

Convergence of a cryptic saddle pattern in benthic freshwater fishes

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Synopsis

Many North American stream fishes have a similar color pattern of four dark saddles against a light background. An interesting feature of the pattern, in addition to its widespread taxonomic distribution, is its consistent configuration. The interval between the first and second saddle is usually the largest, and the last (third) interval is the smallest. All saddled North American freshwater fishes live on uneven, rocky substrates, and nearly all live in flowing water. It is hypothesized that these fishes achieve crypsis through disruptive coloration; the light spaces between the saddles mimic rocks and the dark saddles appear as shadows or gaps between rocks. Saddles are spaced unevenly because rocks in streams are a mixture of sizes; a fish that mimics a series of rocks of similar sizes is more conspicuous than one that mimics rocks of different sizes. The placement of saddles was measured on five North American species. In four of five North American species measured (a sculpin and three darters), the longest spaces are towards the head where the body is also the widest, this is thought to enhance crypsis because pieces of gravel tend to be round or square. In the madtom, the saddle pattern tends more towards even spacing. The madtom may not rely on camouflage to the same extent as other species examined because of decreased predation pressure associated with being nocturnal and possessing sharp spines and venom glands.

Introduction

Many North American, bottom-dwelling stream fishes have a color pattern of four large dark dorsal saddles which continue down the side of the body as bars (Fig. 1). The saddles and bars are usually black, dark brown, or dark gray, and the intervening spaces are typically light brown, yellow, or light gray. Proportionally shorter fishes may have only three saddles, and elongated fishes may have five or six saddles but the condition of four saddles is much more common (Page & Burr 1991). The dark saddle pattern is found in an array of unrelated fishes including sculpins (Scorpaeniformes), several line-

ages of darters (Perciformes), catfishes (Siluriformes), and suckers (Cypriniformes) (Table 1).

An especially interesting feature of the saddle pattern, in addition to its widespread taxonomic distribution, is its consistent configuration. Not only are there usually four saddles, but the saddles are almost always in the same spatial arrangement: the interval between the first and second saddle is the largest, and the last (third) interval is the smallest. In North America, we have identified at least 49 species in six genera and four families of freshwater fishes with this pattern. Based on available information regarding the phylogenetic relationships of these groups (Grady & LeGrande 1992, Page 1983,

