

**Loss of Nuptial Color in Threespine Sticklebacks (*Gasterosteus aculeatus*)**



T. E. Reimchen

*Evolution*, Vol. 43, No. 2 (Mar., 1989), 450-460.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28198903%2943%3A2%3C450%3ALONCIT%3E2.0.CO%3B2-Z>

*Evolution* is currently published by Society for the Study of Evolution.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## LOSS OF NUPTIAL COLOR IN THREESPINE STICKLEBACKS (*GASTEROSTEUS ACULEATUS*)

T. E. REIMCHEN

Department of Zoology, University of Alberta, Edmonton, AB T6G 2E9, CANADA

**Abstract.**—Loss of conspicuous nuptial color in *Gasterosteus aculeatus* (threespine stickleback) has been reported from several localities in western North America and is ascribed to increased rates of predation or to convergent threat displays. I have examined 66 populations of *G. aculeatus* from the Queen Charlotte Archipelago and found extensive variation in the expression of red nuptial color. Males in 31 of the populations lack red throats, while males in five populations have major expression of red nuptial color. I test two hypotheses for nuptial-color loss: that the loss results from increased predation rates and that it involves differences in water spectra (relative transmission at 400 nm). Results, which are consistent with the second hypothesis, show that the greatest expression of red pigment occurs in habitats with the highest water clarity, while loss of red nuptial color is generally found in heavily stained waters. There is no correlation between nuptial-color loss and presence or absence of vertebrate predators. Two new hypotheses for these associations are proposed: signal-masking in spectrally restricted habitats and carotenoid deficiencies in the diet. Previous studies of red nuptial color and its loss in *Gasterosteus* merit additional attention, given the associations with underwater spectra.

Received June 1, 1987. Accepted July 30, 1988

Red nuptial coloration on the throat of male threespine sticklebacks (*Gasterosteus aculeatus*) is a classic example of an epigamic trait that functions to attract females and intimidate rival males (Darwin, 1871; Pelkewijk and Tinbergen, 1937; Rowland, 1984; Rowland and Sevenster, 1985). While this trait is prevalent throughout the circumboreal distribution of the species, there are several populations from western North America in which the red nuptial-color phenotype is replaced by a melanic phenotype (McPhail, 1969; Semler, 1971; Moodie, 1972a; Hagen and Moodie, 1979; Reimchen et al., 1985). Crosses involving fish from one locality indicate that this trait is heritable (McPhail, 1969; Hagen and Moodie, 1979). Several mechanisms have been proposed to account for the evolution of these exceptional populations. Increased risk of mortality of the conspicuous phenotype constitutes the most probable cause in habitats where salmonid predators are common (Semler, 1971; Moodie, 1972a), and this provides one of the few examples of evolutionary loss of conspicuous epigamic traits in response to predation (Anderson, 1982). A second hypothesis, convergent threat display, has been proposed for areas where melanic males are sympatric with *Novumbra hubbsi*, the black Olympic mudminnow (Hagen et al., 1980). Accord-

ing to this hypothesis, melanic males have higher reproductive success due to reduced territorial incursions by *Novumbra*.

In a recent investigation of morphological variation in *G. aculeatus* from several bog lakes in the Queen Charlotte Islands, Reimchen et al. (1985) noted that breeding males were highly melanic and lacked red nuptial color. These habitats were deeply stained, a characteristic that should favor increased prevalence of red nuptial patterns (Levine et al., 1980). My purposes here are 1) to determine whether the relationship between nuptial-color loss and water staining observed in the preliminary survey is a general phenomenon in the archipelago, 2) to examine the importance of predation risk as the mechanism for nuptial-color loss, and 3) to explore new hypotheses for the associations.

### MATERIALS AND METHODS

Sixty-six geographically diverse localities on the Queen Charlotte Islands, British Columbia, with indigenous populations of *G. aculeatus* were sampled as part of ongoing evolutionary studies on this species (Fig. 1A). Surface water samples were collected in opaque vials from the littoral nesting habitat of the sticklebacks during their reproductive season (April–July). Relative transmission for each wavelength on a Digi-

