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NUPTIAL COLOUR LOSS AND SIGNAL MASKING IN GASTEROSTEUS: AN ANALYSIS USING VIDEO IMAGING

by

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(With 5 Figures)
(Acc. 29-III-1995)

Summary

Threespine stickleback vary greatly in male nuptial display, from full red expression between the throat and pelvis to total melanism without any traces of red. The dominant expression for any population is correlated with the underwater spectral irradiance and many populations with melanistic nuptial colour occur in bog habitats where the aquatic spectrum is shifted to long wavelengths. Field observations indicate that in these bog habitats, the typical red nuptial signal is 'spectrally masked' and this might reduce the effectiveness of display during male-male and male-female interactions. We used video imaging techniques to test whether the spectral composition of the visual background influences female preference for nuptial colouration in male threespine sticklebacks. Throat colour preference tests were carried out in which females chose between video images of red and black-throated males superimposed on either a blue or a red background. Despite belonging to a red-throated population, females were found to respond preferentially to the black-throated male image viewed against a red background, indicating that preference was not determined by throat patch hue. This suggests that preference for an epigamic optical signal is likely a function of its efficacy in generating visual contrast rather than its intrinsic spectral characteristics.

Introduction

On the western coast of North America, populations of threespine stickleback (*Gasterosteus aculeatus*) vary greatly in ventral nuptial display, from

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full red expression on the throat and abdomen to total melanism without traces of red. A number of hypotheses have been proposed to explain this variation, including differential predation pressure (McPHAIL, 1969; SEMLER, 1971; MOODIE, 1972) and selection for convergent threat display with the black Olympic mudminnow (*Novumbra hubbsi*) (HAGEN & MOODIE, 1979; HAGEN *et al.*, 1980). Stickleback populations from the Queen Charlotte Islands, an archipelago off the coast of British Columbia, often lack red nuptial display in stained (dystrophic) habitats independent of the presence or absence of vertebrate predators (REIMCHEN *et al.*, 1985). Instead, reproductive males tend to be melanistic. Melanistic nuptial colour may be a highly conspicuous optical signal suited to stained habitats, while red nuptial display may be 'masked' by the ambient spectra (REIMCHEN, 1989). This hypothesis, signal masking, is consistent with the sensory drive hypothesis, which suggests that signal design is largely determined by the sensory perception of the signal receiver (ENDLER, 1992). Signal masking can be defined as a reduction in signal contrast resulting from the signal and the visual background both possessing similar spectral characteristics.

Several studies on a number of species indicate that sensory bias of the signal receiver plays a role in determining optical signal design (ENDLER, 1983, 1991; FLEISHMAN, 1988). However, few studies have attempted to manipulate preference for epigamic signals by imposing a sensory constraint on the signal receiver (but see SIGMUND, 1983; LONG & HOUDE, 1989; MILINSKI & BAKKER, 1990). In the present study, a video imaging technique was used to constrain the ability of female sticklebacks to discriminate between the red throat colour of video recorded males and the visual background. By experimentally altering the visual background to produce a sensory bias, it was possible to investigate whether signal masking (*i.e.* reduced colour contrast) would result in a loss of female preference for red nuptial colour in a population that is monomorphic for this trait. The experimental design allowed for females to choose between spectrally modified mirror images of a single male, thus making it possible to isolate signal contrast as the sole variable related to nuptial colour preference. In this work, we also present data on the spectral characteristics of clear and stained aquatic habitats and discuss this data in relation to optical signal perception.

Methods

Underwater light measurements.

Underwater light measurements were made in two Queen Charlotte lakes. The spectral characteristics of a typical clear water system (Yakoun Lake) and a deeply stained (dystrophic) system (Drizzle Lake) were measured at various depths with an underwater LiCor Spectroradiometer. Downwelling, sidewelling and upwelling irradiance measures were made for each depth sampled. For a detailed description of the acquisition of underwater spectral data see McDONALD (1994).

Origin of experimental fish.

