A limited role for ultraviolet radiation when threespine sticklebacks (*Gasterosteus aculeatus*) prey upon *Daphnia*

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Abstract: Any trait of predatory species that enhances hunting efficiency should be favoured by natural selection. Foraging in threespine sticklebacks (*Gasterosteus aculeatus*) is mainly visually mediated. The visual system of sticklebacks is extended into the ultraviolet (UV) range of the spectrum. We tested, in four different experimental setups, the influence of different spectral compositions, in particular the presence and absence of ultraviolet wavelengths, on the feeding performance of threespine sticklebacks while foraging on live *Daphnia magna*, which absorb UV. In the three experiments with similar background reflections, the foraging behaviour of sticklebacks was unaffected by removing UV wavelengths. But in the fourth experiment, sticklebacks showed a significant difference between the rate of detecting prey against a UV-reflecting or UV-absorbing background. Sticklebacks significantly attacked prey faster when the background lacked UV reflections. Thus, the interaction of prey with its background in UV wavelengths influenced sticklebacks' prey detection. Removing long wavelengths impaired foraging rate, suggesting that long wavelengths may be more important in foraging tasks than UV wavelengths.

Résumé : Toute caractéristique d'une espèce prédatrice qui améliore l'efficacité de la chasse devrait être favorisée par la sélection naturelle. La recherche de nourriture chez l'épinoche à trois épines (*Gasterosteus aculeatus*) se fait surtout au moyen de la vue. Le système visuel des épinoches s'étend vers la région ultraviolette (UV) du spectre. Nous testons, dans quatre montages expérimentaux différents, l'influence des diverses compositions spectrales, en particulier de la présence et l'absence de longueurs d'onde ultraviolettes, sur l'efficacité de l'alimentation d'épinoches à trois épines qui se nourrissent de *Daphnia magna* vivantes qui absorbent l'UV. Dans trois expériences dans lesquelles la réflexion d'arrière-plan est semblable, le comportement de recherche de nourriture des épinoches n'est pas affecté par le retrait des longueurs d'onde UV. Cependant, dans la quatrième expérience, les épinoches ont des taux de détection des proies significativement différents devant un arrière-plan qui reflète les UV et un qui les absorbe. Les épinoches attaquent leurs proies significativement plus rapidement lorsque l'arrière-plan ne reflète pas les UV. Ainsi, l'interaction de la proie et de son arrière-plan en ce qui a trait aux longueurs d'onde UV influence la détection des proies par les épinoches. Le retrait des longueurs d'onde élevées diminue le taux d'alimentation, ce qui laisse croire que les longueurs d'onde élevées peuvent être plus importantes pour les activités de recherche de nourriture que les longueurs d'onde UV.

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Introduction

In predatory species, detecting and successfully hunting for prey is essential for survival and, especially in juveniles, to accelerate growth. Therefore, any trait (e.g., improved visual abilities in visually hunting animals) that enhances the efficiency of prey detection should be favoured by natural and eventually also by sexual selection. The latter is the case when, for example, carotenoid-dependent colorations, which must be acquired through the diet (Rothschild 1975; Kodric-Brown 1989), play a role in mate choice as in threespine sticklebacks (*Gasterosteus aculeatus*) (McLennan and McPhail 1989; Milinski and Bakker 1990) and guppies (*Poecilia reticulata*) (Grether 2000; Pilastro et al. 2004; Karino et al. 2007). Besides mechano-sensory input by the lateral line system (Bleckmann 1993) or chemo-perception (Pohlmann et al. 2001), prey search behaviour in fish is visually mediated (Guthrie and Muntz 1993; Hart and Gill 1994). A prerequisite for visual-mediated detection of prey organisms is a difference in radiance between the prey and its background (Lythgoe 1968). Zooplankters, such as *Daphnia*, belong to the natural prey spectrum of threespine sticklebacks and are camouflaged by being small and relatively transparent (Johnsen and Widder 1998). *Daphnia* are semitransparent, containing lipids and carotenoids, which strongly absorb short wavelengths (Lee et al. 1970). Therefore, *Daphnia* form a strong contrast with a background that reflects ultraviolet (UV) wavelengths. This contrast could enhance the foraging

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efficiency of fish, provided that UV vision contributes to feeding performance. UV-reflecting backgrounds are naturally occurring when prey is viewed, for example, against a sun-lit water column or sandy bottom. For some species, there is strong evidence that UV vision is used in detecting and hunting prey (Browman et al. 1994). Also, in terrestrial species UV vision seems to play a role while foraging, for example, blue tits (*Parus caeruleus* L.) find food faster when UV wavelengths are present (Church et al. 1998), and common kestrels (*Falco tinnunculus* L.) seem to use vole scent marks, which are UV-reflective, to locate prey (Viitala et al. 1995). But in some other studies, no significant effect was found of UV radiation on foraging efficiency (Rocco et al. 2002; Leech and Johnsen 2006). Most investigations about feeding performance in fish concentrated on different light intensities (i.e., different amounts of transmitted light) (e.g., Vinyard and O'Brian 1976; Richmond et al. 2004; Pekcan-Hekim and Lappalainen 2006). A few recent studies have addressed how spectral composition (specific wavelength ranges), rather than intensity, influences foraging efficiency (Utne-Palm 1999; White et al. 2005; Leech and Johnsen 2006).

Many shallow-water fishes are capable of perceiving UV wavelengths (300–400 nm) (Archer et al. 1987; Jacobs 1992; Losey et al. 1999). Also, threespine sticklebacks possess a fourth UV-sensitive visual pigment maximally absorbing (λ_{max}) at 360 nm (Rowe et al. 2004), in addition to the three photopigments with λ_{max} of 435, 530, and 605 nm (Lythgoe 1979). Previous studies in threespine sticklebacks showed significant effects of UV on mate choice (Boulcott et al. 2005; Rick et al. 2006), shoal choice (Modarressie et al. 2006), and orientation by means of landmarks (Boulcott and Braithwaite 2005). The role of UV on foraging success in fishes is ambiguous (Browman et al. 1994; White et al. 2005) and contrasts with the role of long wavelengths in motion detection and foraging success of fishes. In optomotor response experiments on goldfish (*Carassius auratus*), Schaerer and Neumeyer (1996) identified that long wavelength cones (620–660 nm) contribute to motion detection, which also applies to zebrafish (*Danio rerio*) (Krauss and Neumeyer 2003). Additionally, White et al. (2005) found that the exclusion of long wavelengths but not UV wavelengths reduces foraging rates in guppies. Therefore, further studies on the role of UV radiation in foraging tasks of predatory fish species are needed.

