Fin-nipping Piranhas

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Predatory Response of Piranhas to Alternative Prey

Prey selection by South American fin-nipping piranhas was investigated in the field and in laboratory prey-choice experiments. Our comparative data from laboratory assemblage experiments indicate that different piranha species select prey species in different proportions, and that the differences are associated with the body form and swimming behavior of predator and prey. In the field, cichlid fishes were the most preferred prey for fin-nipping piranhas. We tested the hypothesis that some South American cichlid fishes suffer lower levels of fin predation because of their caudal (tail) mimicry of the head region. Most of the large cichlids that inhabit lowland aquatic habitats with piranhas have densely scaled median fins and bright caudal ocelli (eyespots) at the base of the tail that mimic the size and vertical position of the true eye.

Figure 1.
Pygocentrus nattereri *(red belly piranha) is the voracious schooling predator that most people associate with the name piranha. Contrary to popular myth, the diets of the red belly and other piranhas consist not of people, but fish flesh, fins, and even plant material.*
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SOUTH AMERICA'S PIRANHAS (Characiformes: Characidae) exhibit a variety of feeding preferences, including whole fish, chunks of fish flesh, fish fins, scales, and fruit and seeds.[3,6,7,13] A number of piranhas belonging to the genus *Serrasalmus* are voracious predators that specialize in the fins of other fishes (Figures 1, 2, 7–9).[5,7,8,10,13] These fin-nipping piranhas are common in lowland aquatic habitats throughout tropical South America. For example, L G Nico and D C Taphorn[6,7] reported diets of 6 fin-nipping piranhas sympatric in the low llanos (flatlands) of Venezuela's Río Apure basin, and Winemiller[13] documented the ecology of 3 species (*Serrasalmus irritans, S rhombeus, S medinai;* Figures 3&4) from a floodplain system in the western llanos of Venezuela.

Most *Serrasalmus* species in the llanos exhibit their highest preference for fins during the juvenile and subadult stages and switch gradually to whole fish as they grow larger.[5,7,13] However, fins can comprise either a minor or major fraction of the diet of adult fishes depending on the species and season. High rates of fin cropping and extensive fin damage have been documented in the field,[8,10,13,15] but which species are most vulnerable to fin-nipping piranhas is unknown. Preliminary evidence suggests that perciform fishes of the family Cichlidae (Perciformes: Cichlidae) may be particularly vulnerable to fin predation.[5,15]

Prey Defenses

Fish fins are nutritious[6] and represent a renewable food resource that piranhas can crop. But extensive and frequent removal of fin tissue should have a significant negative effect on the survivorship, growth, and reproductive potential of the victims. Fishes can avoid fin predators by a number of mechanisms, including hiding or crypsis. Schooling by small fishes may confuse or frustrate pursuit predators.[9] The threat of injury from spines (eg, *Pimelodus blochii*, Pimelodidae), electric shock (*Electrophorus electricus*, Electrophoridae), or predation from large piscivores (eg, *Cichla ocellaris*, Cichlidae; Figure 6C) may also inhibit fin predators.

Winemiller[15] presented field evidence that the large cichlid *Astronotus ocellatus* suffers significantly lower levels of fin predation (in terms of both frequency and size of nips) than a coexisting cichlid (*Caquetaia kraussii*) of similar size, habitat affinities, and feeding habits. He proposed that *Astronotus* gains some measure of defense against fin predation from its special morphology and coloration pattern that causes the caudal region

As an experimental description of piranha diet, it is a contribution to the field. I think the readership of your journal will benefit from this paper; it is a contribution to our knowledge of the diet of piranhas, and the strategies that their prey use to defend themselves....The manuscript contributes to the knowledge of the complex ecology of large neotropical floodplain rivers.

REVIEWERS

Figure 2.
Piranha jaws in vivo. When the jaws close, the razor-sharp triangular teeth interlock tightly and can cleanly shear pieces of fish flesh, bones, or fins.
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to mimic the fish's head region (Figure 6A&B). The median fins (top, bottom, and tail) of *Astronotus* are almost completely covered with small, dense dark-colored scales. When held in their normal positions, the median fins overlap posteriorly such that the body silhouette is almost perfectly symmetrical when viewed from the side. Mimicry of the head region by the tail is enhanced by the distinct, orange caudal ocellus (eye spot) which closely matches the size, color, and vertical position of the true eye. Except for the caudal eyespot, the coloration pattern of wild-type *Astronotus* is drab olive or gray and cryptic against the normal surroundings of the fish (ie, decaying leaves and roots of floating aquatic plants). *Caquetaia* is believed to be a fairly recent invader of the Orinoco lowlands, having originated from Lake Maracaibo and coastal drainages.[4] Lacking the orange caudal ocellus, densely-scaled median fins, and overlapping margins of the median fins, *Caquetaia* suffers very high levels of fin predation when piranhas are most dense in the western llanos.[15]

The caudal ocellus and densely-scaled median fins of *Astronotus* and other large cichlids (*Cichla* spp, *Crenicichla* spp; Figure 6C&D) of the South American lowlands are deterrents to fin predation with presence of the caudal ocellus highly correspondent with extensive caudal fin squamation.[15] Winemiller hypothesizes that by virtue of their greater size: Larger cichlids are more exposed to fin predators than smaller cichlids; and the head region of a large cichlid poses a greater threat of injury to fin nippers than that of small cichlids. Observations of captive cichlids indicate that they are aware of the predation threat posed by piranhas, and that they frequently repel attacks with frontal agonostic displays and assaults (Winemiller, unpublished observations).[10,15]