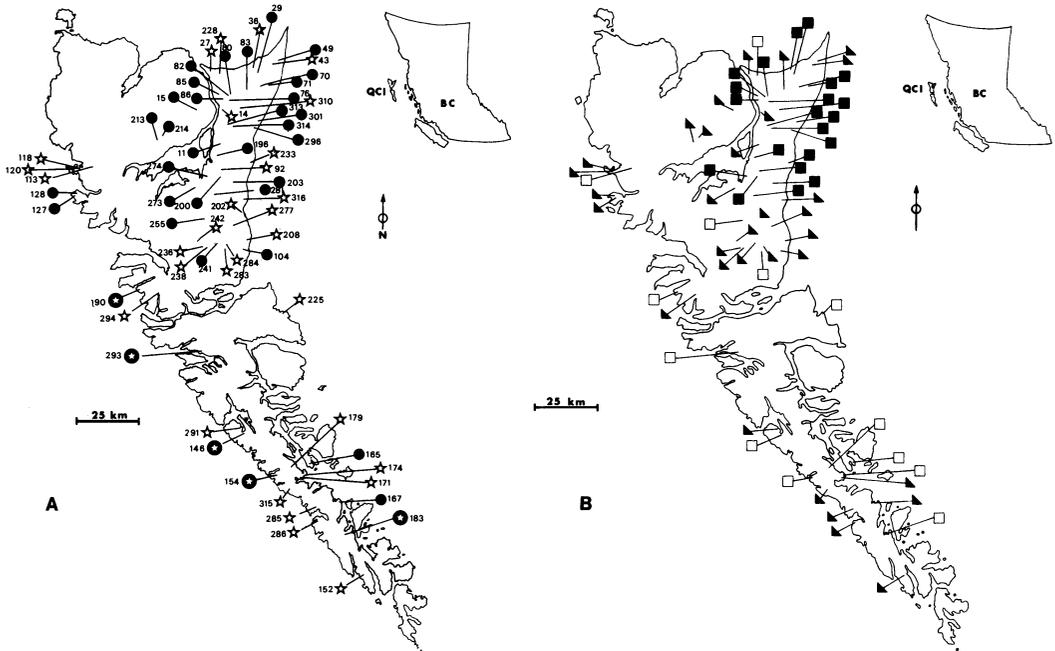


FIG. 1. A) Geographical distribution of nuptial-color phenotypes on the Queen Charlotte Islands (inset: British Columbia). Symbols: solid circle = red throat absent (see category 1 in Fig. 2); star = average red throat (see categories 2–4 in Fig. 2); solid circle with star = extensive red nuptial expression (see category 5 in Fig. 2). Locality numbers correspond to names given in Table 1. B) Geographical distribution of water color ( $T_{400\text{ nm}}$  relative to distilled water) in streams and lakes on the Queen Charlotte Islands. Open square = at least 90.0%; triangle = 70.0–89.9%; closed square = less than 70.0%.

spec spectrophotometer was determined from 380 nm to 700 nm at 20- or 50-nm intervals with recalibration to distilled water (100% transmission) at each wavelength. Most of these habitats are oligotrophic or dystrophic and appear to lack suspended or settled matter. Filtering samples from five representative localities yielded small differences (maximum 4%) from unfiltered samples. For most purposes, I used relative transmission at 400 nm ( $T_{400}$ ) as a standard measure of water color, as these shorter wavelengths are the most variable between localities;  $T_{400} = 50\%$  corresponds to an approximate secchi-disc reading of 1 m. To estimate temporal variability in  $T_{400}$ , I compared water samples from different years (same month) for five localities. Maximum differences between years was 4% relative to the total transmission.

Fish were collected during May–July from nesting areas with standard-size minnow traps or a beach seine; notes on general body coloration of fish (e.g., mottled, counter-

shaded, heavily melanic) were made at the time of collection. Breeding males could be generally ascertained, independent of throat color, by increased body melanism and iridescence in the eye and opercular region. Development of red nuptial pigmentation followed a regular graded series and was subjectively assigned into one of five categories ranging from complete absence to maximum expression (Fig. 2). The former was usually associated with highly melanic fish in which the throat exhibited the same general extent of melanism as the rest of the body surface. The latter category included fish with red pigment extending from the throat to the pelvis and from the mid-ventral surface, dorsolaterally, to the base of the eye and operculum. At most localities, the individual with the most extensive red nuptial development was photographed. In some collections, red pigmentation was lacking on all reproductive males. While this may indicate actual nuptial-color loss in the population, it may also simply reflect col-

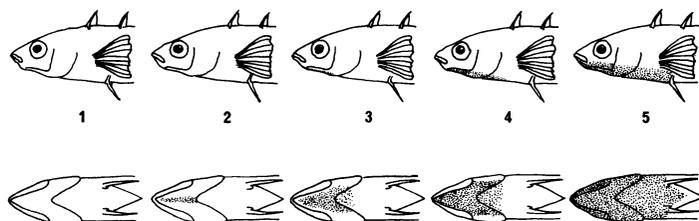


FIG. 2. Representative lateral and ventral red nuptial patterns of *G. aculeatus* from the Queen Charlotte Islands. Red pigment is indicated by shading. The figure shows categories (1–5) used for scoring throat color.

lecting methodology. For example, nuptial expression depends on reproductive phase (Moodie, 1970), and unless territorial individuals were collected during the appropriate period, nuptial color would be lacking. In addition, nuptial color may fade if the male is removed from the territory (Wootton, 1976); this could result in a bias in the data if males were not scored immediately after capture or if they were left in the traps for extended periods. Where possible, I obtained additional samples by seining or by dipnetting several breeding males from nesting territories to verify nuptial color. Because of the phenotypic plasticity, my scoring may underestimate the maximum extent of red nuptial coloration, although the bias should be similar in all populations. Consequently, I used the individuals with the greatest expression of red nuptial pigment as representative of the population. This was reasonable, as the majority of males with nuptial color in any sample had approximately the same or only marginally reduced amount of red nuptial pattern as the male with the maximum expression. For the analyses, I grouped the five nuptial throat colors into three categories: melanic (Fig. 2: category 1), average red (Fig. 2: categories 2, 3, and 4), and extensive red (Fig. 2: category 5). In several populations, there appeared to be evidence for polymorphism in presence or absence of red nuptial pigmentation. However, meaningful estimates of phenotype frequencies could not be obtained, since it was not possible to distinguish a morph lacking red pigment from an individual that had temporarily lost the pigment.

General methodology for assessing predatory regime involved combinations of a seine, minnow traps, and gill nets for cap-

turing predatory fish and visual surveys for avian piscivores. Detailed methodology and results will be presented elsewhere, although general techniques are found in Moodie and Reimchen (1976) and in Reimchen and Douglas (1980, 1984). For the purposes of this study, I coded localities into one of three general classes depending on the dominant predatory taxa: 1) invertebrate, 2) bird, and 3) fish and bird. The major groups of invertebrate predators are odonates and dytiscids; the major avian predators are *Gavia immer*, *G. stellata*, *Podiceps grisegena*, *P. auritus*, *Mergus merganser*, *Lophodytes cuculatus*, and *Ceryle alcyon*; and the major fish predators are *Salmo clarki*, *S. gairdneri*, *Cottus asper*, and *C. aleuticus*. For reproductive males with nuptial color, the risk of predation by invertebrates should be lowest (since invertebrates consume juveniles; Reimchen, 1980), the risk of predation by avian piscivores (which are primarily limnetic) should be moderate, and the risk of predation by large fish predators (which forage in the littoral regions [Moodie, 1972b] and in the horizontal plane where ventrolateral nuptial color would be visible) should be greatest.

