19 Why do Mayflies Lay Eggs on Dry Asphalt Roads? Water-Imitating Horizontally Polarized Light Reflected from Asphalt Attracts Ephemeroptera

Kriska et al. (1998) observed near sunsets that individuals of several mayfly (Ephemeroptera) species swarmed and mated above and landed on dry asphalt roads (Figs. 19.1A-C), shiny black plastic sheets used in agriculture (Figs. 19.1D-I) and windscreens and roofs of cars (Figs. 19.1J,K) in the immediate vicinity of their emergence sites (mountain streamlets), and that after copulation the females laid their eggs *en masse* on dry asphalt roads (Figs. 19.1A-C) instead of laying them on the water surface. These mayflies showed the same behaviour above the more or less horizontal regions of the surface of cars as above asphalt roads, black plastic sheets and water surfaces. Such behaviour was, however, observed only when the colour of the car was red, black or dark grey. White or light cars (metallic coloured or not) did not attract any mayflies. These observations, especially the egg-laying by females, suggest that the mayflies were apparently deceived by and attracted to these shiny surfaces. Previous descriptions of ephemeropteran swarming, mating and egg-laying behaviour have largely ignored or misinterpreted this phenomenon. Although such observations on Ephemeroptera are known to entomologists, they have been mentioned only sporadically as marginal notes in publications or lectures. There were two different interpretations of this phenomenon:

1. It has generally been assumed, that asphalt roads serve as markers for swarming mayflies.
2. Oviposition by mayflies on asphalt roads has been 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 normally mayflies oviposit exclusively onto the water surface and not onto objects serving as markers. However, the behaviour of males and females swarming and mating above asphalt roads are similar to that above water surfaces. The second interpretation cannot explain why egg-laying by Ephemeroptera frequently occurs also on totally dry asphalt surfaces. Kriska et al. (1998) gave a correct and convincing explanation of this surprising behaviour.

In the life cycle of mayflies, only one function is important during the adult stage, the production of progeny. Flight is virtually the only form of locomotion in winged mayflies, therefore the finding of the female, her capture and mating take place in the air. Mating is preceded by peculiar swarming behaviour, during which a group of insects maintains a stationary position with respect to an object of the landscape (Edmunds and Edmunds 1980; Harker 1992). The concentration of males in the swarm and its stationary position are vital conditions for the meeting with females. The maintenance of these conditions is particularly important since the sexually mature stage of mayflies is very short (Brodskiy 1973). Flight in the swarm requires the control of velocity both in relation to a striking visible object of the landscape called the "marker" and, in the presence of wind, relative to the air. Control of the position relative to the marker involves also an optomotor reaction. Markers can be larger objects, the shores of lakes, roads, rows of plants on the littoral, for example (Savolainen 1978). Because of the very short adult stage and the fact that the newly moulted mayflies can dry out quickly, during swarming the mayflies remain relatively close to the water, in which the nymphs develop. 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.

Discovering the causes of the above-mentioned strange behaviour of mayflies is important not only for scientific studies of Ephemeroptera, but also for the protection of this insect group since the 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 fertilisers 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 regarding swarm formation.

In an attempt to clarify the causes of reproductive behaviour of mayflies over asphalt roads, Kriska et al. (1998) conducted a 2-year study on six species of mayfies, using visual observations, video recordings, multiple-choice experiments and video-polarimetric measurements in the field. On the basis of these investigations, they proposed a new interpretation for the peculiar behaviour of Ephemeroptera over asphalt roads. Their explanation was that asphalt surfaces near sunset mimic a highly and horizontally polarizing water surface to water-seeking mayflies which, as Kriska et al. (1998) showed, detect water by means of the horizontal polarization of reflected light.

19.1 Multiple-Choice Experiments with Different Test Surfaces

Although Kriska et al. (1998) frequently observed the reproductive behaviour of *Ephemera danica*, *Ecdyonurus venosus*, *Epeorus silvicola*, *Baetis rhodani*, *Rhithrogena semicolorata* and *Haproleptoides confusa* over dry asphalt roads near sunset, they performed multiple-choice experiments only with *Epeorus silvicola* and *Rhithrogena semicolorata*. These experiments were carried out in late May and early June of 1996 and 1997 in Hungary. The study site was the bank of a section of a mountain creek, from which mayflies emerged in large numbers and where they swarmed near sunset during May and June (Andrikovics 1991; Andrikovics and Kéri 1991). In the immediate vicinity, at a distance of 1-5 m from the creek, an asphalt road ran between trees and bushes almost parallel to the water, and in some places it crossed the stream over small bridges. The creek itself ran in a valley under trees and bushes and was usually completely shadowed by riparian vegetation, except where the road crossed it. The road was several metres higher than the creek, and above it the sky was open. The surface of the asphalt road was relatively smooth and dark grey, but there were several lighter grey patches with a rougher surface.

