Naturwissenschaften (2008) 95:631–638
DOI 10.1007/s00114-008-0365-0

ORIGINAL PAPER

Males do not see only red: UV wavelengths and male territorial aggression in the three-spined stickleback (*Gasterosteus aculeatus*)

Ingolf P. Rick · Theo C. M. Bakker

Received: 30 May 2007 / Revised: 22 January 2008 / Accepted: 15 February 2008 / Published online: 19 March 2008

Abstract Animal colour signals serve important functions in intraspecific interactions, including species recognition, mate choice and agonistic behaviour. An increasing interest concerns ultraviolet (UV) wavelengths, for instance studies on the effect of UV in mating decisions. More recently, some studies also established that UV signals affect intrasexual interactions. We studied the role of UV during aggressive encounters between male three-spined sticklebacks (*Gasterosteus aculeatus*), a species in which UV has an effect on female and male mate choice and shoaling behaviour. To that aim, we compared the aggressive response of a territorial male to male intruders, either seen in UV-including (UV+) or UV-lacking (UV−) conditions. Our prediction was that, if UV wavelengths are used in male–male competition, a territorial male should show less competitive behaviour towards an intruder representing a lower threat, i.e. the one presented without UV light. Male sticklebacks showed significantly lower levels of aggression towards male opponents lacking an UV component to their coloration than male opponents possessing this colour component. Discrimination was not influenced by a difference in brightness between the UV+ and UV− stimuli. Finally, we present some reflectance–spectrophotometrical data of two skin regions (cheek and abdomen) of the experimental males and analysed relationships between colorimetric variables, body variables and behaviour. Our study emphasises that UV visual cues are of importance in different communicational tasks in the three-spined stickleback.

I. P. Rick (✉) · T. C. M. Bakker
Institut für Evolutionsbiologie und Ökologie, University of Bonn,
An der Immenburg 1,
53121 Bonn, Germany
e-mail: irick@evolution.uni-bonn.de

Keywords UV · Aggression · Visual signals · Stickleback · Sexual selection

Introduction

Conspicuous coloration often acts as a status signal in social and accordingly sexual communication, e.g. in agonistic interactions between male conspecifics. Male visual signals such as bright coloration often correlate with territorial defence, fighting ability as well as dominance rank (Andersson 1994) and are used in aggressive interactions in birds (Studd and Robertson 1985), mammals (Wickler 1967), reptiles (Werner 1978; Cooper and Vitt 1988) and fishes (Stacey and Chiszar 1978; Fernald 1980; Bakker and Sevenster 1983). These studies deal with colour traits in the human visible wave range (400–700 nm). More recently, an increasing effort is focusing on ultraviolet (UV) wavelengths to which humans are blind; for instance, studies on the effect of UV in mating decisions (e.g. Bennett et al. 1996; Andersson et al. 1998; Hunt et al. 1998; Smith et al. 2002; Rick et al. 2006). In contrast, information about a potential role of UV signals in intrasexual interactions is comparatively scarce. In birds, Alonso-Alvarez et al. (2004) demonstrated that breeding male blue tits (*Parus caeruleus ultramarinus*), when exposed to two decoys differing in UV reflectance, showed less aggressive behaviour towards the UV-reduced one. In male eastern bluebirds (*Sialia sialis*), UV chroma was positively correlated with success in acquiring nestboxes (Siefferman and Hill 2005). Siebeck (2004) found that male damselfish (*Pomacentrus amboinensis*) discriminated between intruding males depending on their UV reflectance. Recently, Whiting et al. (2006) showed in Augrabies flat lizards (*Platysaurus broadleyi*) that UV throat reflectance is an honest status signal.

We studied the role of UV during aggressive interactions between male three-spined sticklebacks (*Gasterosteus aculeatus*), a species in which UV has an effect on female mate choice (Boulcott et al. 2005; Rick et al. 2006), male mate choice (Rick and Bakker 2008) and shoaling behaviour (Modarressie et al. 2006). Stickleback males, while establishing individual breeding territories, show a characteristic nuptial coloration (red underside and blue-green eyes). Stickleback breeding coloration is a well-known example of a colour pattern that is used in intersexual (Milinski and Bakker 1990) as well as intrasexual interactions (Bakker and Sevenster 1983; Baube 1997). There is a large variation between individual males in the intensity of red nuptial coloration (Wunder 1934; Reisman 1968) and their response to conspecifics (Huntingford 1976; Rowland 1983; Bakker 1986). In intrasexual interactions, males with a brighter nuptial coloration achieve a higher dominance status (Bakker and Sevenster 1983) and have an increased tendency to attack opponents (Rowland 1984; McLennan and McPhail 1989). Furthermore, Candolin (1999b) showed that competition between males increases male differences in red coloration which may reflect dominance status. The author hypothesises that male–male competition thus could increase the honesty of the red coloration as a signal of direct benefits to mating partners.