Data were analyzed with stepwise multiple regression and tested with ANOVA. Spectral data were arcsine-transformed. Interactions between variables were examined with log-linear techniques, with spectral data partitioned into three  $T_{400}$  categories: 25–70%, 71–90%, and 91–99%.

## RESULTS

Among the 66 localities surveyed, red nuptial throat color was absent in 31 populations, moderately expressed in 30 populations, and extensively developed in five populations (Table 1). Throat color tends

TABLE 1. Nuptial color, predation regime, and aquatic spectra ( $T_{400}$  [%]; see text) for Queen Charlotte Island populations of *Gasterosteus aculeatus*. Throat color: 1 = red absent, 2 = average red, 3 = extensive red; Predation regime: 1 = invertebrate, 2 = bird, 3 = fish and bird.

Locality number	Locality	Throat color	Predation regime	$T_{400}$
11	Boulton Lake	1	2	76.9
14	Pure Lake	2	3	76.6
15	Spraint Lake	1	2	80.5
27	Delkatla Pond	3	2	78.5
29	Harelda Lake	1	2	49.5
36	Rouge Lake	2	2	68.1
43	Serendipity Pond	2	1	70.5
49	Gosling Pond	1	1	71.4
70	Richter Lake	1	2	51.9
71	Parkes Lake	1	2	60.5
76	Skonun Lake	1	3	68.0
80	Eriophorum Pond	1	1	45.0
82	Gros Pond	1	1	65.0
83	Solstice Lake	1	2	72.2
85	Drizzle Lake	1	3	67.0
86	Drizzle Creek	1	2	37.9
92	Mayer Lake	2	3	57.1
104	Stellata Lake	1	3	75.7
196	Loon Creek	1	1	60.1
200	Woodpile Creek	1	3	60.8
202	Tiell Pond	2	2	77.3
203	Geike Creek	1	1	62.9
208	Mollitor Pond	2	2	79.3
213	Ain Lake	1	3	86.7
214	Amber Lake	1	3	87.1
225	Sheldon Estuary	2	2	90.8
228	Chown Creek	2	1	91.5
233	Capeball Creek	2	2	46.7
236	Brent Creek	2	3	83.2
238	Elk Creek	2	3	80.5
241	Survey Creek	1	3	84.2
242	Sue Creek	2	3	85.9
255	Yakoun Creek	1	3	90.4
273	Florence Creek	1	1	76.3
274	Pt Clem Creek	1	1	57.0
277	Pontoon Pond	2	2	74.6
113	Coates Lake	2	3	94.5
118	Desolate Lake	2	1	82.0
120	Kiokathli Lake	2	2	75.0
127	Krajina Lake	1	2	86.5
128	Menyanthes Lake	1	2	82.0
146	Wright Lake	3	3	99.0
152	Snub Lake	2	3	82.5
154	Escarpment Lake	3	3	93.6
165	Smith Lake	1	2	95.0
167	Irridens Lake	1	3	87.0
171	Sundew Lake	2	2	86.4
174	Darwin Lake	2	3	90.0
179	Poque Lake	2	3	91.0
183	Lutea Lake	3	3	93.9
190	Stiu Lake	3	3	92.6
281	New Year Lake	1	1	68.6
283	S Anderson Lake	2	3	90.5
284	N Anderson Lake	2	2	88.1
285	Goski Lake	2	2	88.1

TABLE 1. Continued.

Locality number	Locality	Throat color	Predation regime	$T_{400}$
286	Gowgaia Lake	2	3	77.5
291	Fairfax Lake	2	2	89.9
293	Inskip Lagoon	3	2	99.6
294	Dawson Lake	2	2	82.0
296	Slim Lake	1	1	50.4
301	Oeanda Creek	1	1	29.5
310	Dam Lake	2	2	52.2
313	N Otter Lake	1	3	45.8
314	S Otter Lake	1	3	44.5
315	Puffin Lake	2	3	82.7
316	Tiell Estuary	2	2	81.8

to be similar among allopatric populations within watersheds. For example, in the Sangan drainage (localities 76, 80, 82, 83, 85, and 86), all populations lack red nuptial color, while in the Yakoun drainage (localities 236, 238, and 242), all stream populations have moderate red throats, but in a confluent pond to the main river course (locality 255) and an isolated lake (locality 281), the population lacks red throats. The lakes and streams surveyed occur in 45 distinct watersheds (outlets separated by marine waters); melanistic males occurred in 20 of these, moderate reds in 26, and extensive reds in five. Examination of the geographical distribution of the phenotypes (Fig. 1A) indicates that nuptial-color loss is most prevalent in the northeastern region, although melanistic populations occur sporadically throughout the archipelago. Major red expression occurs in the marine population (locality 293) and in disjunct lake populations on western and southern regions of the islands.

Spectral environments differed among the localities principally in the relative loss of short wavelengths, with  $T_{400}$  ranging from 29.5% to 99.5% (Fig. 3), the latter occurring in the marine locality. All heavily stained waters occurred in the northeastern lowlands, which are dominated by *Sphagnum* bogs (Fig. 1B). There was a relationship between water color and predators ( $X^2 = 12.2$ ,  $d.f. = 4$ ,  $P = 0.02$ ), with predatory fishes being more common in habitats with higher water clarity.

