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1985

SPECTRAL SENSITIVITY AND PHOTO-BEHAVIOUR OF THE WATER MITE GENUS *UNIONICOLA*

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SUMMARY

Behavioural response spectra for phototaxis by four European species of water mites that are differently associated with freshwater mussels were determined. The wavelength for maximal stimulation of positive phototaxis and the corresponding energy threshold, were: 560 nm and $3.6 \times 10^{-7} \mu W$ cm^{-2} for the free-living species *Unionicola aculeata*, 560 nm and $2.1 \times 10^{-6} \mu W cm^{-2}$ for the commensal *U. bonzi*, 600 nm and $3.3 \times 10^{-6} \mu W cm^{-2}$ for the obligate symbiont *U. ypsilophora*, and 600 nm and $1.3 \times 10^{-5} \mu W cm^{-2}$ for the parasitic species *U. intermedia*. Sensitivity of these water mites to yellow-orange light is consistent with the spectral transmission of their native stream, the water of which readily absorbs wavelengths shorter than 500 nm.

U. intermedia exhibited wavelength-dependent phototaxis, with maximal positive phototaxis occurring in response to 600 nm light and negative phototaxis occurring at 440 nm. This differential photo-behaviour was not attributable to intensity effects. However, the positive phototaxis of this species to 600 nm light became negative when the mite was exposed to the chemical influence of its molluscan host. The spectral sensitivities of this acarine genus suggest the presence of at least two visual pigments within the taxon.

INTRODUCTION

Analysis of the behavioural responsiveness of aquatic invertebrates to light has focused upon mero- or holo-planktonic species, especially those which engage in diurnal vertical migrations through the water column (Ringelberg, 1964; Thorson, 1964; Hutchinson, 1967; Segal, 1970; Forward, 1976; Kerfoot, 1980; Sulkin, 1984). Although the spectral sensitivities of aquatic species vary considerably, cautious generalization suggests that species from coastal marine areas and eutrophic fresh water often are more responsive to longer wavelengths (500–600 nm) than are oceanic,

deep-sea, or pristine-freshwater species which tend to be maximally sensitive to wavelengths of 460–495 nm (Forward, 1976). Such spectral sensitivities parallel the effects of particulate matter and dissolved organic substances on the spectral transmission of different water masses (Hutchinson, 1967; Jerlov, 1968). However, correlation between spectral sensitivity and the underwater light regime encountered by an aquatic organism is not universal (Forward & Cronin, 1979), since photobehaviour is influenced by physiological, ontogenetic and ecological factors (Forward, 1976; Sulkin, 1984).

Wavelength-specific behaviour including colour dances (Smith & Baylor, 1953; Dingle, 1962) and colour choice (Herman, 1962; Hyatt, 1975) has been described for various aquatic crustaceans. Young (1974) has shown that sensitivity to monochromatic light by *Daphnia* depends upon the orientation of the stimulatory beam. The sign of phototaxis by some aquatic arthropods may also vary with wavelength (Viaud, 1951; LaRow, 1971; Roberts, Dimock & Forward, 1978).

The circum-global water mite genus *Unionicola* (Acari: Unionicolidae) includes species that differ in their dependence upon freshwater sponges or molluscs as part of their life histories (Böttger, 1977; Hevers, 1980). The four European species that are the subjects of the present study are associated with freshwater mussels (Bivalvia: Unionidae). The temporary mussel-mite *Unionicola aculeata* uses a mussel only as a site for oviposition and for post-larval transformations, with the adult being a free-living planktivore (Hevers, 1980). *U. bonzi* and *U. ypsilophora* pass some or all of their adult life in the mantle cavity of a mussel (Davids, 1973; Hevers, 1980). *U. intermedia* is classically parasitic as an adult, piercing the gills of its molluscan host to ingest body fluids (Baker, 1977).

Since some unionicolid mites are significant components of zooplankton communities and engage in diurnal vertical migration (Riessen, 1980), we undertook the present study to broaden the understanding of the photobiology of this taxon. Previous information on the photo-behaviour of the Unionicolidae has been limited to the North American *U. formosa*, for which the response spectra of its photokinetic and phototactic behaviour are known (Waterman, 1937; Roberts *et al*. 1978). Also, the sign of phototaxis by *U. formosa* is specifically reversed from positive to negative upon exposure of the mite to chemical substances from its molluscan host (Welsh, 1931; Roberts *et al*. 1978; del Portillo & Dimock, 1982).

We describe significant interspecific differences in the spectral and intensity sensitivities of these mites, with the free-living species being the most responsive to light and the parasitic species the least so. Spectral sensitivity of the mites parallels the spectral transmission of their habitat water. Three of the species are unaffected by chemical substances from their molluscan hosts, while the positive phototaxis of the parasitic *U. intermedia* is specifically reversed to negative in the presence of water from its host mussel. The sign of phototaxis by *U. intermedia* varies with wavelength, suggesting that this species possesses at least two visual pigments.