Threespine stickleback were collected from Quamichan Lake, British Columbia for a period extending from May to July, 1993. Quamichan Lake is a clear water system with spectral characteristics very similar to that of Yakoun Lake (McDONALD, 1994). Males from the Quamichan Lake population develop the carotenoid based throat pigmentation characteristic of this species. Males were housed solitarily in 20 L home tanks to elicit establishment of breeding territories and nest building behaviour. Only gravid females (as determined by the pronounced angular distension of the abdomen) and reproductive males were used for throat colour preference experiments. Females were collected on a weekly basis and housed communally in 80 L aquaria. Females were tested as soon as possible after capture as they often exuded their egg masses shortly after capture. The holding facility permitted exposure to natural photoperiod and skylight. Water temperature of both the holding tanks and experimental chamber was maintained close to that of the lake from which the fish were taken (16-18°C). Fish were fed daily with brine shrimp.

The video imaging system.

A unique feature of the imaging system was that it allowed spectral alteration of a video image in real time. This permitted image processing while a trial was in progress. Video images were first exported from a VCR to a video imaging board (PIP 512). Since the video imaging board did not have colour capability, colouring of the video image was accomplished with a 486 microcomputer and customized software. Pseudocolouration software (developed by R. RACCA of Racca Scientific Consulting) converted assigned intensities of the video image to a hue of choice (within the capabilities of the monitor). Spectrally altered images were exported from the video board to an RGB colour computer monitor (Sony Trinitron).

Choice of spectral composition of the video images.

At least two differentially sensitive cone photoreceptor mechanisms are required for colour discrimination. Electrophysiological recordings from retinal ganglion cells of the Quamichan Lake fish indicate that medium (green) and long (red) cone photoreceptor mechanisms are present in this population (McDONALD & HAWRYSHYN, 1995). Thus, it is probable that the Quamichan Lake fish are capable of colour discrimination, although behavioural colour discrimination tests would be required to confirm this. The visual backgrounds used for the throat colour preference experiments were chosen to provide different levels of colour contrast for red throat colouration. The spectral composition of the red background and red throat patch were similar (Table 1), and thus likely provided a constraint on the ability to discriminate on the basis of wavelength (colour). Black (the absence of incident photons) can be expected to provide luminance contrast against both the red and blue backgrounds (Table 1). The spectral output of the blue, green and red phosphors of the monitor (Sony Trinitron) are provided in Fig. 1. It is important to note that the use of

TABLE 1. Spectral composition of the throat patches and visual backgrounds

| Spectral element | Percent RGB output | | |
|--------------------|--------------------|-------|-------|
| | Red | Green | Blue |
| Red throat patch | 70.59 | 7.84 | 0.00 |
| Black throat patch | 0.00 | 0.00 | 0.00 |
| Red background | 78.43 | 0.00 | 0.00 |
| Blue background | 0.00 | 0.00 | 78.43 |

The spectral composition of each spectrally altered element in the visual scene is expressed as a percentage of the total red, green and blue output of the RGB computer monitor.

subjective colour naming should not lead the reader to believe that human colour perception is similar to that of sticklebacks.

The filming chamber.

To facilitate relative ease of spectral alteration of the video images, three walls of the filming chamber were painted flat black, while the floor (which consisted of clear aquarium glass) was rendered highly reflective by placing the chamber on glossy white cardboard.