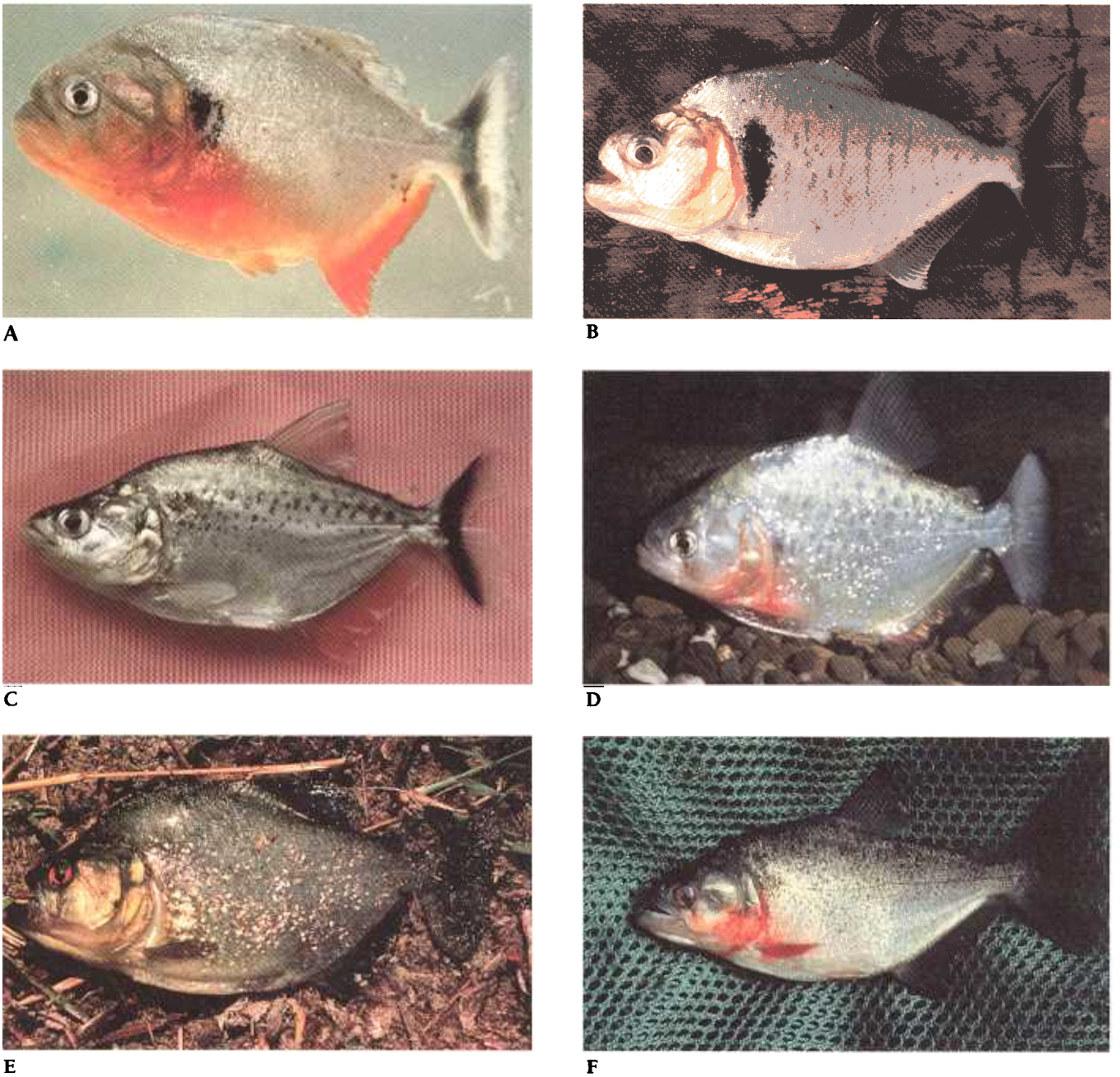
T M Zaret[11,17] hypothesized that the caudal eyespot of the peacock cichlid *Cichla ocellaris* serves primarily as a signal of species identity to larger conspecifics so that cannibalism might be averted. Winemiller[15] argues that the fin predation–caudal head mimicry hypothesis poses a simpler explanation for the presence of bright caudal ocelli in South American cichlids than the earlier hypothesis of inhibition of cannibalism. The inhibition of cannibalism hypothesis seems implausible given the extremely high diversity and abundance of heterospecific predators within the native range of that species (Zaret's hypothesis was initially formulated based on evidence from an introduced population in Lake Gatún, Panama). For a small *Cichla* with a bright eyespot, the advantage of signaling species identity to larger piscivorous conspecifics would be outweighed by the disadvantage of being more conspicuous to other predators.

The fin predation–caudal head mimicry hypothesis and alternative hypotheses can be tested with further comparisons of field data, plus controlled experiments involving manipulation of the false eyespot. We first present an analysis of fin damage in a natural assemblage of fishes in the western llanos of Venezuela. Second, we present results of laboratory experiments with fin-nipping piranhas and alternative prey.

Methods

FIELD DATA

We measured standard length (SL) and fin damage of all fish specimens taken during monthly sampling of Caño Maraca in Portuguesa state, Venezuela, throughout 1984.[16] Caño Maraca is a stream-swamp within the



Río Apure drainage that experiences large changes in habitat characteristics due to highly seasonal rainfall.[16] On both field-preserved specimens and experimental fishes, the depth of each fin nip was measured following the methods reported in Winemiller.[15]

LABORATORY EXPERIMENTS

Six juvenile fin-nipping *Serrasalmus irritans*, 1 juvenile *S medinai*, and 1 juvenile *S elongatus* were collected from ponds (*prestamos*) of the UNELLEZ experimental ranch in Apure state. Fishes were captured by seine and cast net, and later were transported to Knoxville, Tennessee, where behavioral experiments were conducted. The piranhas were housed either separately or as pairs in separate 150-L glass aquaria and fed goldfish (*Carassius auratus*) until their use in the feeding tests.