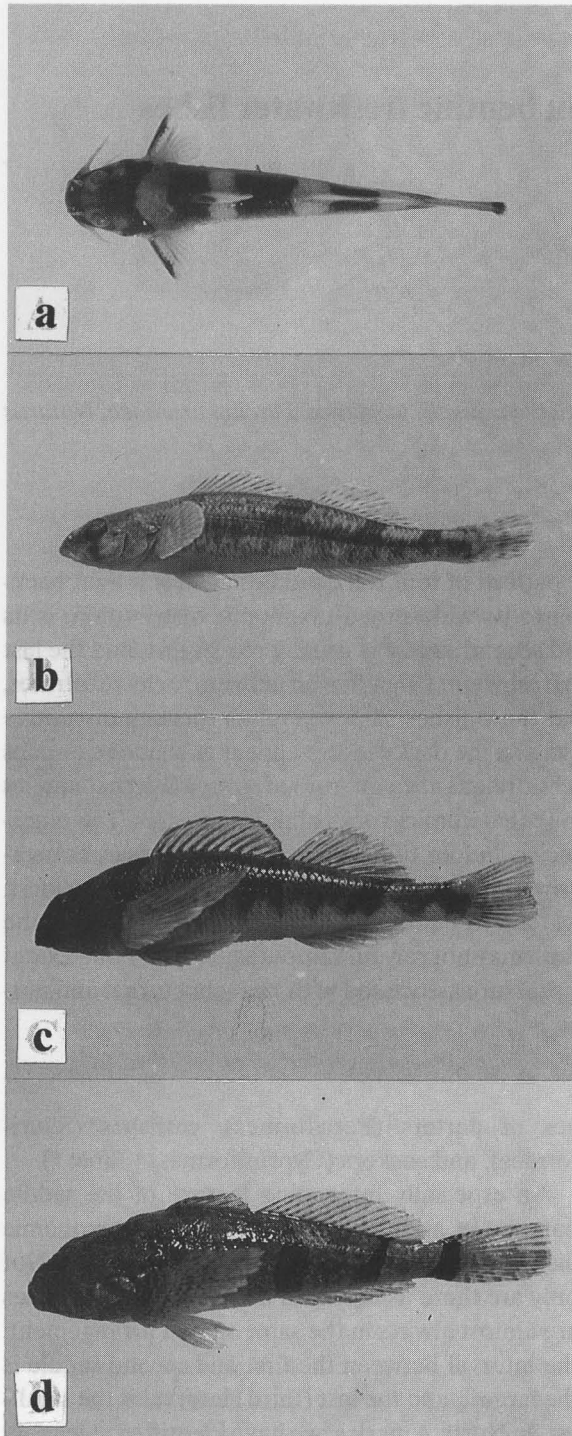


Fig. 1. A pattern of four dorsal saddles is found in many North American benthic fishes. Examples include: a – *Noturus elegans*, b – *Percina tanasi*, c – *Etheostoma blennioides*, d – *Cottus caroliniae* (photographs by: a – Brooks M. Burr, b–d – Lawrence M. Page).

Smith 1992, Stephens et al. unpublished), the pattern has evolved in at least nine separate lineages.

Adaptive significance of the saddle pattern

Color patterns in animals function in one of four ways: crypsis, confusion of predators in ways that do not include hiding, as a warning to predators, or signaling conspecifics. A particular pattern may accomplish one or more of these functions, and all four functions have been hypothesized for animals with dark saddles (A. Thayer 1896, G. Thayer 1909, Cott 1966, Fogden 1974, Barlow 1972, Krebs & Davies 1987).

It is unlikely that fishes with the saddle pattern are trying to warn potential predators because most are small fishes with minimal defense mechanisms. The North American madtoms, many of which have toxins associated with their fin spines, may be exceptions and they may use a saddle pattern to advertise their toxicity.

It also is unlikely that the saddle pattern is useful in signaling conspecifics. Fishes with the saddle pattern are benthic and, consequently, they are viewed laterally by conspecifics. The saddle pattern is best developed dorsally, out of the sight of conspecifics.

It also is unlikely that these fishes are trying to confuse predators by means other than hiding. Barlow (1963, 1972) found that fishes that attempt to confuse predators by utilizing a barring pattern are usually deep-bodied and occur in schools that swim continuously just above the substrate. Predators approaching a school have difficulty selecting individual fishes to attack. In contrast to typical schooling fishes, species with the saddle pattern are benthic, solitary, and move relatively little.

Excluding warning to predators, signaling conspecifics, and confusion of predators without hiding, the best explanation for the saddle pattern appears to be crypsis. A saddle or bar pattern can produce crypsis in two ways: obliterative countershading and disruptive coloration (also confusingly referred to as obliterative coloration) (A. Thayer 1896, G. Thayer 1909, Cott 1966, Lythgoe 1979). Obliterative countershading is similar to simple countershading (light below and dark above), ex-

cept that it requires the addition of either bars or spots. A barred species utilizing obliterative countershading typically has many, alternating, dark and light bars on the side of the body that create a grate. The best-known examples are zebras; a North American fish with obliterative countershading is the logperch, *Percina caprodes*.

Barred, obliteratively countershaded animals are most cryptic under low light conditions due to the eye's perception of the grate pattern through the use of spatial frequency analysis (Lythgoe 1979). Since the minimum spatial frequency that can be detected by the eye increases as light levels decrease (that is, the bars must be wider and further apart to be seen – Kelly 1961), under low light conditions the spatial pattern of a barred animal is too low to be detected, and the animal seems to disappear. Barred, obliteratively countershaded animals are especially cryptic at low light levels, and the

background upon which this pattern is viewed is inconsequential. Light is scattered in aquatic environments, creating an ideal place for this type of crypsis (Lythgoe 1979), and barred fishes living against a homogeneous background, such as open water, can be cryptic.