In this study, we investigated whether UV wavelengths contribute to feeding performance in threespine sticklebacks when feeding on live *Daphnia magna*. We further tested whether the exclusion of longer wavelengths (550–700 nm) as well as the exclusion of both UV and long wavelengths influenced foraging behaviour.

Materials and methods

In total, we conducted four different foraging experiments to study different aspects of UV and long wavelengths on the feeding performance of threespine sticklebacks feeding on live *Daphnia magna* as prey.

Experimental subjects

Several hundred sticklebacks were caught with minnow traps before the start of the breeding season on 16 March 2005 from a shallow pond near Euskirchen, Germany (50°38′N, 6°47′E). The pond is located in a small woodland and is exposed to full sunlight penetration throughout the year. The fish were released into two outdoor stocking tanks (volume 700 L; provided with tap water, flow rate of 3 $L \cdot min^{-1}$, and air ventilation). To guarantee full penetration of UV-rich sunlight, stocking tanks were cleaned regularly. Fish were fed daily ad libitum on a diet of frozen chironomid larvae. As prey organisms, we used *Daphnia magna*, which belongs to the natural prey spectrum of sticklebacks. The *Daphnia* used (mean body length ± SD: 2.165 ± 0.229 mm, $N = 20$) were laboratory-bred and grown on a mixture of mud and chicken faeces. The *Daphnia* were held under the same laboratory lighting and temperature conditions as the test fish.

General experimental procedure

One week prior to trials, fish were gently taken from the outdoor tanks and transferred to four indoor holding tanks (50 cm × 30 cm × 30 cm, length × height × width) with 17 ± 1 °C water temperature and internal filter aeration. Illumination was provided by fluorescent tubes (True Light, Natural Daylight 5500, 36 Watt, 1200 mm; for spectrum, see section on Light measurements below) hanging 15 cm above the water surface with a day–night cycle of 16 h light : 8 h dark. These lights contain a proportion of UV similar to natural sunlight and were also used during experiments. Feeding was performed once a day with live *Daphnia magna* to train test fish to live food in addition to frozen chironomid larvae. To guarantee the same hunger level in all fish over trials, test fish were not fed at least 24 h before the beginning of the experiments. In all four experiments, we used the same-sized test aquarium (Figs. 1*a*–1*d*; 30 cm × 20 cm × 20 cm).

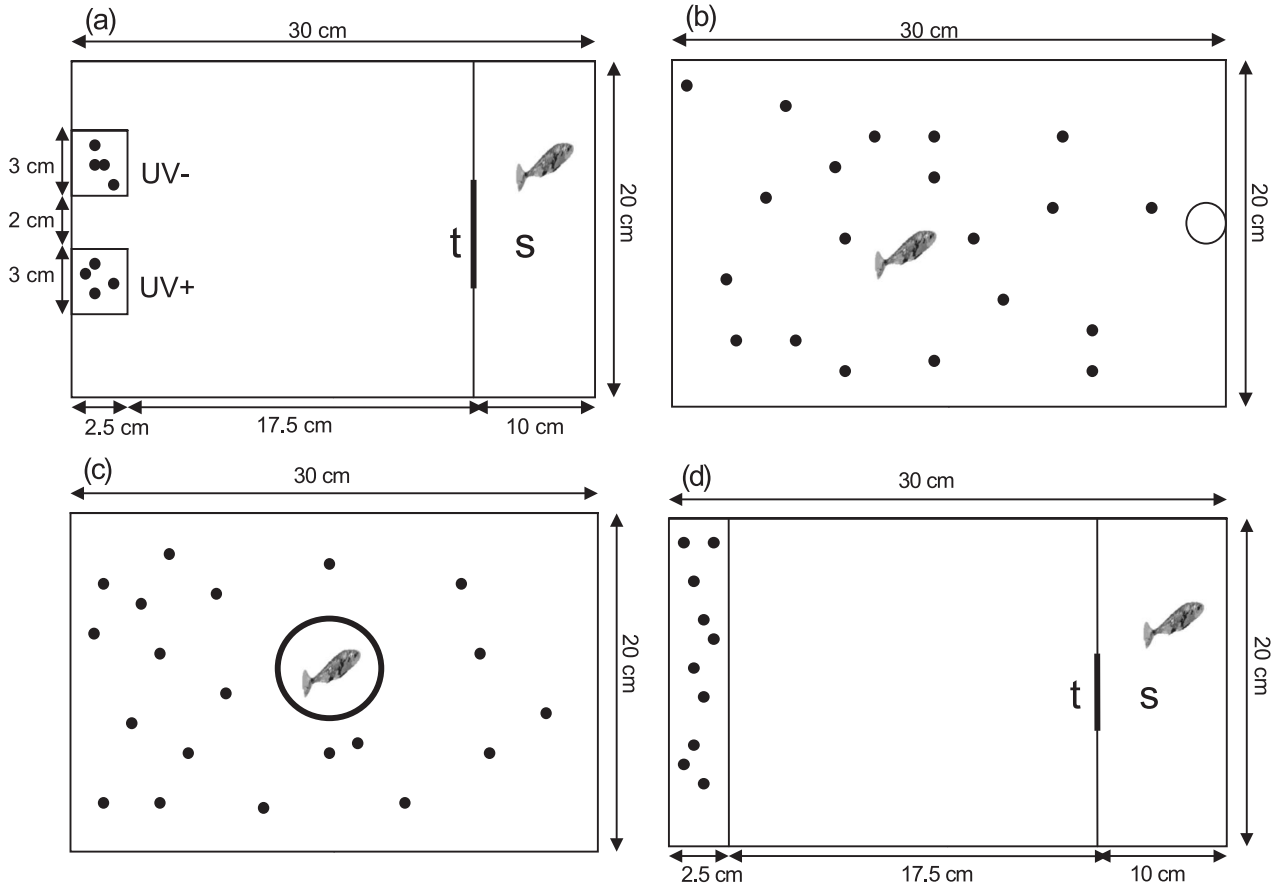
We tested feeding performance under UV-present (UV+) and UV-absent (UV–) lighting conditions using two specific types of optical filters (transmission spectra given in Fig. 2): UV+, GS 2458 and UV–, GS 233, Röhm Darmstadt, Germany. Because these two optical filters differed about 18% in quantal flux and therefore in luminance for UV-sensitive animals (Rick et al. 2006), control experiments were needed. These control experiments were conducted with two UV-transmittive, neutral density filters (Fig. 2: ND1 and ND2, Lee # 209 and Cotech # 298, respectively), which alter luminance independent of hue. They differed about 34% in quantal flux (Rick et al. 2006). The experimental procedure of the control experiments was exactly the same as described for the experiments above with changed quantitative transmission. After each experiment, water was completely exchanged. All setups were surrounded by a black curtain to prevent external, potentially confounding effects.