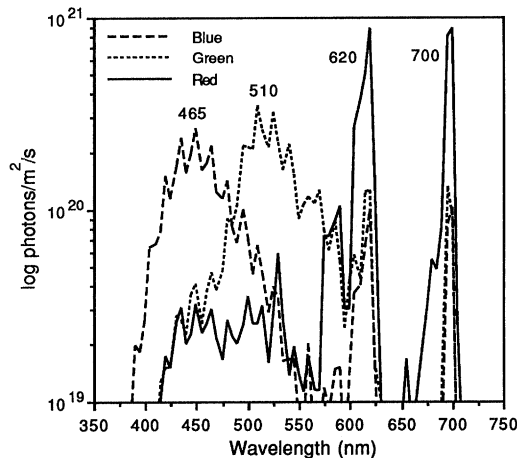


Fig. 1. Spectral output of the blue, green and red phosphors of the Sony Trinitron computer monitor. The wavelength(s) of peak emission for each phosphor is also provided. Although the spectral distribution of the red phosphor emission is different from that of carotenoid based pigmentation, it should be noted that the 620 nm emission peak is very close to the wavelength of peak reflectance (625 nm) for red nuptial colour in sticklebacks (BAUBE, unpublished data). The 700 nm emission peak probably contributes little to visual perception as sensitivity of sticklebacks to this region of the spectrum is minimal (MCDONALD & HAWRYSHYN, 1995).

This permitted high contrast between the fish, which was illuminated from above by a 22 watt fluorescent light, and the background.

The ambient illumination was manipulated such that the ventral portion of the male was the brightest component of the visual scene. This was necessary because spectral alteration of video taped males involved colouring the ventral portion of the male by converting the highest range of intensities in the visual scene to a hue of choice. The background, which exhibited the lowest range of intensities in the visual scene, was spectrally altered in the same fashion. The dorsal and lateral surfaces of the male remained unaffected by the spectral alteration process and appeared as a black and white image.

Filming.

Males that exhibited nest building behaviour were placed in a filming chamber and filmed with a high sensitivity video camera (Panasonic). The camera possessed a mirror imaging function, which permitted generation of mirror images of a single male. To film courtship interactions, nest building males were placed in the filming chamber and provided visual access to a gravid female. A 10 to 15 min. acclimation period was provided for both the male and the female. The use of a one way mirror permitted the male to view a gravid female placed in a 20 l aquarium positioned orthogonally to the filming chamber. The one way mirror also prevented view of the experimenter, while permitting direct sight of the courting male for filming (Fig. 2). Although ritualized courtship behaviours were not observed, the male was often observed to vigorously swim up and down against the front wall of the chamber in unison with the female. This behaviour provided the criterion for operational 'courtship' used in the present study. A six minute segment of vigorous vertical swimming motion of a single male was chosen for use in the colour preference trials.

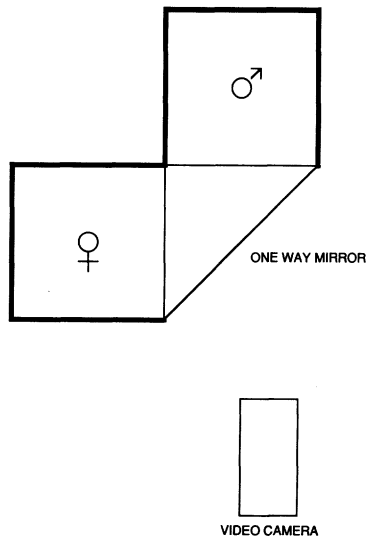


Fig. 2. Set-up for filming males. The one way mirror permitted the male to observe the female without detecting the experimenter. All chamber walls were painted flat black (thick solid lines), with the exception of the orthogonally situated walls which permitted the male and female to view each other.

Experimental chamber design.

Female preference for throat colour was determined by placing a female in a chamber which permitted view of a 14" colour computer monitor. The floor and the two lateral walls of the chamber (36 × 30 cm) were painted flat black to prevent confounding effects from extraneous light. The two remaining walls of the chamber (25.4 × 30 cm) consisted of clear plexiglass and permitted direct view of the monitor by both the female stickleback and the experimenter. A white line on the chamber floor bisected the experimental chamber into two equal halves. This enabled scoring of the time/side analysis. The chamber was positioned 5 cm away from the computer monitor and filled to a depth of 25.4 cm. The ambient light levels were low in the experimental room, with the only ambient illumination, aside from the monitor itself, being a 60 watt incandescent bulb.

Experimental design.