Disruptive coloration acts to break up an animal's body into elements that are no longer identifiable as an animal. G. Thayer (1909) used the example of a copperhead, *Agkistrodon contortrix*, lying on dead leaves. He suggested that the tan spaces between the dark bands on a copperhead represent leaves, and the bands are gaps and dark shadows between the leaves. By breaking up its body into elements similar to the substrate, the copperhead achieves crypsis.

When studying disruptive coloration, it is necessary to consider the background upon which the animal lives in order to suggest an adaptive expla-

Table 1. Species from North America north of Mexico that possess the saddled pattern.

Family	Species	Family	Species
Catostomidae	<i>Hypentelium nigricans</i>	Percidae	<i>C. cognatus</i>
	<i>H. etowanum</i>		<i>C. girardi</i>
	<i>H. roanokense</i>		<i>C. greenei</i>
	<i>Thoburnia atripinnis</i>		<i>C. hypselurus</i>
	<i>T. hamiltoni</i>		<i>C. leiopomus</i>
	<i>T. rhothoeca</i>		<i>C. pygmaeus</i>
Ictaluridae	<i>Noturus albater</i>		<i>C. rhotheus</i>
	<i>N. baileyi</i>		<i>Crystallaria asprella</i>
	<i>N. elegans</i>		<i>Etheostoma blennioides</i>
	<i>N. eleutherus</i>		<i>E. boschungii</i>
	<i>N. flavater</i>		<i>E. caeruleum</i>
	<i>N. flavipinnis</i>		<i>E. collettei</i>
	<i>N. furiosus</i>		<i>E. euzonum</i>
	<i>N. hildebrandi</i>	<i>E. juliae</i>	
	<i>N. miurus</i>	<i>E. kanawhae</i>	
	<i>N. munitus</i>	<i>E. osburni</i>	
	<i>N. stigmosus</i>	<i>E. sellare</i>	
	<i>N. taylori</i>	<i>E. sp. (Sunburst darter)</i>	
Cottidae	<i>N. trautmani</i>	<i>E. tetrazonum</i>	
	<i>Cottus aleuticus</i>	<i>E. trisella</i>	
	<i>C. baileyi</i>	<i>E. variatum</i>	
	<i>C. bairdi</i>	<i>Percina antesella</i>	
	<i>C. beldingi</i>	<i>P. ouachitae</i>	
	<i>C. carolinae</i>	<i>P. tanasi</i>	
		<i>P. uranidea</i>	

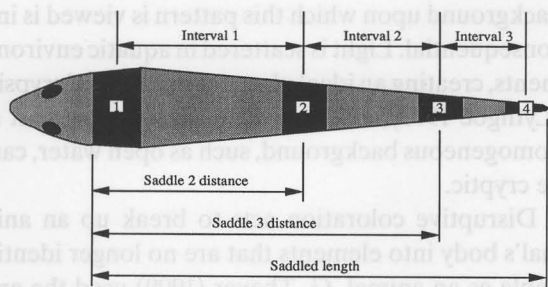


Fig. 2. Measurements used for the comparison of the saddled patterns of five species of North American fishes. Boxed numbers are saddle numbers.

nation for its pattern. It is unlikely that an organism utilizing saddles as disruptive coloration would be found normally against a uniform background because adding structure to an otherwise featureless background would make the organism more visible. In fishes, the saddles may disrupt the body outline when the fish is viewed over a heterogeneous substrate such as gravel.

We examined several aspects of the saddle pattern and the ecological characteristics of North American fishes in order to determine what elements in the pattern are important and which form of crypsis the fishes are utilizing.