Because coloration seems to be an important cue in agonistic interactions between stickleback males, the present study was undertaken to determine whether UV signals affect male–male competition in this species. To that aim, we compared the association of a territorial male with male intruders, either seen in UV-including or UV-lacking conditions. We predicted that, if UV signals are involved in competitive behaviour between stickleback males, a territorial male should show higher levels of aggression towards an intruding male that is perceived as a greater threat by being presented in UV-including conditions. Furthermore, this study looks at the quality of UV and visible coloration in territorial males and its influence on male responsiveness to intruders.

Materials and methods

Experimental subjects

Samples of sticklebacks were collected in April 2006 from a shallow pond near Euskirchen, Germany (50°38′N, 6°47′E). Adult fish were selected for use in experiments and transported to the laboratory where they were maintained in outside stock tanks (volume, 700 l; temperature, 15°C with a tap-water flow rate of 3 l/min and air ventilation). There were approximately equal numbers of each sex. Individuals were fed to excess once daily with frozen chironomid larvae. After 2 weeks, males that showed the typical red courtship coloration were moved individually into aquaria (30×20×20 cm, 12 l) in the laboratory. They were divided into two treatment groups. One group (the subsequent territorial males) was maintained in aquaria which contained a Petri dish with fine gravel to provide males with a nesting site as well as filamentous algae as nesting material. The other group (the subsequent stimulus males) was kept in bare aquaria without any material. All fish were maintained at 17±2°C under a 16:8 light:dark illumination cycle provided by fluorescent tubes (True Light, Aura Light, Germany; Natural Daylight 5500, 36 W, 1200 mm). These lamps produce a proportion of UV similar to natural skylight and were suspended 20 cm above the tanks. Fish were fed ad libitum with frozen chironomid larvae once daily. Black partitions between the aquaria prevented males from seeing each other. To induce nest-building behaviour, we stimulated each territorial male once a day for 10 min by presenting a ripe female in a 500-ml jar in front of the holding aquarium. Males that showed no nest-building activity after 1 week were replaced by new males with courtship coloration from the outside stock tanks.

Choice experiment

The holding aquaria of the territorial males served as test aquaria so that no acclimatisation to a test tank was necessary. Two stimulus males were presented simultaneously in a double-cuvette construction consisting of two stimulus cuvettes (6×7 cm) located at about 20 cm from the nesting dish of the territorial male (Fig. 1). Two double cuvettes were used alternately; one with the UV-transmitting filter (UV+, Plexiglas GS-2458, Röhm, Darmstadt, Germany) on the left and the UV-blocking filter (UV−, Plexiglas GS-233, Röhm) on the right side and the other vice versa. Visual interactions between the two stimulus males were prevented by an opaque grey plastic partition between them. To avoid visual disturbances during the test trials, the exterior walls of the test aquarium were surrounded by opaque grey partitions up to a height of 30 cm. In addition, a black curtain (58×72 cm) in front of the aquaria avoided visual disturbance from the stimulus side. Light conditions during the experimental trials were similar to those of the holding conditions.

Before each experimental trial, a territorial male was visually stimulated by presenting him a ripe female placed in a small transparent box (10×7×17 cm) in front of the holding tank for 5 min. After that, the double cuvette was placed in the tank opposite to the male's nest for 1 h. During this acclimatisation period, we matched the corresponding stimulus male pair by ranking colorations within randomised groups of four males (without nest) using the same procedure described in Rick et al. (2006).

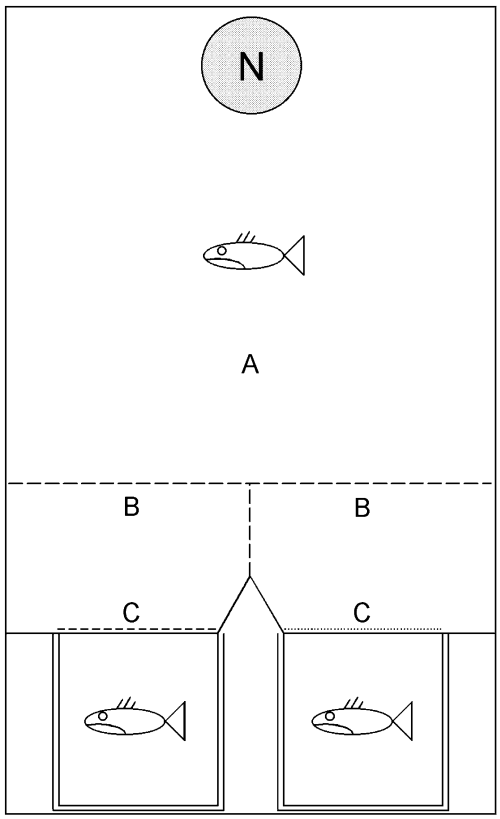

Fig. 1 Experimental set-up used to test male response behaviour towards two stimulus males. The set-up consisted of a section for the territorial male (*A*) and the nesting dish (*N*), two association zones in front of the stimulus sections (*B*) and the two optical filters differing in UV transmission (*C*)

Colour-matched males were used as a pair if their standard length differed by less than 2 mm and their body mass by less than 300 mg. About 30 min before the start of the experiment, the two selected males were also stimulated with ripe females for 5 min.