In the multiple-choice experiments, rectangular test surfaces of different types were laid on the asphalt road near different reaches of the creek where mayflies swarmed near sunset. The 1 m × 2 m test surfaces placed 0.5 m apart were: (i) shiny black plastic sheet, (ii) shiny white plastic sheet, (iii) shiny aluminium foil, (iv) slightly shiny black cloth, (v) matt black cloth and (vi) matt white cloth. In order to avoid the influence of colour on the choice of mayflies, the test surfaces were composed of colourless materials. The number of mayflies landing on and swarming immediately above the test surfaces at a height of no more than 0.1 m within a 0.1 m × 0.1 m rectangular region were counted. The position of the test surfaces relative to each other was changed randomly. These experiments were always carried out under clear skies at sunset. At the beginning of an experiment, the landscape was illuminated by the setting sun and, after sunset, by skylight from above.

19.2 Swarming Behaviour of Mayflies

At the study site, depending on species, the swarming of mayflies began prior to and after sunset every evening from the beginning of May until the end of June. After the emergence of the newly hatched 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, these relatively diffuse swarms were observed everywhere above the streamlet, asphalt road, dirt roads and clearings in the vicinity of the emergence sites. Generally, these swarms developed at places where the sky was visible. As time elapsed, the swarms

gradually approached 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. Thereafter swarming mayflies were observed exclusively above the asphalt road and the 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 (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 below 14-15 ^{o}C and the light intensity became too 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 to roost.

All six mayfly species observed behaved similarly 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 courting and egg-laying occurred above the relatively light grey or rough spots of the asphalt. One of the most typical reactions of female mayflies to the black and smooth asphalt patches was the following: After aerial copulation the females arrived above one of these patches. First, they flew over the patch, then suddenly turned back at its border, and in the presence of a gentle breeze all of them flew into the breeze. Females touched the patch several times and landed on it to lay their eggs. Thus, Kriska et al. (1998) concluded that the darker and smoother the asphalt, the greater is its attractiveness to water-seeking mayflies. Above the asphalt road Kriska et al. (1998) observed the following two flight types for the six Ephemeroptera species, which are typical flight maneouvres usually found only above water surfaces:

1. **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 performed only by females above the middle part of the asphalt road. During egg-laying flight, the females performed a typical, species-specific stereotypical flight pattern (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 in the air. At the end of this flight, the females landed on the asphalt and laid their egg-packet (Fig. 19.1H). In the case of *Ephemera danica*, the females landed on the asphalt and remained on it until their elongated egg-packet was pressed out and laid (Fig. 19.1I). 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).

2. **Surface-touching maneouvres 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 water surfaces at ephemeropteran emergence sites. According to Fischer (1992), such touching of the water surface by male Ephemeroptera allows them either to drink or to test the height above the water surface using their cerci.

19.3 Multiple-Choice Experiments with Swarming Mayflies

Table 19.1 shows the air temperature and the number of *Rhithrogena semicolorata* landing on a given region of three different test surfaces. *Rhithrogena semicolorata* was 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 the reproductive activity reached its maximum. The swarming ceased suddenly approximately 20-30 min after this maximum because of the decreasing temperature and the low light intensity. The shiny white plastic sheet and the aluminium foil were not attractive to *Rhithrogena semicolorata*. The very small number of mayflies landing on these test surfaces was negligible.

As Table 19.2 demonstrates, similar results were obtained for *Epeorus silvicola*. In order to preclude the possibility that temperature differences between the test surfaces resulted in the observed patterns, the temperature of the test surfaces was measured, but no temperature difference was found between the three different surfaces. The temperature of the test surfaces was always significantly higher than the air temperature above the asphalt road. Both temperatures decreased gradually.

In the first series of multiple-choice experiments, Kriska et al. (1998) found that the shiny black plastic sheet reflecting light specularly was the only attractive surface for all six mayfly species. In a control experiment, slightly shining matt black and matt white clothes were used, which reflected light diffusely. The results of this control experiment are presented in Table 19.3 for *Rhithrogena semicolorata*. Again, the shiny black plastic sheet was significantly more attractive than the cloths. The white cloth was unattractive. The black cloth attracted a small number of mayflies. The reason for this was that the matt black cloth was slightly shiny.