General associations among nuptial color, spectral data, and predators are shown

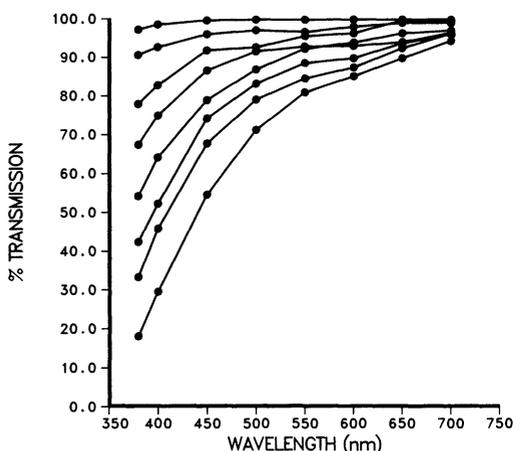


FIG. 3. Relative spectral transmission of water samples from eight representative localities on the Queen Charlotte Islands. Samples shown exhibit the range of water clarity and include samples from the localities where the water was most and least stained. All samples were calibrated against distilled water (100%) at each wavelength.

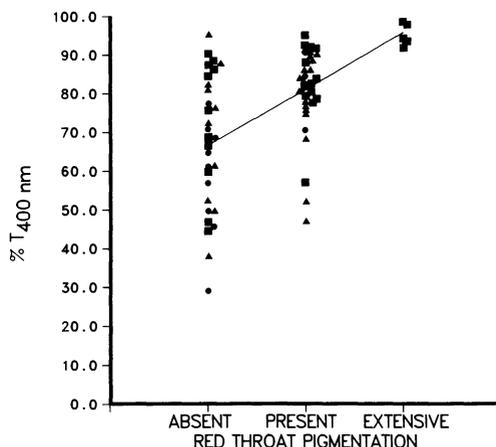


FIG. 4. Relationships among nuptial color, spectral data ( $T_{400}$  [%]), and predators for *Gasterosteus aculeatus* populations from Queen Charlotte Islands. See Figure 2 for grouping of nuptial-color categories. Predatory regime: circle = invertebrate, triangle = bird, square = fish and bird.

in Figure 4. Melanic males occur principally in heavily stained water (mean  $T_{400} = 65\%$ ), average red males usually occur in water with moderate staining (mean  $T_{400} = 81\%$ ), and the five populations with the greatest expression of pigment all occur in localities with exceptional water clarity (mean  $T_{400} = 96\%$ ). These five populations also have increased predation risk, as they are exposed to both avian and salmonid piscivores.

Multiple regression with throat color as the dependent variable and spectra and predators as independent variables indicates that the associations are statistically significant ( $r = 0.61$ ,  $F = 19.0$ ,  $P < 0.001$ ). The independent variables account for 37.6% of the variance, with spectra contributing 35.4% and predation 2.3%. Log-linear analysis shows comparable trends: throat color is statistically associated with spectra (partial  $X^2 = 31.2$ ,  $d.f. = 8$ ,  $P < 0.001$ ), but it is not associated with predation (partial  $X^2 = 2.4$ ,  $d.f. = 4$ ,  $P = 0.7$ ).

#### DISCUSSION

Red nuptial-color loss, generally considered to be a rare occurrence in *G. aculeatus* (Wootton, 1976; Hagen and Moodie, 1979), is common among sticklebacks in the Queen Charlotte Islands. Since freshwater stickle-

backs in separate watersheds are thought to be independently derived from marine forms (Moodie and Reimchen, 1976), the presence of this trait in at least 20 separate watersheds in the archipelago suggests a regular pattern of pigment loss. This extended survey corroborates a trend observed in a previous small-scale study in which nuptial-color loss was shown to be associated with heavily stained waters (Reimchen et al., 1985). However, the results of this study show that nuptial-color loss is not restricted to these stained waters and that the greatest expression of red nuptial display occurs in the habitats with exceptional water clarity.

Reduction in intensity of conspicuous nuptial color in sticklebacks (McPhail, 1969; Semler, 1971; Moodie, 1972b) and other vertebrates (Haskins et al., 1961; Haas, 1976; Endler, 1980; Andersson, 1982; Bredner and Stoner, 1987) has been usually interpreted as a response to increased predation rates. This interpretation does not readily account for the data that I have presented, since populations with nuptial-color loss often occurred in aquatic habitats where vertebrate predators are rare. It is theoretically possible that historically abundant predators are currently absent, but morphological examination of sticklebacks from these localities shows reduction of spines and lateral plates (Reimchen, 1980, un-

publ.; Reimchen et al., 1985), conditions generally found where vertebrate predators are uncommon (Hagen and Gilbertson, 1972; Moodie and Reimchen, 1976; Gross, 1978). Similarly, the five populations with the greatest expression of red nuptial color, including the marine population, exhibit enhanced lateral-plate development (modal number of lateral plates are 7, 8, 8, 35, and 35 for localities 154, 146, 183, 190, and 293, respectively [Reimchen, 1983, unpubl.]) consistent with general adaptations to vertebrate predators (Moodie and Reimchen, 1976). There is no substantive evidence to support the hypothesis that predation is responsible for evolutionary nuptial-color loss in these populations.