The experiment was initiated by simultaneously placing the two stimulus males into the double cuvette. All trials were filmed from above with a webcam and recorded on a laptop. The 2-min observational phase started when the territorial male had entered both association zones (6×6 cm) which previously had been marked on the monitor in front of each filter side. After the test, the two stimulus males were returned to their holding tanks and the double cuvette was removed. On the following day, we repeated the experimental procedure now using the double cuvette with reversed optical filters to control for a potential side bias of the territorial male that depended on the stimulus males. The same pair of stimulus males was tested and males were located on the same sides of the double cuvette as in the first trial.

Films were analysed without knowledge of the filter positions. We measured the time that the territorial male (at least half of the body) spent in the two association zones in front of the stimulus males. In addition, the number of attacks a territorial male conducted towards each stimulus male was counted. All trials were done in normal daylight hours.

Control experiment

Due to the difference in quantal flux between the UV+ and UV− filters, territorial males may show a filter preference based on a perceived difference in brightness between the two filters. Thus, we conducted a series of control trials using two neutral density filters, ND2 (Cotech 298, Zilz, Germany) and ND1 (Lee 209, Zilz), that alter brightness without changing the composition of wavelengths of the stimulus males as perceived by the territorial male. The difference in quantitative transmission between these filters is nearly twice as large as that between the UV treatment filters (ND2 to ND1, mean 34% reduction; UV+ to UV−, mean 18% reduction; see Rick et al. 2006 for details) and the proportion of quantitative transmission relative to the UV+ filter is 68% for the ND2 filter and 44% for the ND1 filter, respectively. The control experiment was performed using new males which were derived from the same population as those used in the UV experiment and were treated similarly. Control trials were conducted after the UV trials, both taking place in May and June prior to the seasonal reproductive peak of sticklebacks, and were carried out as described for the UV treatment.

Reflectance measurements

One week after the choice tests, reflectance measurements of the skin of the territorial males used in the UV experiment were taken. First, standard length and body mass of the males were determined and subsequently they were stimulated with a ripe female for 10 min to enhance colour expression. After that, measurements were taken with a spectrophotometer (Avantes AVS-USB2000, Eerbeek, The Netherlands) connected to a deuterium–halogen light source (Avantes DH-2000) for illumination. A bifurcated 200-µm fibre-optic probe with unidirectional illumination and recording was held at a 90° angle to the body surface with the probe end being inserted in a darkened pipette tip in order to exclude ambient light and to take measurements at a fixed distance of 3 mm from the surface. In order to eliminate measurement errors caused by body movements, males were killed with a blow to the head. Males were then immediately placed on a piece of black fabric. Scans were collected from two small colour patches on the male's left lateral side, one located centrally on the red-coloured cheek below the eye and one on the brightly coloured abdominal skin covering the gonads. Reflectance spectrophotometry of several male body regions (Rick et al. 2004) as well as UV photography of the whole fish (Rick, unpublished data) suggests that these two body regions offer proportionally high UV reflectance compared

to other regions. Reflectance intensity was measured relative to a 98% Spectralon white standard over the range of 300–700 nm at about 0.5-nm resolution in wavelength. Data were recorded with Spectrawin 5.1 (Avantes) and imported into Microsoft Excel. Ten measurements were made in succession averaged for each sample region without changing probe contact. The whole procedure took about 1 min in order to minimise postmortem colour changes caused by, for example, changes in chromatophore pigment dispersion.

All reflectance spectra of the two sample regions were double-peaked. Reflectance was summarised by using the following colour variables: (1) total brightness (sum of reflectance in the interval 300–700 nm), (2) UV chroma (reflectance between 300 and 400 nm, proportional to total brightness; Doucet et al. 2004; Siitari and Huhta 2002), (3) UV contrast (difference in intensity between the UV peak and the lowest value of the reflectance curve; Rick et al. 2004), (4) yellow-red chroma (reflectance between 500 and 600 nm, proportional to total brightness; Pryke et al. 2001) and (5) R50 value (wavelength at the 50% reflectance point between minimum reflectance between 300 and 700 nm and maximum reflectance between 400 and 700 nm; Pryke et al. 2001). Higher R50 values indicate a stronger yellow-redness of the measured region.

Statistical analyses

We tested male behaviour for normality using the Kolmogorov–Smirnov test. All data were normally distributed. We analysed the relative amount of time a territorial male spent near the two males behind UV+ and UV− (or ND1 and ND2) and the number of attacks performed against the two male appearances with a parametric *t* test. Colorimetric and body variables were tested for normality using the Kolmogorov–Smirnov test. If normally distributed, relationships within colorimetric variables and between colorimetric and body variables were analysed with Pearson correlations; otherwise, Spearman rank correlations were used.