Females were provided a choice between red and black-throated mirror images of a single male superimposed on either a red or a blue background. The choice regime allowed the female to view adjacent mirror images of the male on the computer monitor. Females were introduced to the test chamber and provided an adaptation period of 10 min. Before presentation of the video image, the experimenter allowed the female to reach the central region of the tank. This ensured that the female's response was not biased by her initial position. The position of red and black throat colouration was switched randomly among trials to further control for side bias. On the few occasions when females remained responsive after the initial 6 min. trial, throat colours were again switched and the trial repeated. Female responses were recorded with a high sensitivity video camera (Panasonic).

Successful trials were those in which females tracked male video images. Tracking behaviour was said to occur when a female oriented directly toward one of the two video images and moved in unison with it. Females that exhibited tracking behaviour repeatedly altered their orientation such that they swam in the same direction as the image was moving. In some cases, females remained stationary, but rotated their body about the vertical axis such that they maintained direct alignment with the video image.

Results**Underwater light measurements.**

Substantial attenuation of short wavelength light is evident in Drizzle Lake, a dystrophic system (Fig. 3 and 4). At a depth of one meter, the photic environment is dominated by long wavelength light for all lines of sight, with peak water transparency occurring at 705 nm (Fig. 3). Total spectral irradiance at one meter is approximately two orders of magnitude lower than that found for the same depth in Yakoun Lake. Depths beyond 3.5 meters marked the lower limit of sensitivity of the Licor spectroradiometer in Drizzle Lake (Fig. 4). Upwelling irradiance is accordingly extremely low (Fig. 3) and irradiance measures could not be obtained at depths greater than 1 meter. Yakoun Lake has spectral characteristics similar to that of a typical 'green' water mesotrophic lake (NOVALES-FLAMARIQUE *et al.*, 1992). In comparison to Drizzle Lake, the

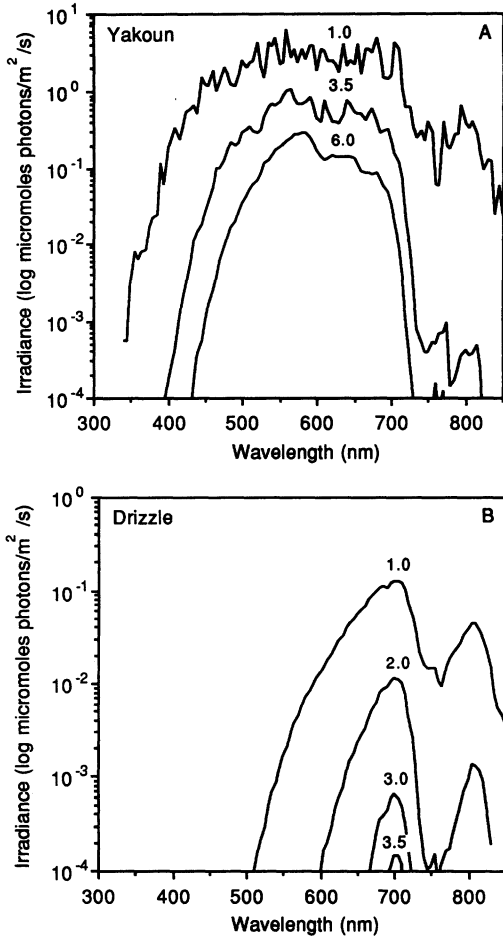


Fig. 3. Downwelling (DW), sidewelling (SW) and upwelling (UW) spectral irradiance for Yakoun (a) and Drizzle Lake (b) at a depth of 1.0 m.

spectral band width (for all lines of sight) is considerably broader and the ambient light levels are substantially higher (Fig. 3 and 4).

Throat colour preference tests.