In the second series of multiple-choice experiments, Kriska et al. (1998) 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 matt black and white surfaces were unattractive to mayflies; the shiny black plastic sheet was the only

attractive one. A similar result was obtained for *Rhithrogena semicolorata*. In this species, the majority of mayflies observed on the cloths and the aluminium foil were copulating pairs; they began to mate while in the air, and dropped accidentally onto these surfaces. The mayflies observed on the black plastic sheet were mainly single male or egg-laying female insects, but copula were also abundant. At the beginning of swarming only a few mayflies landed on the shiny black plastic sheet, but later practically every member of the swarm landed on it periodically. At the end of swarming more individuals had settled onto the plastic than remained flying above it.

The landing of mayflies on the black plastic sheet was so intensive that one could hear the loud strikes of the insect bodies similar to rain drops rattling on the plastic. If any part of the black plastic sheet was covered by a piece of any other test surface, the reproductive activity of mayflies ceased above this region. When the piece of the other test surface was removed, reproductive behaviour of the insects above this part of the black plastic sheet recommenced.

To demonstrate the strong preference of swarming mayflies for the shiny black plastic sheet, the black plastic sheet above which mayflies swarmed in large numbers was lifted and moved 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 unattractive test surface was quickly covered by the black plastic sheet, the mayflies returned and the swarm developed again. 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.

Using a hand net, mayflies (single males and females, egg-laying females, copula) swarming above the black plastic sheet were captured and released onto one of the other test surfaces. These mayflies did not continue their reproductive activity on the new test surface, but they left it and returned to the black plastic. However, if these mayflies were transferred 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.

19.4 Influence of Temperature on the Reaction of Mayflies to the Test Surfaces

The water temperature of the creek was between 12 and 14 ^{o}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 and decreased from approximately 20-22 ^{o}C to 14-15 ^{o}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 still significantly higher and decreased from

approximately 25-26 °C to 16-17 °C during swarming (Table 19.1). The warmest location was always the asphalt road and the test surfaces on it (Table 19.2).

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 to 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, 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 surfaces 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, Kriska et al. (1998) used again the test surfaces, which were laid onto the ground beneath trees and bushes on the bank of the creek. After swarming, the mayflies landed *en masse* not only on the shiny black plastic sheet, but also on other test surfaces independently of their type. The behaviour of roosting mayflies was, however, quite different from that observed during their 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.

19.5 Reflection-Polarizational Characteristics of the Swarming Sites of Mayflies

19.5.1 Reaches of a Mountain Creek

Figure 19.2 shows the measured reflection-polarizational characteristics of three different reaches of a mountain creek from which mayflies emerged and where they swarmed, mated and oviposited yearly in large numbers at sunset. 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. 19.2A1), 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 linear polarization p was high only in those regions of the water surface that were illuminated by skylight (Fig. 19.2A2). The other regions of the water and the shore reflected practically unpolarized light. Because of the undulation of the water surface, the degree p and angle α of polarization (Fig. 19.2A3) changed strongly from site to site on the water surface, giving a relatively wide distribution of these variables (Fig. 19.2A4,5). The E-vectors of light reflected from the water surface were approximately horizontal but, because of the ripples on the water surface, they could diverge strongly from this direction (Fig. 19.2A3,5).

The second reach of the mountain creek was exposed to skylight from above (Fig. 19.2B). The water flowed slowly among stones and pebbles. Here, p 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. 19.2B2). Thus, the spatial distributions of p (Fig. 19.2B2) and α (Fig. 19.2B3) were patchy and the histograms of these variables were again relatively wide (Fig. 19.2B4,5).

In the case of the third reach (Fig. 19.2C), the creek flowed under trees, but its surface was illuminated by skylight from the side. Consequently, p of light reflected from the water surface was relatively high (Fig. 19.2C2,4). However, similarly to the first and second reaches, both p and α of the water-surface-reflected light changed strongly because of ripples (Fig. 19.2C2,3) and their histograms were again wide (Fig. 19.2C4,5).

19.5.2 Sections of an Asphalt Road

Figure 19.3 shows the measured reflection-polarizational characteristics of three different sections of the asphalt road above and on which mayflies swarmed, mated and oviposited. Analysing the patterns and histograms of p and α of the three sections of the asphalt road in Fig. 19.3 and comparing them to those of the reaches of the mountain creek in Fig. 19.2, we can establish several important points. The distribution of p and α of light reflected from the asphalt road is narrow; the E-vector of reflected light is predominantly horizontal and, apart from the lighter and rougher patches of the asphalt surface, p is relatively high, in spite of the fact that the surface was dry. The reflection-polarizational characteristics of wet sections of the asphalt road after rain were also measured with similar results as for the dry asphalt road; however, p was significantly higher when the asphalt was wet (see Table 19.4).