In each experiment, we tested reproductively inactive individuals, except in experiment four in which we used male sticklebacks with nuptial breeding coloration. After the trials, fish were measured for standard length (SL in cm) and body mass (M in g), and their condition factor (CF) was calculated according to $CF = 100 \cdot M \cdot SL^{-3}$ (Bolger and Connolly 1989).

Experiment 1: prey preference test

In the first experiment, we tested feeding preferences of sticklebacks for prey viewed under UV+ and UV– lighting conditions. We conducted a paired feeding-preference de-

Fig. 1. The experimental setups used in experiments (*a*) 1, (*b*) 2, (*c*) 3, and (*d*) 4. Solid dots represent *Daphnia*; thin ring is a plastic feeding tube in (*b*); thick ring is an opaque cylinder in (*c*); t, trapdoor; s, start compartment.



sign, in which fish had the opportunity to attack two simultaneously presented cells (2.5 cm × 3 cm × 10 cm), each containing 40 live *Daphnia*. The cells were installed 2 cm apart inside the test aquarium at the side pane (Fig. 1*a*). One cell was made of UV-transmitting (UV+, GS 2485, Rhöm Darmstadt, Germany) perspex and the other of UV-blocking (UV–, GS 233, Rhöm Darmstadt, Germany) perspex. The walls of the test aquarium were completely covered with grey, opaque plastic partitions, which reflected moderately (reflectance spectrum given in Fig. 3) in the UV. The test aquarium was filled with tap water at a height of 7 cm. Opposite to the prey cells, a start compartment (10 cm × 20 cm × 20 cm) was installed. It was made of grey, opaque plastic and had a small trapdoor (4 cm × 10 cm) positioned midway, which could be lifted by a thin rope. Illumination was provided by a fluorescent tube hanging 55 cm above the water surface (spectrum 3 cm above the bottom of the tank given in Fig. 4*a*).

One experiment comprised two trials, each lasting for 20 min. After 10 min of acclimatization in the start compartment, the test fish was released by lifting the trapdoor. Thereafter, 10 min of feeding preference was filmed with a webcam from 55 cm above the aquarium. After the first trial, the test fish was gently reintroduced, using a hand net, for further 10 min into the start compartment, and the positions of the prey cells were exchanged. Then the trapdoor was lifted again, and the second trial started for another 10 min with exchanged UV+ and UV– prey cell positions. After the experiment, the *Daphnia* used were exchanged by new ones.

To control for differences in luminance between the UV+ and UV– filters, the same experimental procedure was conducted with cells made of two neutral density (ND1 and ND2) filters. We noticed which cell was attacked first and measured the total time test fish spent within a 2 cm preference zone in front of each prey cell after both had been visited. Films were analysed blind, that is, without knowledge of filter positions. A total of 38 fish were tested in both the UV and the ND treatments. For the UV treatment, the mean SL (±SD) of test fish was 3.53 cm (±0.42 cm), mean M = 0.53 g (±0.21 g), and mean CF = 1.15 (±0.16). For the ND treatment, the mean SL (±SD) of test fish was 3.47 cm (±0.45 cm), median M = 0.51 g (range: 0.26–1.18 g), and median CF = 1.19 (range: 0.9–2.1). These experiments were conducted between 26 April and 4 May 2005.

Experiment 2: unpaired predation test

In this experiment, we tested the foraging efficiency of sticklebacks preying upon live *Daphnia* under UV+ and UV– lighting conditions. The test aquarium (Fig. 1*b*) was filled with tap water up to a level of 7 cm. The two side walls were covered with UV-reflecting aluminium foil (reflectance spectrum in Fig. 3), and the back pane was cov-

Fig. 2. Transmission spectra for filters used in the experiments: ultraviolet-transmitting (UV+: thin black), ultraviolet-blocking (UV–: thick black), long-wavelength-blocking (LW–: broken black), and full-spectrum, neutral density (ND1, thin grey; and ND2, thick grey) filters. Measurements were taken with an Avantes AVS-USB2000 spectrophotometer and an Avantes DH-2000 deuterium-halogen light source.

