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WHY DO MAYFLIES LAY THEIR EGGS *EN MASSE* ON DRY ASPHALT ROADS? WATER-IMITATING POLARIZED LIGHT REFLECTED FROM ASPHALT ATTRACTS EPHEMEROPTERA

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Summary

We report on dry asphalt roads acting as 'mayfly traps'; that is, they lure swarming, mating and egg-laying mayflies in large numbers. To explain this surprising behaviour, we performed multiple-choice experiments with Ephemeroptera in the field, and measured and compared the reflection–polarization characteristics of an asphalt road and a mountain creek from which mayflies emerge. We show here that Ephemeroptera can be deceived by and attracted to dry asphalt roads because of the strongly horizontally polarized light reflected from the surface. Asphalt surfaces can mimic a highly polarized water surface to Ephemeroptera. The darker and smoother the asphalt surface, the higher is the degree of polarization of reflected light and the more attractive is the road to mayflies. We show that mayflies detect water by means of polarotaxis; that is, on the basis of the partially and horizontally polarized reflected light. Asphalt roads are excellent markers for swarming Ephemeroptera because of their conspicuous elongated form; the sky above them is usually open, which is the prerequisite of mayfly mating, and the higher temperature of the asphalt prolongs the reproductive activity of mayflies. These additional factors enhance the attractiveness of asphalt roads to swarming mayflies. Thus, asphalt roads near ephemeropteran emergence sites (lakes, rivers and creeks) are a great danger for mayflies, because eggs laid on the asphalt inevitably perish. Asphalt roads can deceive and attract mayflies *en masse* like the ancient tar pits and asphalt seeps or the recent crude or waste oil lakes deceive, lure and trap polarization-sensitive water-seeking insects in large numbers.

Key words: mayfly, Ephemeroptera, reproductive behaviour, asphalt road, insect trap, water detection, polarotaxis, polarization vision, reflection polarization, video-polarimetry.

Introduction

During the last decade, we have observed every year that individuals of several mayfly (Ephemeroptera) species swarmed in large numbers, mated above and landed on dry asphalt roads in the immediate vicinity of their emergence sites (mountain streamlets), and that after copulation the females laid their eggs *en masse* on the roads (Fig. 1A–C) instead of ovipositing them on the water surface. These observations, especially for egg-laying by females, suggest that the mayflies were apparently deceived by and attracted to the asphalt surface, which acts as an insect trap.

Previous descriptions of ephemeropteran swarming, mating and egg-laying behaviour have largely ignored or misinterpreted this enigmatic phenomenon. We have often observed that mayflies also swarm, mate above and oviposit on the shiny bodywork and windscreen of cars. The same reproductive behaviour was frequently observed above and on shiny black plastic sheets used in agriculture (Fig. 1D–I). These artificial shiny surfaces also attract many other water insects. There are numerous observations of water insects being deceived by glass panes, car roofs or wet asphalt streets (Fernando, 1958; Popham, 1964).

Although the above-mentioned observations on Ephemeroptera are known to entomologists, they are only mentioned sporadically as marginal notes in publications or lectures. It has generally been assumed that the roads serve as markers for mayflies to assign the site of swarming and mating (e.g. Brodskiy, 1973; Savolainen, 1978). Oviposition by mayflies on asphalt roads is simply explained by the shiny appearance of wet roads which may lure the insects like the surface of real water bodies. The first interpretation, however, cannot apply to the observed egg-laying on asphalt roads, because mayflies normally oviposit exclusively on the water surface and not on markers. However, males and females swarming and mating above asphalt roads perform the behavioural elements (e.g. egg-laying flight, frequent surface-touching manoeuvres and dropping onto the surface) that are

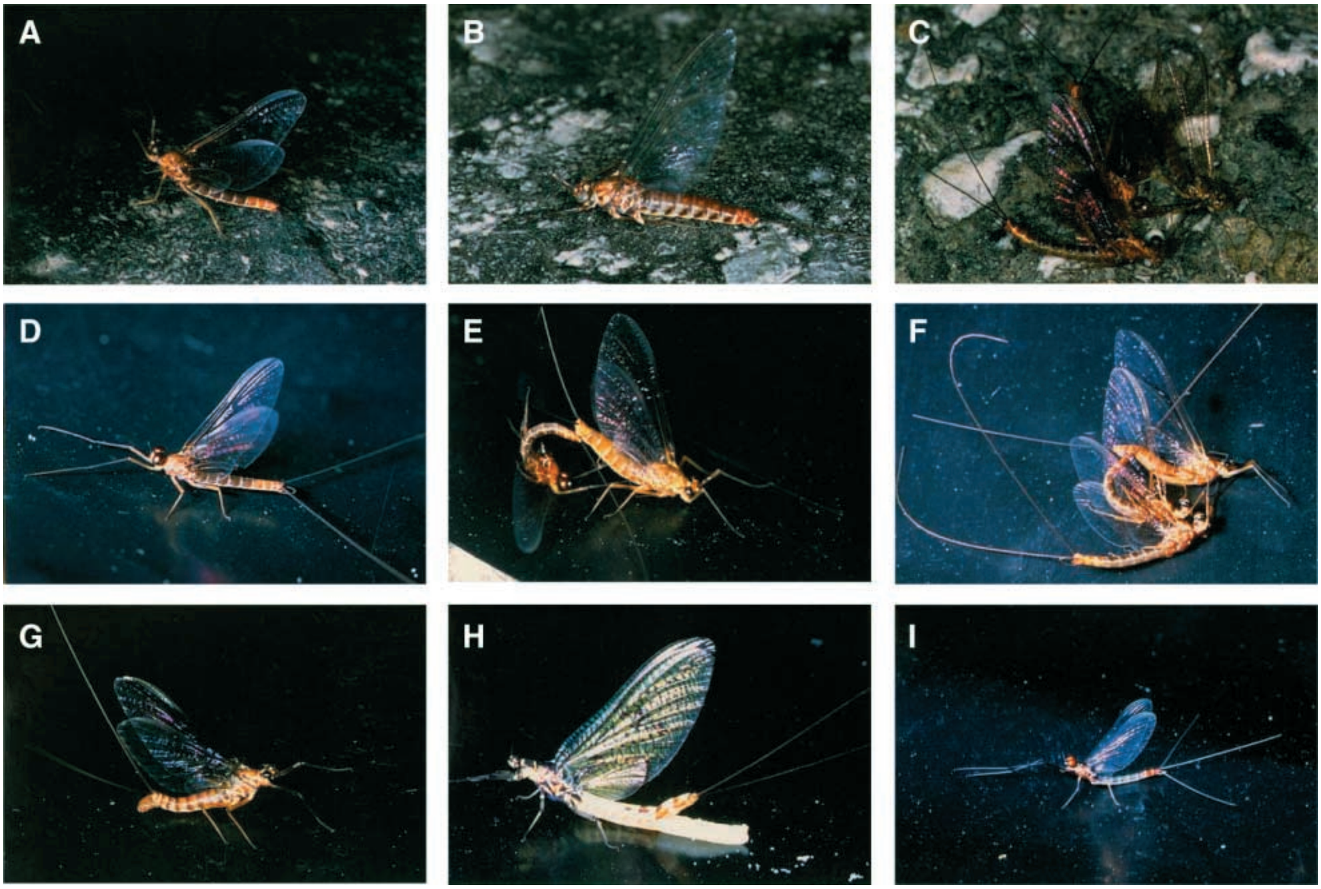


Fig. 1. Examples of mayflies deceived by and attracted to a dry asphalt road (A–C) and to the shiny black plastic sheet used in agriculture (D–I) in the immediate vicinity of a mountain creek near Budapest, Hungary, during May/June 1997. (A) A male *Rhithrogena semicolorata*. (B) A female *Epeorus silvicola*. (C) A female and two male *Epeorus silvicola* attempting to mate. (D) A male *Rhithrogena semicolorata*. (E) A copulating pair of *Rhithrogena semicolorata*. (F) A female and two male *Rhithrogena semicolorata* attempting to mate. (G) An ovipositing *Rhithrogena semicolorata*. (H) An ovipositing *Ephemera danica*. (I) A male *Baetis rhodani*.

characteristic above water surfaces. The second interpretation cannot explain why egg-laying by Ephemeroptera also frequently occurs on totally dry asphalt surfaces. In the present study, we give a possible explanation for this surprising behaviour.