19.5.3 Test Surfaces Used in the Multiple-Choice Experiments

Table 19.4 shows the measured relative radiance I, degree of linear polarization p and angle of polarization α of light reflected from the test surfaces. The shiny black plastic sheet ($p = 55\%$) and the wet asphalt ($p \approx 51\%$) possessed the highest p. The degree of polarization of the dry asphalt ($p \approx 31\%$) was still high and much

higher than that of the slightly shiny black cloth ($p \approx 15\%$), matt black cloth ($p \approx 9\%$) and shiny white plastic sheet ($p = 7.7\%$). The matt white cloth ($p = 3.3\%$) and the shiny aluminium foil ($p = 3.2\%$) 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. The E-vectors of light reflected from the cloths differed significantly from the horizontal because of the surface roughness of these cloths. The shiny aluminium foil reflected the light such that it did not change p and α 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, α of light reflected from the shiny aluminium foil was also random and the relatively low p changed strongly from site to site depending on the direction of view.

19.6 Role of Different Cues in the Reproductive Behaviour of Mayflies Above Asphalt Roads

19.6.1 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.

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 their random positioning. Thus, a role of wind and air humidity in the attractiveness of the shiny black plastic sheet can be excluded.

19.6.2 Temperature

Since there was no temperature difference between the different regions of the asphalt road and the test surfaces laying 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 their swarming (Savolainen

1978). When the air becomes colder than approximately 14-15 °C after sunset, the 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. This higher temperature 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 (approximately 15 min longer) above the asphalt road compared to 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. Kriska et al. (1998) observed the reverse of this phenomenon above asphalt roads.

19.6.3 Colour and Radiance

Based on the above arguments, the high attractiveness of asphalt roads to mayflies can be explained only by optical cues, i.e. by the colour, radiance 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 19.4).

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. Mayflies were attracted only to the shiny black plastic sheet among the test surfaces. This cannot be explained by the relatively small amount of reflected light of this plastic sheet, because the matt black cloth which had a similar relative radiance (there is no any significant difference in radiance; Table 19.4) was not attractive at all. In a specular direction, 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.

19.6.4 Reflection Polarization

Aluminium foil does not change p and α of the incident light after reflection (Horváth and Pomozi 1997). The light reflected from the plastic sheets became polarized parallel to their surface, but p of the white plastic sheet (p = 7.7%) was much smaller than that of the black one (p = 55%) (Table 19.4). The cloths also

possessed very low p; furthermore, the E-vector of light reflected by them was not horizontal. Thus, polarization of reflected light is the most important variable explaining the attractiveness of the shiny black plastic sheet. The black plastic sheet was attractive only if its surface was horizontal; the vertically oriented black plastic sheet, for which the E-vectors would have been vertical, was not attractive at all to mayflies. Thus, one 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 p and α, was unattractive to mayflies. The polarization distribution of the surroundings of the sites of the choice experiments was generally characterized by random orientation of the E-vectors, and by relatively low p (e.g. see Fig. 19.3A). Thus, the light reflected from the aluminium foil was relatively unpolarized in comparison with the black plastic sheet and its E-vector was not horizontal (Table 19.4).

The shiny black plastic sheet was more attractive to mayflies than the dry asphalt surface, and 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. p = 55% was the highest for the shiny black plastic sheet; the dry asphalt road possessed a smaller p ≈ 31%, but higher than that of the slightly shiny black cloth (p ≈ 15%). p of the rougher and lighter patches of the asphalt was lower than that of the smoother and darker regions of the asphalt road (Fig. 19.3C1,2). Therefore, the higher the p 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.

This is in accordance with the results of Schwind (1985b, 1991, 1995), whose test surfaces attracted also *Cloeon* species (Ephemeroptera). He found that the probable spectral range where *Cloeon* is sensitive to polarization is between 450 and 480 nm. In the experiments of Kriska et al. (1998), the slightly shiny black cloth with p = 15% was slightly attractive while the matt black cloth (p = 9.1%) was relatively unattractive to the six mayfly species investigated. This indicates that the threshold of polarization sensitivity of their visual system is between 9% and 15%.