Interspecific variation

We attempted to determine whether the exact placement of the saddles on the body (i.e., 'saddle midpoints') and the relative spacing of the saddles within a species were consistent in the saddled pattern in different phyletic lineages. We made measurements on specimens of five North American species housed at the Illinois Natural History Survey: a sculpin, *Cottus carolinae* (60 specimens), three darters, *Etheostoma blennioides* (46), *E. variatum* (60) and *Percina uranidea* (23), and a catfish, *Noturus flavater* (10). We consider the presence of saddles to be a derived state independently evolved in all five lineages represented by species examined. Although two of the darters are in *Etheostoma* they are not sister taxa (Stephens et al. unpublished), and the saddles are thought to be the result of convergence.

Measurements were confined to the area of the body termed the saddled length (Fig. 2), defined as the length from the anterior border of the first saddle to the posterior border of the fourth saddle. All species showed intraspecific variability in the width (distance from the anterior saddle margin to the posterior saddle margin) of the saddles; therefore,

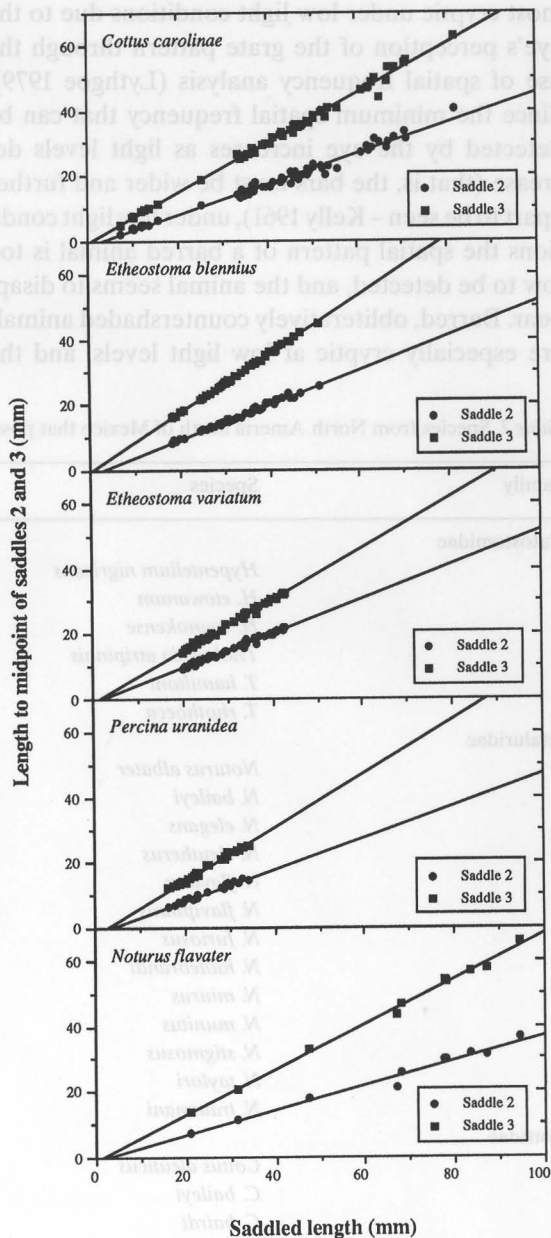


Fig. 3. Linear regressions of saddle 2 distance and saddle 3 distance on saddled length in five species of North American fishes.

Table 2. Tukey tests for saddle 2 distance and saddle 3 distance. Values greater than 0.05 (boldface) indicate that there is no significant difference between the two species in the placement of the saddle.

Species	<i>C. carolinae</i>	<i>E. blenni</i>	<i>E. variatum</i>	<i>P. uranidea</i>	<i>N. flavater</i>
<i>a. Saddle 2 distance</i>					
<i>C. carolinae</i>	1.00000				
<i>E. blenni</i>	0.00002	1.00000			
<i>E. variatum</i>	0.00002	0.12155	1.00000		
<i>P. uranidea</i>	0.07618	0.00002	0.00002	1.00000	
<i>N. flavater</i>	0.00002	0.00002	0.00002	0.00002	1.00000
<i>b. Saddle 3 distance</i>					
<i>C. carolinae</i>	1.00000				
<i>E. blenni</i>	0.00002	1.00000			
<i>E. variatum</i>	0.08980	0.00002	1.00000		
<i>P. uranidea</i>	0.79586	0.00002	0.01604	1.00000	
<i>N. flavater</i>	0.00002	0.00002	0.00002	0.00002	1.00000

