11 Polarization Vision in Aquatic Insects and Ecological Traps for Polarotactic Insects

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Abstract

We review the polarization vision of aquatic insects, which detect water from a distance by the horizontally polarized light reflected from the water surface. Reflection–polarization characteristics of different water bodies, as functions of sky conditions and solar elevation, are examined in relation to how they influence the detection of water bodies by polarotactic aquatic insects. Examples are given showing how aquatic insects can be deceived by, attracted to and trapped by highly and horizontally polarizing artificial reflectors, such as oil surfaces, horizontal black plastic sheets, asphalt roads, red or black car-bodies and black gravestones. We explain why mirages and polarizing black burnt stubble-fields do not attract polarotactic aquatic insects. The existence of a polarization sun-dial, which dictates the optimal time of day for dispersal by flying aquatic insects, is demonstrated. We finish by examining some unexpected aspects of polarization vision in insects: a polarotactic mayfly that never leaves the water surface and thus does not need polarotaxis, and polarotactic vision of several tabanid flies.

Polarization Vision in Aquatic Insects

Human observers can detect the presence of a distant water body by means of learned visual cues associated with water, such as mirroring of landmarks on the water surface, rippling of the surface or aquatic plants on the shore. These water-specific visual cues arise from the spatiotemporal distribution of the intensity and colour of light originating from water and the surrounding objects. As all these cues must be learned, a completely inexperienced human being (who has never encountered an open water surface) would be unable to recognize water.

The inexperienced person's lack of knowledge about water is similar to the situation when an aquatic insect leaves the water for the first time, driven by resource shortages or unsuitable environmental conditions. Larval and many adult aquatic insects live in water where they can gather information only about their aquatic environment. When adults leave the water for the first time, they face the task of detecting water while dispersing in order to return to water to avoid dehydration, oviposit, or simply return to the aquatic environment. As they have no opportunity to learn the visual cues associated with water, they need a genetically fixed and reliable method to detect water visually and from a distance. This sensory capability is polarization vision.

In the early 1980s, Rudolf Schwind (1983a,b, 1984a,b, 1985a,b) discovered that the backswimmer, *Notonecta glauca*, detects water by means of the horizontally polarized light reflected from the water surface, rather than by the intensity or colour of water-reflected light, or by the glittering or mirroring of the water surface. In the ventral eye region of *Notonecta*, Schwind *et al.* (1984) found ultraviolet-sensitive photoreceptors with horizontal and vertical microvilli that are highly sensitive to horizontally and vertically polarized light (Schwind, 1983b). This eye region is called the 'ventral polarization-sensitive area'. These photoreceptors can determine whether the direction of polarization of light from the optical environment is horizontal or not. In *Notonecta*, exactly or nearly horizontally polarized light stimulus elicits a typical plunge reaction, whereby the insect stops flying and attempts to re-enter the water (Schwind, 1984b). This attraction to horizontally polarized light is called positive polarotaxis.

Following from these initial studies, positive polarotaxis has been discovered in over 250 species of aquatic insects and from many different groups, including bugs, beetles, dragonflies, mayflies, tabanid flies and caddisflies (Schwind, 1985a,b, 1989, 1991, 1995; Kriska *et al.*, 1998, 2006a, 2007; Wildermuth, 1998; Horváth *et al.*, 1998; Bernáth *et al.*, 2001; Wildermuth and Horváth, 2005; Csabai *et al.*, 2006). The eyes of many aquatic insects are sensitive to the polarization of light in the visible or ultraviolet spectral ranges (Schwind, 1989, 1991, 1995). These insects find water using horizontally polarized light reflected from the water surface (Schwind and Horváth, 1993; Horváth, 1995). The spectral sensitivity of the polarization-sensitive photoreceptors of insects living in water is generally matched to the spectral composition of underwater light, which is quite diverse in different types of aquatic habitats (Lythgoe, 1979). Aquatic insects detect polarization in that region of the spectrum that is characteristic of their preferred habitat (Schwind, 1995). Depth, turbidity, transparency, colour, surface roughness of the water and substratum composition, as well as illumination, strongly influence the reflection–polarization characteristics of water bodies. These polarization patterns provide important information on the quality of freshwater habitats for polarotactic insects and can aid the orientation of these insects from a distance.