Moodie (1972a, 1972b) described a melanistic stickleback population from Mayer Lake, Queen Charlotte Islands (see Fig. 2: locality 92), in which only 15% of reproductive males developed red throats. In experimental tanks, sticklebacks with red throats were attacked by trout (*Salmo gairdneri*) more frequently than were melanistic males and he hypothesized that the conspicuous red males in the natural habitat have a greater risk of predation than melanistic males from resident *S. clarki* predators. This study has been cited in a review of sexual selection (Andersson, 1982) as one of the few demonstrations that the cost of conspicuous nuptial color involves increased predatory risk. While this is intuitively reasonable, there are several factors that allow a different interpretation of nuptial-color loss in this locality. Mayer Lake, as determined from the present spectral survey, is heavily stained ( $T_{400} = 57\%$ ), consistent with the broad association between nuptial-color loss and water staining observed elsewhere in the archipelago. The results of the predation experiments are not compelling, since they were carried out in clear water, where the red nuptial color pattern would be highly visible and conspicuous (as discussed below). Red and melanistic model sticklebacks suspended in the lake (and therefore under natural photic conditions) were attacked equally frequently by resident trout (Moodie, 1970), suggesting that red nuptial color was not more susceptible to predation in these stained waters. In localities adjacent to Mayer Lake, such

as Boulton Lake, which is also stained ( $T_{400} = 77\%$ ), trout predation is rare or absent (Reimchen, 1980), yet red nuptial color is absent as well (see Fig. 1: locality 11), demonstrating that predation risk is not essential for nuptial-color loss. The present evidence suggests that reexamination of this widely cited example of nuptial-color loss as a consequence of predation pressure (see Wootton [1976] for review) may be warranted.

McPhail (1969) and Hagen and Moodie (1979) argue that loss of red nuptial coloration in the Olympic Peninsula *G. aculeatus* is causally related to the presence of *Novumbra*, the black Olympic mudminnow. Both of these studies present compelling evidence that the black stickleback only occurs in creeks where *Novumbra* is present and that, within a creek, red-throated sticklebacks replace black sticklebacks where *Novumbra* are absent. McPhail (1969) showed experimentally that fry of black males are less susceptible to predation by sympatric *Novumbra* than are fry of red-throated males, due to the evasive movements of the fry. He concludes that it is the increased risk of fry predation that produces loss of red-throated males in these localities. However, Hagen and Moodie (1979) were unable to find direct evidence of predation by *Novumbra* on *G. aculeatus* fry. Using aquaria, they demonstrated that black male sticklebacks incur fewer territorial intrusions by *Novumbra* than do red-throated males, and as a consequence, the black males have higher reproductive output (Hagen et al., 1980). They suggested that black throat color in sticklebacks is perceived as a conspecific threat display by *Novumbra*, and as a result, selection has favored a loss of red nuptial color and a convergence towards the black color of *Novumbra*.

While this may be a sufficient and satisfactory explanation for nuptial-color loss in these localities, it is useful to explore whether additional parameters are involved. Based on results from the present study, I predict the occurrence of stained habitats for Olympic Peninsula populations of black stickleback. Only qualitative descriptions were made of water color in these studies; some headwater pools have clear water (Hagen, pers. comm.), but the general habitat of *No-*

*novumbra* and melanic stickleback is described as "highly stained" (McPhail, 1969, pers. comm.) and tea-colored (Moodie, pers. comm.). These data, although anecdotal, are consistent with my prediction. In the lower reaches of the streams, red males replace black-throated males, coincident with the absence of *Novumbra* (McPhail, 1969; Hagen and Moodie, 1979). This change would seem incongruent with the water-color associations and highly consistent with postulated *Novumbra* associations. However, in the well-studied case at Conner Creek, the red-throated sticklebacks probably represent a distinct brackish-water population, since eggs and fry of red males have 100% survival in seawater compared to 0% survival for eggs and fry of black males (McPhail, 1969). These brackish habitats should have increased water clarity relative to the creeks, due to both dilution from clear marine waters and from increased salinity which results in precipitation of humic acids (Sieburth and Jensen, 1968). Therefore, spectral habitats in the Olympic Peninsula and their associated throat-color phenotypes in sticklebacks are similar to those observed on the Queen Charlotte Islands. The distributional correlation between black males and *Novumbra* may not be causal, as previously argued (McPhail, 1969; Hagen and Moodie, 1979; Hagen et al., 1980), but rather, a response to a third environmental variable. Spectral data from the creeks in the Olympic Peninsula would provide insight into alternate proposals.

There are two divergent hypotheses that could account for the relationship between nuptial color and water spectra: the first, spectral masking, invokes selective differences between phenotypes and is therefore of evolutionary interest; the second hypothesis, carotenoid deficiency, is based on non-heritable environmental induction of nuptial color. Assuming heritability of this trait, the loss of red nuptial color may be a functional adaptation to signal-masking in a spectrally restricted habitat. Principles of underwater vision and photodetection of objects have been extensively developed by Duntley (1962), Lythgoe (1966, 1972), and Munz and McFarland (1977), and comparisons between clear and stained habitats are possible. In shallows of a clear lake, downwelling and upwelling light will be broad-

spectrum and very similar in hue, although intensity of upwelling light is relatively low (approximately 1% or less than that of downwelling light; Tyler and Preisendorfer, 1962). With increasing path length, such as is found with horizontal lighting, long waves attenuate, and the spectrum becomes progressively blue-shifted and monochromatic, usually reaching a transmission maxima between 470 and 520 nm. Conversely, in stained lakes, dissolved humic acids produce rapid attenuation of the short wavelengths; with increasing depth or increasing path length, intensity is greatly reduced, and the spectrum becomes increasingly red-shifted and monochromatic, reaching transmission maximum near 700 nm (Bowling et al., 1986).

Consider a male stickleback that has a red throat with a broad band reflectance above 600 nm. Consider further that this fish is near the substrate in shallow water and that it is being viewed horizontally at close range (ca. 50 cm) against open water (Fig. 5A). In clear water, broad-spectrum downwelling light reflected off a stickleback will include the full range of hues on the fish, but these hues will be viewed against low intensity horizontal light which is blue-shifted and monochromatic. The red throat viewed against the blue background represents maximum hue contrast (Fig. 5B). Conversely, in stained waters, fish in shallow water will be illuminated with broad-spectrum downwelling light and will be perceived against low-intensity red-shifted horizontal lighting. A red throat will have less hue contrast and could potentially exhibit the same wavelength distribution as the horizontal lighting against which it is being perceived (Fig. 5C). The component of the nuptial signal that is related to hue will be masked by the spectral characteristics of horizontal lighting; the extent of hue-masking should be proportional to the relative loss of blue and green spectral hues in the horizontal field (i.e., proportional to the amount of staining).