Kriska et al. (1998) could not determine the spectral range in which the studied mayflies are sensitive to polarization. These Ephmeroptera swarm at dusk when the only light source is the sky. Thus, they can detect the water surface by means of the polarization of reflected skylight, in which the short wavelength range (UV and blue) of the spectrum dominates (Coulson 1988). Both asphalt and water surfaces reflect the entire spectrum of the skylight. Kriska et al. (1998) observed that mayflies were deceived by and attracted to asphalt roads not only under clear skies (when skylight is rich in the UV component beside the blue one), but also under partially cloudy skies or even at total overcast (when the UV component of skylight is strongly reduced or even absent). From this one can expect that the polarotactic water detection of the Ephemeroptera studied functions in the blue, as in *Cloeon*.

The best known fact about the visual system of Ephemeroptera is the presence of large dorsal eyes, called turban eyes, in the male of some families. The eyes of these insects are characterized by a strong sexual dimorphism. In addition, these insects also have lateral eyes just as the females do. The males of one of the mayfly species studied by Kriska et al. (1998), *Ephemera danica*, however, do not possess turban eyes, the morphology of their eyes is very similar to that of the females. Most works published on the ephemeropteran visual system deal predominantly or entirely with the dorsal eyes (e.g. Horridge 1976; Horridge and McLean 1978). The function of the dorsal eyes is to distinguish the female in flight (the female usually enters the top of a swarm, and the turban eyes allow the male to search the area above it), while with the lateral eyes the male and female orients itself in relation to the elements of the landscape, to the water surface, for instance. Although in some mayfly species the microvilli structure of the retina in the dorsal as well as lateral eye has already been investigated (e.g. Burghause 1981), unfortunately nothing is known about the polarization sensitivity of the visual system in mayflies. The observations of Kriska et al. (1998) show that mayflies are polarization sensitive and detect the water by means of the horizontal polarization of reflected light.

19.7 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. At sunset it always reflects horizontally polarized light, the p of which is almost 100% near the Brewster angle (57.5^{o}). 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 p. Thus, a brook is horizontally polarized when the surface-reflected light dominates and vertically polarized if the light returning from the water dominates. The greater the proportion of light returning from the water in comparison to that reflected from the water surface, the lower is the net p (Figs. 19.2A,B). In Fig. 19.2C, p of 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 water-surface-reflected light is great (due to the bright illumination from the side).

The highly and at sunset always horizontally polarized asphalt roads with a relatively homogeneous distribution of p and α (Fig. 19.3) can therefore be much more attractive to mayflies than the surface of a streamlet (Fig. 19.2). 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 to the light reflected from water. This was also observed in the multiple-choice

experiments of Kriska et al. (1998), when mayflies swarming above the asphalt road were attracted to the highly polarized shiny black plastic sheet after it was laid onto the road. A relatively small black plastic sheet (a few m^2) attracted all the mayflies swarming above the asphalt road within several tens metres.

According to Schwind (1991), insects inhabiting running waters, e.g. plecopterans living near brooks (Zwick 1990), may not locate their habitats using polarization, because polarization is reduced or even distorted by waves (see Fig. 19.2B). Nevertheless, the observations and multiple-choice experiments of Kriska et al. (1998) show that this is not true of the Ephemeroptera, at least for the six species studied.

According to Brodskiy (1973), considering swarming site, mayflies form three groups:

1. species swarming over water,
2. species swarming over the littorial but maintaining visual contact with the water,
3. species swarming in conditions where there is no visual contact with water.

It is clear that the fertilized eggs of the mayfly species belonging to groups 2 and 3 can be exposed to the danger that they are laid on the surface of a highly polarized asphalt road running near the emergence site of their parents. Similar danger may not be expected in the case of the species of group 1, because these mayflies cannot be attracted by a surface (in spite of its high p and horizontal E-vector) which is positioned farther away from the water.

The mayfly species observed by Kriska et al. (1998) possess the following typical behaviour, which is considered the most generalized one in Ephemeroptera (Brodskiy 1973): At the time of the nuptial flight the males are spread out along the shore line of the water basin and under optimal weather conditions they collect together in a swarm. The females fly from the water over the row of plants on the littorial intersecting it at a right angle and, when no swarm is encountered, fly back again with a change in altitude. This continues until the females fly through a swarm. They are visually detected and then captured by the males. Mating usually takes place in flight, after which the male again returns to the swarm. A single female can be repeatedly fertilized, after which she lays her eggs into the water. From this behaviour it follows that one of the prerequisites of mayfly mating is to swarm above places where the sky is visible, because the females usually are detected visually and captured by the males from below (Brodskiy 1973). One of the few exceptions is *Ephemera danica* without turban-like dorsal eyes and with a ventrally oriented chasing flight. 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. Among roads, highly and horizontally polarizing 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,
– their strong and horizontal polarization at sunset mimics a water surface, and
– at sunset they have a slightly higher temperature than the surrounding areas.