Sixteen females displayed tracking behaviour. To enable comparison between the two treatments, females were scored as responding preferentially to a particular throat colour if they tracked the male image expressing it for a greater period of time than the male image expressing the

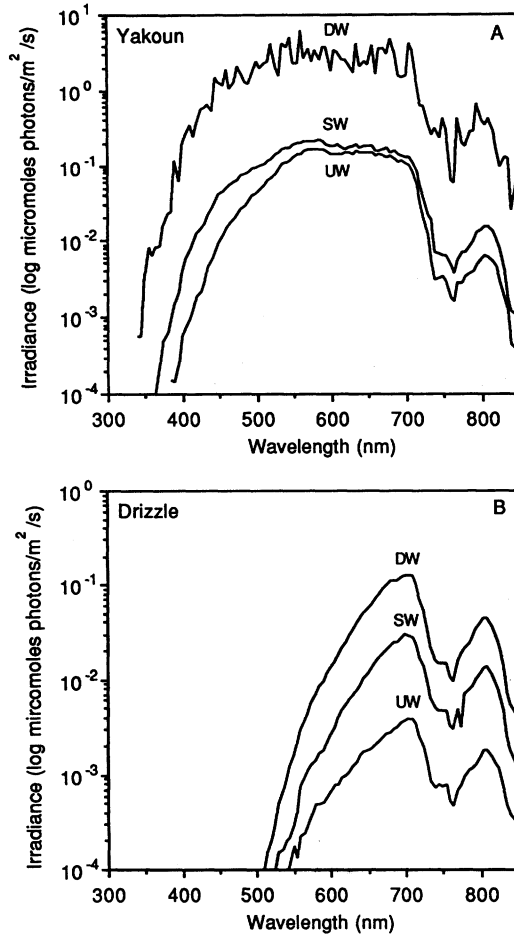


Fig. 4. Downwelling spectral irradiance for Yakoun (a) and Drizzle Lake (b) at various depths (meters).

alternate colour. This is a robust measure of preference as in all but one trial females tracked a focal image for at least 76.1% of the total response duration (Fig. 5). Female preference for red or black nuptial colour was shown to be influenced by background colour, as evidenced by a significant difference (Fisher's exact test, $p = 0.0128$, 1-tailed) between red and blue background treatments (Table 2, Fig. 5). Females spent significantly more time tracking the black-throated image under the red background treatment (Wilcoxon matched-pairs signed-ranks test, $N = 5$, $T^+ = 15$, p

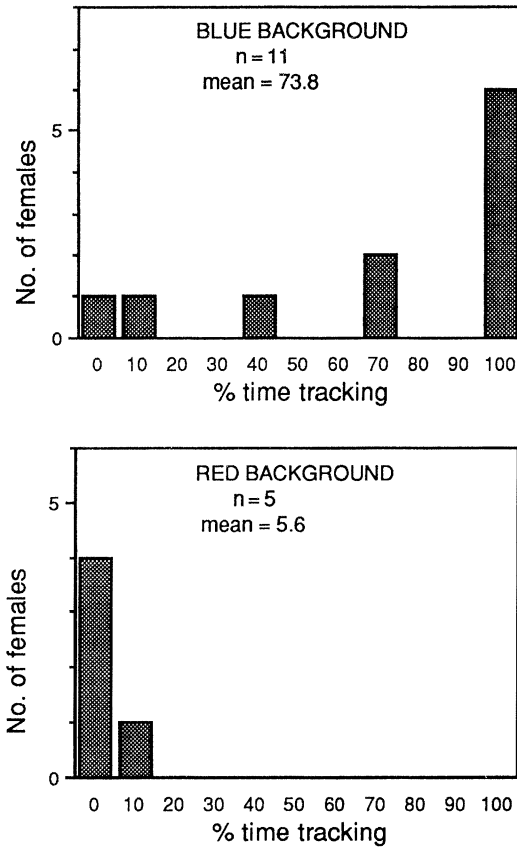


Fig. 5. Percentage of the total response duration each female spent tracking a red-throated male image (response to the red-throated image/response to the red-throated image + the response to the black-throated image).

= 0.0313, 1-tailed). Under the blue background treatment, females spent proportionately more time tracking the red-throated image ($N = 11$, $T^+ = 53.5$, $p < 0.0414$, 1-tailed).