A second component to contrast is relative brightness. Reflective surfaces will have enhanced brightness if their pigments match the dominant wavelengths in spectrally narrow aquatic habitats, since these surfaces will reflect more than surrounding surfaces (Lythgoe, 1979; Levine et al., 1980). Spe-

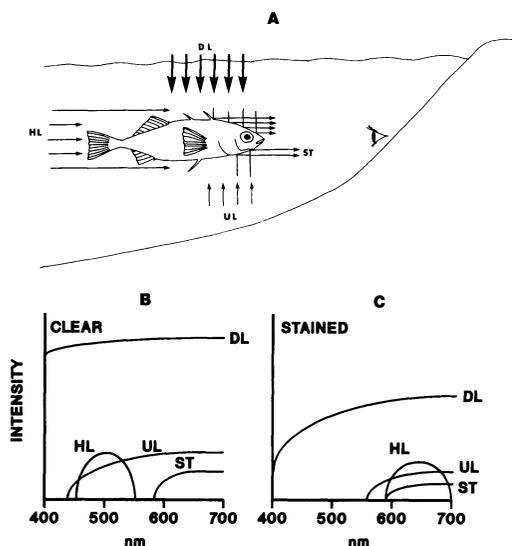


FIG. 5. Generalized model for signal-masking. A) Schematic diagram of a stickleback and principal sources of illumination in shallow water; B) general spectra in clear water; C) general spectra in stained water. DL = downwelling light; HL = horizontal light; UL = upwelling light; ST = reflectance off throat of stickleback. Differences in hue and light intensity (vertical axis) are approximations.

cifically, red objects in stained water will appear brighter than other objects. It is for this reason that red displays are common in freshwater fishes (Noble, 1938) and are predicted to occur most commonly in habitats with increased organic staining (Lythgoe, 1979; Levine et al., 1980). However, increased brightness does not necessarily result in increased contrast. Because fish are illuminated principally from above, dorsal surfaces receive much more light than ventral surfaces. Highly reflective ventral surfaces on the fish compensate for shadow (countershading) and yield reduced contrast with the background (Cott, 1940; Lythgoe, 1979). Since upwelling light is shifted toward long wavelengths in stained habitats, red pigment on the throat would be more reflective than other pigments and could result in minimum contrast with the background by compensating for shadow. A red ventral patch would be particularly ineffective for nuptial display in these stained waters for the same reasons that a white or silver ventral patch would be ineffective in clear-water habitats. Any throat with relatively low reflectivity would generate con-

trast with the background in producing reversed countershading, which is a highly conspicuous signal (Cott, 1940). This may account for the prevalence of black-throated males among these populations, since black would have minimum reflectance and therefore maximum contrast with horizontal lighting. This effect would be influenced by the relative amounts of upwelling light. For example, in habitats with nonreflective substrates, (e.g., in some dystrophic lakes and streams), the virtual absence of upwelling light will accentuate the reversed countershading. If this line of reasoning is correct, the occurrence of black-throated males in the Olympic Peninsula may not be the result of convergence towards *Novumbra* but, rather, a result of sexual selection operating for maximum contrast within *Gasterosteus*. Interspecific threat signals may reinforce the selective regime and accentuate convergence in nuptial signals, but this would represent a secondary effect.

The hypothesis of signal-masking generates interesting questions concerning photic regimes in aquarium studies. Previous experimental work on red nuptial-color loss in sticklebacks (McPhail, 1969; Moodie, 1970; Hagen and Moodie, 1979; Hagen et al., 1980) was carried out in clear water, rather than in stained waters similar to those from which the populations were collected. That red-throated males were at increased predation risk, had courtship advantages, and incurred greater number of *Novumbra* intrusions than melanic males is not unexpected in a photic regime where red males had maximum contrast. Whether this pattern would also occur in stained waters, where red-throated males may contrast less with the background than melanic males, remains to be determined. A second problem with behavioral experiments in aquaria concerns the spectral width of horizontal light. Because of its short path length, horizontal lighting in aquaria will be broad-spectrum, similar in hue and intensity to downwelling light as opposed to monochromatic or narrow-band spectra in natural habitats. Consequently, if any behavioral interactions are a function of contrast between the male's throat and horizontal light, the visual signals of territorial and courtship displays will differ from those observed in natural settings. This might account for some

of the conflicting results in experiments on epigamic function of nuptial pattern in *G. aculeatus* (for reviews, see Wootton [1976] and Baerends [1985]), which have been carried out without attention to spectral characteristics of horizontal light. Hailman (1977) and Endler (1978) have emphasized the necessity of considering characters subject to sexual selection in the context of the ambient conditions under which the traits are being perceived. This is particularly true for aquatic species, because their habitats differ greatly in attenuation rate of select wavelengths and spectral curves differ substantially over short distances.

While signal-masking constitutes a plausible mechanism for the general loss of red nuptial color in *G. aculeatus*, there are various difficulties with this hypothesis. There were exceptions to the geographical trends, in that red nuptial color occurred in several heavily stained lakes, while populations with loss of red pigment occasionally occurred in clear-water lakes. One would anticipate that the reduction in hue contrast in stained waters could be readily compensated by increased brightness contrast if red pigment were expressed on lateral (rather than ventral) surfaces, such as the operculum. However, in the few cases where red nuptial color was present, it was restricted to mid-ventral regions of the throat. Furthermore, the hypothesis does not explain why the greatest expression of red, which included the entire ventral surface from the lower jaw to the pelvis as well as lateral surfaces, occurred in waters of the highest clarity. Based on these difficulties and on several field observations which suggested yearly fluctuations in throat-color intensity (Reimchen, 1984), it is instructive to examine whether population differences in nuptial color of Queen Charlotte Island sticklebacks represent non-genetic responses to pigment availability.