An experimental assemblage of South American fishes (Table 1) was

Figure 3.
Examples of fin-nipping piranhas from Venezeula: A, Pygocentrus caribe, *juveniles are facultative fin predators and adults shear off chunks of fish flesh. B,* Serrasalmus manueli, *juveniles are fin specialists and adults shear off fine fish flesh and sometimes eat fruit. C,* S rhombeus, *juveniles are fin specialists and adults shear off fish flesh and consume whole fishes. D,* S medinai, *juveniles and small adults are fin specialists. E,* S irritans, *juveniles and adults are fin specialists. F,* S elongatus, *juveniles and small adults are fin specialists.*
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Figure 4.
Serrasalmus rhombeus *feeds heavily on fish fins when young and later shifts to a diet of whole fish and fish flesh. Unlike the red belly piranhas,* S rhombeus *tends to hunt alone or in small loose-knit groups.*
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Table 1. Frequencies of Nip Damage from 3 Piranha Species in an Experimental Fish Assemblage

PREY SPECIES	*n*	*S ELONGATUS*	*S IRRITANS*	*S MEDINAI*
Anostomus spp (ff)	2	0	0	0
Hemigrammus sp (ff)	2	1c	1c	0
Metynnis spp (db)	4	1	2c	7c
Moenkhausia sanctaefilomenae (ff)	2	1c	0	0
Piaractus brachypopmus (db)	1	0	1c	7c, 4d
Thayeria boehlkei (ff)	3	2c	0	0
CHARACIFORMES	14	5c	4c	14c, 4d
Apternotus albifrons GYMNOTIFORMES	1	0	0	0
Bunocephalus sp (ff)	1	0	0	0
Corydoras spp (db)	6	1c	2c	2c
Chaetostoma sp (ff)	1	0	0	0
Farlowella sp (ff)	1	0	0	0
Pekoltia vittatus (db)	1	0	0	0
Platydoras amaurus (db)	1	0	0	0
Pimelodella sp (ff)	1	0	0	0
Pterygoplichthys sp (db)	2	1c	4c, 3d, 1a, 1p	0
Rineloricaria sp (ff)	1	0	1p	0
Trachelyichthys sp (ff)	1	0	0	0
SILURIFORMES	16	2c	6c, 3d, 1a, 2p	2c
Poecilia reticulata CYPRINODONTIFORMES	3	1c	1c	0
Aequidens curviceps (db)	1	1c	0	0
Apistogramma sp (ff)	2	0	2c	0
Satanoperca pellegrini (db)	26	10c, 1d	26c, 1d	12c, 1d, 1p
Mesonauta festivum (db)	2	0	1d	1d
Nannocara anomalum (ff)	2	0	0	0
PERCIFORMES	33	11c, 1d	29c, 1d	12c, 2d, 1p
TOTAL FISHES	67	19c, 1d	40c, 4d, 1a, 2p	28c, 6d, 1p

a=anal fin, c=caudal fin, d=dorsal fin, db=deep-bodied (deep-bodied fishes were those in which maximum body depth, including the extended dorsal fin, was ~>0.5 TL, where TL=SL + length of caudal fin.), ff=fusiform, p=pectoral fin.

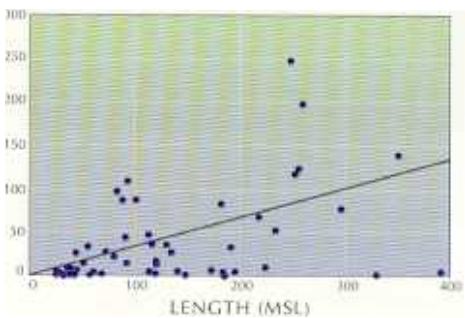

Figure 5.
Relationship between the maximum standard length recorded (MSL) and the total number of fin nips counted in the sample of each species at Caño Maraca, Venezuela, in 1984 (number of nips=0.337[MSL]–1.60; r^2=0.23; F=16.81; DF=1,58; p<0.0001; slope different from zero, t=4.10, *p<0.0001).*

acclimated in a 475-L aquarium landscaped to simulate a stream-edge habitat. Some of the fishes were captured in Venezuela and transported to the lab, but the majority were purchased from a local fish supplier. The aquarium water was aerated, filtered, and maintained at 25°C. Three small submersible pumps maintained moderate water current in half of the aquarium, and rocks, woody debris, and plastic plants provided cover. Artificial light was maintained on a 14-h-light : 10-h-dark cycle. Resident fishes were fed frozen brine shrimp. A single juvenile *S elongatus* (SL=65 mm) was introduced to the assemblage and allowed to hunt for 1 week. After the removal of the piranha, the frequencies and locations of fin nips on residents were recorded. Residents were monitored each day until all fishes had completely regenerated their fins, a period of 31 to 39 days. Once regeneration was complete, the test was repeated with a single juvenile *S medinai* (SL=63 mm) for 2 days (yielding a total number of nips comparable to the previous test). Complete fin regeneration was again permitted before the last test, which consisted of the introduction of a single juvenile *S irritans* (SL=64 mm) for 2 days. No fishes died during these fin-predation tests in the experimental assemblage.

To test for the effect of the presence or absence of a contrasting caudal

A

B

C

D

eyespot in *Astronotus*, we set up the following conditions in 4 150-L aquaria: 4 wild-type *Astronotus* with 4 red *Astronotus* and 1 *S irritans* (3 aquaria), and 8 wild-type *Astronotus* with 1 *S irritans* (1 aquarium). Wild-type and "red" variety *Astronotus* were purchased from tropical fish wholesalers in the United States and were housed in a 2-m-diameter plastic wading pool and fed goldfish, frozen brine shrimp, and commercial pellets before use in the experiments. Except for the presence of a bright orange caudal ocellus, wild-type *Astronotus* are mottled tan and gray and can fade to a dull gray depending on environment and mood. Red *Astronotus* are the product of selective breeding and differ from wild-type fish in lacking the caudal ocellus and having uniform orange-brown flanks. Each experimental aquarium contained gravel, 3 large rocks, 2 pieces of woody debris, and 1 plastic plant anchored to the bottom. In addition, each aquarium contained a box filter for aeration and a submerged aquarium heater that maintained water at 25°C. *Astronotus* were fed pellets and brine shrimp during the experiments. After 5 days, the experiment was terminated and fish lengths and nip depths were measured.