The Optomotor Response to Polarization Patterns in Aquatic Insects

The optomotor response is a turning reaction displayed in response to a cylindrical pattern of vertical black and white stripes being rotated around an animal.

This behaviour demonstrates the ability of an animal to detect movement of the optical environment on the basis of brightness cues; it helps to stabilize the animal's orientation in its environment and to maintain a straight course during locomotion (Varjú, 1959). If the underlying visual subsystem is sensitive to linear polarization, an optomotor response is likely to be elicited also by a rotating pattern of alternating direction of polarization.

Both the above- and underwater optical environments of backswimmers (Notonectidae) and waterstriders (Gerridae) (composed of the underwater world, the water surface, the riparian vegetation and the sky) are rich in polarized light. To test whether this polarization cue can be exploited for motion detection, in behavioural laboratory experiments Horváth and Varjú (2003, pp. 276–292) investigated the optomotor response of the waterstrider *Gerris lacustris* and the backswimmer *Notonecta glauca* to over- and underwater brightness and polarization patterns. They found that the latero-frontal *eye* regions in *Gerris* and *Notonecta* respond to certain contrasts in the direction of polarization, especially vertical versus horizontal polarization (Fig. 11.1). The function of this polarization-sensitive optomotor response may be a contrast enhancement for motion perception during compensation for passive drift and rotation of the body. They also showed that, in *Gerris* and *Notonecta*, the polarization-sensitive optomotoric reaction is mediated by the green receptors. In the aquatic habitat of these insects, brightness and polarization contrasts occur mainly in the visible and especially in the green part of the spectrum (e.g. riparian vegetation, water plants and phytoplankton in water).

Reflection–polarization Characteristics of Different Water Bodies

In this and subsequent sections we make a distinction between 'dark water bodies' and 'bright water bodies'. Dark water bodies reflect little light, because they are deep, the water contains dark suspended particles or the bed sediments are dark. Bright water bodies reflect a lot of light, because the water is clear and shallow, the water contains bright suspended particles or the bed sediments are bright.

Schwind and Horváth (1993) and Horváth (1995) investigated, theoretically, the reflection–polarization characteristics of flat water surfaces in relation to the solar elevation. Using different kinds of imaging polarimetry, Horváth and Varjú (1997), Gál *et al*. (2001a) and Bernáth *et al*. (2002) measured the reflection–polarization patterns of various freshwater habitats in the red (650 nm), green (550 nm) and blue (450 nm) spectral ranges, under different meteorological conditions. According to Fig. 11.2D,E, the light reflected from the so-called Brewster zone (an annular region, the centre line of which is a circle at a nadir angle of 57.5°) of dark water surfaces is highly and always horizontally polarized. Thus, the light reflected from the Brewster zone is very attractive to polarotactic aquatic insects, even though the reflectivity R of the Brewster zone is only moderate as R increases nearly exponentially toward the horizon (Fig. 11.2F). What these insects identify as water are only those areas that reflect light with degrees of linear polarization p higher than the threshold p^* of their polarization sensitivity

