELA (N = 10).

Prey	N	Volume (ml)	Proportion (Vol.)
<i>Crenicichla saxatilis</i> (Cichlidae)*	1	11.0	0.30
<i>Pellona</i> sp. (Clupeidae)	2	7.5	0.21
<i>Poptella orbicularis</i> (Characidae)	2	3.3	0.09
<i>Geophagus surinamensis</i> (Cichlidae)		3.3	0.09
<i>Pygocentrus notatus</i> (Characidae)	2	3.0	0.08
<i>Curimatella immaculata</i> (Curimatidae)		2.4	0.07
<i>Anostomus</i> cf. <i>trimaculatus</i> (Anostomidae)		2.0	0.05
<i>Cichlasoma festivum</i> (Cichlidae)		1.7	0.05
<i>Microgeophagus ramirezi</i> (Cichlidae)		0.8	0.02
<i>Eigenmannia virescens</i> (Sternopygidae)		0.7	0.02
Unidentified fish		0.4	0.01
<i>Megalampodus sueglesi</i> (Characidae)		0.15	<0.01

* Species having distinct caudal ocellus.

Crenicichla spp. have evolved ocelli as mimics of the intraspecific recognition signal of *Cichla ocellaris* as a means to avoid predation by the latter. Sixteen specimens of *C. ocellaris* from the low llanos were examined for stomach contents (Table 2). A single, 85 mm *Crenicichla saxatilis* with a bright caudal ocellus was the most important prey consumed by volume in this small sample (stomachs of six individuals were empty). The single occurrence of *C. saxatilis* with a bright eyespot within the stomach of one of 10 specimens of *Cichla ocellaris* offers no support for Zaret's hypothesis, whereas ingestion of two juvenile piranhas (*Pygocentrus notatus*) illustrates a predation threat to fin-nippers posed by the anterior region of the large piscivore.

Both *Crenicichla saxatilis* and *Cichla ocellaris* appear to suffer comparatively low levels of fin predation. Twenty-three specimens of *Crenicichla saxatilis* collected with piranhas as Caño Maraca averaged only 0.26 nips per fish (all caudal). Although the average number of nips per individual of *Cichla ocellaris* was not significantly lower than the value obtained for *Caquetia kraussii* in the earlier comparison (caudal

= 4.8 nips per fin; all fins = 8.0 nips per fish), the average depth of 50 fin nips on 14 Apure specimens was 5.9 mm (SD = 3.0), a value lower than that obtained for *C. kraussii* (t-test = 7.86, $P < 0.0001$) but not *A. ocellatus* (t-test = 0.94, $P > 0.05$).

Comparisons of fin damage on other llanos fishes suggest that cichlids are more vulnerable to fin predation than native ostariophysan fishes (Northcote et al., 1986; Sazima and Pombal, 1988; Winemiller, unpubl.). To test this hypothesis, an experiment was conducted for 3 d using four specimens of *S. irritans* (30–160 mm), each housed in a separate aquarium with a mixture of 16 characiform, siluriform (catfishes), and cichlid prey (>25.0 mm). Cichlids were attacked most frequently (11 nips recorded on three *Aequidens pulcher*; no nips on one *Crenicichla geayi* with a bright caudal eyespot), followed by catfishes (14 nips on 17 individuals representing eight species), and characins (18 nips on 42 individuals representing seven species). Predation attempts by the piranhas were most frequent during twilight conditions in the aquaria.

To test the head-mimicry hypothesis, experiments using *S. irritans* and manipulations of ocellus markings on cichlids were set up in large concrete pools during the 1989 llanos dry season. The experiment was terminated prematurely after the grease paint used for masking and enhancing *Astronatus ocellatus* and *Caquetia kraussii* ocelli wore off. During the trial, both cichlids frequently were observed to turn and repel piranhas with frontal displays (i.e., mouth open, opercula and branchiostegal membranes flared) when the latter approached or hovered near their caudal regions. Persistent piranhas were sometimes driven off with charges and bites by both cichlids. Experiments of similar design using models or another marking technique could test the fin-predation/head-mimicry hypothesis.

Fin damage inflicted by piranhas is undoubtedly a major selective pressure on large, slow-moving fishes that inhabit lowland aquatic habitats of South America. Conspicuous ocelli in *A. ocellatus* and certain other large cichlids probably serve as false eyes for caudal-head mimicry that partially deters fin-nipping. Although not mutually exclusive, the fin-predation/head-mimicry hypothesis explains the function of caudal ocelli on neotropical cichlids more parsimoniously than Zaret's inhibition of cannibalism hypothesis, because it invokes fewer interrelated assumptions.

ACKNOWLEDGMENTS

D. C. Taphorn, L. G. Nico, A. Barbarino, L. K. Winemiller, P. Rodriguez, and E. R. Pianka provided technical assistance in the field. Special thanks go to D. C. Taphorn and la Universidad de los Llanos Occidentales Ezquiel Zamora for providing a base of operations in Venezuela. A collecting permit was obtained from the Dirección Administración y Desarrollo Pesquero of the Republic of Venezuela. I thank E. R. Pianka, L. K. Winemiller, M. Morris, and C. Hubbs for helpful comments on the manuscript. I thank R. L. Beach for assistance in preparation of the manuscript. Field work was funded by the National Geographic Society and the Denton A. Cooley Professorship (E. R. Pianka).

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