The mating of mayflies is preceded by a peculiar swarming behaviour, during which a group of insects maintains a stationary position with respect to an element of the landscape called the ‘marker’. Concentration of the males in the swarm and its constant position are particularly important for mayflies since their sexually mature stage is of very short duration (Brodskiy, 1973). Markers can be large objects of relatively rare occurrence: the shores of lakes, roads or rows of littoral plants, for example (Savolainen, 1978). Because of the short-lived adult stage and the fact that the newly moulted adult mayflies can dry out quickly, during swarming the mayflies remain relatively close to the water basin in which development of the nymphal stage takes place. Thus, it is essential for the markers to be near water. This is why the role of markers in ephemeropteran swarming has been intensively studied and why it became a widespread view that asphalt roads near ephemeropteran emergence sites can be markers for swarming and mating.

Discovering the causes of the above-mentioned strange behaviour of mayflies may be important not only for scientific studies of Ephemeroptera, but also for the protection of this insect group since the huge number of eggs (an egg-packet of a female mayfly contains 6000–9000 eggs) laid onto the asphalt roads do not survive. Mayflies are in great danger because their aquatic habitat is becoming more polluted with herbicides, pesticides, excess fertiliser and industrial waste. Almost all mayfly species are threatened, and many of them have suffered a severe decline during the last decades as a result of habitat destruction by agricultural and urban development and land drainage. As a consequence, mass swarming of Ephemeroptera is now a rare phenomenon. Thus, it is particularly important to determine whether the egg-laying of mayflies on asphalt roads can be prevented. Little attention has been paid to this aspect of ephemeropteran swarming behaviour despite the considerable attention paid to the scientific study of swarm formation.

In an attempt to clarify the causes of reproductive behaviour of mayflies on asphalt roads, a 2 year study was conducted on six species of mayfly, using visual observations, video recordings, multiple-choice experiments and video-polarimetric measurements in the field. On the basis of our investigations, we propose a new interpretation for the peculiar behaviour of Ephemeroptera on asphalt roads. Our explanation is that asphalt roads mimic a highly and horizontally polarized water surface to water-seeking mayflies which, as we show here, detect water by means of the horizontally polarized reflected light, like many other water insects (Schwind, 1985, 1991, 1995; Schwind and Horváth, 1993; Horváth, 1995; Horváth and Zeil, 1996; Horváth and Varjú, 1997).

Materials and methods

Multiple-choice experiments with swarming mayflies using different test surfaces

Although we frequently observed the reproductive behaviour of *Ephemera danica* (Müll.), *Ecdyonurus venosus* (Fabr.), *Epeorus silvicola* (Etn.), *Baetis rhodani* (Pict.), *Rhithrogena semicolorata* (Curt.) and *Haproleptoides confusa* (Hag.) above dry asphalt roads, we performed multiple-choice experiments only with *Epeorus silvicola* and *Rhithrogena semicolorata*. Our experiments were carried out in late May and early June of 1996 and 1997 near the village of Dömörkapu located approximately 30 km from Budapest, Hungary. Our study site was the bank of a typical reach of a mountain creek, called Bükkös patak, from which mayflies emerge in large numbers and where they swarm during May and June (Andrikovics, 1991; Andrikovics and Kéri, 1991). In the immediate vicinity (at a distance of 1–5 m) of the creek, an asphalt road runs between trees and bushes almost parallel to the water and in some places it crosses the stream over small bridges. The creek itself runs in a valley under trees and bushes and is usually completely shadowed by riparian vegetation, except where the road crosses it. The road is several metres higher than the creek, and above it the sky is open. The surface of the asphalt road is relatively smooth and dark grey, but there are several patches of a lighter grey with a rougher surface.

In the multiple-choice experiments, we laid rectangular test surfaces of different types onto the asphalt road at different reaches of the creek where mayflies swarmed. The 1 m×2 m test surfaces were placed 0.5 m apart. The test surfaces we used were (i) shiny black plastic (polyethylene) sheet, (ii) shiny white (milky) plastic (polyethylene) sheet, (iii) shiny aluminium foil, (iv) slightly shiny black cloth, (v) matt black cloth and (vi) matt white cloth. To avoid the influence of colour on the choice of mayflies, the test surfaces were composed of neutral grey (uncoloured) reflecting materials. On several occasions, we counted the number of mayflies landing on and swarming immediately above (height no more than 0.1 m) a 0.1 m×0.1 m rectangular region of the test surface. The position of the test surfaces with respect to each other was changed randomly in order to avoid the possible influence of their position on the number of mayflies attracted.

Our experiments were always carried out under clear skies. At the beginning of an experiment, the landscape was illuminated by direct light from the setting sun, and after sunset by skylight from above.

Both visual observations and video-recordings were made of the swarming behaviour of mayflies above the asphalt road and the test surfaces. We also used photographs to document the landing and egg-laying of mayflies on the asphalt road and the test surfaces.

During the experiments, we measured the water temperature, the air temperature immediately above the creek and the asphalt road, and the temperature of the asphalt and test surfaces.

Video-polarimetric recordings of an asphalt road, a creek and the test surfaces

Using video-polarimetry, we measured the reflection–polarization characteristics of some reaches of a mountain creek (from which mayflies emerge and where they swarm, mate and oviposit), an asphalt road (above which mayflies swarm every year) and the test surfaces (used in the multiple-choice experiments described above). This method is described in detail by Horváth and Varjú (1997). In the case of scenes with flowing water, several digitized pictures were averaged prior to the calculation of the reflection–polarization characteristics in order to eliminate the effect of motion.

Using our video-polarimeter, we could measure the polarization of light through the three colour channels of the video camera: red (R, wavelength $\lambda^{red}=\lambda_{max}=730\pm65$ nm, mean ± S.D.), green (G, $\lambda^{green}=600\pm65$ nm) and blue (B, $\lambda^{blue}=470\pm65$ nm). Because the recorded scenes – the creek (the shore and bottom of which were covered by grey pebbles and stones), asphalt and test surfaces – were colourless, their polarization was practically independent of the spectral range. The grey asphalt surface (wet or dry), test surfaces and creek bed had the common spectral feature that they reflected approximately equally the entire visible spectrum of the incident light, as do all neutral grey objects. Thus, when presenting the measured reflection–polarization characteristics, we omit reference to the spectral range in which the measurement was obtained.

Results

The swarming behaviour of the mayflies

Depending on the species, the swarming of mayflies began prior to and after sunset every evening from the beginning of May until the end of June in both years. After the emergence of the insects from the mountain creek, the males gathered in several diffuse swarms in the air at a distance of approximately 4–5 m from the ground. At the beginning of swarming, we observed these relatively diffuse swarms everywhere above the streamlet, asphalt road, dirt roads and clearings in the vicinity of the emergence sites. Generally, these swarms developed in places where the sky was visible. As time elapsed, the swarms gradually became nearer to the ground and more females flew through them in order to copulate with the males. After mating, the females returned to the streamlet or landed on the asphalt road and laid their eggs on the water or asphalt surface.

Later, as the air temperature and intensity of ambient light decreased, the swarms gradually left the dirt roads and clearings. We then observed swarming mayflies exclusively above the asphalt road and those reaches of the creek open to the sky. In these swarms, both the males and females flew periodically up and down, displaying the species-specific nuptial dances (see Fischer, 1992), or flew parallel to the water or asphalt surface against the prevailing breeze. They frequently touched the water or asphalt surface, or dropped onto it for a few seconds. When the air temperature decreased to below approximately 14–15 °C and the light intensity was low, mayfly swarming suddenly ceased, and the insects disappeared from both the water and asphalt surfaces. They then landed on the leaves of neighbouring trees, bushes and grass in order to roost.