In one trial for each of the experimental treatments, a female remained responsive until the end of the initial 6 min. test period. Throat colour position was switched and these females retested. Under the red background treatment, the female tracked the black-throated male image for a greater period of time, both before (100% of response duration) and after (91%) throat colours were switched. Under the blue background treat-

TABLE 2. Female responses to red and black-throated male video images as a function of background colouration

| Variable | Treatment | |
|--------------|----------------|-----------------|
| | Red background | Blue background |
| Red throat | 0 | 8 |
| Black throat | 5 | 3 |

Fisher's exact $p = 0.0128$, 1-tailed.

ment, the female preferentially tracked the red-throated male image before (76.9%) and after (100%) throat colours were switched. These findings provide evidence that side bias was not a confounding factor. As females chose between mirror images of the same male, it is highly probable that preference was associated solely with throat colour contrast.

In an attempt to determine whether females which did not display tracking behaviour responded preferentially to a particular throat colour, a time per side analysis was carried out. Only females which exhibited swimming behaviour directed towards the video screen (but did not track the images) were used for this analysis. The amount of time each female spent on each side of the test chamber swimming at the video screen was recorded (for both blue and red background treatments). Under both the red ($N = 16$, $T^+ = 55.5$, $p > 0.50$, 1-tailed) and blue ($N = 14$, $T^+ = 47$, $p > 0.50$, 1-tailed) background treatments, time spent per side did not differ significantly.

Discussion

These results demonstrate that female preference for throat colour of video recorded male threespine sticklebacks (*Gasterosteus aculeatus*) can be altered by manipulating throat colour contrast against the visual background. Despite belonging to a red-throated population, females were found to respond preferentially to the black-throated male image viewed against a red background, indicating that preference was not determined by throat patch hue. Throat colour providing luminance contrast (*i.e.* the black throat patch viewed against the red background) and possibly colour contrast (*i.e.* the red throat patch viewed against the blue background) was effective in eliciting female responses. We can not be sure,

however, that under the blue background treatment, red throat colour provided strong colour contrast as we did not compensate for the subjective brightness of the emissions of the different phosphors. These findings suggest that preference for an epigamic optical signal is likely a function of the signal's efficacy in generating visual contrast rather than its intrinsic spectral characteristics.

Our experimental conditions did not permit complete assurance that the observed behaviours can be interpreted as sexual responses. It is possible, for example, that the tracking response we observed was investigatory behaviour rather than courtship. Nevertheless, our findings strongly suggest that a male expressing a nuptial signal which confers greater detectability relative to other males should be more successful in attracting and maintaining the attention of females. Put differently, males which are more readily perceived can be expected elicit a preferential response. Thus, upon first encountering a courting male, female preference may be determined more by male conspicuousness than by a sexual response to a particular trait.

A number of studies lend support to our findings. For example, BLOUW & HAGEN (1990) found that during the initial stages of courtship, female threespine sticklebacks responded preferentially to males of the newly described white stickleback species (*Gasterosteus*). The white stickleback is a close relative of the threespine stickleback and reproductive males of this species are highly conspicuous by virtue of their iridescent, white dorsal colouration, which threespine stickleback males do not possess. BLOUW & HAGEN (1990) found that there were no backgrounds that consistently matched the iridescent white colour at the nesting sites they examined, suggesting that white stickleback males are conspicuous in their natural habitat. Female threespine sticklebacks stopped responding to white stickleback males only when they were introduced to the nest which, unlike that of the threespine stickleback, is situated above the substrate and constructed of fine filamentous algae. It appears then that differences in the position and composition of the nest, rather than nuptial colouration, were factors related to the ultimate rejection of white stickleback males as potential mates. In another study by BAUBE *et al.* (this volume), it was found that female threespine sticklebacks preferred red-throated dummies to green-throated dummies. Using a colour vision model, BAUBE *et al.* calculated that red throat colour should provide

greater colour contrast against both the dorsal colouration of the dummies and the visual background used in their experiment. These findings (BLOUW & HAGEN, 1990; BAUBE *et al.*, this volume; present study) all indicate that the primary determinants of nuptial colour hue are a function of the necessity to increase the detectability of courting males.