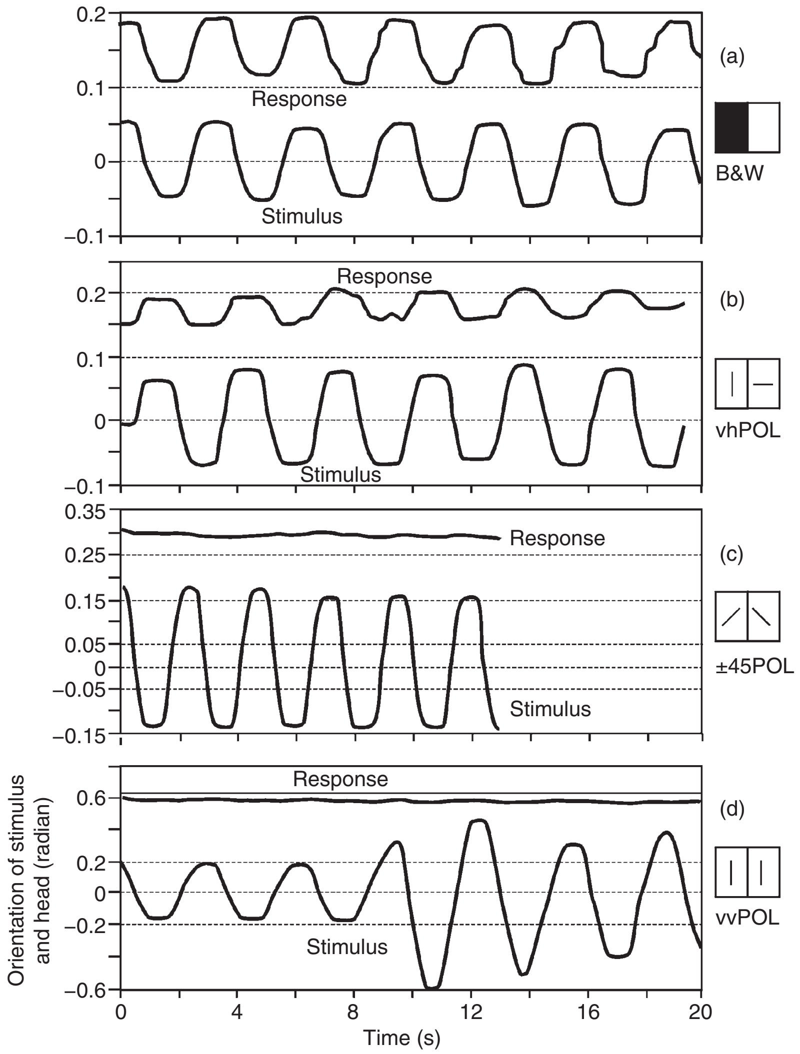

Fig. 11.1. Examples of the optomotor response of *Gerris lacustris* for different lateral stimuli in white light: (A) black-and-white intensity pattern (B–D) linear polarization patterns. The stimulus types are indicated by their symbols on the right side; bars represent the direction of polarization. The abscissa is the time and the ordinate is the oscillating orientation of the stimulus and the head of *Gerris* (response). The response is nearly zero to the ±45POL (C) and vvPOL (D) stimuli, while it is strong to the B&W (A) and vhPOL (B) ones.

($p > p^*$), and with angles of polarization α differing from the horizontal ($\alpha = 90°$ from the vertical) by less than a threshold $\Delta\alpha > |90° - \alpha|$. For example, the black region in Fig. 11.2G shows the area detected as water by a polarotactic insect whose thresholds are $p^* = 5\%$, $\Delta\alpha = 5°$.