Results

Choice experiment

In the UV treatment, 14 territorial males and 28 intruders were tested. Five intruders were used twice with an interval of at least 1 week between both tests. Territorial male sticklebacks significantly preferred to assess male opponents in UV+ conditions with respect to both the number of males that spent more time near the UV+ male than near the UV− male (sign test, N_1=12, N_2=2, P=0.013) and the relative amount of time spent near the UV+ male (mean±SD=59.6±16.1%) and UV− male (40.4±16.1%; paired *t* test, t_{13}=2.221, P=0.045; Fig. 2a). Accordingly, territorial males exhibited significantly more attacks towards the UV+ opponent (mean±SD=49.43±14.34) than towards the UV− opponent (37.86±15.51; paired *t* test, t_{13}=2.277, P=0.040; Fig. 2b).

Control experiment

In the ND treatment, ten territorial males and 20 intruders were tested. All intruders were used only once. One out of

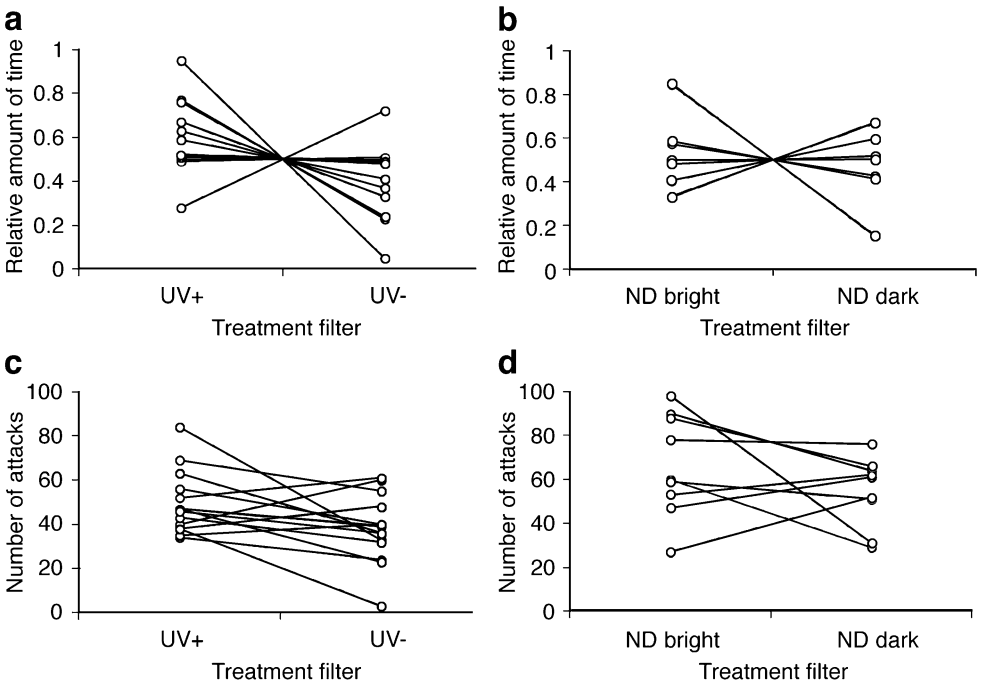

Fig. 2 Proportion of time spent by 14 males within the association zones in front of males behind the UV+ and UV− filter (**a**) as well as behind the ND bright and ND dark filter (**b**). The *lower graphs* give the number of attacks performed towards males behind the UV+ and UV− filter (**c**) as well as behind the ND bright and ND dark filter (**d**)

ten males did not assess both opponents and was therefore excluded from statistical analyses. Differences in brightness did not significantly affect male responsiveness towards male opponents under UV+ conditions; that is, territorial males did not significantly prefer to assess an opponent under either ND1 conditions (mean±SD=54.4±19.5%) or ND2 conditions (45.6±19.5%; paired t test, t_8=0.681, P=0.515). Accordingly, there was no significant difference in the number of attacks territorial males conducted towards the ND1 male (mean±SD=66.67±23.35) or ND2 male (54.67±15.83; paired t test, t_8=−1.284, P=0.235). Mean levels of aggression, measured as the total number of attacks conducted towards both filters, were significantly higher for the ND treatment (mean±SD=121.3±28.38) than for the UV treatment (mean±SD=87.29±23.04; t test, t_{21}=−3.162, P=0.005).

Reflectance measurements

The reflectance spectra of the two sample regions were bimodal, peaking at 343.0±6.8 nm (cheek) and 342.6±6.5 nm (gonadal region) in the ultraviolet waveband and at 542.6±16.0 nm (cheek) and 578.6±40.7 nm (gonadal region) in the human visible waveband, respectively (Fig. 3).

UV chroma and male standard length were positively correlated for cheek (r=0.672, n=14, P=0.008; Fig. 4a) but no significant correlation was found for gonadal region (r=0.380, n=14, P=0.180). No significant correlations were found between UV chroma and body mass or body condition factor [BCF=100×(body mass, g)/(standard length, cm)^3] for the two sample regions (correlation range −0.017 to 0.297, all P>0.18). For cheek, a greater total brightness was correlated with a lower yellow-red chroma (r=−0.748, n=14, P=0.002), whereas it was not significantly related to UV chroma (r=0.177, n=14, P=0.544), R50 value (r=0.258, n=14, P=0.373) or any body variable (correlation range 0.074 to 0.207, all P>0.47). For gonadal region, a greater total brightness was positively correlated, although not significant, with lower standard length (r=−0.519, n=14, P=0.057) and it was not significantly related to any other body variable (correlation range −0.181 to 0.048, all P>0.54) or colour variable (correlation range −0.134 to 0.018, all P>0.65).