To test for the effect of eyespots, we masked the natural eyespots of 1 group of *Astronotus* with a 10% $AgNO_3$ (silver nitrate) solution. We swabbed $AgNO_3$ over the region of the caudal eyespot of 8 wild-type *Astronotus* and returned them to the stock pool. After 14 days, the scales in the area treated with $AgNO_3$ had turned opaque gray and all of the eyespots were completely masked. To test for the effect of fin squamation and

Figure 6.
A, Astronotus ocellatus, *a South American cichlid with a caudal ocellus and scaled median fins that result in mimicry of the head region by the caudal region, B, close-up of caudal ocellus of* Astronotus, *C,* Cichla ocellaris, *a large piscivorous cichlid from South America with a caudal ocellus and scaled median fins, and D,* Crenicichla geayi, *a South American pike cichlid with a caudal ocellus.*
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Aquarium 1
Serrasalmus irritans–100 mm SL
unmasked *Astronotus ocellatus*–115, 133 mm
masked *Astronotus ocellatus*–113 mm
Lepomis macrochiras–124, 125, 126 mm

Aquarium 2
Serrasalmus–78 mm
unmasked *Astronotus*–130 mm
masked *Astronotus*–124, 125 mm
Lepomis–125, 127, 150 mm

Aquarium 3
Serrasalmus–67 mm
unmasked *Astronotus*–100, 117, 126, 129 mm

Aquarium 4
Serrasalmus–68 mm
masked *Astronotus*–100, 102, 105, 107 mm
Lepomis–78, 89, 92, 100 mm

Table 2. Nipped Individuals, Caño Maraca, 1984

	NIPPED INDIVIDUALS IN SAMPLE	TOTAL INDIVIDUALS IN SAMPLE	PERCENTAGE
Characiformes	784	14822	5.3
Gymnotiformes	54	667	8.1
Siluriformes	234	3434	6.8
Cyprinodontiformes	3	341	0.1
Perciformes	306	1684	18.2
Perciformes (minus *Apistogramma*)	306	1505	20.3

Perciform numbers are presented with and without the dwarf cichlid *Apistogramma*. Order was significantly associated with the relative frequencies of nipped individuals in relation to frequencies of sampled individuals. (χ^2=345.1; *DF*=4, p<0.0001, the Perciformes minus *Apistogramma* category was not included in the test.)

eyespots, we used *Lepomis* collected from Melton Hill Lake, Tennessee, as an alternative perciform prey that lacks both the caudal ocellus and densely-scaled median fins. Whereas a suite of species-specific differences covaries with these traits, *Lepomis* was chosen because its size, relative body shape, fin arrangement, and swimming mode are similar to those of *Astronotus*. The *Lepomis* were housed for 1 month with *Astronotus* in a 2-m-diameter plastic wading pool and fed earthworms and frozen brine shrimp. Because we had a limited number of piranhas, the same individual *S irritans* were used for both sets of experiments. Except for 6 individuals, we used different wild-type cichlids in the 2 sets of experiments. We set up the following conditions in 150-L aquaria: 4 unmasked wild-type *Astronotus* with 4 *Lepomis* and 1 *S irritans*; 4 masked *Astronotus* with 4 *Lepomis* and 1 *S irritans*; 1 masked *Astronotus* with 2 unmasked wild-type *Astronotus*, 3 *Lepomis*, and 1 *S irritans;* 2 masked *Astronotus* with 1 unmasked wild-type *Astronotus*, 3 *Lepomis*, and 1 *S irritans*. An attempt was made to match the sizes of alternative prey within each tank. Each experiment was terminated after 24 hours, and fish lengths and nip depths were measured. Because group sample sizes within each aquarium were small and responses to treatments were consistent between aquaria, we grouped individuals across aquaria and used analysis of variance to test for main effects of independent variables and Scheffe's *F*-test to test for mean differences.

Results

FIELD DATA

Except for a single immature specimen of *S medinai* collected at the start of the peak dry season (January), piranhas were present at the Caño Maraca field site only during the wet season (June to August) and the transition to dry season (September to December).[13] During the peak dry season, resident fishes at Caño Maraca must contend with a much reduced aquatic environment, high temperatures (>30°C), and frequent hypoxia.[14] Near the end of the transition season, the 4 piranha species at Caño Maraca (*Pygocentrus caribe, S irritans, S medinai, S rhombeus*) migrate downstream to deeper, more stable aquatic environments. They return to the site with the beginning of each new wet season.[13] Characteristic piranha-nip scars on the fins of fishes at Caño Maraca correlated with the presence of piranhas at the site. Eleven nips were recorded among the 6825 specimens collected during the dry season, and all of

Table 3. Fin Nips on Fishes from Caño Maraca, Venezuela, when *Serrasalmus* Piranhas Were Present, June to December 1984

	SL	DORSAL	CAUDAL	ANAL	PELVIC	PECTORAL	TOTAL
CHARACIFORMES							
nr species = 29							
nr individuals = 784							
sum		196	797	239	98	22	1350
mean	81.8	0.25	1.02	0.30	0.12	0.03	1.72
SD	40.5	0.55	0.67	0.61	0.42	0.28	1.68
GYMNOTIFORMES*							
nr species = 4							
nr individuals = 54							
sum		-----	32	61	-----	0	93
mean	197.6	-----	0.59	1.13	-----	0	1.72
SD	78.0	-----	0.50	1.35	-----	0	1.16
SILURIFORMES							
nr species = 17							
nr individuals = 234							
sum		84	247	17	18	6	372
mean	90.3	0.36	1.05	0.07	0.08	0.03	1.59
SD	54.8	0.72	0.56	0.26	0.28	0.16	1.18
CYPRINODONTIFORMES							
nr species = 2							
nr individuals = 3							
sum		0	3	0	0	0	3
mean	20.7	0	1	0	0	0	1
SD	0.61	0	0	0	0	0	0
PERCIFORMES							
nr species = 5							
nr individuals = 306							
sum		70	353	108	26	31	588
mean	62.7	0.23	1.15	0.35	0.09	0.10	1.92
SD	40.4	0.56	0.85	0.81	0.32	0.45	2.25

Data are grouped by prey order.
*Gymnotiforms lack dorsal and pelvic fins. Most gymnotiforms also lack caudal fins, however piranha nips suffered by the caudal tip were scored as caudal nips.

these were from the earliest dry season samples (18&28 January 1984). In contrast, >2400 nips were recorded among the 22 499 fishes sampled during the wet period of June to December.