MATERIALS AND METHODS

Adult *Unionicola bonzi*, *U. ypsilophora* and *U. intermedia* were recovered from the mantle cavity of their molluscan hosts, *Unio pictorum, Anodonta cygnea* and
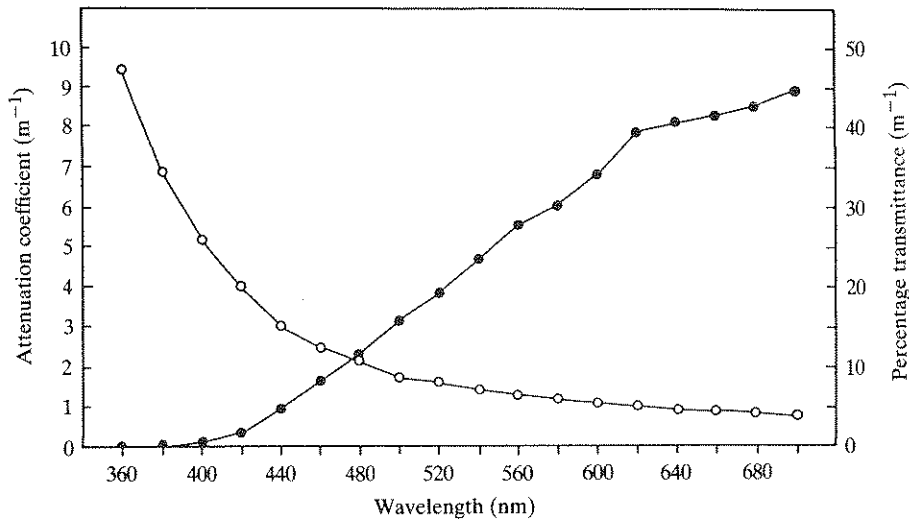
Fig. 1. Spectral properties of unfiltered water from the Gein. The attenuation coefficient (left ordinate, open circles) and percentage transmittance (right ordinate, solid circles) were calculated for monochromatic light passing through 1 m of water.

A. anatina, respectively. Adult *U. aculeata* were sieved from laboratory aquaria as they transformed from tritonymphs and emerged from *A. anatina*. The mussels were collected by hand at a depth of about 1 m primarily from the 'Gein', a slowly flowing stream about 10 km south east of Amsterdam. Some *A. anatina* were also collected from a shallow canal along the 'old dike' near St. Maartensbrug, The Netherlands. Mussels and mites were maintained under a seasonally appropriate photoperiod in the laboratory of the Department of Aquatic Ecology, University of Amsterdam, where the experimental studies were conducted (July–October, 1983).

The Gein has a high dissolved organic content, as evidenced by the colour of the water, which resembles tea. The absorption spectrum of unfiltered water from the Gein was determined with a Beckman Model 25 (Beckman Instruments, California, U.S.A.) dual beam spectrophotometer with a 4-cm light path. The results (Fig. 1) indicated that the water from the Gein was most transparent to red light of 620–700 nm, with the attenuation coefficient increasing exponentially at shorter wavelengths.

Phototaxis was measured as movement towards (positive) or away from (negative) a stimulus light. The experiments were performed in a chamber ($118 \times 16 \times 20$ mm, i.d.) constructed of clear 3-mm Lucite which was provided with thin, removable partitions that could simultaneously be raised or lowered, in which latter position they subdivided the chamber into five 20-mm compartments. The chamber was illuminated horizontally from one end with a 4-cm^2 beam of light from a slide projector (250 W tungsten filament bulb). The light was filtered first through a 'hot mirror' (Baird Atomic Co., Massachusetts, U.S.A.) and a Corning No. 1–75 infrared-absorbing filter (Corning Glass Works, New York, U.S.A.) to reduce the radiation above 700 nm. The stimulus light was then filtered through interference filters (half bandwidth $= 7$–9 nm; Ditric Optics Co., Massachusetts, U.S.A.) to control

wavelength, and neutral density filters (Ditric Optics) to control intensity. All neutral density filters had been individually calibrated with white light to determine their respective absorption characteristics. Light intensity was measured (at the illuminated end of the chamber) with a LiCor Model LI–185 quantum sensor (Lambda Instrument Co., Nebraska, U.S.A.).

The protocol of the basic phototaxis assay included the following. Mites (primarily females) were removed from their mussel hosts at least 24 h before use and were washed several times in filtered lake water (Lake Maarsseveen, an oligotrophic lake). A group of about 20 *U. bonzi, U. aculeata* or *U. intermedia*, or 15 of the larger *U. ypsilophora* (body length about 1·0 mm *vs* 0·3–0·7 mm for the other species) was dark-adapted for at least 1 h in 1 ml of Lake Maarsseveen water in a 2·5-ml microcentrifuge tube. The experimental chamber was filled to a depth of 1·5 cm with filtered Maarsseveen water (temperature = 19–23 °C) and the partitions were inserted.

In total darkness one tube of mites was poured into the centre compartment of the experimental chamber, the partitions were removed, and the mites were held for 30 s in the dark. The stimulus light was then illuminated for 60 s (preliminary experiments had shown that all species could traverse the length of the chamber within 20 s). At the end of the stimulus period the partitions were quickly re-inserted, the room lights were turned on, and the number of mites in each of the five compartments was determined. The 'dark control' was similar to the light experiments except that two mutually interfering wavelength filters plus an additional no. 3 neutral density filter were interposed in the light path to maintain the experimental chamber in total darkness.

In all experiments with *U. ypsilophora* a fitted piece of thin filter paper was inserted over the floor of the chamber, since this animal's crawling locomotion is ineffective on smooth surfaces; the other species actively swim. At the end of each trial the chamber and partitions were thoroughly washed and any filter paper was replaced. All experiments were performed between 10.00 h and 16.30 h to minimize potential complications from any rhythmic behaviour.