For cheek, there was a significant negative correlation between R50 value and condition factor (r=−0.548, n=14, P=0.043; Fig. 4b) but no significant correlation was found for standard length (r=0.269, n=14, P=0.352) or body mass (r=−0.317, n=14, P=0.270). Additionally, for gonadal region, no significant correlation was found between R50 value and standard length (Spearman r=0.166, n=14, P=0.570), body mass (Spearman r=0.231, n=14, P=0.427) or condition factor (Spearman r=0.317, n=14, P=0.270). UV chroma was positively associated, although not significant, with R50 value for cheek (r=0.478, n=14, P=0.084) and for gonadal region (r=0.131, n=14, P=0.656).

When comparing the two regions for each male, UV chroma of cheek was significantly correlated with UV chroma of gonadal region (r=0.660, n=14, P=0.01; Fig. 4c) and yellow-red chroma of cheek was significantly correlated with yellow-red chroma of gonadal region (r=0.772, n=14, P=0.001; Fig. 4d).

Furthermore, we found a significant negative relationship between male association index (the difference in the relative amount of time spent near the UV+ and UV− filters in the UV treatment) and UV chroma of cheek (r=−0.552, n=14, P=0.041) but no significant correlation was found for gonadal region (r=−0.320, n=14, P=0.264). Male behaviour was not significantly correlated with any of the body variables (correlation range −0.302 to 0.049, all P>0.29).

Discussion

Territorial three-spined stickleback males showed significantly higher levels of aggression towards male opponents possessing a UV component to their coloration than male opponents lacking this colour component. To our knowledge, in only one further study in fish a similar effect of UV on male–male interactions has been found (Siebeck 2004).

In the control experiment with ND filters, territorial males, when presented with male intruders in either high or

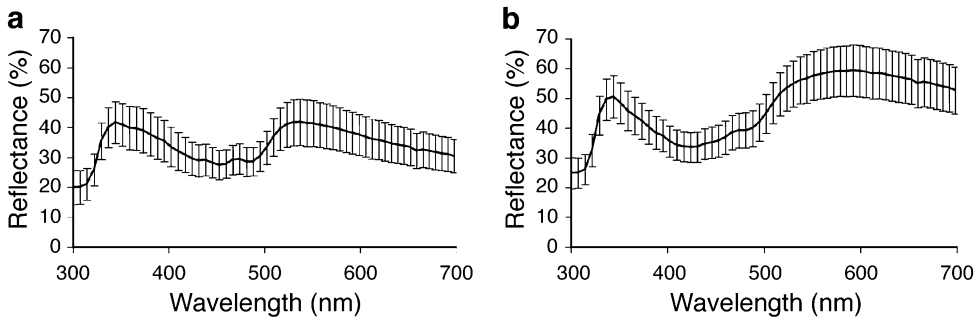

Fig. 3 Spectral reflectance for the cheek (**a**) and the gonadal region (**b**) of 14 territorial males. Plotted are the means of the reflectance intensities (%)±SE between 300 and 700 nm