All six mayfly species observed showed the same behaviour above and on the asphalt road as at the water surface. The density of swarming, mating and ovipositing mayflies was highest above those patches of the asphalt road where the surface was smoother and darker than the surrounding regions. No reproductive behaviour occurred above the relatively light grey or rough spots of the asphalt. One of the most typical reactions of female mayflies to the smooth, black asphalt patches was the following: after copulation in the air, the females arrived above one of these patches. First, they flew across the patch, then suddenly turned back at its border, and in the presence of a gentle breeze, they all flew into the breeze. Females touched the patch several times and landed on it to lay their eggs. Thus, we assume that the darker and smoother the asphalt, the greater is its attractiveness to water-seeking mayflies. Experiments to test this hypothesis are in progress.

Above the asphalt road, we observed two types of flight for the six Ephemeroptera species, which are typical flight manoeuvres usually found only above a water surface. (i) *Egg-laying flight of females*. The females, generally facing into the slight breeze, flew to and fro parallel to and immediately above the asphalt surface, dancing up and down in a zig-zag pattern and sometimes touching the asphalt. This type of flight was shown only by females above the middle part of the asphalt road. During egg-laying flight, the females showed a typical, species-specific stereotypical flight pattern (see Fischer, 1992), which resembled the nuptial dance of the swarming males and occurred simultaneously with it. As egg-laying flight progressed, an increasing number of eggs was pressed out from the genitalia of the females. At the end of this flight, the females landed on the asphalt and laid their egg-packet (Fig. 1G). In the case of *Ephemera danica*, the females landed on the asphalt and remained on it until their elongated egg-packet had been pressed out and laid (Fig. 1H). The functions of egg-laying flight are finding an optimal site for oviposition, and/or allowing a larger number of eggs to be pressed out, and/or acting as a defence against attacks by swarming males (Fischer, 1992). (ii) *Water-touching manoeuvres of males*. The males also periodically touched the asphalt surface during their flight, usually facing into the wind. Some of the individuals touched the asphalt periodically only with their cerci while flying up and down immediately above the road. Others landed on the asphalt, stayed on it for 1 s and then took off, to land again some seconds later. Similar water touching by male mayflies (e.g. *Baetis vernus*, *Ecdyonurus venosus*, *Rhithrogena semicolorata* and *Ephemera danica*) was observed by Fischer (1992) above natural water surfaces at ephemeropteran emergence sites. According to Fischer (1992), such touching of the water surface by male Ephemeroptera allows them either to drink water or to test the height above the water surface using the cerci.

Multiple-choice experiments with swarming mayflies

We performed the multiple-choice experiments with all six mayfly species; however, quantitative data were gathered only for *Rhithrogena semicolorata* and *Epeorus silvicola*, a typical medium- and large-sized mayfly species, respectively.

Table 1 shows the air temperature and the number of *Rhithrogena semicolorata* landing on a given region of three different test surfaces (a shiny black plastic sheet, a shiny white plastic sheet and a shiny aluminium foil). *Rhithrogena semicolorata* is attracted almost exclusively to the shiny black plastic sheet. At the beginning of swarming above the asphalt road (at approximately 19:00 h), only a few mayflies landed on the black plastic, but their number increased rapidly over time. At 20:40 h, the reproductive activity reached its maximum on this plastic. Swarming ceased suddenly approximately 20–30 min after this maximum because of the decreasing temperature and the low light intensity. The shiny white plastic

Table 1. *Air temperature and the number of* Rhithrogena semicolorata *landing on a 0.1 m × 0.1 m area of three test surfaces (a shiny black plastic sheet, a shiny white plastic sheet, a shiny aluminium foil) for 30 s* versus *time on 23 May 1996*

		Number of insects landing		
Time (h)	Air temperature (°C)	Shiny black plastic sheet	Shiny white plastic sheet	Shiny aluminium foil
19:06	25.5	1	0	0
19:09	25.5	3	1	0
19:12	25.0	4	0	0
19:32	24.0	8	0	0
19:35	24.0	9	2	0
19:41	23.5	13	1	0
20:09	21.5	16	0	0
20:20	21.0	33	1	0
20:25	20.5	57	1	2
20:33	20.0	97	1	0
20:40	19.0	166	0	0
20:48	18.0	85	0	2
20:56	17.0	29	2	0
21:02	16.0	9	1	0

Table 2. *Air temperature, temperature of the test surfaces and the number of* Epeorus silvicola *landing on a 0.1 m × 0.1 m area of three test surfaces (a shiny black plastic sheet, a shiny white plastic sheet, a shiny aluminium foil) for 30 s* versus *time on 3 June 1996*

			Number of insects landing		
Time (h)	Air temperature (°C)	Temperature of the test surfaces (°C)	Shiny black plastic sheet	Shiny white plastic sheet	Aluminium foil
19:10	25.0	27.5	11	0	0
19:12	25.0	27	9	0	0
19:15	24.5	27	9	0	0
19:19	24.0	26.5	24	0	0
19:22	23.5	26	26	1	0
19:25	23.0	25.5	19	1	0
19:29	22.0	24.5	16	0	0
20:03	21.5	23.5	3	0	0

sheet and the aluminium foil were not attractive to *Rhithrogena semicolorata*. The very small number of mayflies observed landing on these test surfaces is negligible in comparison with the number landing on the black plastic sheet.

As Table 2 demonstrates, similar results were obtained for *Epeorus silvicola*. To preclude the possibility that temperature differences between the test surfaces resulted in the observed patterns, we measured the temperature of the test surfaces. We found no temperature differences between the surfaces. The temperature of the test surfaces was always significantly higher than the air temperature above the asphalt road (Table 2; paired *t*-test, $P<0.01$). Both temperatures decreased gradually as a function of time, because both the swarming of mayflies and the multiple-choice experiments began immediately prior to sunset.

In the first series of multiple-choice experiments (carried out in 1996), we found that the shiny black plastic sheet (which reflected light specularly, i.e. in such a way that the angle of incidence is equal to the angle of reflection, and only a small amount of light is reflected in other directions) was the only attractive surface for all six mayfly species studied. As control surfaces, we used a slightly shiny black cloth and a matt white cloth that reflected light diffusely (that is, in all directions). The results of the control experiment are presented in Table 3 for *Rhithrogena semicolorata*. Again, the shiny black plastic sheet was significantly more attractive than the cloths (paired *t*-test, $P<0.001$). The white cloth was unattractive; however, the black cloth attracted a small number of mayflies. The reason for this was that this black cloth was slightly shiny. This is discussed below in detailing the reflection–polarization characteristics of the test surfaces.

Table 3. *The number of* Rhithrogena semicolorata *landing on a 0.1 m × 0.1 m area of three test surfaces (a shiny black plastic sheet, a slightly shiny black cloth, a matt white cloth) for 30 s* versus *time on 17 June 1996*

	Number of insects landing		
Time (h)	Shiny black plastic sheet	Slightly shiny black cloth	Matt white cloth
19:33	25	6	0
19:38	18	3	0
19:43	20	3	2
19:48	25	2	0
19:53	23	5	1
19:58	22	4	0
20:03	24	4	0
20:08	16	3	0
20:13	23	4	0
20:18	21	4	0

The slightly shiny black cloth reflected partially horizontally polarized light. Its degree of polarization was much lower than that of the shiny black plastic sheet (see Table 6; Fig. 4).

Table 4. *The number of* Epeorus silvicola *landing on and flying immediately above (within a height of 0.1 m) a 0.1 m × 0.1 m area of three test surfaces (a shiny black plastic sheet, a matt black cloth, a matt white cloth) for 30 s* versus *time on 6 May 1997*

	Number of insects landing		
Time (h)	Shiny black plastic sheet	Matt black cloth	Matt white cloth
20:12	13+50	0+3	0+0
20:14	20+150	1+2	0+0
20:20	160+170	0+0	0+0
20:27	32+32	0+0	0+0
20:30	16+10	0+0	0+0

The numbers of mayflies are given in the format $a+b$, where a is the number of insects landing on the surface and b is the number of insects swarming above it.