the exact positions of the saddles were defined as the midpoints of the saddles along the dorsal midline. The midpoint of each saddle was determined by averaging the measurements taken at the anterior and posterior edges of the saddle. In *C. carolinae*, the midpoint of the first saddle had to be estimated using the average width of the other three saddles because the posterior margin of the first

saddle was usually indistinct on preserved specimens.

Patterns of the species were compared in two ways. The first was a comparison between species of two saddle distances (Fig. 2): the distance between the anterior margin of the first saddle and the midpoint of saddle 2 ('saddle 2 distance'), and the distance between the anterior margin of the first saddle and the midpoint of saddle 3 ('saddle 3 dis-

Table 3. Tukey tests for comparison of intervals within species. No comparisons were significant. Degrees of freedom: *N. flavater* = 27, *C. carolinae* = 177, *P. uranidea* = 66, *E. variatum* = 177, *E. blenni* = 135.

<i>Cottus carolinae</i>				<i>Percina uranidea</i>			
Interval #	1	2	3	Interval #	1	2	3
1	1.00000			1	1.00000		
2	0.00002	1.00000		2	0.00011	1.00000	
3	0.00002	0.00002	1.00000	3	0.00011	0.00011	1.00000
<i>Etheostoma blenni</i>				<i>Noturus flavater</i>			
Interval #	1	2	3	Interval #	1	2	3
1	1.00000			1	1.00000		
2	0.00002	1.00000		2	0.04160	1.00000	
3	0.00002	0.00002	1.00000	3	0.00076	0.00013	1.00000
<i>Etheostoma variatum</i>							
Interval #	1	2	3				
1	1.00000						
2	0.00002	1.00000					
3	0.00002	0.00002	1.00000				

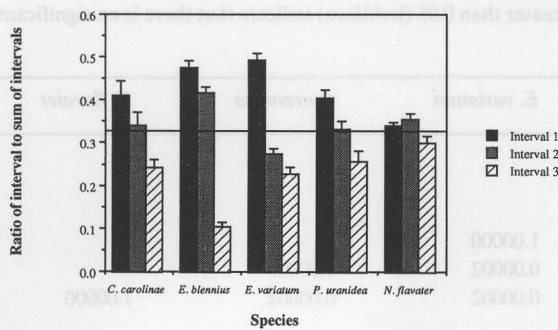


Fig. 4. The relative spacing of all five species examined differed significantly from an evenly spaced pattern indicated by the line at 0.333. The error bars indicate one standard deviation.

ance'). Saddle 4 was excluded from this comparison because the saddled length and the distance to the midpoint of saddle 4 were nearly equal, differing only by half of the width of saddle 4. Ratios of the saddle 2 distance and saddle 3 distance to saddled length were determined for each individual and then arcsine transformed to normalize the values. An ANCOVA was applied to the arcsine transformed measurements of each saddle separately, holding the log transformed saddled length as the covariate. The ANCOVA was followed by Tukey tests in order to compare individual pairs of species. The data were also plotted as a linear regression of saddle distance to saddled length (Fig. 3).

The second comparison determined whether the placement of the saddles on the body within a species deviated from an evenly spaced pattern. An interval was defined as the distance between the midpoints of successive saddles (Fig. 2). A ratio of each interval to the sum of the intervals was determined and arcsine transformed. These intervals were chosen instead of measuring the interspaces directly because the sum of the ratios of the intervals equals 1, making it easier to compare the relative interval size both intraspecifically and interspecifically. To test whether species deviated from an evenly spaced pattern, an ANOVA was performed for each species on the arcsine transformed ratios of interval lengths to saddled length. The ANOVA's were each followed by Tukey tests in order to determine if any of the following was true within a species: interval 1 = interval 2, interval 1 = interval 3, and interval 2 = interval 3.