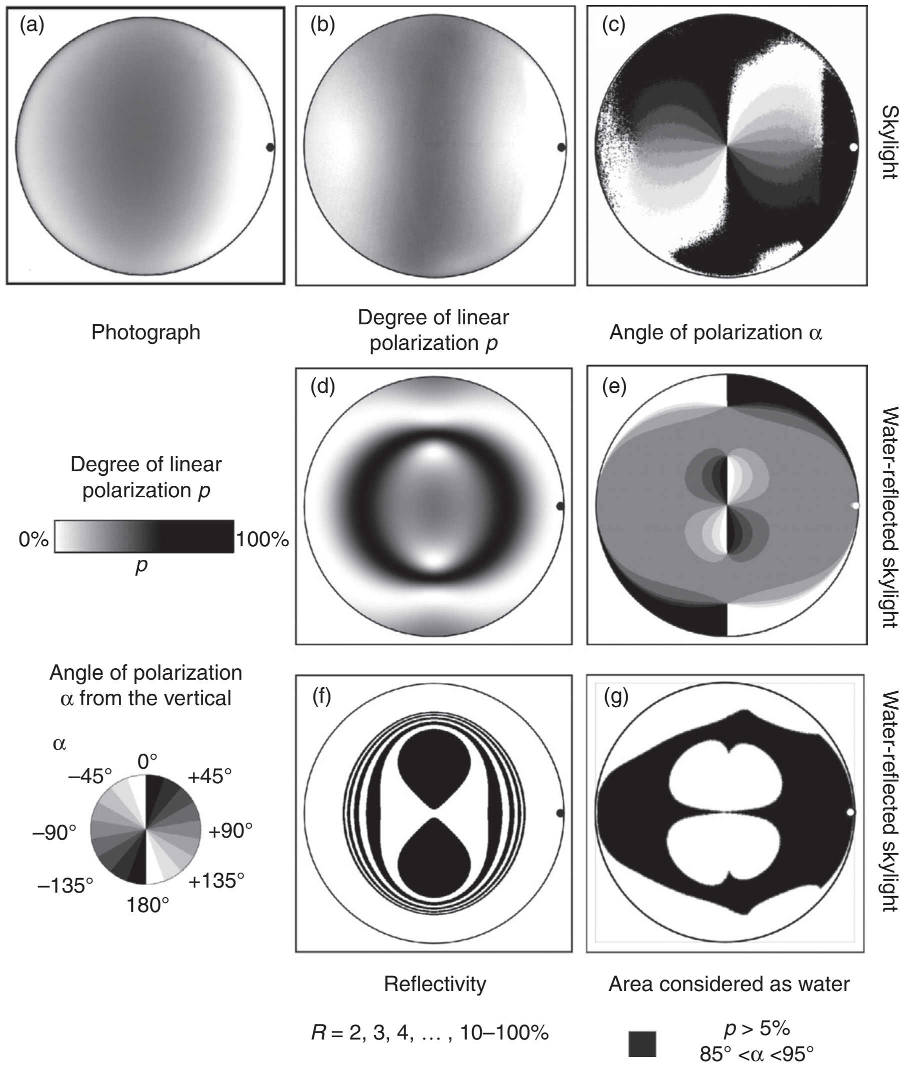

Fig. 11.2. Polarization patterns of the clear sky (A–C) and the flat water surface (D–F), and the area (black) detected as water by a polarotactic aquatic insect (G) at sunset. In the circular patterns the centre is the zenith (A–C) or the nadir (D–G) and the perimeter is the horizon. The two central 8-shaped black patches in pattern F represent $R \leq 2\%$, the concentric oval and annular, alternately black and white narrow zones around these patches represent $R = 3, 4, 5, \ldots 10\%$ towards the periphery, the outermost annular white zone represents $R > 10\%$. The sun (A–C) and its mirror image (D–G) is represented by a dot on the horizon.

The light coming from the surface of a water body is a combination of that reflected from the water surface (which is partially horizontally polarized) and that refracted from within the water body (which is partially vertically polarized). The net polarization of light by water is governed, therefore, by the polarization