In 1997, we used totally matt black cloth as one of the control surfaces. The other two test surfaces were a shiny black plastic sheet and a matt white cloth. The number of *Epeorus silvicola* swarming immediately above and landing on these surfaces is given in Table 4. The matt black and white surfaces were unattractive to mayflies; the shiny black plastic sheet was the only attractive surface. A similar result was found for *Rhithrogena semicolorata* (Table 5). In this species, the majority of mayflies observed on the cloths and the aluminium foil were copulating pairs; they began to mate while still in the air and dropped accidentally onto these surfaces. The mayflies observed on the black plastic sheet were mainly single males or egg-laying females, but copula were also abundant. Table 4 also shows the typical pattern observed in all six species: at the beginning of swarming, only a few mayflies landed on the shiny black plastic sheet, but later almost every member of the swarm landed on it periodically. At the end of swarming, we observed that more individuals had settled onto the plastic than were flying above it.

Table 5. *The number of* Rhithrogena semicolorata *landing on a 0.1 m × 0.1 m area of four test surfaces (a shiny black plastic sheet, a matt black cloth, a matt white cloth, a shiny aluminium foil) for 30 s* versus *time on 11 May 1997*

	Number of insects landing			
Time (h)	Shiny black plastic sheet	Matt black cloth	Matt white cloth	Shiny aluminium foil
19:10	6	0	0	0
19:15	8	0	1	0
19:20	8	0	1	0
19:25	11	0	0	1
19:39	12	1	0	0
19:43	13	1	0	2
19:47	12	0	0	0
19:51	21	0	0	0
19:54	20	3	0	0
19:57	18	4	0	1
20:00	26	4	0	4
20:03	23	3	0	0
20:06	28	2	0	0
20:09	31	2	0	1
20:12	35	0	0	1
20:13	29	2	0	0
20:15	60	2	0	1
20:16	63	5	0	1
20:21	64	0	0	0
20:25	63	0	0	0
20:28	58	0	0	0
20:31	26	0	0	0
20:34	8	0	0	0
20:37	8	0	0	0

The landing of mayflies on the black plastic sheet was so intensive that we could hear the loud strikes of the insect bodies similar to rain drops rattling on the plastic. If we covered any part of the black plastic sheet with a piece of any other test surface, then reproductive activity of mayflies ceased above this region, but not above the surrounding sheet. When the piece of the other test surface was removed, reproductive behaviour of the insects above this part of the black plastic sheet recommenced.

Displacing the black plastic sheet

To demonstrate the strong preference of swarming mayflies for the shiny black plastic sheet, we lifted the black plastic sheet above which mayflies swarmed in large numbers and moved it slowly such that its surface remained horizontal. The swarming mayflies followed the slowly moving plastic. When the black plastic sheet with the cloud of swarming mayflies was moved above one of the other test surfaces and then the black plastic was quickly removed, the mayfly cloud dissipated rapidly. When the black plastic was replaced on the unattractive test surface, the mayflies returned and quickly developed a swarm. If the black plastic was held vertically, the mayflies did not swarm over or next to it, nor did they follow its movement. The same was true for all other test surfaces in this experiment.

Transferring the mayflies from the black plastic sheet to other test surfaces

Using a hand net, we captured mayflies (single males and females, egg-laying females, copulating pairs) swarming above the black plastic sheet and released them onto one of the other test surfaces. We observed that these mayflies did not continue their reproductive activity on the new test surface, but left it and returned to the black plastic. However, if we transferred them to another black plastic sheet, they began their reproductive behaviour again, showing that the captured mayflies did not fly away from the new test surface because of the netting procedure, but because of the unattractive or repellant nature of the test surface.

The influence of temperature on the reaction of mayflies to the test surfaces

The water temperature of the creek was between 12 and 14 °C, and did not change during swarming on a given day. The air temperature above the creek (at a distance of 1 m from the water surface) was significantly higher than that of the water (paired *t*-test, $P<0.001$) and decreased from approximately 20–22 °C to 14–15 °C between the start and end of swarming each day. The air temperature above the asphalt road (at a distance of 1 m from the surface) was significantly higher still (paired *t*-test, $P<0.001$) and decreased from approximately 25–26 °C to 16–17 °C during swarming (Table 1). The warmest location was always the asphalt road and the test surfaces on it (Table 2; paired *t*-test, $P<0.01$).

The swarming of mayflies began immediately prior to or after sunset when the air temperature was still relatively high above both the asphalt surface and the creek. The swarming ceased when the air temperature decreased below 14–16 °C. The higher air temperature above the asphalt road prolonged the reproductive behaviour of mayflies by approximately 15 min in comparison with the reaches of the creek from which the sky was visible, presumably making the asphalt more attractive to mayflies than the creek. However, since there was no temperature difference among the test surfaces investigated, the different reactions of mayflies to the different test surfaces cannot be explained by their thermal perception. Similarly, a role of olfaction in the choice of the test surface by mayflies can be excluded (see below). Mayflies must have preferred the asphalt road and the black plastic sheet and avoided the other test surfaces because these surfaces were visually attractive, non-attractive or even repellant.

Mayflies roosted on the leaves of trees and bushes after their reproductive activity. To study the role of the substratum chosen by the insects as a roosting place, we again used the test surfaces, which were laid onto the ground beneath trees and bushes on the bank of the creek. We observed that, after swarming, the mayflies landed *en masse* not only on the shiny black plastic sheet, but also on the other test surfaces irrespective of their type (using paired *t*-test, there were no significant differences between surfaces chosen). The behaviour of roosting mayflies was, however, quite different from the behaviour observed during swarming. Roosting mayflies did not dance, fly up and down, or oviposit on the test surfaces, but simply settled on them and remained motionless, apparently using the test surfaces as roosting places and not as reproduction sites. Because of the lower temperature, the roosting of mayflies on the shore of the creek began earlier than at the border of the warmer asphalt road.

Reflection–polarization characteristics of the swarming sites of mayflies

From the above observations, it is clear that mayflies select reproduction sites predominantly on the basis of visual cues (see also Discussion). We can hypothesize that the detection of water surfaces as oviposition sites occurs by polarotaxis as in many other water insects (Schwind, 1985, 1991, 1995). Thus, using video-polarimetry, we determined the reflection–polarization characteristics of several reaches of a mountain creek and compared them with those of an asphalt road and the test surfaces.

Reaches of a mountain creek

Fig. 2 shows the measured reflection–polarization characteristics of three different reaches of a mountain creek from which mayflies emerge and where they swarm, mate and oviposit yearly in large numbers. All three scenes had a slightly undulating water surface and were recorded from a direction of view of the camera of 60° measured from the vertical, which is slightly larger than the Brewster angle of asphalt (57.5°) and water (53°) with refractive indices of 1.57 and 1.33, respectively. In the first reach of the creek (Fig. 2A, row 1), the water was relatively slow and calm and a small pond was present in the shadow of trees. Through the foliage, skylight illuminated the water surface from above and to the right. The degree of polarization is high only in those regions of the water surface that are illuminated by the skylight (Fig. 2A, row 2). The other regions of the water and the shore reflect practically unpolarized light. Because of the undulation of the water surface, the degree of polarization and the E-vector alignment (Fig. 2A, row 3) change strongly from site to site on the water surface, giving a relatively broad distribution of these variables (Fig. 2A, rows 4, 5). The E-vectors of light reflected from the water surface are approximately horizontal but, because of the ripples on the water surface, they can diverge strongly from this direction (Fig. 2A, rows 3, 5).

The second reach of the mountain creek was exposed to skylight from above (Fig. 2B). The water flowed slowly among stones and pebbles. Here, the degree of polarization of light reflected from the undulating surface of the turbulent water was also relatively low, and the dry stones and pebbles were largely unpolarized (Fig. 2B, row 2). Thus, the spatial distributions of the degree (Fig. 2B, row 2) and direction (Fig. 2B, row 3) of polarization are very patchy and the histograms of these variables are again relatively broad (Fig. 2B, rows 4, 5). In the case of the third reach (Fig. 2C), the creek flowed under trees, but its surface was illuminated by skylight from the side. Consequently, the degree of polarization of light reflected from the water surface is relatively high (Fig. 2C, rows 2, 4). However, similarly to the first and second reaches, both the degree and direction of polarization of the light reflected from the water surface change strongly because of the ripples (Fig. 2C, rows 2, 3), and their histograms are again broad (Fig. 2C, rows 4, 5).