Asphalt roads can be much more attractive to mayflies than real creeks, because the latter run frequently under trees and bushes. Mayflies do not swarm or mate above those reaches of the creek which are in the shelter of trees, that is, from which the sky is not visible. Egg-laying also takes place on the reaches of streamlets where the sky is visible, and from which polarized skylight can be reflected to guide the mayflies to the water surface.

In the attractiveness of asphalt roads to mayflies at sunset it is of particular importance that at dusk the E-vector of polarized light reflected from the rough asphalt surface is always horizontal due to the diffuse illumination from the sky. Mayflies (like many polarotactic water-seeking insects) are attracted only by horizontal E-vector. If the asphalt surface is illuminated by direct sunlight during the day when the sun is above the horizon, the E-vector of light reflected from the asphalt is not horizontal, and thus, asphalt roads are no longer attractive to mayflies, even if p of reflected light is high.

19.8 An Efficient Method to Study Ephemeropteran Swarming Behaviour in the Field

The experiments of Kriska et al. (1998) suggest that a shiny black plastic sheet can 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 some square metres would attract the whole swarm, allowing the study of mayflies, or their capture. This simple method could facilitate field studies on Ephemeroptera.

19.9 Possible Measures to Prevent Mayfly Egg-Laying onto Asphalt Roads

After the discovery of the causes of the reproductive behaviour of mayflies above asphalt roads, the experts of protection of animals and the environment could take the necessary measures to prevent the egg-laying by mayflies and to reduce the amount of eggs laid and perished on asphalt surfaces. One could, for example treat the sections of the asphalt roads running near the emergence sites of Ephemeroptera in such a way that their surface becomes relatively light and rough to reduce their reflection polarization. This could be performed by rolling down of small-sized lighter gravel on the asphalt surface. This treatment of the asphalt surface reduces significantly p of reflected light, which abolishes its attractiveness

to mayflies. Not only the highly polarizing asphalt roads, but also the huge shiny black plastic sheets used in the agriculture can deceive and attract mayflies in a large number, if they are laid on the ground near the ephemeropteran emergence sites. Thus, also these black plastic sheets can be dangerous to mayflies. It would be advisable to forbid the farmers to use such black plastic sheets near the swarming and egg-laying sites of Ephemeroptera.

Tables

Table 19.1. Observation time t (local summer time = UTC + 2), air temperature T_{air} (°C) and the number N of *Rhithrogena semicolorata* landing within 30 s on a 0.1 m × 0.1 m area of three test surfaces. S7: shiny black plastic sheet; S4: shiny white plastic sheet; S3: shiny aluminium foil. (After Table 1 of Kriska et al., 1998, p. 2276).

t	T_{air} (°C)	N (S7)	N (S4)	N (S3)
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 19.2. As Table 19.1 for *Epeorus silvicola*. Here also the temperature T_{sur} (°C) of the test surfaces is given. (After Table 2 of Kriska et al. 1998, p. 2277).

t	T_{air} (°C)	T_{sur} (°C)	N (S7)	N (S4)	N (S3)
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

Table 19.3. As Table 19.1 for *Rhithrogena semicolorata,* without air temperature. S7: shiny black plastic sheet; S6: slightly shiny black cloth; S2: matt white cloth. 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 (Table 19.4). (After Table 3 of Kriska et al. 1998, p. 2277).

t	*N* (S7)	*N* (S6)	*N* (S2)
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

Table 19.4. The relative radiance I, degree of linear polarization p and angle of polarization α of light reflected from the test surfaces measured by video polarimetry. I is calculated relative to the shiny aluminium foil; α is measured from the vertical. Values are mean ± standard deviation ($N = 560 \times 736$ = number of pixels in a video picture). S1: wet asphalt; 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. (After Table 6 of Kriska et al. 1998, p. 2281).