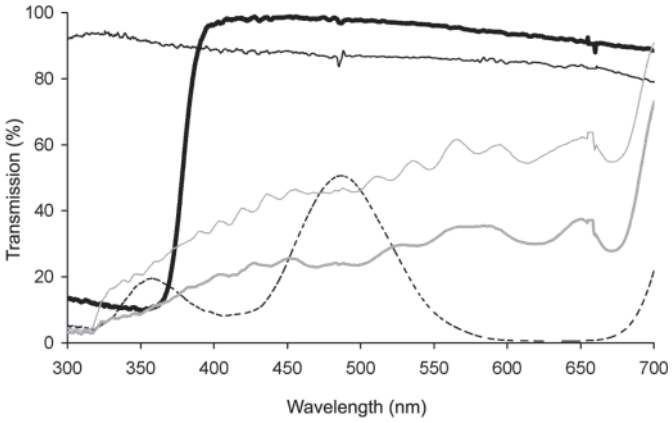
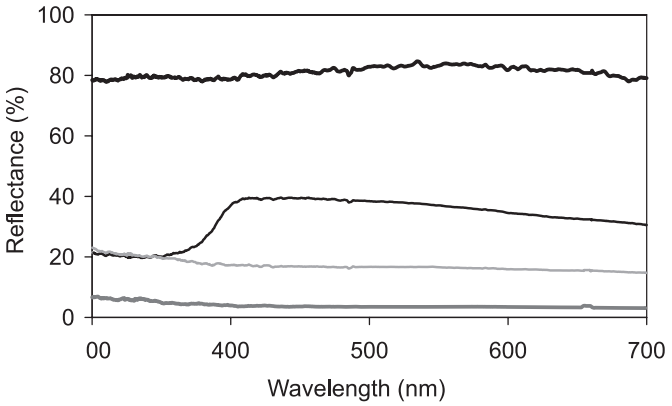


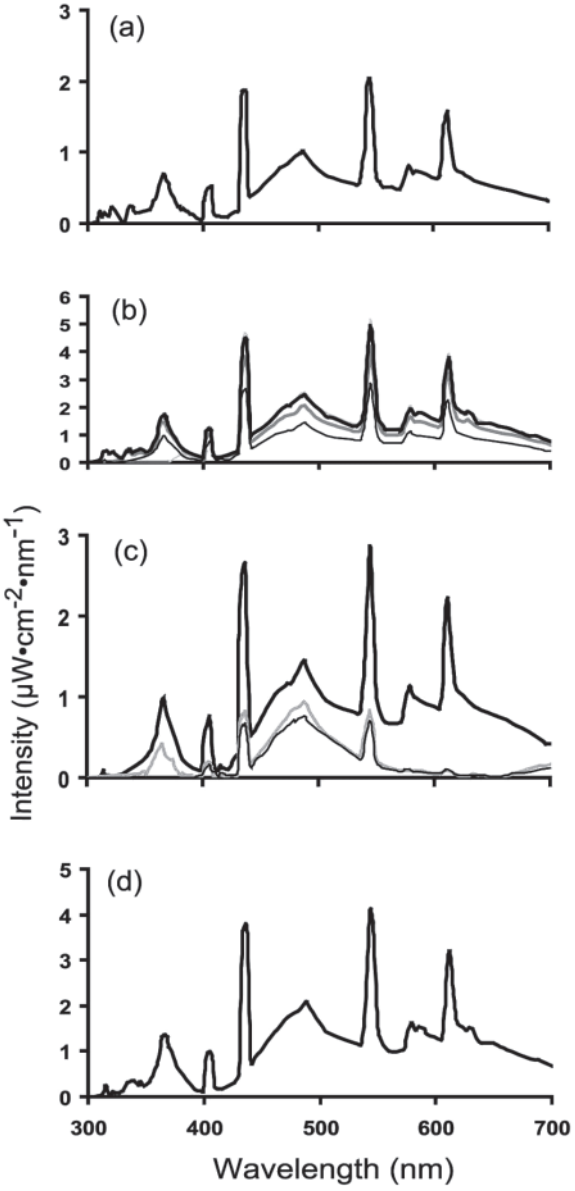
Fig. 3. Mean reflectance spectra from 10 measurements of the different backgrounds used in the experiments: thick black: duct tape; thin black: grey plastic partitions; thin grey: aluminium foil; and thick grey: black tar – bitumen.



ered with black tar – bitumen (reflectance spectrum in Fig. 3) roof sheeting. The latter facilitated observation because of enhanced contrast of *Daphnia* against the back pane. The front window remained clear for observation. Again, the test aquarium was illuminated 17 cm from above by a fluorescent tube (True Light, Natural Daylight 5500, 36 Watt, 1200 mm), emitting a proportion of UV wavelengths in addition to the visible spectrum (spectrum 3 cm above the bottom of the tank given in Fig. 4*b*). A plastic tube (diameter 7 mm) was installed on one side wall as prey feeder. The whole setup, excluding a small observation window (10 cm × 4 cm), was surrounded by a black curtain to exclude external, potentially confounding effects.

The test fish was gently introduced into the test aquarium using a hand net. All test fish had 10 min of acclimatization, while every 2 min within this period of time 50 mL of tap water was introduced through the plastic tube into the aquarium. At the tenth minute, 50 mL of tap water containing 10

Fig. 4. Intensity measurements (expressed as $\mu W \cdot cm^{-2} \cdot nm^{-1}$) of the lighting conditions in the different setups. (*a*) Experiment 1 (UV+), (*b*) Experiment 2 (thick black, UV+; thin grey, UV–; thick grey, ND1; and thin black, ND2), (*c*) Experiment 3 (thick black, UV+; grey, UV+,LW–; thin black, UV–,LW–), (*d*) Experiment 4 (UV+).



live *Daphnia magna* was added through the plastic tube. Thirty fish (mean SL (±SD) of test fish was 4.63 cm (±0.7 cm), mean M = 1.28 g (±0.51 g), and mean CF = 1.24 (±0.18)) were tested under UV+ lighting conditions using a UV-transmitting optical filter, and 30 fish (mean SL (±SD) of test fish was 4.66 cm (±0.64 cm), mean M = 1.34 g (±0.50 g), and mean CF = 1.26 (±0.16)) under UV– lighting conditions using a UV-blocking optical filter. The UV filters were placed on top of the test aquarium. In the control experiments, we tested a total of 60 fish (30 under ND1 and 30 under ND2 conditions). For the ND1 treatment, the mean SL (±SD) of test fish was 4.81 cm (±0.57 cm), median M = 1.42 g (range: 0.58–2.2 g), and median CF = 1.21 (range: 1.01–2.5). The mean SL (±SD) of test fish in the ND2 treat-

ment was 4.51 cm (±0.72 cm), median M = 1.29 g (range: 0.39–2.29 g), and median CF = 1.22 (range: 1.10–3.19).