In terms of nip-scar frequencies recorded in our sample of fishes from Caño Maraca, characiform fishes (tetras and their relatives) were the group most often exploited by piranhas, followed by perciform cichlid fishes (Table 2). However, characiforms were by far the most abundant fishes at the site, so that, per capita, perciform fishes were the group most preferred by fin-nipping piranhas (Table 3). Cichlids comprised <2% of the total individuals sampled at the site, yet they represented >18% of the individuals with piranha fin-nips (Table 3). Because it inhabits dense vegetation in shallow water at the edge of the swamp, the dwarf cichlid *Apistogramma hoignei* is essentially inaccessible to piranhas. If we exclude the dwarf cichlid from the calculations, the remaining cichlids comprised >20% of all nipped individuals (Table 2). Cyprinodontiforms (annual killifishes) were the least numerous and the least exploited fishes, both on an absolute and per capita basis (Tables 2&3). Like the dwarf cichlid, small killifishes inhabit shallow, vegetated fringe habitats of the swamp and probably come into contact with fin-nipping piranhas only infrequently. Per capita, siluriforms (catfishes) and gymnotiforms (weakly electric knifefishes) suffered intermediate fin damage when based on either the sample of nipped fishes (Table 2) or the total sample of fishes (Table 3).

WILD-TYPE VS "RED" *ASTRONOTUS*

AQUARIUM 1
Serrasalmus irritans–77 mm SL
Wild-type *Astronotus ocellatus*–96, 101, 105, 111 mm
"Red" *Astronotus ocellatus*–89, 90, 91, 94 mm

AQUARIUM 2
Serrasalmus–69 mm
Wild-type *Astronotus*–85, 86, 88, 90 mm
"Red" *Astronotus*–83, 84, 87, 91 mm

AQUARIUM 3
Serrasalmus–86 mm
Wild-type *Astronotus*–97, 100, 100, 103 mm
"Red" *Astronotus*–87, 89, 89, 96 mm

AQUARIUM 4
Serrasalmus–64 mm
Wild-type *Astronotus*–99, 109, 110, 115 mm
"Red" *Astronotus*–84, 85, 90, 90 mm

AQUARIUM 5 (CONTROL)
Serrasalmus–98 mm
Wild-type *Astronotus*–102, 111, 115, 117, 117, 121, 122, 123 mm

The fin-nipping habit of these piranhas has obvious advantages. Fins are an abundant and renewable resource that can be cropped and replenished, much like vegetation that is browsed by herbivores. Also, by attacking the fins of larger fishes, these piranhas avoid resource competition with piscivores of similar size that swallow their prey whole.

Figure 7.
Catoprion mento *(wimple piranha) is a specialist that feeds on the scales of other fishes. The lower jaw protrudes when open. When the teeth on the lower jaw are raked across the flanks of the victim, scales are removed like a row of shingles.*
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Siluriforms were the 2nd most abundant group and gymnotiforms were the 2nd rarest (Table 3); both groups are dominated by nocturnal fishes that hide in aquatic vegetation during the day.

The caudal fin is most frequently attacked by piranhas, generally suffering at least 3-fold greater incidence of damage than the 2nd most attacked fin (Table 3). Except for the catfishes (siluriforms), the anal fin (unpaired ventral fin) is the 2nd most attacked fin. Most catfishes inhabit the stream bottom, hence their anal fins (ventrally positioned fins) are less exposed to piranhas than their dorsal fins. When fin nips were summed for each fish species, larger species were shown to suffer more fin nips than smaller species (Figure 5). When the dorsal and anal fins of perciforms are attacked, these attacks are nearly always directed only at the soft-rayed portions rather than the spiny portions.

LABORATORY EXPERIMENTS WITH FISH ASSEMBLAGES

In the assemblage experiment, 3 individual fin predators representing 3 species were introduced 1 at a time into the same artificial environment (Table 1). The average numbers of nips recorded per day for each of the predators were 3 (*S elongatus*), 17.5 (*S medinai*), and 23.5 (*S irritans*). *S elongatus* (Figure 3F) has the most fusiform-elongate body form of the 3 piranhas tested and attacked mostly the cichlid (*Satanoperca pellegrini*) and fusiform characids (Table 4). If fusiform characids are the preferred prey of *S elongatus*, then its comparatively low rate of success could have been associated with the lower abundance of fusiform characids in our experimental assemblage. *S elongatus* usually hovered near cover (eg, vegetation, woody debris) and attacked prey by stalking or ambush. Here we define stalking as slow movement (usually with rapid fin fluttering) toward a target that appears unaware of the predation threat, followed by a rapid attack. Ambushing is defined as gliding behind or near cover followed by a rapid dash toward passing prey.

S irritans (Figure 3E) preyed heavily upon cichlids and to a lesser extent on slow-moving stout-bodied catfishes, such as *Pterygoplichthys* and *Corydoras* spp (Tables 1&4). The predatory behavior of *S irritans* was similar to that observed for *S elongatus*, except that stalking was observed much more frequently than ambushing.

S medinai (Figure 3D) preyed most heavily upon deep-bodied characiforms (*Piaractus, Metynnis*) followed by cichlids (Tables 1&4). The predatory behavior of *S medinai* was very different from that of the other 2 piranhas. *S medinai* is an active swimmer and appears to prefer roving the open midwater column to hovering at stations near cover. We observed only a few ambush attacks and none of *S medinai*'s open-water attacks appeared to involve the stealth (fin-fluttering) exhibited by the other piranhas. On several occasions, *S medinai* removed long narrow strips of fin tissue from large prey by initiating the bite near the center of the fin rather than at the fin margin, the latter being the usual mode of attack. The first contact with the fin appeared to be with the lower jaw in these attacks. Attacks initiated near the center of a fin left long narrow nip wounds.