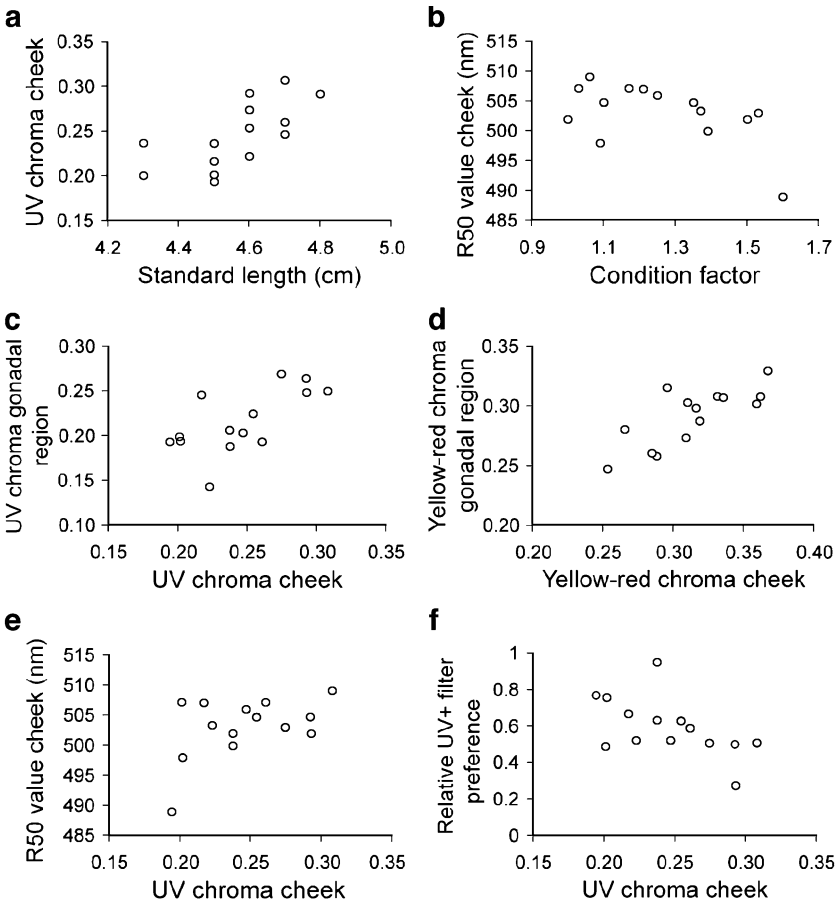

Fig. 4 Relationships between UV chroma of cheek and standard length (**a**), R50 value of cheek and condition factor (**b**), UV chroma of gonadal region and UV chroma of cheek (**c**), yellow-red chroma of gonadal region and yellow-red chroma of cheek (**d**), R50 value and UV chroma of cheek (**e**) and relative UV+ filter preference and UV chroma of cheek (**f**) (N=14 males)

low brightness conditions, did not show a significant difference in agonistic behaviour between both conditions. This result is influenced by a higher individual variation in the number of attacks in the control experiment compared to the UV experiment. Surprisingly, mean levels of aggression (number of attacks) for the ND treatment are significantly higher than for the UV treatment. Perhaps, due to their reduced perceptibility under the comparatively darker full-spectrum conditions, both male intruders in the control experiment represented an overall greater threat to the territorial males. Nevertheless, our data suggest that the increased levels of aggression towards UV+ male intruders in the UV experiment were rather not affected by a higher achromatic brightness caused by the UV+ filter. However, a better understanding of potential chromatic and achromatic channels involved in stickleback visual processing would help in the interpretation of our results.

In animal contest theory, a low degree of asymmetry is thought to increase the probability of escalation between opponents (Riechert 1998). In our experiment, the higher aggression level towards the UV+ opponent may have resulted from a lower asymmetry in quality between the territorial male and the UV+ opponent compared to the UV− opponent. Similarly, Baube (1997) found in a study on male dominance in sticklebacks that a smaller difference in red coloration between two male contestants was correlated with an increased fighting duration, and Bakker and Sevenster (1983) found that when the contestants had similar dominance experiences, the fights escalated more. Our results revealed that this may be true for the UV part of male coloration as well.

One might argue that, in our experiments, the higher aggression towards the UV+ male was due to the fact that species recognition was impeded when UV wavelengths are absent on the UV− side. However, it is unlikely that a limited set of abnormal male colour stimuli of UV− males but species-appropriate behaviour and morphology would lead to a reduction in species recognition. During our experimental trials, territorial males showed distinct behavioural patterns of intrasexual aggression (Rowland 1984) including biting, bumping and threatening towards both the UV+ and UV− opponents.

Earlier studies on the effects of male red coloration on stickleback aggression have found inconsistent results (Tinbergen 1953; Peeke 1969; Rowland 1982; Bakker and Sevenster 1983; Baerends 1985) which could have been partially influenced by different light conditions used in aquarium experiments (Reimchen 1989). The lack of UV wavelengths in laboratory studies on male aggressiveness may have further contributed to the inconsistent results.

Reflectance data of territorial males revealed that the coloration of both sample regions (cheek and gonadal region) was produced by broadband reflectance of structural coloration as well as absorption of carotenoids in the 400–500-nm range, thereby creating a bimodal reflectance pattern. Similar reflectance curves were found in birds in studies on plumage colour (Bleiweiss 2004, 2005) and colour of integumentary ornaments (Mougeot and Arroyo 2006). The latter study found a significant negative correlation between UV chroma and R50 value (λ Rvis50) of red comb colour in red grouse (*Lagopus lagopus scoticus*), which was interpreted as a masking effect of UV reflectance by carotenoid pigmentation. With regard to stickleback cheek coloration, we did not detect such a negative relationship. In contrast, we found a positive association between the two colour variables which rather suggests a mutual amplifying effect of UV coloration and carotenoid pigmentation. Moreover, chroma values for UV and yellow-red were positively correlated between the two sampled skin regions indicating that the expression of both colour components is not restricted to one body region.

Further knowledge of the morphology and pigmentation of the epidermal surface is necessary to better analyse the relationship between both colour components and its behavioural and evolutionary significance in the three-spined stickleback.

When comparing colorimetric variables with body variables, we obtained a strong positive relationship between UV chroma for the cheek region and standard length. Thus, the UV signal could potentially help a rival male or a courting female to assess size or age of the nest owner more precisely. But no significant correlation was found between UV chroma and body mass or condition factor. In contrast, in a former study on stickleback coloration, a positive relationship between UV peak contrast, another measure of UV reflectance, and condition factor has been found for the gonadal region (Rick et al. 2004). Accordingly, when comparing UV peak contrast (difference in intensity between the UV peak and the lowest value of the reflectance curve) and condition factor of males used in the present study, we found no significant relationship for the gonadal region (r=0.483, N=14, P=0.080) and for the cheek region (r=0.267, N=14, P=0.356). However, compared to UV peak contrast, UV chroma is a more reliable measure to quantify UV coloration in sticklebacks as it takes into account the double-peaked nature of the spectra.