We measured (*i*) time elapsed after introduction until first prey consumption, (*ii*) duration of time until five *Daphnia* (half of the presented prey items) were eaten, and (*iii*) the time interval between the consumption of the first and fifth *Daphnia*. This experiment was conducted between 28 November and 9 December 2005.

Experiment 3: exclusion of short and long wavelengths

In this experiment, individual fish were consecutively tested under three different lighting conditions. We excluded either the long wavelengths (UV+,LW–; Rosco Supergel filter 73; transmission spectrum in Fig. 2) or both the short and long wavelengths (UV–,LW–) or gave the full spectrum (UV+,LW+; 300–700 nm). Each fish was tested under all three lighting conditions (spectra 3 cm above the bottom of the tank given in Fig. 4*c*) in a randomly determined order.

The test fish was introduced in an opaque, plastic cylinder (diameter 6 cm) positioned in the middle of the test aquarium (Fig. 1*c*), and 20 *Daphnia* were introduced into the aquarium. After 10 min of acclimatization, the cylinder was lifted through a thin rope and the trial started. One trial lasted for 10 min or until 10 *Daphnia* were eaten.

Again, during observation we recorded time elapsed until (*i*) first prey consumption and (*ii*) last prey consumption. A total of 22 fish were tested. Trials were conducted between 20 April and 2 May 2006. Data were transformed $(1/\sqrt{(x+1.1)})$ to meet the normality assumptions for parametric statistical tests. The mean SL (±SD) of test fish was 3.31 cm (±0.36 cm), mean M = 0.46 g (±0.12 g), and mean CF = 1.27 (±0.26).

Experiment 4: background reflection

In this experiment, we tested explicitly the influence of UV-reflecting and nonreflecting backgrounds on foraging behaviour of male sticklebacks. The test aquarium (Fig. 1*d*) was divided into three compartments. The middle compartment (17.5 cm × 20 cm × 20 cm) formed the testing arena. The prey compartment (2.5 cm × 20 cm × 20 cm) containing 10 *Daphnia* was separated by UV-transmitting perspex from the middle compartment. The start compartment (10 cm × 20 cm × 20 cm) was positioned at the other side of the middle compartment and separated from it by a grey, opaque partition with a trapdoor positioned midway. The side wall of the prey compartment facing the partition with the middle compartment also consisted of UV-transmitting perspex. A plastic plate that was covered by UV-reflecting, Teflon-coated tape (reflectance spectrum in Fig. 3) was mounted behind the side wall of the prey compartment. In the nonreflecting trial, a UV-blocking perspex was inserted between the reflecting background and the side wall. Again, the test aquarium was illuminated 17 cm from above by a fluorescent tube (True Light, Natural Daylight 5500, 36 Watt, 1200 mm), emitting a proportion of UV wavelengths in addition to the visible spectrum (spectrum 3 cm above the bottom of the tank given in Fig. 4*d*).

The foraging behaviour of 32 males (16 with a UV+ and 16 with a UV– background) was filmed from above. The films were analysed blind, that is, without knowledge of the background of the prey compartment. The time elapsed until the first attack on the prey compartment and the time spent within a 4 cm preference zone (adjusted to male body length) in front of the prey compartment within 10 min after the first attack were measured. In the UV+ treatment, the mean SL (±SD) of test fish was 4.59 cm (±0.21 cm), mean M = 1.35 g (±0.18 g), and mean CF = 1.40 (±0.25). Test fish used in the UV– treatment had mean SL (±SD) of 4.49 cm (±0.26 cm), mean M = 1.34 g (±0.24 g), and mean CF = 1.46 (±0.15). Trials were conducted on 17 and 18 November 2005.

Light measurements

Irradiance in the test tanks was measured using a calibrated spectrometer (Avantes AVS-USB2000, Eerbeek, the Netherlands). A 2 mm diameter fiber optic probe with CC-UV/VIS cosine corrector was fitted to the spectrometer. The probe was placed 3 cm above the bottom of the tank, and light was collected at an angle of 45°. The spectral irradiance was measured from 300 to 700 nm under the different experimental lighting conditions (Figs. 4*a*–4*d*).

Statistical analysis

All analyses were performed using SPSS 11.0 for Windows (SPSS Inc., Chicago, Illinois). When data were not normally distributed according to the Kolmogorov–Smirnov test with Lilliefors correction and could not be transformed, nonparametric statistics was applied. Given P values are two-tailed throughout. Bonferroni corrections were applied to correct for the effects of multiple testing.