Spectral sensitivity of the four species was assessed by generating a response spectrum to light of approximately equal quantal intensities at 20-nm intervals from 420–680 nm. Preliminary intensity-response studies at 480 nm indicated that *U. aculeata* and *U. bonzi* were more sensitive than *U. ypsilophora* and *U. intermedia*. Thus, stimulus lights were balanced at approximately 4×10^{11} quanta m^{-2} s^{-1} for *U. bonzi* and *U. aculeata* and $3·8 \times 10^{12}$ quanta m^{-2} s^{-1} for *U. ypsilophora* and *U. intermedia*. The actual quantal intensities employed at each wavelength are presented in Table 1.

Three groups of *U. aculeata* and *U. bonzi* and four of *U. ypsilophora* (about 60 mites/species) were tested at each wavelength. The unexpected response spectrum of *U. intermedia* (see Results) prompted us to repeat the entire survey with that species (for a total of about 120 mites at each wavelength). About 115 mites of each species were used for the dark controls. Some mites were used at more than one wavelength (with re-testing occurring no sooner than 3 h and usually 24 h later), but not twice at the same wavelength. In all, 310 *U. bonzi*, 240 *U. aculeata*, 305 *U. ypsilophora* and 590 *U. intermedia* were used for the response spectra. All mussel-mites were used within 4 days of being removed from a mussel; *U. aculeata* was fed *Daphnia* during laboratory maintenance.

Table 1. *Quantal intensities used at each wavelength for determining response spectra for phototaxis of* Unionicola

Wavelength (nm)	Quanta $m^{-2} s^{-1}$	
	With *U. aculeata* and *U. bonzi*	With *U. ypsilophora* and *U. intermedia*
420	$3 \cdot 83 \times 10^{11}$	$3 \cdot 63 \times 10^{12}$
440	$4 \cdot 02 \times 10^{11}$	$3 \cdot 81 \times 10^{12}$
460	$4 \cdot 10 \times 10^{11}$	$3 \cdot 89 \times 10^{12}$
480	$3 \cdot 90 \times 10^{11}$	$3 \cdot 78 \times 10^{12}$
500	$3 \cdot 78 \times 10^{11}$	$3 \cdot 59 \times 10^{12}$
520	$4 \cdot 02 \times 10^{11}$	$3 \cdot 82 \times 10^{12}$
540	$4 \cdot 21 \times 10^{11}$	$3 \cdot 99 \times 10^{12}$
560	$3 \cdot 78 \times 10^{11}$	$3 \cdot 70 \times 10^{12}$
580	$3 \cdot 83 \times 10^{11}$	$3 \cdot 63 \times 10^{12}$
600	$3 \cdot 99 \times 10^{11}$	$3 \cdot 78 \times 10^{12}$
620	$4 \cdot 25 \times 10^{11}$	$4 \cdot 03 \times 10^{12}$
640	$3 \cdot 91 \times 10^{11}$	$3 \cdot 71 \times 10^{12}$
660	$4 \cdot 02 \times 10^{11}$	$3 \cdot 81 \times 10^{12}$
680	$4 \cdot 25 \times 10^{11}$	$4 \cdot 03 \times 10^{12}$
$\bar{X}$ ($\pm$ s.d.) =	$3 \cdot 99$ ($\pm 0 \cdot 16$) $\times 10^{11}$	$3 \cdot 79$ ($\pm 0 \cdot 15$) $\times 10^{12}$

The threshold for positive phototaxis (at λ_{max}) was estimated from intensity-response data for each species. The influence of a host mussel on the photo-behaviour of each species was assessed by conducting the phototaxis assay under the conditions that had elicited maximal positive phototaxis in the spectral response analysis, but with the mites in paper-filtered (gravity flow) water from the mantle cavity of the respective species of mussel. The effects of several intensities of 440, 520 and 600 nm light on the photo-behaviour of *U. intermedia* were also determined.

Most of the behavioural data are presented as percentage positive or negative phototaxis based upon the number of mites in the compartment closest to or farthest from the stimulus light at the end of an experiment. The means and associated standard errors for the three to six (depending upon the species) replicate determinations of the percentage phototaxis were calculated from arcsine transformations of the percentage data. The data have been analysed by analysis of variance (ANOVA) following arcsine transformation of the percentages and Levene's test for equality of variances. The data were further analysed by Dunnett's and Student-Newman-Keuls (SNK) multiple range tests. Some data were examined with the Kolmogorov-Smirnov goodness of fit test when comparisons of the distribution of mites in all five compartments of the experimental chamber were in order. All statistical analyses followed the procedures of Zar (1974).