Interestingly, in our study, yellow-redness of the cheek region (R50 value) and condition factor were negatively correlated, which is different from results by Milinski and Bakker (1990) and Bakker and Mundwiler (1994) who found either a positive or no significant relationship between male condition factor and redness in Swiss freshwater populations. Other studies on a marine stickleback population from Long Island, New York were unable to demonstrate a significant correlation between physical condition and redness (Rowland 1984; Baube 1997). The negative relationship we found here may be a tactic by which males in poorer condition invest strongly into red coloration (Candolin 1999a), and thus become more attractive to females (Bakker and Milinski 1991). Sample size and feeding regime may account for the ambiguous results.

Counterintuitively, in our choice experiment, we found a significantly negative relationship between UV chroma and UV+ filter association of the territorial males. Perhaps males with poorer UV reflectance have to compensate their lack of coloration and thus invest more into aggressive behaviour against the UV+ male, which they visually estimated as a greater threat. Since we did not measure body reflectance of the stimulus males, we cannot check whether differences in reflectance between the corresponding intruders and the territorial male affected the aggressive response behaviour.

Finally, the colour parameters we have determined here should only give approximate information about a potential signalling value of colour expression in male sticklebacks. For a more detailed analysis of intraspecific colour communication, it would be important to consider the involved visual system as well as the light environment in which signalling occurs and include these variables in a visual model of colour perception.

In conclusion, stickleback males use UV wavelengths in aggressive interactions. Considering that UV light, in our study population, is also used in female mate choice (Rick et al. 2006) and male mate choice (Rick and Bakker 2008), it can be assumed that UV signalling in this species has evolved as an important cue for sexual selection.

Acknowledgments We are grateful to Ricarda Modarressie, Sebastian Baldauf, Timo Thünken, Joachim Frommen for discussion and comments on the manuscript and Susanne Lindsteding and Nicole Henning for their help with data collection. We gratefully acknowledge the permission of Jürgen Wittler for catching sticklebacks at the field site. Manuscript preparation was supported by a grant from the Deutsche Forschungsgemeinschaft (BA 2885/1–3). The study conforms to the legal requirements of Germany.

References

Alonso-Alvarez C, Doutrelant C, Sorci G (2004) Ultraviolet reflectance affects male–male interactions in the blue tit (*Parus caeruleus ultramarinus*). Behav Ecol 15:805–809

Andersson S (1994) Costs of sexual signalling in the lekking Jackson widowbird. Condor 96:1–10

Andersson S, Ornborg J, Andersson M (1998) Ultraviolet sexual dimorphism and assortative mating in blue tits. Proc R Soc Lond B 265:445–450

Baerends GP (1985) Do dummy experiments with sticklebacks support the IRM-concept. Behaviour 93:258–377

Bakker TCM (1986) Aggressiveness in sticklebacks (*Gasterosteus aculeatus* L.): a behaviour-genetic study. Behaviour 98:1–144

Bakker TCM, Sevenster P (1983) Determinants of dominance in male sticklebacks (*Gasterosteus aculeatus* L.). Behaviour 86:55–71

Bakker TCM, Milinski M (1991) Sequential female choice and the previous male effect in sticklebacks. Behav Ecol Sociobiol 29:205–210

Bakker TCM, Mundwiler B (1994) Female mate choice and male red coloration in a natural three-spined stickleback (*Gasterosteus aculeatus*) population. Behav Ecol 5:74–80

Baube CL (1997) Manipulations of signalling environment affect male competitive success in three-spined sticklebacks. Anim Behav 53:819–833

Baube CL, Rowland WJ, Fowler JB (1995) The mechanisms of colour-based mate choice in female threespine sticklebacks: hue, contrast and configurational cues. Behaviour 132:979–996

Bennett ATD, Cuthill IC, Partridge JC, Maier EJ (1996) Ultraviolet vision and mate choice in zebra finches. Nature 380:433–435

Bleiweiss R (2004) Ultraviolet plumage reflectance distinguishes sibling bird species. Proc Natl Acad Sci U S A 101:16561–16564

Bleiweiss R (2005) Variation in ultraviolet reflectance by carotenoid-bearing feathers of tanagers (Thraupini: Emberizinae: Passeriformes). Biol J Linn Soc 84:243–257

Boulcott PD, Walton K, Braithwaite VA (2005) The role of ultraviolet wavelengths in the mate-choice decisions of female three-spined sticklebacks. J Exp Biol 208:1453–1458

Candolin U (1999a) The relationship between signal quality and physical condition: is sexual signalling honest in the three-spined stickleback. Anim Behav 58:1261–1267