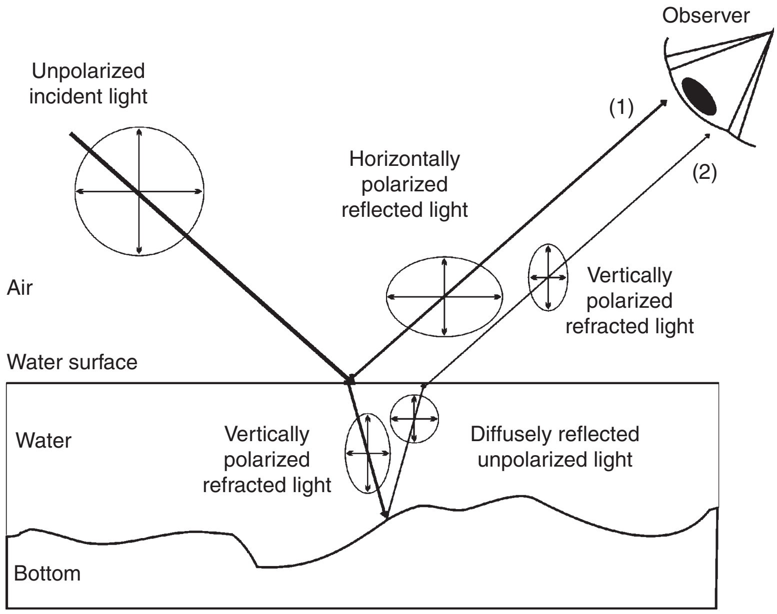

Fig. 11.3. Polarization of light returned from a body of water for unpolarized incident light. The returned light has two components: (1) the partially horizontally polarized light reflected from the water surface, and (2) the partially vertically polarized refracted light coming from the water. The ellipses and circles with vertical and horizontal double-headed arrows symbolize the 'linear polarization ellipse' of light.

characteristics of these two components (Fig. 11.3). If, in a given part of the spectrum, the intensity of the first component is larger/smaller than that of the second one, then the water-returned light is partially horizontally/vertically polarized. If the intensities of both components are equal, the water returns unpolarized light. Consequently, the reflection–polarization characteristics of water bodies strongly depend on the spectrum of light backscattered by the particles suspended in water and of the light reflected by the bottom of water.

Shadows also influence the reflection–polarization characteristics of water bodies: in the case of dark waters, horizontally polarized surface-reflected light always dominates, and thus the direction of polarization is always horizontal for shaded and sunlit regions. The p of light reflected from the shaded regions of dark waters is lower than that from the sunlit regions because, in shaded areas, the amount of horizontally polarized, surface-reflected light is reduced. In the sunlit or shaded regions of bright waters, the direction of polarization can be horizontal or vertical, and p can be higher or lower, respectively. The p of light from bright water bodies is always much less than that from dark waters. Under windy conditions, the water surface undulates and this distorts the reflection–polarization patterns of flat water surfaces, reducing the extent of polarization.

Bernáth *et al.* (2002) showed that, from a distance and at an angle of view of 20° from the horizontal, dark water bodies are indistinguishable from bright ones based on the intensity and the polarization angle of the reflected light. Dark waters do, however, reflect light with a higher degree of linear polarization p than bright waters, in any part of the spectrum and in any direction of view with respect to the sun. Polarization-sensitive aquatic insects, therefore, may be able to use the p of reflected light as a visual cue to distinguish dark and bright water bodies from far away.

The reflection–polarization characteristics of the water surface are influenced also by the polarization of the sky. As moonlit and sunlit skies have the same polarization pattern, if the positions of the moon and sun coincide (Gál *et al*., 2001b), the reflection–polarization patterns of a water surface are the same under sunlit and moonlit conditions for the same position of the sun and moon.

Polarization Sun-dial of Flying Aquatic Insects

Flying polarotactic aquatic insects are attracted to any surface where $p > p^*$ and $|\alpha - 90°| < \Delta\alpha^*$. The percentage Q of a reflecting surface identified polarotactically as water is the angular proportion Q of all viewing directions (relative to the angular extension of 2π steradians of the whole lower hemisphere of the field of view of the hypothesized insect) for which both criteria are satisfied. The higher the Q-value for a reflecting surface in a given visual environment, the larger its polarotactic detectability, i.e. the higher the probability that insects seeking water can find it by polarotaxis.

Using 180° field-of-view imaging polarimetry, Bernáth *et al*. (2004) measured the reflection–polarization characteristics of horizontal bright and dark reflectors (imitating bright and dark waters), in the red, green and blue spectral ranges in relation to the solar elevation angle θ from sunrise to sunset, under clear and partly cloudy skies. They found experimental evidence that the proportion $Q(\theta)$ of reflecting surfaces detectable polarotactically as water is always maximal at the lowest (dawn and dusk) and highest (noon) θ for dark waters, while $Q(\theta)$ is maximal at dawn and dusk (low solar elevations) for bright waters under both clear or partly cloudy skies (Fig. 11.4).