Results

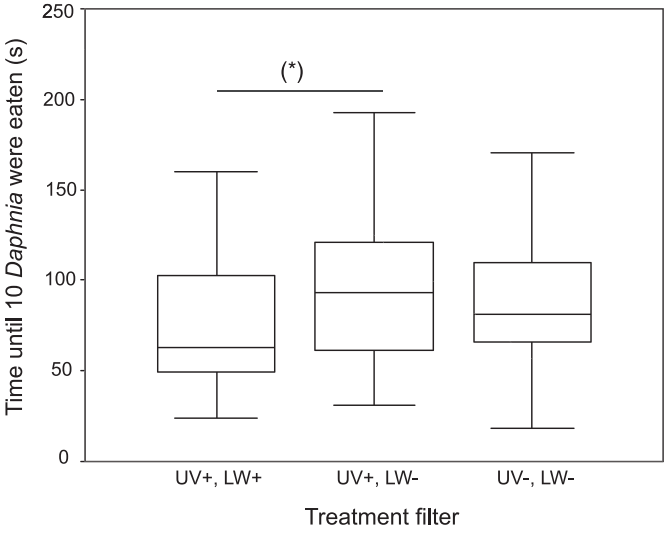
Experiment 1

Both prey cells, UV+ and UV–, were first attacked at a similar rate, both in the first (UV+ = 20; UV– = 18; χ^2 test, $\chi^2_1 = 0.105$, $P = 0.746$) and second trials (UV+ = 17; UV– = 19; χ^2 test, $\chi^2_1 = 0.111$, $P = 0.739$). The neutral-density trials gave similar results. The ND1 prey cell was first attacked 18 times during the first trials, whereas the ND2 prey cell was attacked 20 times (χ^2 test, $\chi^2_1 = 0.105$, $P = 0.746$) and no significant difference was found with respect to the first attack in second trials (χ^2 test, $\chi^2_1 = 0.027$, $P = 0.869$). The time test fish spent within the preference zone in front of the UV+ prey cell did not differ significantly from time spent in front of the UV– prey cell (mean ± SD, UV+ = 55.83 ± 49.07 s; UV– = 65.97 ± 46.57 s; Wilcoxon matched-pairs signed-ranks test: $n = 30$, $Z = –1.546$, $P = 0.122$). No significant difference was found between the time test fish spent in front of the ND1 and ND2 prey cells (mean ± SD, ND1 = 66.24 ± 48.13 s; ND2 = 69.16 ± 48.59 s; Wilcoxon matched-pairs signed-ranks test: $n = 38$, $Z = –0.587$, $P = 0.557$).

Experiment 2

Testing the feeding performance of sticklebacks on live *Daphnia* under UV+ and UV– lighting conditions showed no significant difference in time elapsed until the first *Daphnia* was eaten between the UV+ and UV– treatments (Mann–Whitney U test, $N_1 = 27$, $N_2 = 26$, $U = 306$, $P = 0.423$). This result suggests that UV wavelengths did not enhance prey detection. There was also no significant difference in time elapsed until the first *Daphnia* was eaten in the

Fig. 5. Median time (s) (± quartiles, percentiles) elapsed until 10 *Daphnia* were eaten under three different lighting conditions in which ultraviolet wavelengths (UV–), long wavelength (LW–), or both (UV–,LW–) were removed. The asterisk (*) signifies $P < 0.05$ after Bonferroni correction between the treatments UV+,LW+ and UV+,LW–.



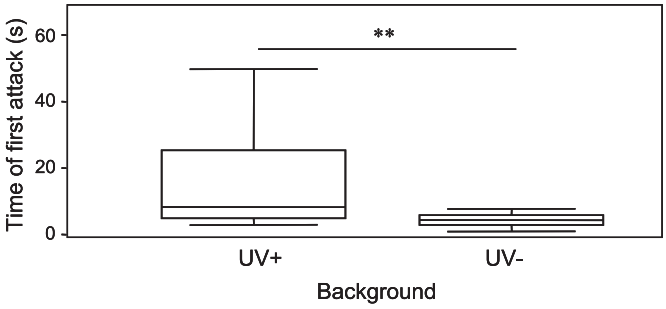
luminance control experiment with the ND1 and ND2 filters (Mann–Whitney U test, $N_1 = 26$, $N_2 = 29$, $U = 340$, $P = 0.533$). Thus, the difference in luminance also seemed to have no influence on feeding performance. The fish tested under UV+ and UV– conditions, as well as those tested under ND1 and ND2 lighting conditions, did not significantly differ with respect to SL, M, or CF (all $P > 0.5$).

Also, no significant differences were observed in time elapsed until the fifth *Daphnia* was eaten either in the UV+,UV– or ND1,ND2 treatments (Mann–Whitney U test, $N_1 = 25$, $N_2 = 26$, $U = 309.5$, $P = 0.77$; and $N_1 = 21$, $N_2 = 26$, $U = 222$, $P = 0.275$, respectively). Furthermore, the time interval between the first and the fifth consumed *Daphnia* did not differ significantly either in the UV+,UV– or ND1,ND2 treatments (Mann–Whitney U test, $N_1 = 25$, $N_2 = 26$, $U = 300$, $P = 0.637$; and $N_1 = 21$, $N_2 = 26$, $U = 229.5$, $P = 0.352$, respectively). Thus, all fish fed at the same rate of five *Daphnia*, once the first was detected.

Experiment 3

The time elapsed until first prey capture did not differ significantly among the three (UV+,LW–; UV–,LW–; and UV+,LW+) different lighting conditions (repeated measures ANOVA: $F_{[2,22]} = 1.369$, $P = 0.277$). However, time elapsed until 10 *Daphnia* were eaten tended to differ under the three given lighting conditions (repeated measures ANOVA: $F_{[2,18]} = 3.239$, $P = 0.066$; Fig. 5). When removing the long wavelengths from the spectrum (UV+,LW–), sticklebacks needed significantly more time to consume 10 *Daphnia* compared with the full spectrum conditions UV+,LW+ (paired t test: $t = 2.358$, df = 17, $P = 0.031$; Fig. 5). However, after adjusting significance levels according to Bonferroni, this result was not significant. The two other comparisons (UV–,LW– vs. UV+,LW+ and UV+,LW– vs. UV–,LW–) were also not significant ($P = 0.348$ and $P = 0.221$, respectively).

Fig. 6. Median time (s) (± quartiles, percentiles) elapsed until first attack on *Daphnia* presented either in front of a UV-reflecting (UV+) or a UV-nonreflecting (UV–) background. **, $P < 0.01$ for both scenarios.



Experiment 4

The time elapsed until prey was attacked, and thus the rate at which prey was detected, differed significantly between the UV+ and UV– treatment. Males attacked prey significantly faster when the background lacked UV reflections in comparison with a UV-reflecting background (Mann–Whitney U test, $N_1 = 16$, $N_2 = 16$, $U = 52.5$, $P = 0.003$; Fig. 6). Males in the UV+ treatment did not differ from males in the UV– treatment with respect to SL, M, or CF (t test, all $P > 0.241$). Furthermore, neither SL, M, nor CF was significantly correlated to the latency of the first attack (Spearman's rank correlation coefficient, all $P > 0.165$). No significant differences between the UV+ and UV– treatment were found with respect to the time spent in front of the prey compartment within the testing period of 10 min (t test, $t = –1.542$, df = 30, $P = 0.138$).