LABORATORY EXPERIMENTS WITH 2 PREY SPECIES

In prey-choice experiments involving bluegill sunfish (*Lepomis*) and oscar cichlids (*Astronotus*), sunfish received significantly greater fin damage than the cichlids (Table 5). If we exclude the caudal fin, the depth of nips

Table 4. Fin Nip Frequencies by Prey Body Form and by Taxonomic Order

	S ELONGATUS	*S IRRITANS*	*S MEDINAI*
BODY FORM			
fusiform	7 (33%)	7 (15%)	2 (6%)
deep-bodied	14 (67%)	40 (85%)	33 (94%)
χ^2=7.66, *DF*=2, p<0.025			
ORDER			
Characiform	6 (30%)	5 (11%)	18 (51%)
Perciform	12 (6%)	30 (64%)	15 (43%)
Siluriform	2 (10%)	12 (25%)	2 (6%)
χ^2=18.95, *DF*=4, p<0.001			

Results from χ^2 tests of association show that the relative frequency of fin nips was significantly associated with piranha species and both prey body form and taxonomic group.

Table 5. *Astronotus–Lepomis* Experiment

	CAUDAL FIN	FINS OTHER THAN CAUDAL
INDEPENDENT VARIABLE=SPECIES (*ASTRONOTUS* VS *LEPOMIS*)*		
NR OF NIPS	*F*=65.85; *DF*=1, 26; p<0.0001	*F*=21.63; *DF*=1, 26; p<0.0001
MEAN (SD)		
Lepomis	3.86 (1.10)	1.64 (1.08)
Astronotus	0.79 (0.89)	0.14 (0.53)
DEPTH OF NIPS	*F*=7.83; *DF*=1, 49; p<0.01	*F*=0.004; *DF*=1, 22; p=0.950
MEAN (SD)		
Lepomis	9.12 mm (5.85)	
Astronotus	40.9 mm (1.76)	
INDEPENDENT VARIABLE=PRESENCE OR ABSENCE OF EYESPOT (UNMASKED *ASTRONOTUS* VS OCELLUS-MASKED *ASTRONOTUS*)**		
NR OF NIPS	*F*=0.08; *DF*=1, 12; p=0.778	*DF*=1, 1; no comparison made
DEPTH OF NIPS	*F*=0.01; *DF*=1, 9; p=0.936	*DF*=1, 1; no comparison made

*wild-type *Astronotus* having dense opaque scales covering the median fins and caudal ocelli vs *Lepomis* lacking both features
**wild-type *Astronotus* with ocelli vs wild-type *Astronotus* with masked ocelli
Correlations between fish length and nips means are presented only for comparisons with p<0.05 based on Scheffe's *F*.

did not differ, but *Lepomis* suffered a greater frequency of nips than *Astronotus* (Table 5). No significant differences in frequencies or depths of fin nips were obtained for *Astronotus* with masked ocelli ($AgNO_3$-stained) compared with unmanipulated *Astronotus*, however, these sample sizes were small because the incidence of nips to *Astronotus* was low in the *Lepomis* experiment (Table 5). Neither the depth nor the number of caudal nips was significantly correlated with fish length (eg, number of nips with SL: *Astronotus* r^2=0.002[n=14], *Lepomis* r^2=0.305 [n=14], both species r^2=0.167).

LABORATORY EXPERIMENTS WITH 2 PREY MORPHS

In terms of the depth of fin nips, red variety *Astronotus* lacking the caudal eyespot suffered significantly more fin predation than wild-type conspecifics with eyespots (Table 6). The frequency of fin damage was not significantly different between the wild-type and red varieties (Table 6). When wild-type *Astronotus* were housed with an equal number of red con-

The observed differences in depth of nip could be attributed to differences in fin structure* (Astronotus *vs* Lepomis) *or body coloration and selected behavior ("red" vs wild morph).

A REVIEWER

Figure 8.
Pygopristis denticulatus *(white piranha) inhabits streams of forested regions and feeds heavily on fruit and seeds.*
AARON NORMAN

The size of piranhas in the experiments with Astronotus *may have been too large to be frightened by the threat of predation by the* Astronotus. *A positive result might have been obtained had we used smaller piranhas, however this is not really a viable option, since they would be quickly eaten within the confines of an aquarium.*

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Table 6. *Astronotus* Eyespot Experiment Using Wild-Type

INDEPENDENT VARIABLE=PRESENCE OR ABSENCE OF OCELLUS (WILD-TYPE *ASTRONOTUS* VS RED *ASTRONOTUS*)*

	CAUDAL FIN	FINS OTHER THAN CAUDAL
NR OF NIPS	F=0.07; DF=1, 30; p<0.795	F=2.17; DF=1, 30; p<0.151
DEPTH OF NIPS	F=16.02; DF=1, 73; p<0.0001	F=6.95; DF=1, 37; p<0.025
MEAN (SD)		
wild-type	5.00 mm (2.16)	6.17 mm (3.25)
red	7.81 mm (3.76)	9.58 mm (4.30)

INDEPENDENT VARIABLE=EXPERIMENTAL GROUP (WILD-TYPE *ASTRONOTUS* HOUSED WITH REDS VS CONTROL WILD-TYPE ONLY GROUP)**

	CAUDAL FIN	FINS OTHER THAN CAUDAL
NR OF NIPS	F=0.67; DF=1, 22; p=0.421	F=0.98; DF=1, 22; p=0.332
DEPTH OF NIPS	F=5.53; DF=1, 59; p<0.025	F=0.08; DF=1, 25; p=0.779
MEAN (SD)		
wild-type (alone)	5.00 mm (2.16)	
wild-type housed with red	6.77 mm (3.74)	

*ocellated wild-type *Astronotus* vs red variety lacking ocelli
**wild-type *Astronotus* from experimental groups (those housed with red morphs) vs wild-type *Astronotus* from a control group (those housed only with other wild-types)
Means are presented only for comparisons with p<0.05 based on Scheffe's F.

specifics (experimental wild-types), the depth of caudal fin nips was greater for the control group (Table 6). This suggests that damage suffered by wild-type fishes is less severe when non-ocellated red morphs are also present in the same tank. Again, the number of nips was not significantly different between experimental wild-type and control wild-type fish.