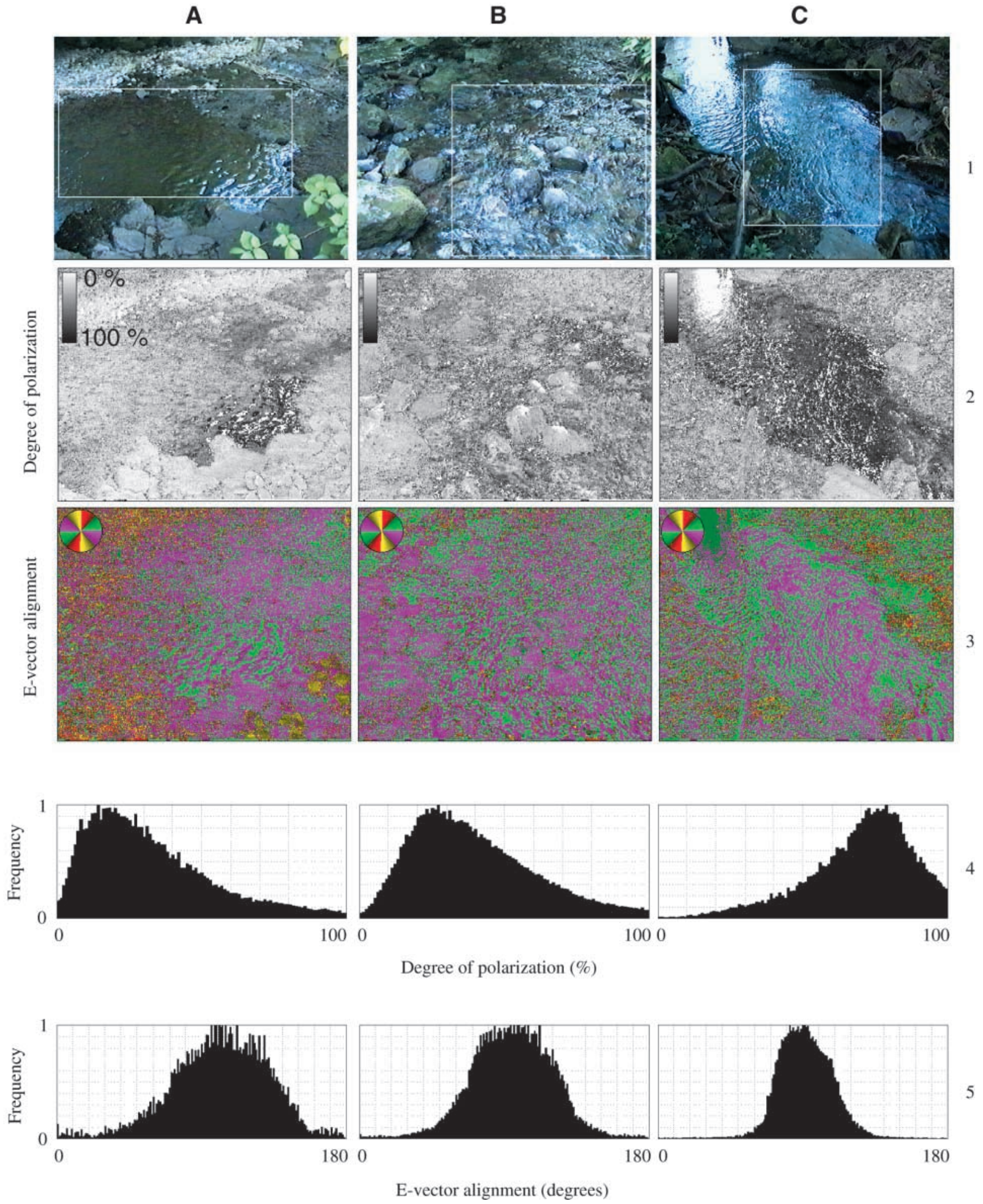
Sections of an asphalt road

Fig. 3 shows the measured reflection–polarization characteristics of three different sections of the asphalt road above and on which the investigated mayflies swarmed, mated and oviposited. Analysing the patterns and histograms of the degree and direction of polarization of light reflected from the three sections of the asphalt road in Fig. 3 and comparing them with those of the reaches of the mountain creek in Fig. 2, we can establish several important points. The distribution of the degree of polarization and the E-vector alignment of the light reflected from the asphalt road is narrow; the E-vector of the reflected light is predominantly horizontal and, apart from the lighter and rougher patches of the asphalt surface, the degree of polarization is relatively high, in spite of the fact that the surface was dry. We also measured the reflection–polarization characteristics of light reflected from wet sections of the asphalt road after rain. We obtained similar results as for the dry asphalt road; however, the degrees of polarization were significantly higher when the asphalt was wet (paired *t*-test, $P<0.001$; see Table 6; Fig. 4).

Test surfaces used in the multiple-choice experiments

Fig. 4 shows the reflection–polarization patterns of the different test surfaces measured using video-polarimetry. Table 6 shows the measured relative brightness, degree of polarization δ and E-vector alignment α of light reflected from the test surfaces. From Fig. 4 and Table 6, the following observations can be made. Light reflected from the shiny black plastic sheet (δ=55 %) and the wet asphalt ($\delta\approx$51 %) possessed the highest degrees of polarization ($P<0.001$). The degree of polarization of light reflected from the dry asphalt ($\delta\approx$31 %) was still strong and much higher ($P<0.001$) than that from the slightly shiny black cloth ($\delta\approx$15 %), the matt black cloth ($\delta\approx$9 %) and the shiny white plastic sheet (δ=7.7 %). The matt white cloth (δ=3.3 %) and the shiny aluminium foil (δ=3.2 %) reflected practically unpolarized light.

Because of the approximately smooth and horizontal reflecting surfaces, the direction of polarization of light reflected from the wet and dry asphalt and the shiny black and white plastic sheets was not significantly different from horizontal ($P<0.001$). The E-vectors of light reflected from the cloths differed significantly from the horizontal direction ($P<0.001$) because of the surface roughness of these cloths. The shiny aluminium foil reflected the light such that it did not



change the degree and direction of polarization of the incident light. Since the surroundings (sky and randomly oriented leaf blades of the vegetation) of the swarming sites and the site of the multiple-choice experiments possessed randomly oriented E-vectors, the directions of polarization of light reflected from the shiny aluminium foil were also random, and the relatively low degree of polarization changed strongly from site to site depending on the direction of view.

Fig. 2. The reflection–polarization characteristics of three different reaches of a mountain creek (a typical emergence and swarming site of the mayflies studied) measured using video-polarimetry. All three scenes with a slightly undulating water surface were recorded from a direction of view of the camera of 60 ° measured from the vertical. (A) In this relatively slow and calm reach of the creek, a small pond is present, shadowed by trees. Through the foliage, skylight illuminated the water surface from above and to the right. (B) A reach of the creek illuminated from above by the clear sky where the water flowed slowly among stones and pebbles. (C) A reach where the creek flowed under trees, but its surface was illuminated by skylight from the side. Row 1 shows the spatial distribution of the brightness and colour of the scene as seen through the video-polarimetry camera. The small rectangular areas demarcated by white lines within the pictures in row 1 represent the regions for which the histograms of the degree and direction of polarization are given in rows 4 and 5. Row 2 gives the patterns of the degree of polarization δ of the scenes. The colour scale is given in the top left corner: the darker the grey tone, the higher is δ (black, δ=100 %, white, δ=0 %). Row 3 shows the patterns of the E-vector alignment α of the scenes measured from the vertical. The darker the violet/green or red/yellow colour, the more the E-vector alignment deviates from the horizontal or vertical, respectively (red, $0^\circ\leqslant\alpha<45^\circ$; green, $45^\circ\leqslant\alpha<90^\circ$; violet, $90^\circ\leqslant\alpha<135^\circ$; yellow, $135^\circ\leqslant\alpha\leqslant180^\circ$). Row 4 shows histograms (frequencies) of the distribution of the degree of polarization calculated for the rectangular windows in row 1. In row 5 are histograms (frequencies) of the distribution of the E-vector alignment calculated for the rectangular windows in row 1.