	S1	S2	S3	S4	S5	S6	S7	S8
I (%)	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
p (%)	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
α (°)	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

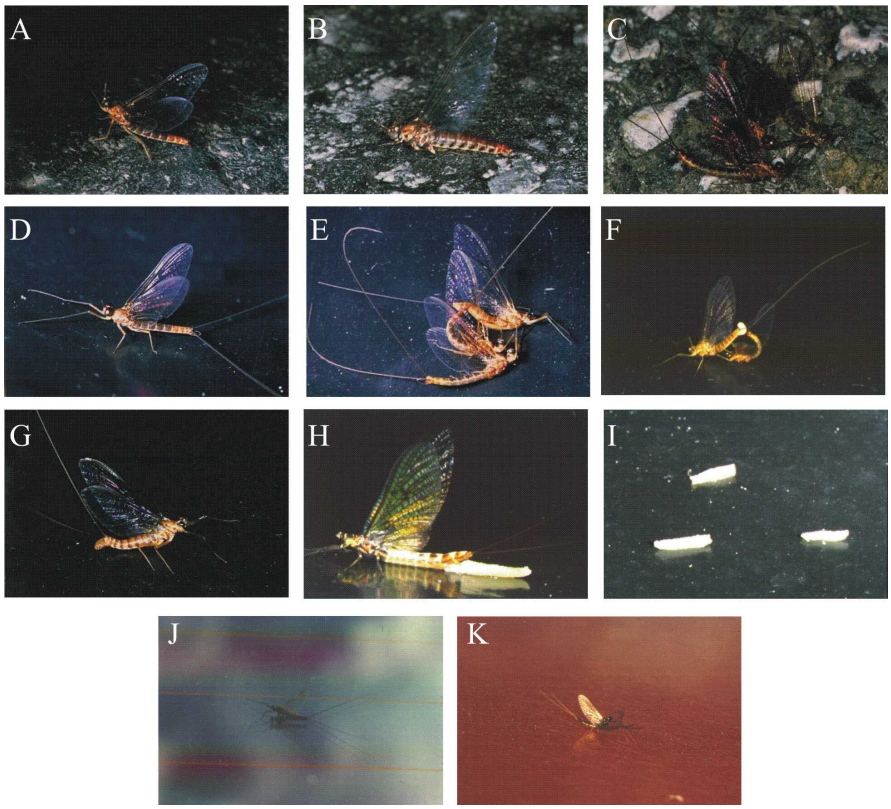

Fig. 19.1. Examples of mayflies deceived by and attracted to a dry asphalt road (A-C), a shiny black plastic sheet used in agriculture (D-I), the windscreen (J) and the red bodywork (K) of a car in the immediate vicinity of a mountain creek near Budapest during May/June 1997. A: a male *Rhithrogena semicolorata*; 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: egg-packets of *Ephemera danica*, J,K: a male *Baetis rhodani*. (After Fig. 1 of Kriska et al. 1998, p. 2274).