The significance of each of the linear regressions of saddle 2 distance and saddle 3 distance on saddled length (Fig. 3) was quite high for each of the five species ($p < 0.00005$). All fishes, large or small, plotted closely to the regression line indicating that the effects of allometry are small.

The ANCOVA showed that there are differences between species in the exact position of the saddles, suggesting that exact placement of the saddles may not be very important in the evolution of the saddled pattern. However, there are striking similarities among the species. Tukey Tests (Table 3) indicate that the positions of saddle 2 and saddle 3 are not significantly different in *C. carolinae* and *P. uranidea* ($0.05 < p < 0.10$ and $0.75 < p < 0.80$), suggesting that the pattern is the same in the two species. Saddle 2 in *E. blennioides* is not significantly different from that of *E. variatum* ($0.10 < p < 0.15$), and the position of saddle 3 of *E. variatum* is not significantly different from that of *C. carolinae* ($0.75 < p < 0.80$).

In all species examined except *N. flavater*, all four saddles are spaced unevenly ($p < 0.001$) (Fig. 4, Table 2), and all intervals were significantly different from one another within a species (all $p < 0.0005$). In *N. flavater*, the pattern also was uneven ($p < 0.001$), but interval 2 was only slightly significantly larger than interval 1 ($0.04 < p < 0.05$). With two intervals of nearly the same size, the pattern of *N. flavater* tends more towards an evenly spaced pattern than that of the other four species in which interval 1 always was the largest and interval 3 was the smallest.

Ecological characteristics of North American fishes with the saddle pattern

To identify ecological characteristics of North American fishes with the saddle pattern, we used the information in Page (1983) and Page & Burr (1991). We scored substrate and flow preferences as well as presence or absence of 3–5 dark dorsal saddles for all species of the families Catostomidae (61) and Ictaluridae (38), all darters (Percidae) (146), and all *Cottus* (Cottidae) (24). Substrate was scored as either uniform (sand, mud, and bedrock) or un-

even (gravel, cobble, and boulders). Flow was scored as no/low flow (pools and lakes) or flow (riffles and runs).

The preference for flowing or standing water and the preference for uniform or uneven substrate were examined in 269 species, 49 of which have the saddle pattern. All of the saddled species live on uneven, rocky substrates, and nearly all ($N = 46$) live in flowing water. These results were analyzed using a Chi-square contingency table (Table 4) which showed that saddled species prefer uneven substrates and flowing water. A Chi-square test was also applied to determine the relationship of flow to substrate. A significant interaction between substrate type and flow ($p < 0.0001$) was found, as expected, because faster flowing water tends to wash out the smaller particles such as sand and mud while leaving the gravel, cobble, and boulders (Moyle & Cech 1988). Because phylogenies are lacking for most groups of North American fishes, it is impossible to exclude the effects of phylogeny, and the Chi-square test probably suffers from pseudoreplication. However, the data strongly suggest a positive relationship between living in flowing water over a rocky substrate and having the saddle pattern.

Discussion

We propose that the selective advantage leading to the multiple evolution of the saddle pattern is through disruptive coloration. The fishes with the saddle pattern are always found on gravel, and we propose that dark saddles mimic shadows or gaps between rocks while the light spaces between the saddles represent rocks. Species with the saddle pattern also prefer flowing water. However, three of the saddled species live in pools with little or no flow. The pools in which these species live are rocky, and we assume that the main habitat element that has promoted the evolution of the saddle pattern is uneven, rocky substrates. Flow may have aided in the evolution of the pattern because of additional shadows cast by surface ripples created by flowing water.