Discussion

The aim of this study was to quantify whether ultraviolet photoperception contributes to prey search behaviour and foraging efficiency in threespine sticklebacks using *Daphnia magna* as prey. We found that the presence of UV wavelengths did not enhance prey detection. The feeding performances of threespine sticklebacks preying upon live *Daphnia* either under UV-present or UV-absent lighting conditions did not differ significantly. These findings are in concordance with a study of White et al. (2005), who demonstrated that neither the presence nor absence of UV wavelengths affected foraging efficiency of guppies feeding on *Daphnia pulex*. This suggests that in threespine sticklebacks, UV wavelengths are not essential for detecting and successfully hunting prey. This may have been expected, as *Daphnia* absorb UV wavelengths (Lee et al. 1970). The contrast of *Daphnia* with its background in UV wavelengths may therefore be more important to the foraging efficiency of its predators.

In contrast with these findings, another study that also investigated the influence of the presence and absence of UV wavelengths on foraging behaviour showed that UV perception enhanced prey detection in juvenile rainbow trout (*Oncorhynchus mykiss*) and juvenile pumpkinseed (*Lepomis gibbosus*) preying upon live *Daphnia pulex* (Browman et al. 1994). In the study of Browman et al. (1994), prey density

was very high (100 prey items·L^{-1}), whereas prey densities in our experiments (range: 2.38–7.84 prey·L^{-1}) as well as in White et al. (2005) (1.79 prey·L^{-1}) were much lower. Whether the presence of UV wavelengths also would have enhanced prey detection at high prey densities in guppies and sticklebacks can therefore not be excluded.

Sticklebacks tested in the present study comprised fish with SL values between 3.3 and 4.8 cm, and it can therefore not be excluded that fish of smaller and (or) larger size potentially make use of the UV wave range during foraging. Furthermore, sticklebacks feed on a wide range of different prey organisms, such as insect larvae, cladocera, copepoda, as well as fish fry (Hart and Gill 1994). It is conceivable that UV wavelengths could play a role in foraging on other types of prey than *Daphnia*.

Sticklebacks significantly attacked prey faster when the background lacked UV-reflections than when it strongly reflected UV light. Prey detection depends on the ambient light conditions and especially on the relationship of prey–background radiance (Lythgoe 1968). *Daphnia* are semitransparent and contain lipids and carotenoids, which absorb short as well as UV wavelengths (Lee et al. 1970). They should therefore form a strong contrast to a UV-reflecting background (Loew and McFarland 1990; Flamarique and Browman 2001) and be more visible to predators that are sensitive to ultraviolet wavelengths (Loew and McFarland 1990; Browman et al. 1994). Unexpectedly, the effect of background on foraging efficiency in our study was reversed. Possibly, the background reflections in UV were too intense and bedazzled the predator. However, sticklebacks still attacked prey in front of the UV-reflecting background. Alternatively, the *Daphnia* that were used in our experiments may have exhibited different absorption or reflection properties and may thereby have contrasted more strongly against a background that lacked UV reflections. This needs further investigation. UV-reflection properties of the background had a pronounced effect on feeding efficiency. Thus, UV, or more precisely, the contrast of prey with its background in the UV wave range plays a role in foraging success of sticklebacks. Future studies have to show whether this is also true under the lighting conditions that occur in nature.

We also tested the influence of long wavelengths on the feeding performance of sticklebacks preying upon *Daphnia magna*. When removing the long wavelengths from the spectrum, the foraging rate of sticklebacks was reduced compared with full spectrum conditions. Although this result was statistically not significant, the tendency of a reduced foraging rate agrees with the findings of White et al. (2005) on guppies. Therefore, long wavelengths may be more important during feeding performance than UV wavelengths. Long wavelengths contribute to motion detection, for example, in goldfish (Schaerer and Neumeyer 1996) and zebrafish (Krauss and Neumeyer 2003). The ability to detect prey movements in the absence of long wavelengths could therefore have been reduced in our sticklebacks.

Surprisingly, the exclusion of both UV and long wavelengths did not impair foraging rates. In this experiment, mechano- as well as olfactory perception of prey was possible and may have compensated the impaired visual perception in prey detection. Stimuli of the lateral line system can even override the visual stimuli (Janssen and Corcoran 1993). However, this explanation seems unlikely, because removing only long wavelengths did reduce foraging efficiency.

In conclusion, our results suggest that UV light has a limited influence on sticklebacks' foraging efficiency when they prey upon *Daphnia magna*. Removing UV wavelengths had no significant impact on foraging success, but UV-reflection properties of the background had an effect on foraging rate. Additionally, the exclusion of long wavelengths tended to reduce foraging rates. Therefore, it seems that in sticklebacks UV vision and reflections of UV wavelengths are more essential during social interactions than in foraging tasks.

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References

Archer, S.N., Endler, J.A., Lythgoe, J.N., and Partridge, J.C. 1987. Visual pigment polymorphism in the guppy *Poecilia reticulata*. Vision Res. **27**: 1243–1252.

Bleckmann, H. 1993. Role of the lateral line in fish behaviour. *In* Behaviour of teleost fishes. *Edited by* T.J. Pitcher. Chapman and Hall Press, London, UK. pp. 201–246.

Bolger, T., and Connolly, P.L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. **34**: 171–182.

Boulcott, P., and Braithwaite, V. 2005. Ultraviolet light and visual behaviour in the three-spined stickleback, *Gasterosteus aculeatus*. Physiol. Biochem. Zool. **78**: 736–743.

Boulcott, P.D., Walton, K., and Braithwaite, V.A. 2005. The role of ultraviolet wavelengths in the mate-choice decisions of female three-spined sticklebacks. J. Exp. Biol. **208**: 1453–1458.

Browman, H.I., Flamarique, I.N., and Hawryshyn, C.W. 1994. Ultraviolet photoreception contributes to prey search behavior in two species of zooplanktivorous fishes. J. Exp. Biol. **186**: 187–198.

Church, S.C., Bennett, A.T.D., Cuthill, I.C., and Partridge, J.C. 1998. Ultraviolet cues affect the foraging behaviour of blue tits. Proc. R. Soc. Lond. B Biol. Sci. **265**: 1509–1514.