Red pigments in fishes, which are generally carotenoids, are derived from the diet, either from direct consumption of primary producers or from consumption of zooplankton and other herbivores which store the pigments. While the presence of integumentary chromatophores, in which the carotenoids are deposited, is genetically determined in most fishes, dietary deficiencies of carotenoids will reduce pigment intensity

(Fox, 1976; Simpson et al., 1981). For example, *Salmo trutta* fed on a diet lacking carotenoids, lose the bright red tips of adipose fins and the red skin spots (Steven, 1947). Reduced proportion of crustaceans (which are a rich source of carotenoids [Goodwin, 1954]) in salmonid diets result in white rather than red muscle tissue (Nilsson and Andersson, 1967).

Total carotenoids in natural habitats are highly correlated with algal standing crop (Gorham et al., 1974), and it seems possible that stained lakes, which have exceptionally low light penetration and low primary productivity, would yield low levels of carotenoids. Furthermore, reduced intensity of blue and blue-green wavelengths results in decreased carotenoid production by algae (Brandt et al., 1976); such spectral deficiencies characterize stained waters (Bowling et al., 1986). The two heavily stained lakes with red-throated populations, which are the major exceptions to the general trend, have elevated levels of calcium and sulphur relative to surrounding lakes (Reimchen, unpubl.), characteristics favorable to carotenoid production (Gorham et al., 1974). These factors indicate that carotenoids may be limiting in some habitats. If so, the general reduction in nuptial color in stained waters could be environmentally induced, rather than an evolutionary response associated with aquatic spectra.

#### ACKNOWLEDGMENTS

I thank M. A. Bell, S. D. Douglas, and J. S. Nelson for constructive comments on the manuscript and D. D. Beatty, P. Chambers, G. E. E. Moodie, C. Paszkowski, and M. V. H. Wilson for discussion. I am also grateful to S. D. Douglas, M. Hearne, J. Westly, and L. Buckland-Nicks for technical assistance. This work was supported with funds from Natural Sciences and Engineering Research Council of Canada and from the Ecological Reserves Unit, Government of British Columbia.

#### LITERATURE CITED

- ANDERSSON, M. 1982. Sexual selection, natural selection and quality advertisement. *Biol. J. Linn. Soc.* 17:375-393.
- BAERENDS, G. P. 1985. Do the dummy experiments with sticklebacks support the IRM-concept? *Behaviour* 93:258-277.