Discussion

PREY SELECTION BY PIRANHAS

Fish fins appear to be an abundant and nutritious food resource for South American piranhas of the genus *Serrasalmus*. The identification of fish fins from stomach contents is a feasible means for analyzing the feeding ecology of piranhas.[5–7, 13] However, accurate identification of prey species based on material removed from stomachs is usually not possible.[13,15] Direct observation and experimentation are probably the only economical means for obtaining data on the specific identity of prey.

Our prey-choice experiments with a diverse fish assemblage provide preliminary evidence that juvenile piranhas may exhibit species-specific hunting behavior and prey preferences. All 3 of the juvenile piranhas fed on cichlid fins with great frequency. In addition to attacking cichlids, the hovering fusiform piranha (*S elongatus*) was the only species that fed heavily upon fusiform midwater tetras (Characidae). Similarly, the round, deep-bodied piranha (*S medinai*) was the most active swimmer and the only species that preyed heavily upon round, deep-bodied tetras that occupy the open midwater column habitats. The piranha with the intermediate body shape (*S irritans*) was primarily a stealth feeder and exploited mostly cichlids and deep-bodied catfishes. Though our samples were extremely limited, each of the 3 piranha species appears to differentiate itself from the others by preying most heavily upon those fishes having

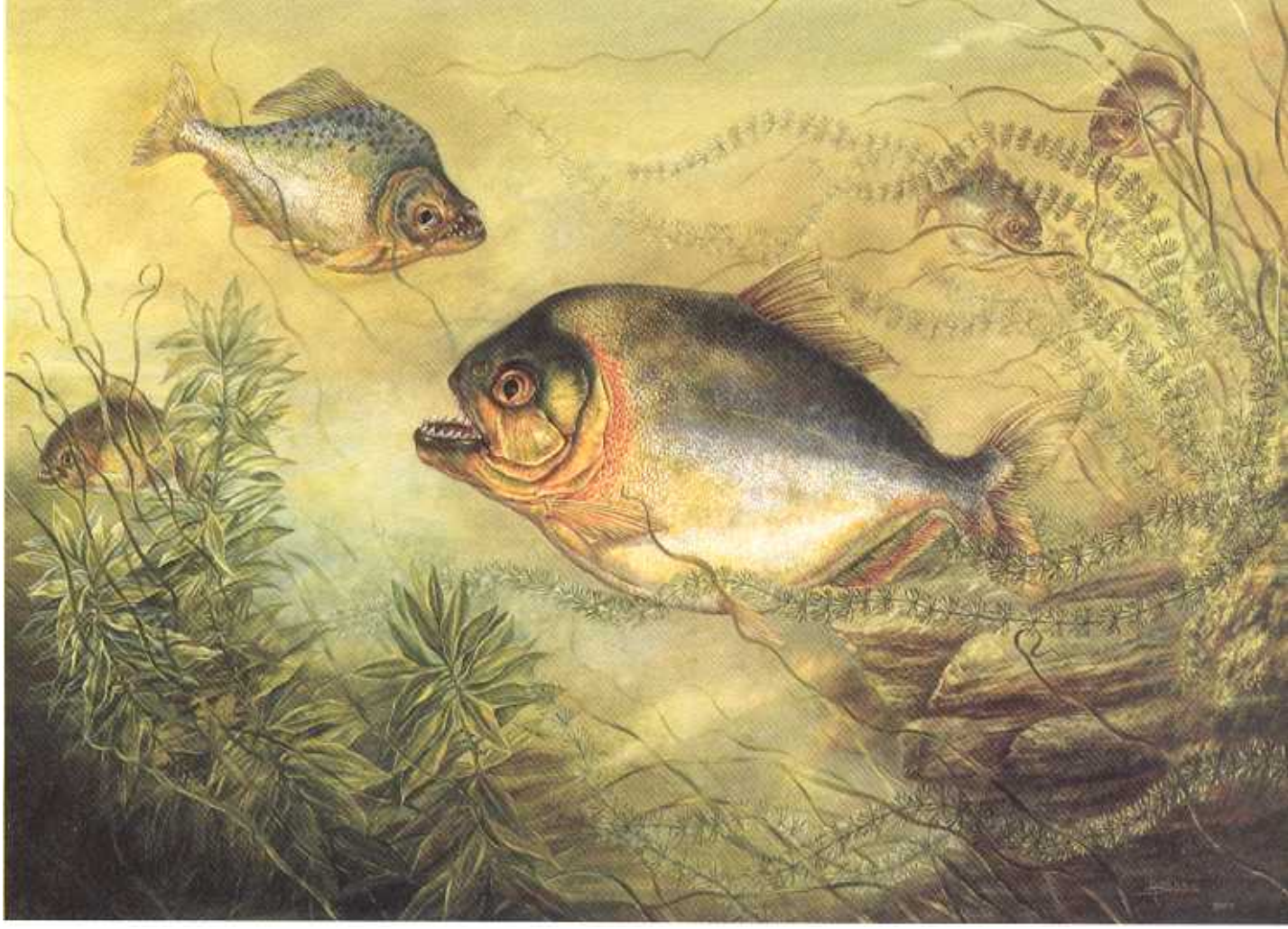

Figure 9.
As conspicuous predators of neotropical fish communities, piranhas, eg, Pygocentrus *sp, affect not only the population dynamics of their prey, but they also influence many aspects of prey behavior by posing a threat.*
ROSALIA DEMONTE

body shapes and habitat preferences most similar to its own.

Evidence from both field data on nip damage and laboratory prey-choice experiments indicates that cichlids are either particularly vulnerable to piranhas, or that they are greatly preferred by them. Why should either be the case? It seems unlikely that the fin tissue of cichlids is more nutritious than that of most other South American fishes. Without biochemical data this possibility remains a possible factor in determining piranha feeding responses, albeit an unlikely one. Winemiller[15] argues that larger cichlids provide easy targets for small fin-nipping piranhas because: they are relatively slow; most have large, broad fins; they are diurnally active, large, and hence relatively conspicuous; and they occupy the same habitats as small juvenile piranhas (eg, near stream margins, often near aquatic vegetation or other physical structures). Prey availability also influences profitability, and cichlids are generally abundant in backwater habitats, like Caño Maraca, that serve as nursery areas for piranhas. Cichlids (perciforms) were not the most abundant taxonomic groups at Caño Maraca, but they were nipped with disproportionately greater frequency than other fish orders (Tables 2&3).