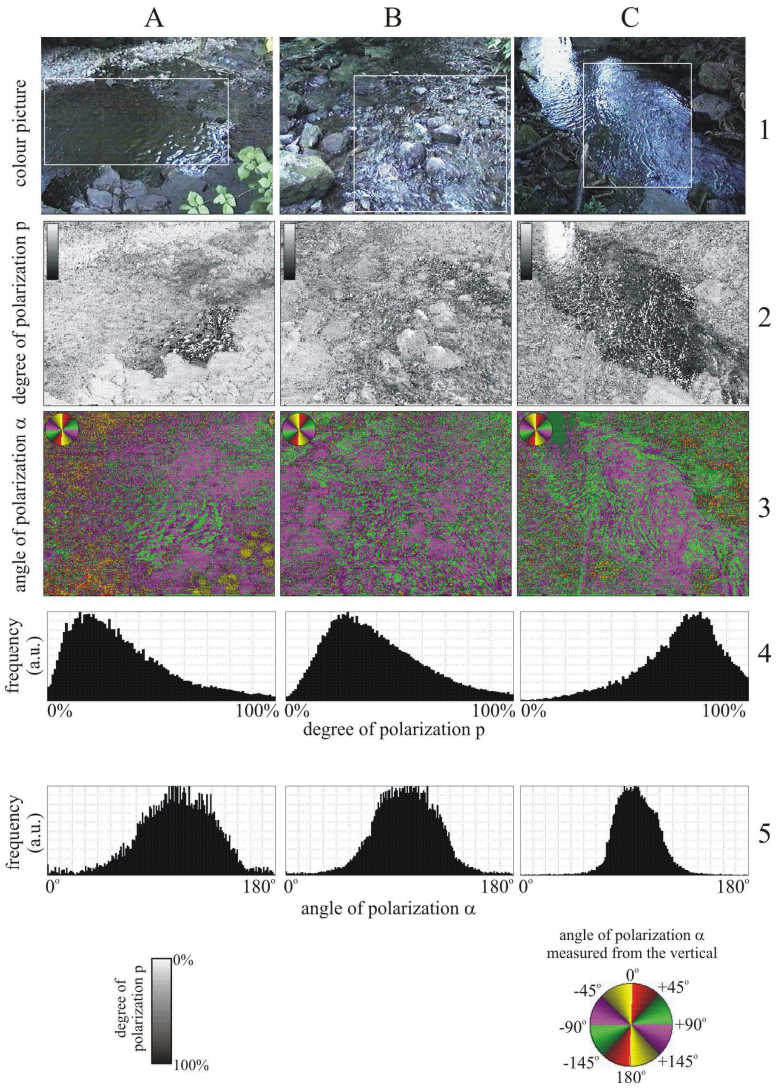

Fig. 19.2. The reflection-polarizational characteristics of three different reaches of a mountain creek (a typical emergence and swarming site of the mayflies studied) measured by video polarimetry at 450 nm. All three scenes with a slightly undulating water surface were recorded from a direction of view of the camera of 60° relative to the vertical. A: In this relatively slow and calm reach of the creek a small pond was shadowed by trees. Through the foliage skylight illuminated the water surface from above and from 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. Rows 4 and 5 show the frequencies (in arbitrary units) of p and α calculated for the rectangular windows in row 1. (After Fig. 2 of Kriska et al. 1998, p. 2280).

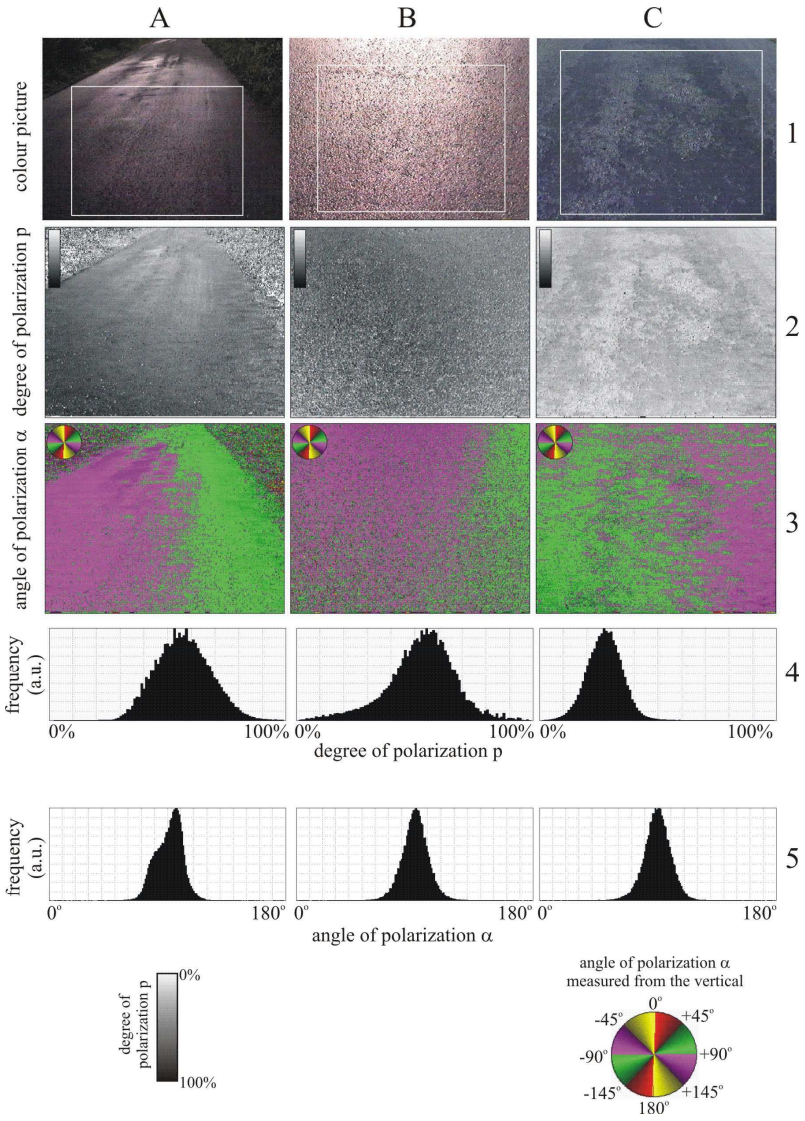

Fig. 19.3. The reflection-polarizational characteristics of three different sections of the asphalt road above and on which mayflies swarmed, mated and oviposited. In each case, the asphalt surface was dry, and the scenes were recorded from a direction of view of the camera of 60° with respect to the 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 as in Fig. 19.2. (After Fig. 3 of Kriska et al. 1998, p. 2282).