- BOWLING, L. C., M. S. STEANE, AND P. A. TYLER. 1986. The spectral distribution and attenuation of underwater irradiance in Tasmanian inland waters. *Freshw. Biol.* 16:313-335.
- BRANDT, A. B., K. A. SHARIPOV, M. I. KISILEVA, AND N. N. FURKOVSKAYA. 1976. Dynamics of the accumulation of carotenoids during the developmental cycle of a synchronous chlorella culture in various spectral regions. *Chem. Abstr.* 85:2618.
- BREDER, F., AND G. STONER. 1987. Male predation risk determines female preference in the Trinidad guppy. *Nature* 329:831-833.
- COTT, H. B. 1940. *Adaptive Coloration in Animals*. Methuen, London, U.K.
- DARWIN, C. 1871. *The Descent of Man and Selection in Relation to Sex*. Murray, London, U.K.
- DUNTLEY, S. Q. 1962. Underwater visibility, pp. 452-455. *In* M. H. Hill (ed.), *The Sea*. Interscience, N.Y.
- ENDLER, J. A. 1978. A predator's view of animal color patterns. *Evol. Biol.* 11:319-364.
- . 1980. Natural selection and color patterns in *Poecilia reticulata*. *Evolution* 34:76-91.
- FOX, D. L. 1976. *Animal Biochromes and Structural Colors*. Univ. California Press, Berkeley.
- GOODWIN, T. W. 1954. *Carotenoids; Their Comparative Biochemistry*. Chemical Publ., N.Y.
- GORHAM, E., J. W. G. LUND, J. E. SANGER, AND W. E. DEAN, JR. 1974. Some relationships between algal standing crop, water chemistry and sediment chemistry in the English Lakes. *Limnol. Oceanogr.* 19: 601-617.
- GROSS, H. P. 1978. Natural selection by predators on the defensive apparatus of the three-spined stickleback, *Gasterosteus aculeatus* L. *Can. J. Zool.* 56:398-413.
- HAAS, R. 1976. Sexual selection in *Nothobranchius guentheri* (Pisces: Cyprinodontidae). *Evolution* 30: 614-622.
- HAGEN, D. W., AND L. G. GILBERTSON. 1972. Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific northwest, America. *Evolution* 26:32-51.
- HAGEN, D. W., AND G. E. E. MOODIE. 1979. Polymorphism for breeding colors in *Gasterosteus aculeatus*. I. Their genetic and geographic distribution. *Evolution* 33:641-648.
- HAGEN, D. W., G. E. E. MOODIE, AND P. F. MOODIE. 1980. Polymorphism for breeding colors in *Gasterosteus aculeatus*. II. Reproductive success as a result of convergence for threat display. *Evolution* 34:1050-1059.
- HAILMAN, J. P. 1977. *Optical Signals*. Indiana Univ. Press, Bloomington.
- HASKINS, C. P., E. F. HASKINS, J. J. A. McLAUGHIN, AND R. E. HEWITT. 1961. Polymorphism and population structure in *Lebistes reticulatus*, an ecological study, pp. 320-395. *In* W. F. Blair (ed.), *Vertebrate Speciation*. Univ. Texas Press, Austin.
- LEVINE, J. S., P. S. LOBEL, AND E. F. MACNICHOL. 1980. Visual communication in fishes, pp. 447-475. *In* M. A. Ali (ed.), *Environmental Physiology of Fishes*. Plenum, N.Y.
- LYTHGOE, J. N. 1966. Visual pigments and underwater vision, pp. 375-390. *In* R. Bainbridge, C. C. Evans, and O. Rackham (eds.), *Light as an Ecological Factor*. Blackwell, Oxford, U.K.
- . 1972. The adaptation of visual pigments to their photic environment, pp. 566-603. *In* H. J. A. Dartnall (ed.), *Handbook of Sensory Physiology*, Vol. VII/1. Springer-Verlag, Berlin, W. Ger.
- . 1979. *The Ecology of Vision*. Clarendon, Oxford, U.K.
- McPHAIL, J. D. 1969. Predation and the evolution of a stickleback (*Gasterosteus*). *J. Fish. Res. Board Can.* 26:3183-3208.
- MOODIE, G. E. E. 1970. Predation as a mechanism in the evolution of an unusual population of sticklebacks in the Queen Charlotte Islands, Canada (Pisces: Gasterosteidae). Ph.D. Diss. Univ. Alberta, Edmonton, Canada.
- . 1972a. Morphology, life history and ecology of an unusual stickleback (*Gasterosteus aculeatus*) in the Queen Charlotte Islands, Canada. *Can. J. Zool.* 50:721-732.
- . 1972b. Predation, natural selection and adaptation in an unusual stickleback. *Heredity* 28: 155-167.
- MOODIE, G. E. E., AND T. E. REIMCHEN. 1976. Phenetic variation and habitat differences in *Gasterosteus* populations of the Queen Charlotte Islands. *Syst. Zool.* 25:49-61.
- MUNZ, F. W., AND W. N. MCFARLAND. 1977. Evolutionary adaptations of fishes to the photic environment, pp. 193-274. *In* F. Crescitelli (ed.), *Handbook of Sensory Physiology*, VII/5. Springer-Verlag, Berlin, W. Ger.
- NILSSON, N. A., AND G. ANDERSSON. 1967. Food and growth of an allopatric brown trout in northern Sweden. *Inst. Freshw. Res. Rep.* 47:120-125.
- NOBLE, G. K. 1938. Sexual selection among fishes. *Biol. Rev.* 13:133-158.
- PELKWIJK, J. J. TER, AND N. TINBERGEN. 1937. Eine reizbiologische analyse einiger verhaltensweisen von *Gasterosteus aculeatus* L. *Z. Tierpsychol.* 1:193-204.
- REIMCHEN, T. E. 1980. Spine deficiency and polymorphism in a population of *Gasterosteus aculeatus*: An adaptation to predators? *Can. J. Zool.* 58: 1232-1244.
- . 1983. Structural relationships between spines and lateral plates in threespine stickleback *Gasterosteus aculeatus*. *Evolution* 37:931-946.
- . 1984. Status of unarmoured and spine-deficient populations (Charlotte unarmoured stickleback) of three-spine stickleback, *Gasterosteus* sp., on the Queen Charlotte Islands, British Columbia. *Can. Field-Natur.* 98:120-126.
- REIMCHEN, T. E., AND S. D. DOUGLAS. 1980. Observations of loons (*Gavia immer* and *G. stellata*) at a bog lake on the Queen Charlotte Islands. *Can. Field-Natur.* 94:398-404.
- . 1984. Seasonal and diurnal abundance of aquatic birds on the Drizzle Lake Reserve, Queen Charlotte Islands. *Can. Field-Natur.* 98:22-28.
- REIMCHEN, T. E., E. M. STINSON, AND J. S. NELSON. 1985. Multivariate differentiation of parapatric and allopatric populations of threespine stickleback in the Sangan River watershed, Queen Charlotte Islands. *Can. J. Zool.* 63:2944-2951.
- ROWLAND, W. J. 1984. The relationships among nuptial coloration, aggression, and courtship of male

- three-spined sticklebacks, *Gasterosteus aculeatus*. Can. J. Zool. 62:999-1004.
- ROWLAND, W. J., AND P. SEVENSTER. 1985. Sign stimuli in the threespine stickleback (*Gasterosteus aculeatus*): A re-examination and extension of some classic experiments. Behaviour 93:241-257.
- SEMLER, D. E. 1971. Some aspects of adaptation in polymorphism for breeding colours in the three-spine stickleback (*Gasterosteus aculeatus*). J. Zool. Lond. 165:291-302.
- SIEBURTH, J. M., AND A. JENSEN. 1968. Studies on algal substances in the sea. I. Gelbstoff (humic material) in terrestrial and marine waters. J. Exp. Mar. Biol. Ecol. 2:174-189.
- SIMPSON, K. L., T. KATAYAMA, AND C. O. CHICHESTER. 1981. Carotenoids in fish feeds, pp. 463-538. In J. C. Bauernfeind (ed.), Carotenoids as Colorants and Vitamin A Precursors. Academic Press, N.Y.
- STEVEN, D. M. 1947. Carotenoid pigmentation of trout. Nature 160:540-541.
- TYLER, J. E., AND R. W. PREISENDORFER. 1962. Transmission of energy within the sea, pp. 397-451. In M. N. Hill (ed.), The Sea, Vol. 2. Interscience, N.Y.
- WOOTTON, R. J. 1976. The Biology of the Sticklebacks. Academic Press, London, U.K.

Corresponding Editor: J. A. Endler