PREY DEFENSES AGAINST PIRANHAS

Approximately half the 83 fish species documented at Caño Maraca were nipped infrequently or not at all. Several traits may account for this apparent lack of susceptibility to, or avoidance by, fin-nipping piranhas. First,

The South American fish fauna is the most species-rich on Earth. Associated with this rich taxonomic variety is a diversity of ecological roles and species associations, many of which seem rather bizarre in reference to ecological findings in temperate zones. Feeding specialization, such as fin nipping, and defensive adaptations, like eyespots and head mimicry by the tail region, become less surprising as scientists obtain more information from the tropics.

small fishes may have fins so small that they do not provide adequate targets for piranhas, or they are not profitable in terms of net energy gained (eg, energy consumed–energy expended to capture and process the resource). We found a positive correlation between maximum length of species and the frequency of fin damage in the field. The Caño Maraca site is dominated by small fishes, most of which were rarely exploited by small fin-nipping piranhas. In addition, small fishes can find refuge in the narrow spaces within dense stands of aquatic plants or in the shallow water at the very margins of streams and swamps. Many small characiforms, catfishes (Siluriformes), guppies, and killifishes (Cyprinodontiformes) probably avoid encounters with fin predators by means of this fine-scale habitat separation. Even some of the large nocturnal fishes probably avoid encounters with piranhas by hiding in dense vegetation during daylight (eg, knifefishes and catfishes). At the Caño Maraca site, the dwarf cichlid *Apistogramma hoignei* suffered no fin predation, and this likely resulted from the combined effects of size-dependent profitability (smaller fins provide a smaller target) and habitat selection.

Some of the larger fishes may defend themselves against piranha attacks using spines or frontal displays and biting. Many catfishes have venomous secretions associated with their sharp pectoral and dorsal spines (eg, *Pimelodella* spp [Pimelodidae] and *Corydoras* spp [Callichthyidae]). The predatory characiform *Hoplias malabaricus* (Erythrinidae) has jaws armed with teeth nearly as formidable as those of the piranhas (Figure 2), yet it suffered moderately high incidence of fin predation at Caño Maraca (143 total nips; 24% of all individuals were nipped). Nearly all South American cichlids have only small coniform teeth used for grasping, yet some successfully ward off fin-nipping piranhas with frontal attacks and aggressive displays.[15] I Sazima and F A Machado[10] describe the group defense tactic used by cichlids (*Cichlasoma dimerus* and *Mesonauta festivum*) against fin-nipping *Serrasalmus* in western Brazil. These cichlids organized themselves into a defensive ring near the substrate with their tails oriented toward the center of the ring and their heads oriented outward to fend off piranhas. This group defense would be particularly adaptive given our finding that piranhas attack the caudal fin much more frequently than other fins (Table 3).[2,7,8,10]

If larger cichlids are among the most conspicuous and profitable of prey for fin nippers, and if cichlids can repel piranha attacks with frontal displays and bites, then features that confound the discernment of a cichlid's head and tail regions would be advantageous. We tested the hypothesis that the dense, opaque fin scales and caudal eyespots of the largest South American cichlids are adaptions that reduce fin-predation by piranhas.[15] *Astronotus* received fewer nips than a perciform fish of similar size (*Lepomis*) under the controlled conditions of the laboratory. Even though an entire suite of species-specific traits is associated with the treatment effect in these experiments, we believe that the presence of dense, small opaque scales on the median fins of *Astronotus* was a key trait leading to the observed differences. These dense scales obscure many of the visual cues that might identify fins for piranhas. The fins of *Lepomis*, as well as the vast majority of bony fishes (including cichlids from other parts of the world), are transparent, and have soft fin-rays running along their length. The fins of *Astronotus* and other large South American cichlids, such as *Cichla* and *Crenicichla* spp, that coexist with piranhas (Figure 5), are more rigid and opaque, and often closely match the colors of the head region.

The caudal eyespot in South American cichlids probably enhances mimicry of the head region by the tail region by confounding visual cues received by fin-nipping piranhas. Our experimental treatment for the presence or absence of eyespots was inconclusive. On the one hand, wild-type *Astronotus* with eyespots showed significantly less fin damage than red *Astronotus* that lack eyespots (nip depth, Table 6). On the other hand, our $AgNO_3$-treated wild-type *Astronotus* without eyespots did not experience greater fin damage than untreated wild-types. Based on the results of the various experiments, we conclude that dense scales on the median fins are the primary masking characteristic, and that the presence of caudal eyespots probably transmits additional confounding visual cues to the receiver. The piranhas in our eyespot-manipulation experiments may have been too large to be threatened by *Astronotus*. Tail mimicry of the head region would only be an effective deterrent to fin predation if the size ratio between predator and prey were large enough to pose a real threat to small serrasalmine piranhas.

To reduce levels of fin damage, eyespots need not be 100% effective in frightening away potential fin predators. For a small piranha, the decision whether to approach or flee an object transmitting cues associated with the head region of a large predatory cichlid must be made quickly. These small piranhas often rely on stealth, so that when they receive confusing visual signals, they hesitate and miss opportunities for attack. This confusion, or startle effect, on predators has also been proposed as an adaptive function of the eyespot patterns on the tail region of butterfly fishes (Chaetodontidae) of coral reefs[12] and on the wings of butterflies and moths.[1]

In addition to the insights gained from the field data, the other aquarium tests showed taxonomic prey preferences, positive results in the* Lepomis–Astronotus *experiments (obvious species differences were the presence of both dense fin scales and eyespots), and some support for an effect of eyespots (the red vs wild-type experiment).

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