RESULTS

The photo-behaviour of *Unionicola* was significantly influenced by wavelength ($P < 0 \cdot 001$, ANOVA), with three of the four species exhibiting only positive phototaxis to those wavelengths to which they were responsive (Figs 2, 3). The free-living species *U. aculeata* was maximally responsive to 560 nm light, but its responses to wavelengths from 480 to 580 nm were statistically indistinguishable ($P > 0 \cdot 05$,
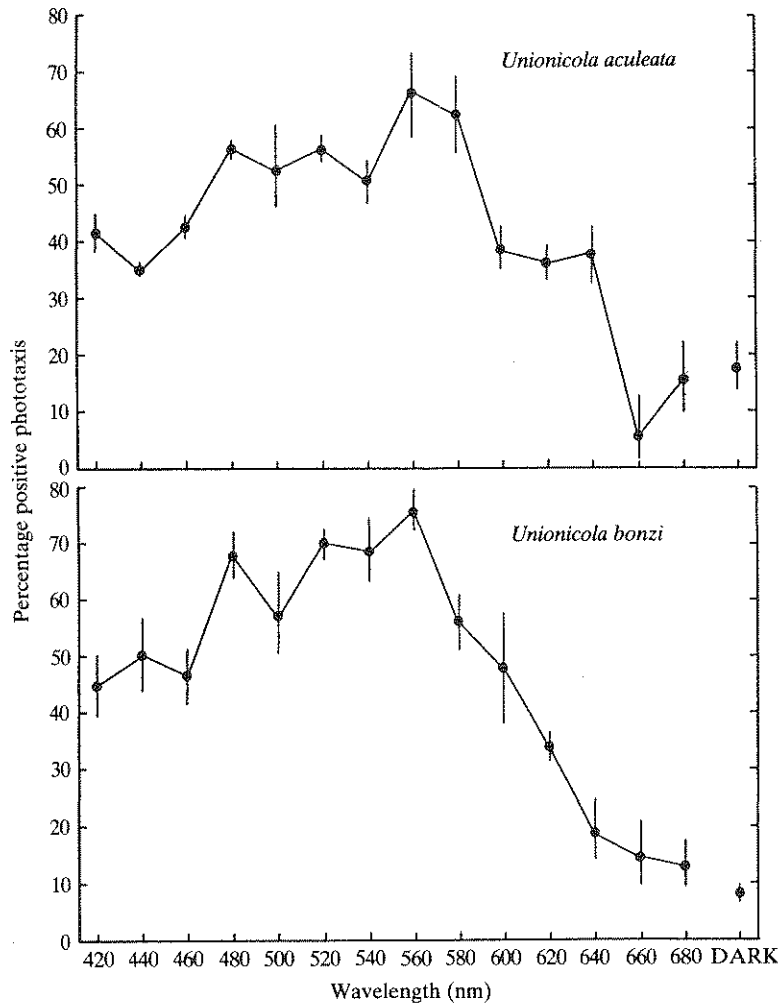
Fig. 2. Response spectra for positive phototaxis by *Unionicola aculeata* (top) and *U. bonzi* (bottom) to quantally equivalent wavelengths. Points are the $\bar{x} \pm$ s.e. for the percentage response of three groups of mites (about 20/group; $N = 54$–63) to each wavelength. The DARK points are control distributions of six groups ($N = 110$–120) with no stimulus light.

SNK; Fig. 2). The response of this mite to light of 660 nm and 680 nm was not, however, significantly different from the dark control ($P > 0.05$, Dunnett's).

The spectral sensitivity of phototaxis by the more commensalistic species *U. bonzi* resembled that of *U. aculeata* (Fig. 2). Maximal responsiveness occurred at 560 nm but did not differ significantly from the responses to light between 480 nm and 580 nm ($P > 0.05$, SNK). Similarly this mite exhibited no significant response to 640–680 nm light ($P > 0.05$, Dunnett's).

The response spectrum of the obligate symbiont *U. ypsilophora* was more complex than that of either *U. aculeata* or *U. bonzi* (Fig. 3). Significant positive phototaxis occurred at all wavelengths except 420, 440, 660 and 680 nm ($P < 0.05$, Dunnett's). *U. ypsilophora* was maximally responsive to light of 600 nm, but its responses to the
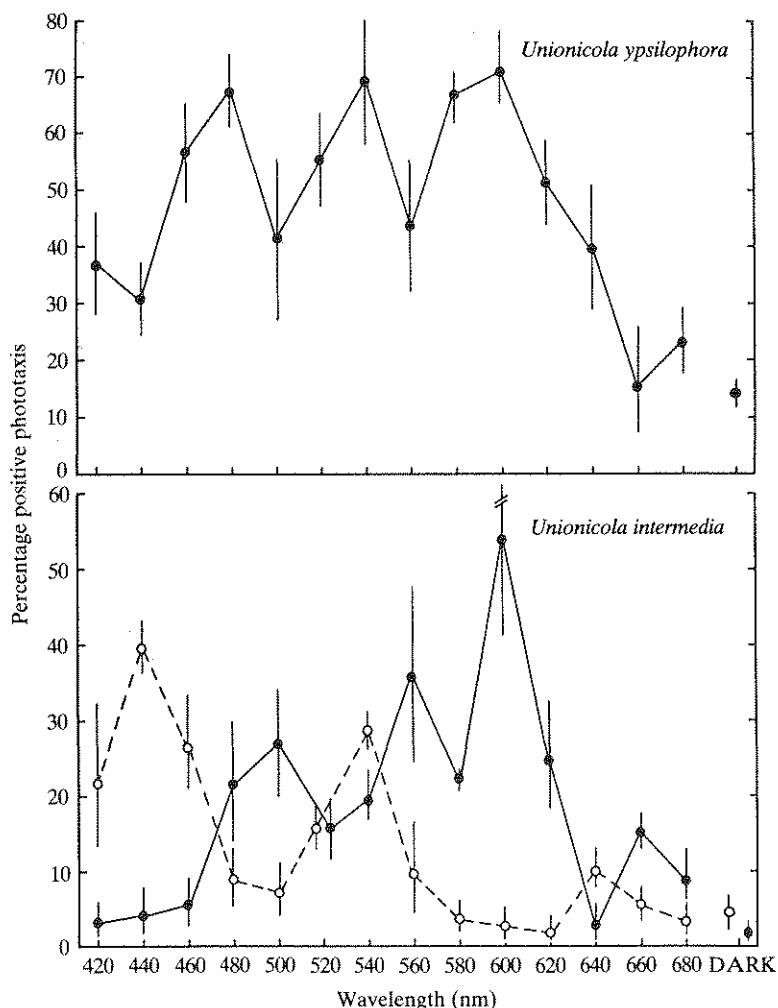
Fig. 3. Response spectra for positive phototaxis by *Unionicola ypsilophora* (top), and positive (solid circles, solid line) and negative (open circles, dashed line) phototaxis by *U. intermedia* (bottom) to quantally equivalent wavelengths. Points are the x̄ ± s.e. for the percentage response of four groups of mites (about 15/group; N = 55–63) for *U. ypsilophora* (top) and six groups (about 20/group; N = 104–123) for *U. intermedia* (bottom) to each wavelength. The points at 520 nm for *U. intermedia* have been displaced for clarity. The DARK points are control distributions of 6–8 groups (N = 110–120) with no stimulus light.