Candolin U (1999b) Male–male competition facilitates female choice in sticklebacks. Proc R Soc Lond B 266:785–789

Cooper WE, Vitt LJ (1988) Orange head coloration of the male broad-headed skink (*Eumeces laticeps*), a sexually selected social cue. Copeia 1988:1–6

Doucet SM, Shawkey MD, Rathburn MK, Mays HL, Montgomerie R (2004) Concordant evolution of plumage colour, feather microstructure and a melanocortin receptor gene between mainland and island populations of a fairy-wren. Proc R Soc Lond B 271:1663–1670

Fernald RD (1980) Response of male cichlid fish, *Haplochromis burtoni*, reared in isolation to models of conspecifics. Z Tierpsychol 54:85–93

Hunt S, Bennett ATD, Cuthill IC, Griffiths R (1998) Blue tits are ultraviolet tits. Proc R Soc Lond B 265:451–455

Huntingford FA (1976) The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. Anim Behav 24:245–260

McLennan DA, McPhail JD (1989) Experimental investigations of the evolutionary significance of sexually dimorphic nuptial coloration in *Gasterosteus aculeatus* L.—the relationship between male color and male behavior. Can J Zool 67:1778–1782

Milinski M, Bakker TCM (1990) Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. Nature 344:330–333

Modarressie R, Rick IP, Bakker TCM (2006) UV matters in shoaling decisions. Proc R Soc Lond B 273:849–854

Mougeot F, Arroyo BE (2006) Ultraviolet reflectance by the cere of raptors. Biol Lett 2:173–176

Peeke HVS (1969) Habituation of conspecific aggression in three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour 35:137–156

Pryke SR, Lawes MJ, Andersson S (2001) Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. Anim Behav 62:695–704

Reimchen TE (1989) Loss of nuptial color in threespine sticklebacks (*Gasterosteus aculeatus*). Evolution 43:450–460

Reisman HM (1968) Effects of social stimuli on secondary sex characters of male three-spined sticklebacks (*Gasterosteus aculeatus*). Copeia 4:816–826

Rick IP, Bakker TCM (2008) UV wavelengths make female three-spined sticklebacks (*Gasterosteus aculeatus*) more attractive for males. Behav Ecol Sociobiol 62:439–445

Rick IP, Modarressie R, Bakker TCM (2004) Male three-spined sticklebacks reflect in ultraviolet light. Behaviour 141:1531–1541

Rick IP, Modarressie R, Bakker TCM (2006) UV wavelengths affect female mate choice in three-spined sticklebacks. Anim Behav 71:307–313

Riechert SE (1998) Game theory and animal contests. In: Dugatkin LA, Reeve HK (eds) Game theory and animal behavior. Oxford University Press, Oxford, pp 64–93

Rowland WJ (1982) The effects of male nuptial coloration on stickleback aggression—a re-examination. Behaviour 80:118–126

Rowland WJ (1983) Color intensity as a predictor of responsiveness in male threespine sticklebacks. Am Zool 23:880–880

Rowland WJ (1984) The relationships among nuptial coloration, aggression, and courtship of male three-spined sticklebacks, *Gasterosteus aculeatus*. Can J Zool 62:999–1004

Siebeck UE (2004) Communication in coral reef fish: the role of ultraviolet colour patterns in damselfish territorial behaviour. Anim Behav 68:273–282

Siefferman L, Hill GE (2005) UV-blue structural coloration and competition for nestboxes in male eastern bluebirds. Anim Behav 69:67–72

Siitari H, Huhta E (2002) Individual color variation and male quality in pied flycatchers (*Ficedula hypoleuca*): a role of ultraviolet reflectance. Behav Ecol 13:737–741

Smith EJ, Partridge JC, Parsons KN, White EM, Cuthill IC, Bennett ATD, Church SC (2002) Ultraviolet vision and mate choice in the guppy (*Poecilia reticulata*). Behav Ecol 13:11–19

Stacey PB, Chiszar D (1978) Body color pattern and aggressive-behavior of male pumpkinseed sunfish (*Lepomis gibbosus*). Behaviour 64:271–297

Studd MV, Robertson RJ (1985) Evidence for reliable badges of status in territorial yellow warblers (*Dendroica petechia*). Anim Behav 33:1102–1113

Tinbergen N (1953) The evolution of mating behavior patterns. Evolution 7:391–391

Werner DI (1978) On the biology of *Tropidurus delanonis*, Baur (Iguanidae). Z Tierpsychol 47:337–395

Whiting MJ, Stuart-Fox DM, O'Connor D, Firth D, Bennett NC, Blomberg SP (2006) Ultraviolet signals ultra-aggression in a lizard. Anim Behav 72:353–363

Wickler W (1967) Socio-sexual signals and their intra-specific imitation among primates. In: Morris D (ed) Primate ethology. Weidenfeld and Nicolson, London, pp 69–147

Wunder (1934) Gattenwahlversuche bei Stichlingen und Bitterlingen. Zool Anz Suppl (Verh Dtsch Zool Ges) 7:152–158