Csabai *et al*. (2006) found evidence for the influence of this effect on polarotactic attraction of aquatic insects in the field by 24-h trapping. The trap consisted of a strongly and horizontally polarizing shiny black plastic sheet laid on the ground, which is as attractive to polarotactic aquatic insects as a natural dark water surface (see below). They found that aquatic insects belonging to 99 taxa (78 Coleoptera and 21 Heteroptera) flew predominantly in mid-morning, around noon or at nightfall (Fig. 11.5). There are at least four different types of diurnal flight activity rhythm in these insects, characterized by peak(s): (i) in mid-morning; (ii) in the evening; (iii) both in mid-morning and the evening; and (iv) around noon and in the evening (Fig. 11.5). These activity maxima are quite general and cannot be explained exclusively by daily fluctuations of air temperature, relative humidity, wind speed and risks of predation, which are all somewhat stochastic (weather-dependent) and cannot be perceived in the water.

From the temporal coincidence between peaks in the diel flight activity of aquatic insects (Fig. 11.5) and the polarotactic detectability $Q(\theta)$ of water surfaces

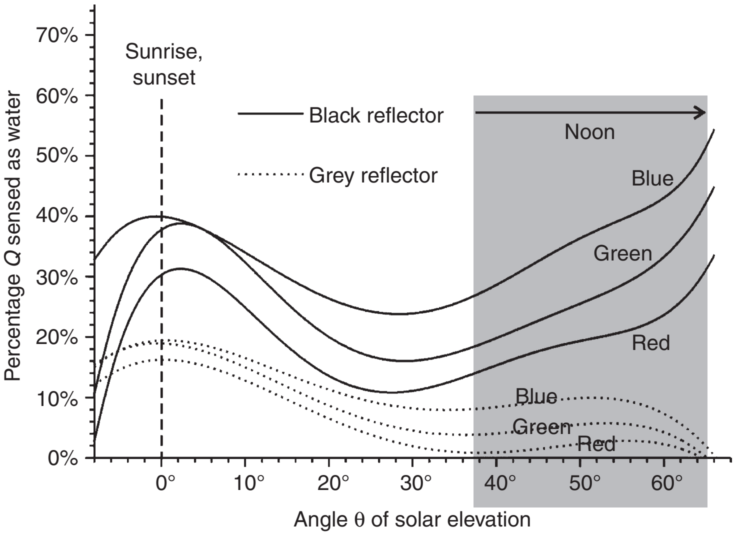

Fig. 11.4. Polarotactic detectability Q, that is, the percentage Q (%) of a black (continuous) and a grey (dashed) horizontal reflector that would be sensed as water by water-seeking polarotactic aquatic insects as a function of the solar elevation angle θ in the blue (450 nm), green (550 nm) and red (650 nm) parts of the spectrum under a clear sky. The angular shift of solar culmination (noon) from the beginning to the end of the 4-month monitoring of aquatic insects is marked by a grey band, where a horizontal arrow shows the shift direction.