span of wavelengths from 420 to 640 nm were statistically indistinguishable by a multiple range test ($P > 0.05$, SNK). However, the peaks in the response spectrum at 480, 540 and 600 nm were significantly different from the corresponding minima at 440, 500 and 560 nm when the distributions of all mites within the experimental chamber were examined ($P < 0.05$, Kolmogorov-Smirnov).

Unlike that of the other species, the photo-behaviour of the parasitic species *U. intermedia* was polyphasic both with respect to spectral sensitivity and to the sign of phototaxis as a function of wavelength (Fig. 3). Two distinctly different response spectra were evident, one for positive and one for negative phototaxis. Significant

positive phototaxis occurred only at wavelengths of 500, 560 and 600 nm ($P < 0.05$, ANOVA, Dunnett's). The maximal response at 600 nm and the peak at 560 nm were statistically discrete from each other and from all other 'positive' responses ($P < 0.05$, SNK). However, this mite was markedly negatively phototactic to wavelengths within the blue and green parts of the visible spectrum, i.e. from 420 to 460 nm and at 540 nm, with maximal negative responsiveness occurring at 440 nm. No statistically significant negative phototaxis occurred at any other wavelength ($P > 0.05$, SNK; Fig. 3).

The development of this mite's positive phototaxis to 600 nm light and of its negative photo-response to 440 nm light as a function of increasing light intensity is illustrated in Fig. 4. The wavelength-specific photo-behaviour of *U. intermedia* persisted over several log units of intensity (Fig. 4). No significant positive phototaxis occurred at any intensity of 440 nm light. However, the magnitude of the negative response to 440 nm light decreased at the highest intensity tested as the mites became more evenly distributed throughout the compartments of the test chamber towards the 'negative' end, perhaps *via* a photokinetic response coupled with avoidance of the
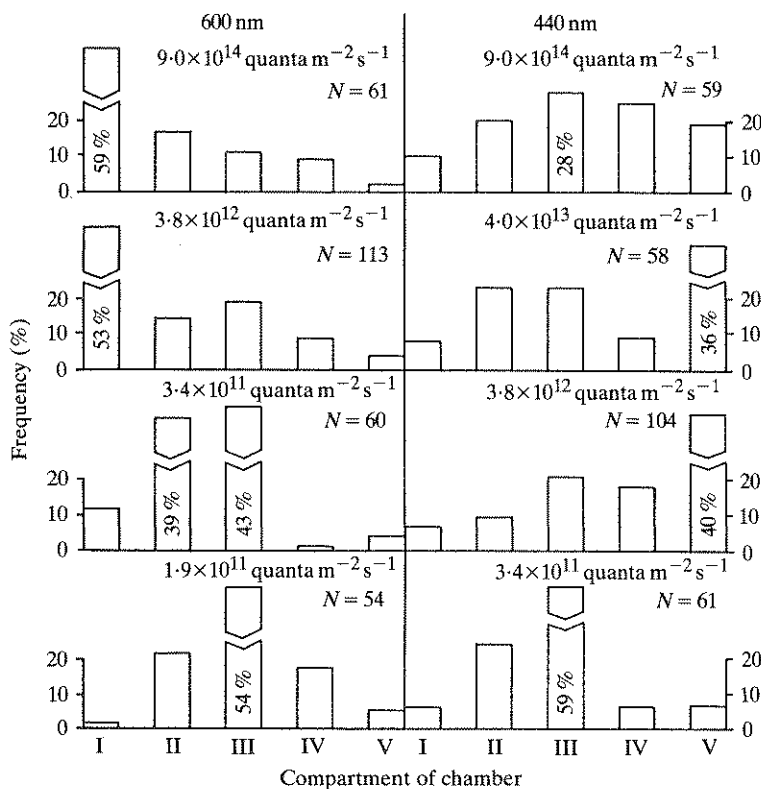