Discussion

An appropriate explanation for the reproductive behaviour of mayflies above asphalt roads is that certain sensory (olfactory, thermal or visual) cues deceive and attract these insects. To investigate these cues, we performed multiple-choice experiments with swarming mayflies. We used colourless reflecting test surfaces because we wanted to study the role of the brightness and polarization of reflected light in the reproductive behaviour and detection of water by mayflies. We wished to avoid the more complex investigation of the role of colour in this behaviour. The latter is a task for future studies.

The role of olfaction, wind and air humidity

The asphalt road and the test surfaces did not possess any characteristic smell detectable by the human olfactory system. The black and white plastic sheets were composed of the same polyethylene; consequently, their odour must be the same, as in the case of the matt black and white cloths. Similarly, there might not be any significant difference between the smell of the smooth/dark and light/rough regions of the asphalt surface. It is, therefore, improbable that olfaction plays a role in the attractiveness of the shiny black plastic sheet and the asphalt surface to mayflies. This is consistent with the results of other authors (Schwind, 1985, 1991, 1995; Horváth *et al*. 1998), who found that water-seeking insects find their aquatic habitat visually and not by means of olfaction.

Mayflies generally avoid those sites where the wind is strong and the air humidity is low (Brodskiy, 1973). Any small possible differences in wind velocity and relative humidity among the test surfaces were compensated for by the random positioning of these surfaces in the multiple-choice experiments. Thus, a role of wind and air humidity in the attractiveness of the shiny black plastic sheet can be excluded.

The role of temperature

Since there were no temperature differences between the different regions of the asphalt road and the test surfaces lying on it, the attractiveness of the smoother and darker regions of the asphalt surface and the shiny black plastic sheet cannot be explained in terms of temperature. Mayflies must have thermal sensitivity in order to perceive the optimal temperature range for swarming (Savolainen, 1978). When the air becomes colder than approximately 14–15 °C after sunset, swarming ceases and the mayflies roost on the leaves of grass, trees and bushes on the shore of their emergence site. The air above asphalt roads is always warmer than that above the water surface, because the sunshine warms the dark asphalt more than the water. This higher temperature above asphalt roads is advantageous for mayflies as it prolongs their reproductive activity. Note, however, that it is unlikely to be the higher temperature that attracts mayflies to asphalt roads. The higher temperature only affects the duration of the swarming period

Table 6. *The reflection–polarization characteristics of the test surfaces measured using video-polarimetry*

	S1 Wet asphalt	S2 Matt white cloth	S3 Shiny aluminium	S4 Shiny white plastic sheet	S5 Matt black cloth	S6 Slightly shiny black cloth	S7 Shiny black plastic sheet	S8 Dry asphalt
Relative brightness (%)	38.8±3.4	99.7±5.4	100±5.7	97.6±4.3	24.4±2.8	17.6±3.2	22.6±2.4	26.0±3.1
Degree of polarization, δ (%)	50.9±3.4	3.3±0.9	3.2±1.1	7.7±1.5	9.1±2.1	15.1±2.8	55.0±5.4	30.6±3.4
E-vector alignment, α (degrees)	89.1±1.4	58.8±4.3	57.7±2.1	91.3±1.1	81.9±5.4	73.1±4.9	90.5±1.2	90.9±1.3

Relative brightness is calculated relative to the shiny aluminium foil; E-vector alignment is measured with respect to the vertical.
Values are means ± S.E.M. (N=560 × 736 = number of pixels in a video frame).

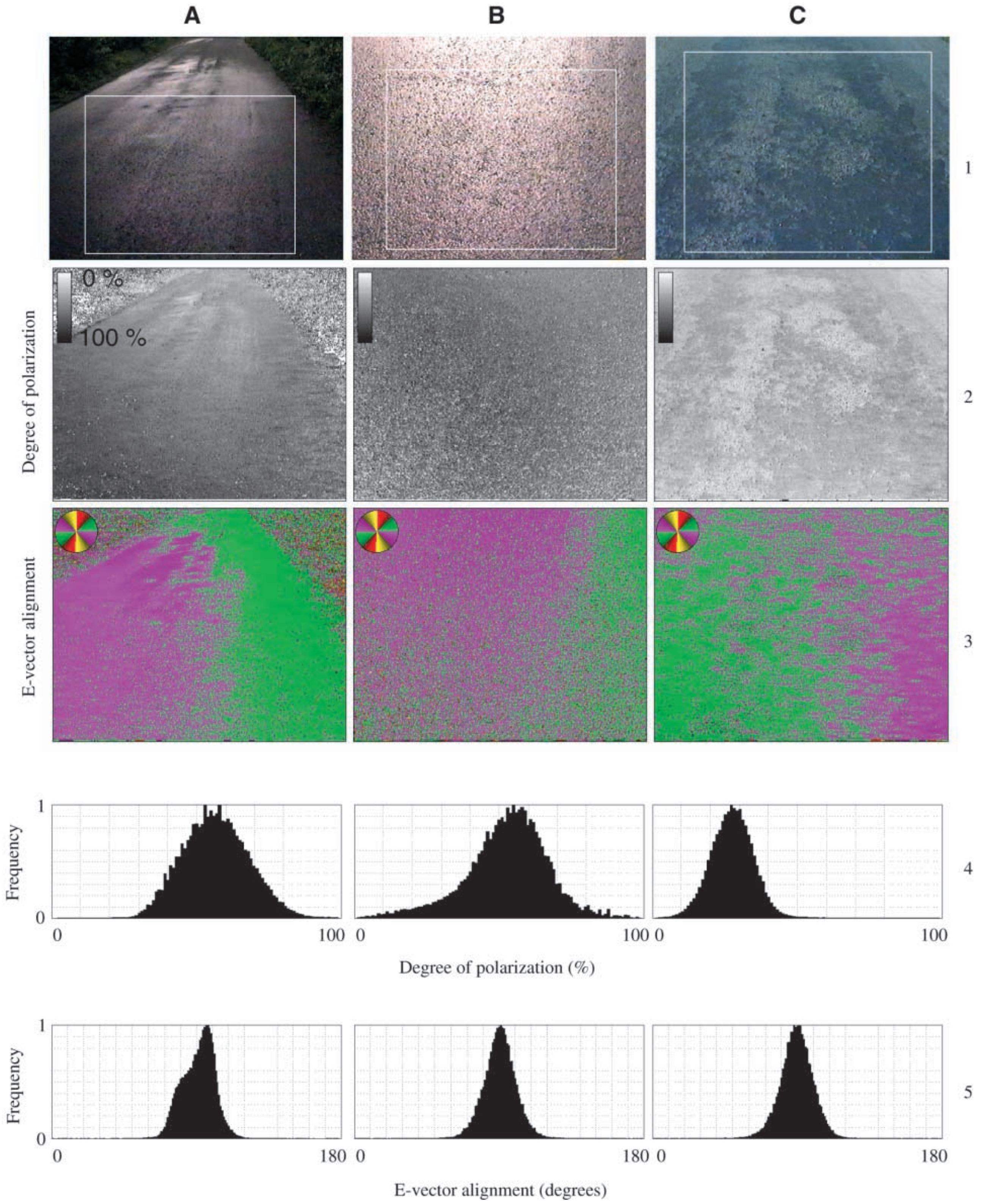


Fig. 3. The reflection–polarization characteristics of three different sections of the asphalt road above and on which the mayflies swarmed, mated and oviposited. In each case, the asphalt surface was dry, and the scenes shown were recorded from a direction of view of the camera of 60° with respect to the vertical. (A) A long section of the asphalt road illuminated by direct light from the setting sun under a clear sky. The camera viewed towards the solar meridian. (B) A short, smooth and dark section of the asphalt road illuminated by direct sunlight prior to sunset. The camera viewed towards the solar meridian. (C) A short section of the asphalt road with smooth and rough, bright and dark patches illuminated by skylight from above after sunset. Other details are as in Fig. 2.