A number of studies on species other than the threespine stickleback also report findings consistent with those presented here. For example, in a study by SIGMUND (1983) on visual display in an *Anolis* lizard (*Anolis carolinensis*), it was found that contrast of a male's dewlap with background colouration can have a significant influence on female mate choice. Females were shown to exhibit no preference between males with red or green dewlaps, provided that dewlap colour contrasted with the background. Since only red dewlaps occur in the population examined by SIGMUND, one may conclude that female choice was based upon the conspicuousness of the nuptial signal and not a result of a fixed preference for a particular hue. As females rarely chose a male with a green dewlap if it did not contrast with the background, it is unlikely that green dewlaps were chosen simply because of their novelty. SIGMUND suggested that these results provide evidence that red dewlap colouration evolved to enhance contrast against the green foliage in front of which *Anolis* lizards typically display.

Similarly, ENDLER (1983) demonstrated that female guppies (*Poecilia reticulata*) tend to favour males which contrast with background colour over those which resemble it. He was also able to show, using a multi-generational study, that selection operates to increase the frequency of males which contrast with the background. Thus, it seems likely that nuptial colouration in the guppy has evolved to enhance the detectability of males, and furthermore that a given photic regime can influence optical signal design.

Although there is evidence to suggest that there is genetic variation for the strength of female preference for red nuptial colour in threespine sticklebacks (BAKKER, 1993), it is apparent that the efficacy of signal transmission and detection must also play an important role in determining colour preference. Indeed, the findings presented here indicate that female preference for red nuptial colour can be significantly reduced by its superimposition on a low contrast visual background. However, it

remains to be determined whether red nuptial colour is spectrally masked in natural habitats.

It is important to note that although red nuptial colour would provide minimal hue contrast in red-shifted habitats (REIMCHEN, 1989), it would conversely provide high luminance contrast if expressed laterally (rather than ventrally). There are two reasons for this. First, reflective surfaces with a spectral distribution similar to that of the ambient spectra reflect relatively more light than surfaces that are spectrally offset (LYTHGOE, 1979). Second, laterally situated nuptial colour would receive substantial illumination from the downwelling irradiance. Since sidewelling irradiance is substantially lower than downwelling irradiance (Fig. 3), laterally expressed red would appear considerably brighter than the background (at least at proximal distances). However, REIMCHEN (1989) found that in red environment populations where red nuptial colour was present, expression was limited to the mid-ventral region of the throat. Upwelling irradiance in dystrophic systems is generally extremely low (Fig. 3), and thus would probably not render red ventral colouration conspicuous.

It has been hypothesized that the melanistic appearance of reproductive males from red environment systems may provide a high contrast optical signal (REIMCHEN, 1989). Specifically, REIMCHEN suggests that melanistic nuptial colour would result in reversed countershading (HAILMAN, 1977). However, it should again be noted that ambient light levels in dystrophic systems are extremely low (Fig. 3 and 4). Hence, melanistic nuptial expression may provide poor contrast against the low backwelling irradiance. There are, however, some scenarios where the efficacy of melanistic nuptial expression would likely be quite high. Firstly, the nesting sites of some of the Queen Charlotte lakes are in littoral regions where the substrate is highly reflective (pers. obs.). Melanistic males nesting in microhabitats where ambient light levels are elevated might very well appear quite conspicuous. Secondly, differences in the spatial stereometry of courtship in dystrophic systems may influence the conspicuousness of melanistic nuptial colour. As far as the authors are aware, this possibility has not been addressed. Here it is significant to note that male ninespine sticklebacks (*Pungitius pungitius*) possess melanistic nuptial colour and that females view courtship behaviour largely from a position below the male (MORRIS, 1958). A melanistic male silhouetted against the down-

welling light would certainly provide a highly conspicuous visual stimulus.

In conclusion, it is evident that the behavioural results presented here indicate that signal masking can influence colour preference and that signal design is likely largely determined by parameters related to the generation of visual contrast. These findings are consistent with the sensory drive hypothesis (ENDLER, 1992). However, it is also evident that the conspicuousness of red nuptial colour in dystrophic habitats must be quantified to determine if signal masking does indeed occur in nature.

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