Fig. 4. Effect of wavelength and intensity on the magnitude and sign of phototaxis of *Unionicola intermedia*. Histograms depict the mean percentage of 3–6 groups of mites (about 20/group) in each of the five compartments of the experimental chamber in response to 600 nm light (left side of figure) and 440 nm light (right side). Since the chamber was illuminated directionally from compartment I to V, the percentage in compartment I depicts 'positive' and that in compartment V, 'negative', phototaxis.
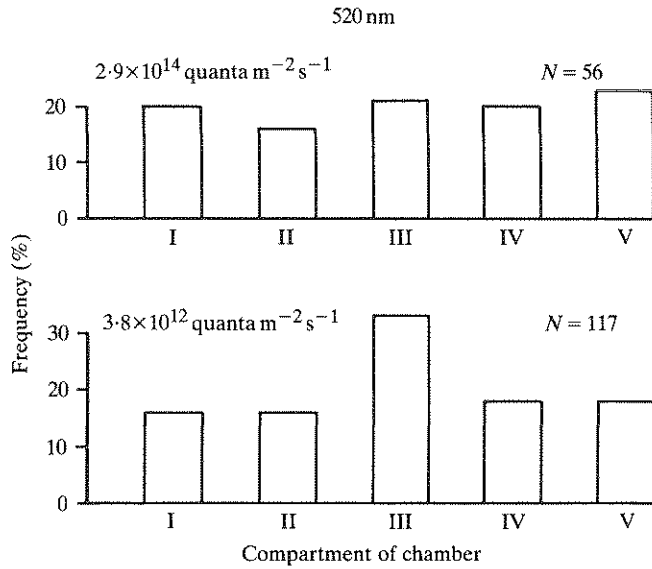
Fig. 5. Response of *Unionicola intermedia* to 520 nm light. Histograms depict the mean percentage of 3–6 groups of mites (about 20/group) in each of the five compartments of the experimental chamber. The stimulus light was directed from compartment I to compartment V.
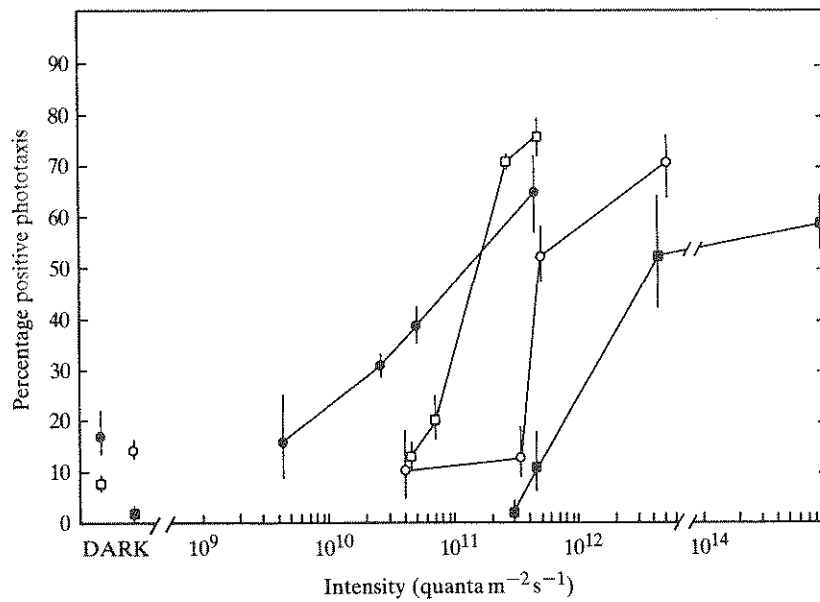

Fig. 6. Intensity-response relationships for positive phototaxis by *Unionicola aculeata* (solid circles), *U. bonzi* (open squares), *U. ypsilophora* (open circles) and *U. intermedia* (solid squares). Each point is the $\bar{x} \pm$ s.e. for the percentage response of 2–3 groups of mites ($N = 40$–60) to 560 nm light (*U. aculeata* and *U. bonzi*) or 600 nm light (*U. ypsilophora* and *U. intermedia*). The DARK points are the respective control distributions of each species with no stimulus light.
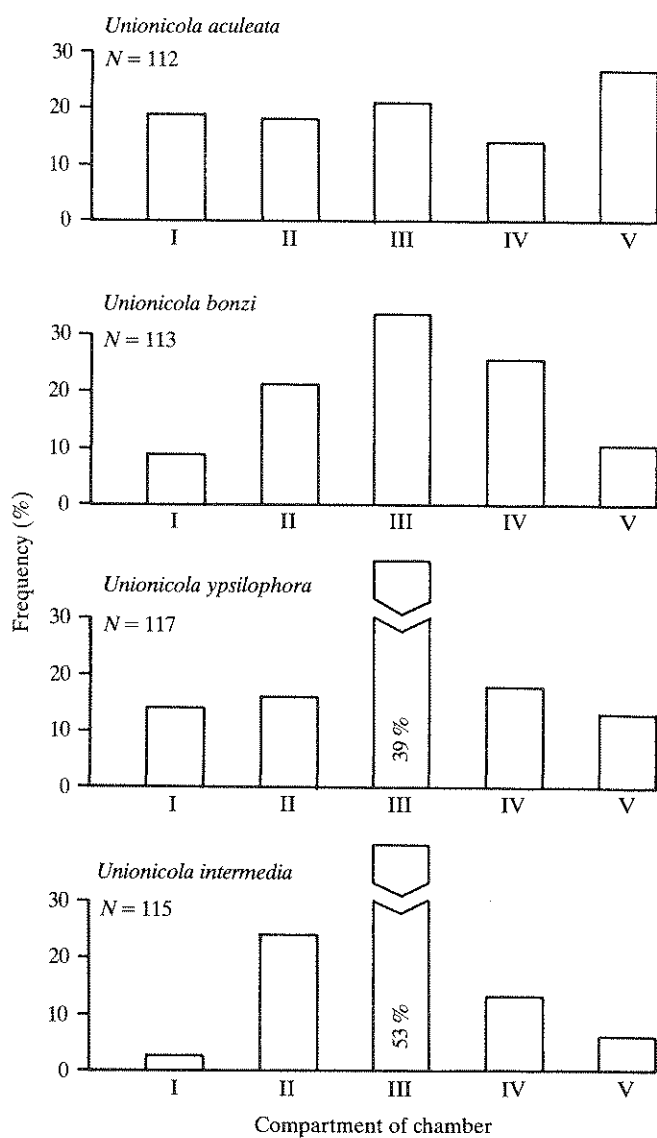
Fig. 7. Distribution of unionicolid mites in the experimental chamber in total darkness. Histograms depict the mean percentage of 3–8 groups of mites (about 15–20/group) in each compartment. The mites were introduced initially into compartment III.