Additional evidence supporting the claim that

the saddle pattern is not primarily for obliterative countershading is the fact that the saddles of saddled species collected over sand are faded or lost. *Cottus carolinae*, in particular, blanches to the color of the sand and the saddles are barely visible as slightly darker areas on the back. If the saddle pattern served some function other than mimicking rocks, the saddles presumably would not fade when the fishes moved onto sand. Also, pelagic fishes normally lacking saddles sometimes develop some form of saddle or bar pattern when they become benthic (Barlow 1963, Hailman 1982, Neil 1984). This change often corresponds to a change in behavior from active movement to slow or no movement. Finally, although juvenile hog suckers (*Hypentelium* spp.), which live in rocky riffles, are strongly saddled, hog suckers lose their saddle pattern as they grow and move into deeper, slower, less rocky habitats.

The five species examined, and many more species, have converged upon a pattern of four saddles. In the five species examined, all except *N. flavater* possess a highly uneven pattern: interval 1 was the largest and interval 3 was the smallest. This observation leads to three questions: 1. What is the advantage of a pattern of unevenly spaced saddles? 2. Why are the spaces between the saddles larger towards the head? 3. Why doesn't *N. flavater* conform to the pattern of the other four species?

What is the advantage of a pattern of unevenly spaced saddles?

When viewed from above (Fig. 5), each saddle delineates a light space that has the appearance of a rock, and a fish with four saddles is broken into a series of five 'rocks' (head, caudal fin, and three interspaces). Animals maximize their crypsis by mimicking a random sample of the background (Endler 1978). Because rocks in streams are a mixture of sizes and slopes, a fish that mimicked a series of rocks of similar proportions would be more conspicuous than one that mimicked a series of rocks of different sizes. The five 'rocks' of different sizes on a four-saddled fish blend into the substrate.

Why are the spaces between the saddles larger towards the head?

The body of a fish tapers from head to tail and, consequently, the widest space always will be the

space nearest the head. Because pieces of gravel in a stream are usually round or slightly elliptical, a fish can best mimic the substrate by having the longest spaces near the head.

Although the general pattern is for spaces to be longest near the head, *C. carolinae* has the ability to widen its first saddle such that the first space becomes smaller. *C. carolinae* can also go to the opposite extreme by eliminating its first saddle so that the first space is much larger and includes the head. The ability to change the relative size of the saddles enhances the sculpin's ability to camouflage itself. A sculpin would be expected to eliminate the first saddle when it is among large gravel, but widen the first saddle when it is among smaller gravel.

Why doesn't *N. flavater* conform to the pattern of the other four species?

N. flavater deviates from the pattern exhibited by the other four species examined in that interval 1 and interval 2 are barely significantly different from one another. It seems likely that, to a fish living on a rocky substrate, an uneven pattern is more cryptic than an even pattern; therefore, *N. flavater* must not rely on camouflage to avoid predation to the same extent as the other species examined. Organisms under decreased predation pressure can afford to be less cryptic than organisms under high predation pressure (Endler 1978, 1986). Madtoms reduce their predation pressure in two ways. The first is that they



Fig. 5. *Cottus carolinae* in Big Creek Hardin Co., IL. This individual shows the sculpin's ability to widen its first saddle and, concomitantly, shrink the first space (photograph by Jonathan W. Armbruster).

Table 4. Contingency table for the effects of flow (a) and of substrate (b) on the saddle pattern. The Chi-square values indicate that saddled species are found more often in flowing water and on an uneven substrate than would be expected by chance.

a	Flow	No flow	Total
Saddles absent	110	110	220
Saddles present	46	3	49
Total	156	113	269
$X^2 = 13.2177$ (d.f. = 1)			
$p < 0.001$			

b	Uneven	Uniform	Total
Saddles absent	167	53	220
Saddles present	49	0	49
Total	216	53	269
$X^2 = 29.8948$ (d.f. = 1)			
$p < 0.0001$			

are nocturnal, hiding under rocks during the day when visually oriented predators abound. Secondly, madtoms possess sharp pectoral fin spines with venom glands at their bases. With this additional protection, *N. flavater* can afford to be less cryptic than other saddled species. In contrast to *N. flavater*, some species of madtoms (e.g. *N. miurus* and *N. flavipinnis*) have a more uneven saddle pattern. The color patterns and degree of toxicity in madtoms deserve additional study.

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