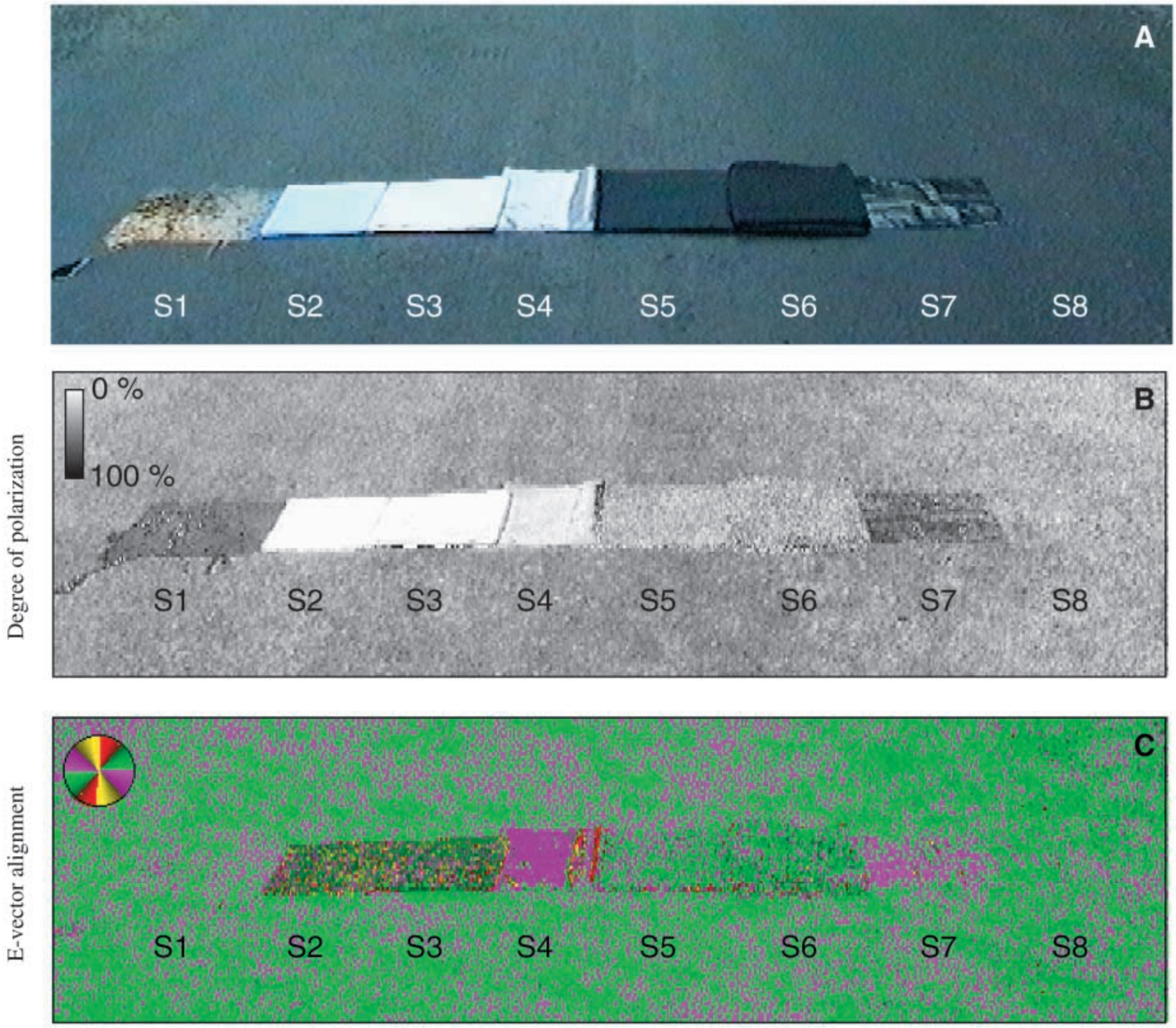


Fig. 4. The reflection–polarization characteristics of eight different test surfaces measured using video-polarimetry. The scene was illuminated by skylight from above after sunset and recorded from a direction of view of the camera of 70 ° with respect to the vertical. The rectangular pieces of the test surfaces were laid on a dry asphalt road, a small rectangular area of which (S1) was moistened by water. S1, wet asphalt surface; S2, matt white cloth; S3, shiny aluminium foil; S4, shiny white plastic sheet; S5, matt black cloth; S6, slightly shiny black cloth; S7, shiny black plastic sheet; S8, dry asphalt surface. (A) The colour picture of the scene as seen through the video-polarimetry camera. (B) The pattern of the degree of polarization of the scene. (C) The pattern of the E-vector alignment of the scene. Other details are as in Fig. 2.

(approximately 15 min longer) above the asphalt road compared with the cooler water surface. For species swarming at dusk over water, a gradual increase in swarming altitude has been reported (Brodskiy, 1973) as the insects avoid cold air near the ground. We observed the reverse of this phenomenon above asphalt roads.

The role of colour and brightness

On the basis of the above arguments, the high attractiveness of asphalt roads to mayflies can be explained only by optical cues, i.e. by the colour, brightness or polarization of reflected light. Because a black or grey asphalt surface reflects the whole spectrum of the incident light and its reflectivity is almost independent of the wavelength, as for the colourless test surfaces used in the experiments, the role of colour in the choice by mayflies can be excluded. The shiny aluminium foil and the plastic sheets reflected the light specularly, the matt cloths reflected it diffusely. Among the test surfaces, the brightest was the aluminium foil; the white plastic sheet and the white matt cloth reflected a slightly, but not significantly, smaller amount of light; and the black plastic sheet and the black cloths were the darkest (Table 6). If mayflies were attracted to the asphalt surface by positive phototaxis, then the shiny aluminium foil, the shiny white plastic sheet and the matt white cloth should have been the most attractive to them. Since the reverse was found, one can conclude that mayflies were not guided by phototaxis to the asphalt surface.

We found that mayflies were attracted only to the shiny black plastic sheet among the test surfaces. This cannot be explained by the relatively small amount of light reflected from this plastic sheet, because the matt black cloth, which had a similar relative brightness (using a paired *t*-test, there is no significant difference in brightness; Table 6), was not attractive at all. In a specular direction (i.e. when the angle of incidence is equal to the angle of reflection), a shiny black surface reflects more light than a matt black one; however, it was established above that the amount of light reflected is not the cue used by mayflies.

The role of reflection polarization

Aluminium foil does not change the degree and direction of polarization of the incident light (Horváth and Pomozi, 1997). The light reflected from the plastic sheets became polarized parallel to their surface, but the degree of polarization of light reflected from the white plastic sheet (δ=7.7 %) was much smaller than that from the black one (δ=55 %) (Table 6). The light reflected from the cloths also possessed very low degrees of polarization; furthermore, the E-vector of light reflected from them was not horizontal. Thus, we suggest that polarization of reflected light might be the most important variable explaining the attractiveness of the shiny black plastic sheet. We observed that the black plastic sheet was attractive only if its surface was horizontal; the vertically oriented black plastic sheet, for which the E-vectors of reflected light would have been vertical, was not attractive to mayflies. Thus, we can conclude that only horizontally polarized reflected light attracts mayflies.

This is also supported by the fact that the shiny aluminium foil, which did not change the degree and direction of polarization of reflected light, was unattractive to mayflies. The polarization distribution of the surroundings of the sites of our choice experiments was generally characterized by random orientation of the E-vectors and by relatively low values of the degree of polarization (e.g. see Fig. 3A). Thus, the light reflected from the aluminium foil was relatively unpolarized in comparison with the light reflected from the black plastic sheet and its E-vector was not horizontal (Table 6).