most fully illuminated compartment (Fig. 4). In contrast, only positive phototaxis occurred at 600 nm (Fig. 4). In addition, this species failed to exhibit any tactic response to light of intermediate wavelength (520 nm) even at a quantal intensity two orders of magnitude higher than that employed in the response-spectrum analysis (Fig. 5). Thus, the transition from negative to positive phototaxis as a function of increasing wavelength was apparently independent of light intensity.

Intensity-response relationships for each species of mite at the respective

Table 2. *Threshold intensities for positive phototaxis of water mites of the genus* Unionicola

Species	λ_{max}	Intensity		Source
		Quanta $m^{-2} s^{-1}$	$\mu W\, cm^{-2}$	
U. aculeata	560 nm	10^{10}	$3 \cdot 6 \times 10^{-7}$	This study
U. bonzi	560 nm	6×10^{10}	$2 \cdot 1 \times 10^{-6}$	This study
U. ypsilophora	600 nm	10^{11}	$3 \cdot 3 \times 10^{-6}$	This study
U. intermedia	600 nm	4×10^{11}	$1 \cdot 3 \times 10^{-5}$	This study
U. formosa	500 nm	9×10^{11}	$3 \cdot 6 \times 10^{-5}$	Roberts, Dimock & Forward (1978)

Table 3. *The effect of water from the mantle cavity of a host mussel on the phototaxis of unionicolid mites*

Species	Type of water (test wavelength)	% Phototaxis*		N
		+	(−)	
U. aculeata	Lake water (560 nm)	65·5	4·8	53
	Water from Anodonta anatina (560 nm)	61·4	9·4	73
U. bonzi	Lake water (560 nm)	75·4	1·8	57
	Water from Unio pictorum (560 nm)	81·6	0·0	68
U. ypsilophora	Lake water (600 nm)	70·5	3·3	61
	Water from Anodonta cygnea (600 nm)	68·9	1·3	67
U. intermedia	Lake water (600 nm)	52·6	4·7	113
	Water from Anodonta anatina (600 nm)	13·5	44·7	75

*Total may not equal 100 %; see text.

wavelength that induced maximal positive phototaxis (λ_{max}) are depicted in Fig. 6. For each species the response to the lowest intensity illustrated was not significantly different from the dark control (Fig. 7) as determined both by ANOVA and the Kolmogorov-Smirnoff analysis (i.e. $P > 0 \cdot 05$). However, each of the four species exhibited significant positive phototaxis to the next higher test intensity ($P < 0 \cdot 05$, Kolmogorov-Smirnov). Thus, the thresholds for positive phototaxis were estimated from these intensity-response curves and are presented in Table 2, together with the only comparable published data available for any other species in this genus.

The positive phototaxis of *U. aculeata*, *U. bonzi* and *U. ypsilophora* was unaffected by exposing these mites to water from the mantle cavity of the mussels with which they had been associated in the field (Table 3). However, the phototactic response of the

parasitic species *U. intermedia* to 600 nm light changed from positive to negative when that mite was tested in water from its molluscan host, *Anodonta anatina*. Exposure of *U. intermedia* to water from the mantle cavity of this mussel had no effect on the negative phototaxis to 440 nm light (Fig. 3).

<div align="center">DISCUSSION</div>

The photobiology of water mites has received little experimental attention. However, the present study and previous work with the North American *Unionicola formosa* (Waterman, 1937; Roberts *et al.* 1978) reveal that the phototactic behaviour of the genus exhibits broad spectral sensitivity. The response maxima at 560 nm and 600 nm for the four European species that we have examined (Figs 2, 3) occur at longer wavelengths than the corresponding peak sensitivity for positive phototaxis by dark-adapted *U. formosa* (500–540 nm, Roberts *et al.* 1978). This yellow-orange spectral sensitivity resembles that of various invertebrates (Wasserman, 1973; Forward, 1976; Menzel, 1979; Dimock & Parno, 1981) and parallels the spectral transmission of the water inhabited by the mites which we employed in this study (Fig. 1). The relative insensitivity of these four species to red light (>620 nm), which nevertheless is transmitted by their habitat water, is clear (Figs 2, 3) and is typical of other invertebrates possessing a 'rhodopsin' type visual pigment (Menzel, 1979). Although the *in situ* spectral distribution of underwater illumination at the collection sites has not been determined, the spectral responsiveness of these mites is consistent with behavioural evidence for the attractiveness of yellow-orange light-traps to various water mites (C. Davids, personal observations).