Flamarique, I.N., and Browman, H.I. 2001 Foraging and prey-search behaviour of small juvenile rainbow trout (*Oncorhynchus mykiss*) under polarized light. J. Exp. Biol. **204**: 2415–2422.

Grether, G.F. 2000. Carotenoid limitation and mate preference evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulata*). Evolution, **54**: 1712–1724.

Guthrie, D.M., and Muntz, W.R.A. 1993. Role of vision in fish behaviour. *In* Behaviour of teleost fishes. *Edited by* T.J. Pitcher. Chapman and Hall, London, UK. pp. 89–121.

Hart, P.J.B., and Gill, A.B. 1994. Evolution of foraging behaviour in the threespine stickleback. *In* The evolutionary biology of the

threespine stickleback. *Edited by* M.A. Bell and S.A. Foster. Oxford University Press, Oxford, UK. pp. 207–239.

Jacobs, G.H. 1992. Ultraviolet vision in vertebrates. Am. Zool. **32**: 544–554.

Janssen, J., and Corcoran, J. 1993. Lateral line stimuli can override vision to determine sunfish strike trajectory. J. Exp. Biol. **176**: 299–305.

Johnsen, S., and Widder, E.A. 1998. Transparency and visibility of gelatinous zooplankton from the Northwestern Atlantic and Gulf of Mexico. Biol. Bull. **195**: 337–348.

Karino, K., Shinjo, S., and Sato, A. 2007. Algal-searching ability in laboratory experiments reflects orange spot coloration of the male guppy in the wild. Behaviour, **144**: 101–113.

Kodric-Brown, A. 1989. Dietary carotenoids and male mating success in the guppy — an environmental component to female choice. Behav. Ecol. Sociobiol. **25**: 393–401.

Krauss, A., and Neumeyer, C. 2003. Wavelength dependence of the optomotor response in zebrafish (*Danio rerio*). Vision Res. **43**: 1273–1282.

Lee, R.F., Nevenzel, J.C., and Paffenhöfer, G.-A. 1970. Wax esters in marine copepods. Science (Washington, D.C.), **167**: 1510–1511.

Leech, D.M., and Johnsen, S. 2006. Ultraviolet vision and foraging in juvenile bluegill (*Lepomis macrochirus*). Can. J. Fish. Aquat. Sci. **63**: 2183–2190.

Loew, E.R., and McFarland, W.N. 1990. The underwater visual environment. *In* The visual system of fish. *Edited by* R.H. Douglas and M.B.A. Djamgoz. Chapman and Hall Press, London, UK. pp. 1–43.

Losey, G.S., Cronin, T.W., Goldsmith, T.H., Hyde, D., Marshall, N.J., and McFarland, W.N. 1999. The UV visual world of fishes: a review. J. Fish Biol. **54**: 921–943.

Lythgoe, J.N. 1968. Visual pigments and visual range under water. Vision Res. **8**: 997–1012.

Lythgoe, J.N. 1979. The ecology of vision. Clarendon Press, Oxford, UK.

McLennan, D.A., and McPhail, J.D. 1989. Experimental investigations of the evolutionary significance of sexually dimorphic nuptial colouration in *Gasterosteus aculeatus* (L.): the relationship between male colour and female behaviour. Can. J. Zool. **68**: 482–492.

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

Modarressie, R., Rick, I.P., and Bakker, T.C.M. 2006. UV matters in shoaling decisions. Proc. R. Soc. Lond. B Biol. Sci. **273**: 849–854.

Pekcan-Hekim, Z., and Lappalainen, J. 2006. Effects of clay turbidity and density of pikeperch (*Sander lucioperca*) larvae on predation by perch (*Perca fluviatilis*). Naturwissenschaften, **93**: 356–359.

Pilastro, A., Simonato, M., Bisazza, A., and Evans, J.P. 2004. Cryptic female preference for colorful males in guppies. Evolution, **58**: 665–669.

Pohlmann, K., Grasso, F.W., and Breithaupt, T. 2001. Tracking wakes: the nocturnal predatory strategy of piscivorous catfish. Proc. Natl. Acad. Sci. U.S.A. **98**: 7371–7374.

Richmond, H.E., Hrabik, T.R., and Mensinger, A.F. 2004. Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. J. Fish Biol. **65**: 195–205.

Rick, I.P., Modarressie, R., and Bakker, T.C.M. 2006. UV wavelengths affect female mate choice in three-spined sticklebacks. Anim. Behav. **71**: 307–313.

Rocco, V., Barriga, J.P., Zagarese, H., and Lozada, M. 2002. How much does ultraviolet radiation contribute to the feeding performance of rainbow trout, *Oncorhynchus mykiss*, juveniles under natural illumination? Environ. Biol. Fishes, **63**: 223–228.

Rothschild, M. 1975. Remarks on carotenoids in the evolution of signals. *In* Coevolution of animals and plants. *Edited by* L.E. Gilbert and P.H. Raven. University of Texas Press, Austin, Texas. pp. 20–47.

Rowe, M.P., Baube, C.L., Loew, E.R., and Phillips, J.B. 2004. Optimal mechanisms for finding and selecting mates: how threespine stickleback (*Gasterosteus aculeatus*) should encode male throat colors. J. Comp. Physiol. A, **190**: 241–256.

Schaerer, S., and Neumeyer, C. 1996. Motion detection in goldfish investigated with the optomotor response is "color blind". Vision Res. **36**: 4025–4034.

Utne-Palm, A.C. 1999. The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. J. Fish Biol. **54**: 1244–1258.

Viitala, J., Korpimäki, E., Palokangas, P., and Koivula, M. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet-light. Nature (London), **373**: 425–427.

Vinyard, G.L., and O'Brien, W.J. 1976. Effects of light and turbidity on reactive distance of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. **33**: 2845–2849.

White, E.M., Church, S.C., Willoughby, L.J., Hudson, S.J., and Partridge, J.C. 2005. Spectral irradiance and foraging efficiency in the guppy, *Poecilia reticulata*. Anim. Behav. **69**: 519–527.