We found that the shiny black plastic sheet was more attractive to mayflies than the dry asphalt surface, and that the latter was much more attractive than the slightly shiny black cloth. However, the smoother and darker regions of the asphalt road were much more attractive than the rougher and lighter patches. We found that the degree of polarization of reflected light was highest for the shiny black plastic sheet (δ=55 %); light reflected from the dry asphalt road possessed a smaller degree of polarization ($\delta\approx$31 %), but a higher degree of polarization than that of the slightly shiny black cloth ($\delta\approx$15 %). The degree of polarization of light reflected from the rougher and lighter patches of the asphalt was lower than that reflected from the smoother and darker regions of the asphalt road (Fig. 3C, rows 1, 2). Therefore, the higher the degree of polarization of reflected light, the greater is its attractiveness to mayflies. Hence, mayflies swarming, mating and egg-laying on asphalt roads are predominantly visually deceived by and attracted to the asphalt surface because the strongly and horizontally polarized reflected light imitates a water surface.

Our results are in accordance with the earlier results of Schwind (1985, 1991, 1995), whose test surfaces also attracted *Cloeon* species (Ephemeroptera). He found that the probable spectral range where the polarization vision system of *Cloeon* functions is between 450 and 480 nm.

We found that the slightly shiny black cloth with a degree of polarization δ of reflected light of 15 % was slightly attractive (see Table 3), while the matt black cloth (δ=9.1 %) was relatively unattractive to the six mayfly species investigated. This indicates that the threshold of the polarization sensitivity of their visual system is between 9 % and 15 %. Apart from some anatomical studies (e.g. Horridge, 1976; Horridge and McLean, 1978; Burghause, 1981) on the dorsal (turban) and lateral eyes in male and female Ephemeroptera, nothing is known about the polarization sensitivity of the visual system in mayflies. Our observations make it very probable that mayflies possess well-developed polarization vision and detect the water surface on the basis of reflected polarized light.

Generally, aquatic insects and those living in moist substrata are influenced in their choice of habitat not only by horizontally polarized reflected light (visible from remote distances), but also by non-optical factors; shortly after landing on a substratum, they may find it unsuitable and leave again (Schwind, 1991). However, we did not observe such behaviour in the six Ephemeroptera species studied. Perhaps the highly and horizontally polarized light reflected from the asphalt surface or the shiny black plastic sheet was such a strong visual cue that it suppressed the signals of other sensory organs.

Comparison of the attractiveness of asphalt roads and water surfaces to mayflies

Since the asphalt is black or dark grey and non-transparent, an asphalt road is an efficient specular reflector and polarizer if its surface is smooth; it always reflects horizontally polarized light, the degree of polarization of which is almost 100 % near the Brewster angle (57.5 °). Light penetrating into the asphalt has no effect on the polarization because it is totally absorbed. The situation in the case of a streamlet, however, is different, because light reflected specularly from the water surface is horizontally polarized, whereas light penetrating into water and emanating from it is vertically polarized due to refraction. This vertically polarized component reduces the net degree of polarization. Thus, the light reflected from a brook is horizontally polarized when the surface-reflected light dominates and vertically polarized when the light returning from the water dominates. The greater the proportion of light returning from the water in comparison with that reflected from the water surface, the lower is the net degree of polarization (Fig. 2A,B). In Fig. 2C, the degree of polarization of light reflected from the water surface is relatively high, because only a small amount of light is coming from the water (due to the sheltering vegetation), and the amount of light reflected from the water surface is high (due to the bright illumination from the side).

The highly and always horizontally polarized light reflected from asphalt roads and the relatively homogeneous distribution of the degree and direction of polarization (see Figs 3, 4) can therefore be much more attractive to mayflies than the surface of a streamlet (Fig. 2). An asphalt road can reflect and polarize the incident light in such a way that the reflected light becomes a supernormal stimulus for water-seeking mayflies in comparison with the light reflected from the water. This was also observed in our multiple-choice experiments, when mayflies swarming above the asphalt road were attracted to the highly polarized light reflected from shiny black plastic sheet when it was laid onto the road. A relatively small black plastic sheet (a few square metres) attracted all the mayflies swarming above the asphalt road within several tens of metres.

According to Schwind (1991), insects inhabiting running waters, e.g. plecopterans living near brooks (Zwick, 1990), may not locate their habitats using polarization vision because polarization is reduced or even distorted by waves (see Fig. 2B). Nevertheless, our observations and multiple-choice experiments show that this is not true of the Ephemeroptera, at least for the six species studied by us.

One of the prerequisites of mayfly mating is to swarm above places where the sky is visible, because the females are usually detected visually and captured by the males from below (Brodskiy, 1973). The sky is generally open above highways and asphalt or dirt roads; thus, in this respect, roads near the emergence site of mayflies provide a good swarming place. After mating, the polarotactic females return to water to oviposit. Highly and horizontally polarized light reflected from asphalt roads with a smooth and dark surface can deceive and attract them.

Hence, asphalt roads are visually attractive on several levels to mayflies: the sky above them is visible, the strong and horizontal polarization of reflected light mimics a water surface, and they have a slightly higher temperature than the surrounding areas. Asphalt roads can be much more attractive for mayflies than real creeks, because the latter frequently run under trees and bushes. Mayflies do not swarm or mate above those reaches of the creek that are in the shelter of trees; that is, from which the sky is not visible. Egg-laying also takes place on the reaches of the streamlets where the sky is visible and from which polarized skylight can be reflected to guide the mayflies to the water surface.

Other choice experiments with mayflies

Using different shiny black and white plastic markers oriented horizontally or vertically, Savolainen (1978) studied the ability of some mayfly species to recognize the markers in their visual environment. His observation that individuals of *Ephemera vulgata* were deceived by horizontal plastic sheets is consistent with our results. In contrast to our choice experiments, Fischer (1992) could attract male *Baetis vernus* in large numbers to a horizontally oriented matt black cloth laid on the grass of a meadow, and the mayflies followed the cloth if it was moved slowly. However, he carried out no control experiments and gave no information about the optical characteristics of the test surface, so that comparisons with our results are difficult.

The results of Savolainen (1978) and Fischer (1992) were interpreted regarding the effects of markers on the swarming of mayflies. All earlier experiments studying the swarming site preference of mayflies have concentrated exclusively on the brightness contrast of markers; reflection polarization as an optical cue was not taken into consideration. Some authors (e.g. Fischer, 1992) have hypothesized that the recognition of the surface of creeks or lakes by the visual system of Ephemeroptera is made on the basis of brightness contrasts. Our results on the polarotaxis of Ephemeroptera demonstrate that this view is erroneous.

Asphalt roads as analogies with ancient tar seeps and recent oil lakes

Our observations on mayflies deceived by and attracted to highly and horizontally polarized light reflected from asphalt roads recall the earlier observations of Horváth and Zeil (1996) that both male and female dragonflies were visually deceived by the high and horizontal polarization of light reflected from crude oil lakes in the desert of Kuwait where they attempted to touch the surface or lay their eggs and perished in the black liquid oil. Recently, G. Horváth and G. Kriska (unpublished data) have observed that mayflies are attracted to and trapped in large numbers by the waste oil lake in Budapest. Asphalt roads and crude or waste oil lakes resemble the Pleistocene natural tar pits and asphalt seeps in Rancho la Brea, Los Angeles, USA (Akersten *et al*. 1983), and Starunia, Western Ukraine (Angus, 1973; Kowalski, 1997), which also trapped water insects *en masse* probably because of their high reflection polarization (Horváth and Zeil, 1996).

A new method for studying ephemeropteran swarming behaviour in the field

Our experiments suggest that a shiny black plastic sheet could be used for the investigation of reproductive behaviour in Ephemeroptera. In the field, under natural conditions, it is often difficult to observe mayfly swarms, because they are formed in unapproachable sites, above the water surface or at high altitudes, for instance. The placement of a shiny black plastic sheet of several square metres would attract the whole swarm, allowing the study of the mayflies or their capture. This simple method could facilitate field studies by students of Ephemeroptera.

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