The influence of wavelength on the sign of phototaxis by *U. intermedia* (Figs 3–5) constitutes one of the few quantitative demonstrations of wavelength-dependent phototaxis among aquatic invertebrates. Roberts *et al.* (1978) showed that dark-adapted *U. formosa*, a species that is negatively phototactic only in the presence of chemical substances from its molluscan host, shifted from a markedly negative phototaxis at 460–480 nm to predominantly positive phototaxis at 520–600 nm, with a nearly symmetrical 50 % positive/50 % negative phototaxis at 500 nm. From an analysis of the influence of light intensity on the phototaxis of *U. formosa* those authors speculated that the wavelength-dependent photo-behaviour might be a consequence of differential perception of the intensity of quantally equivalent stimulus lights of different wavelengths (Roberts *et al.* 1978), i.e., wavelength-specificity but not necessarily colour vision (Menzel, 1979). However, since *U. intermedia* exhibits distinctly different photo-responsiveness to short *vs* long wavelengths (Fig. 3), and that behaviour is not interconvertible as a function of intensity (Figs 4, 5), this species, at least, within the genus has a clearly wavelength-dependent component of its photobiology.

The breadth of the response spectra for positive phototaxis by *U. aculeata*, *U. bonzi* and *U. ypsilophora* could result from the possession by these mites of a single visual pigment that absorbs over a broad range of wavelengths or from their having multiple visual pigments. Broad spectral sensitivity has been attributed to either (or both) physiological mechanism in various invertebrates, including some aquatic arthropods (Waterman, Fernandez & Goldsmith, 1969; Wasserman, 1973; Menzel, 1979).

However, differential spectral sensitivity, including colour vision, does not always require the presence of multiple visual pigments (Kong, Fung & Wasserman, 1980).

The multi-modal spectral sensitivity of *U. ypsilophora*, with response maxima at 480, 540 and 600 nm (Fig. 3), suggests a multiple visual pigment basis for this mite's photosensitivity. However, perhaps the strongest indication of the occurrence of at least two separate photophysiological systems in this genus is evidenced by the photo-behaviour of *U. intermedia*. The differential spectral sensitivity of positive *vs* negative phototaxis by this mite (Figs 3–5) may involve the coupling of specific motor patterns to photoreceptors with different visual pigments. The pattern of response to u.v. and green light by the terrestrial spider mite *Tetranychus urticae* apparently is a function of the differential distribution of u.v. and green receptors in anterior *vs* posterior eyes of that species (McEnroe & Dronka, 1966; Mills, 1974). Comparable data on structural-functional relationships of water mite eyes are not available.

The threshold intensities for positive phototaxis by the four European unionicolids that we have examined (about 4×10^{-7} to $2 \times 10^{-5} \mu\mathrm{W\,cm}^{-2}$) are similar to the sensitivity of *U. formosa* (about $4 \times 10^{-5} \mu\mathrm{W\,cm}^{-2}$, Roberts *et al.* 1978) and to the thresholds for photo-responsiveness of many aquatic organisms (Forward, 1976). The differential sensitivities of these four species perhaps parallel their ecological/ evolutionary affinities, with *U. aculeata* (free-living) having the lowest threshold and *U. intermedia* (parasitic) having the highest (Fig. 6; Table 2). This sequence may reflect a greater role of vision in the biology of adult *U. aculeata* [and perhaps also *U. bonzi*, the extent of whose dependence upon a host mussel is not fully known (Davids, 1973; Hevers, 1980)] than for the more sedentary or parasitic life styles of *U. ypsilophora* and *U. intermedia*.

The well established (Welsh, 1931; Roberts *et al.* 1978; del Portillo & Dimock, 1982) influence of a molluscan host on the photo-behaviour of *U. formosa* obviously is not a universal behavioural characteristic within the genus, since only *U. intermedia* of the four species that we have examined exhibited host-induced negative phototaxis (Table 3). The physiological basis for this reversal of phototaxis remains unknown.

The lack of response of *U. ypsilophora* to molluscan products, as well as the differences in the response spectra of *U. ypsilophora* (Fig. 3) and *U. formosa* (Roberts *et al.* 1978), supports the contention of Mitchell (1957) and Vidrine (1980) that the European *U. ypsilophora* and the North American *U. formosa* are separate species. The *U. ypsilophora* of earlier North American workers (Welsh, 1931; Waterman, 1937) is probably *U. formosa*.

The functional significance of the photo-behaviour that we have described is largely unknown. Since *U. aculeata* is a free-living planktivore, its highly sensitive photo-behaviour may be adaptive for visually mediated predation, perhaps involving either shape recognition or motion detection, or through an indirect influence of light on vertical migration. This species is an adept swimmer and also is very active in the dark, as evidenced by its nearly uniform distribution among the five compartments of the experimental chamber in total darkness (Fig. 7). At the other extreme, the parasitic species *U. intermedia* is least sensitive to light (Fig. 6; Table 2) and remains quite inactive in the dark, with more than 50 % of the individual mites remaining in the central-most compartment of the experimental chamber in the absence of a light stimulus (Fig. 7).

The negative phototaxis of *U. intermedia* to the blue or blue-green part of the visible spectrum may in some way be associated with its host-induced negative response to 600 nm light, both of which responses could increase the probability of this mite encountering a benthic molluscan host by swimming away from the sunlit surface waters. However, negative phototaxis to the shorter wavelength blue light could also involve avoidance of potentially deleterious effects of such relatively higher energy radiation (Hairston, 1976). Although this high energy radiation is rapidly attenuated in the primary area of our field collections (Fig. 1), the submarine light field elsewhere in the range of this species is unknown. It is also possible that the behaviour that we have observed among these adult mites is a retention of behavioural traits that are adaptive for larval or nymphal unionicolid water mites, the photobiology of which is completely unknown. Perhaps the multi-modal response of the obligate symbiont *U. ypsilophora* to visible light (Fig. 3) is transitional between the photo-behaviour of the free-living *U. aculeata* and that of the parasitic *U. intermedia*.

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