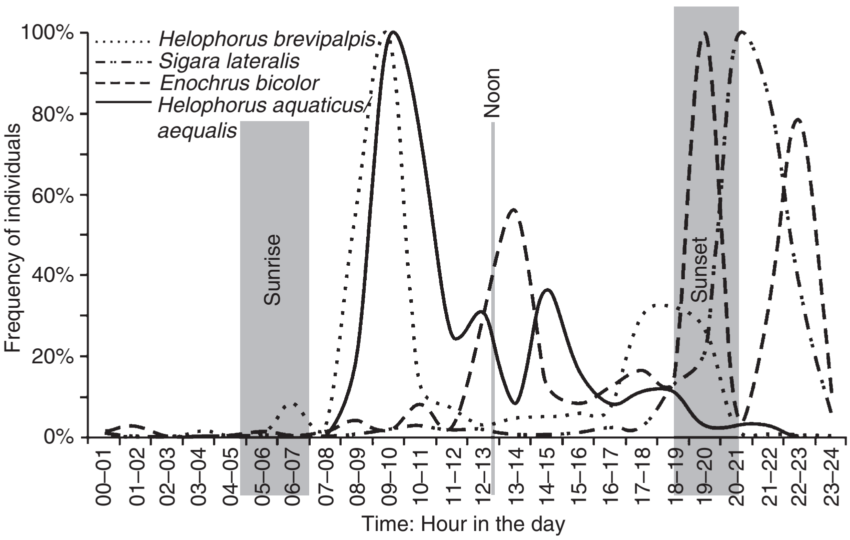

Fig. 11.5. Four different typical daily rhythms of dispersal by flying aquatic insects (*Helophorus brevipalpis*, *Sigara lateralis*, *Enochrus bicolor*, *Helophorus aquaticuss/ aequalis*). Time: local summer time = UTC + 2. The temporal shifts of sunrise and sunset from the beginning to the end of the 4-month monitoring of aquatic insects are marked by grey bands.

(Fig. 11.4), Csabai *et al*. (2006) concluded that the optimal times of day for aquatic insects to disperse are the periods of low and high solar elevations θ. The θ-dependent reflection–polarization patterns, combined with the influence of other factors, such as air temperature (usually too low for flight at sunrise), clearly explain why polarotactic aquatic insects disperse to new habitats in mid-morning, around noon or at dusk. These three optimal periods for dispersal, governed by the reflection–polarization pattern of the water surface, can be easily and reliably identified from the solar elevation θ, even underwater where air temperature, humidity and wind speed cannot be perceived. This phenomenon is called the 'polarization sun-dial' for dispersing aquatic insects.

Ecological Traps for Polarotactic Aquatic Insects

Here we examine evidence for ecological traps, *sensu* Schlaepfer *et al*. (2002), for polarotactic aquatic insects.

Oil surfaces

Kennedy (1917) gave an account of many individuals of the dragonfly *Anax junius* being killed as a result of mistaking an open surface of crude oil for water, and Kennedy (1938) cited cases where dragonflies were attracted to pools of petroleum. Similar phenomena were observed in oil ponds in the desert of Kuwait (Horváth and Zeil, 1996) and a waste oil lake in Hungary (Bernáth *et al*., 2001). Many dragonflies, mayflies, water beetles (Dytiscidae, Coleoptera) and water bugs (*Belostoma* sp., Nepidae, Heteroptera) were found at the edge of these oil ponds, with females in particular often being trapped as they tried to lay eggs. Dragonflies were also frequently observed fighting and defending territory (Horváth et al. 1998), behaviours that are typical only above water surfaces (Corbet, 1999).

Horváth and Zeil (1996) suggested that polarotactic aquatic insects were attracted by the high and horizontal polarization of light reflected from the oil surface. Horváth et al. (1998) tested and supported this hypothesis in multiple-choice field experiments with dragonflies in Hungary. They compared the numbers of dragonflies being caught in water, crude oil and salad-oil traps with different reflection–polarization characteristics. They showed that positive polarotaxis is the most important mechanism guiding dragonflies during habitat choice and oviposition site selection, and this is why dragonflies can be deceived by, and attracted to, crude and waste oil, tar or asphalt. Using horizontally aligned test surfaces with different reflection–polarization characteristics in multiple-choice field experiments with dragonflies, Wildermuth (1998) obtained the same result.

There are several reasons, why oil and tar surfaces are more attractive than water surfaces to polarotactic animals: (i) oil is a better polarizing reflector than water, because oil has a higher refractive index (1.39–1.57) than water (1.33); (ii) due to the higher viscosity of oil, the reflection polarization of light is less distorted by wind-induced ripples; (iii) as dark oil is not transparent, the light reflected from flat oil surfaces is always horizontally and much more highly polarized than that reflected from transparent waters, due to the lack of vertically polarized refracted light.

Fig. 11.6 shows the patterns of the degree of linear polarization p and angle of polarization α of light reflected from the surface of crude oil, clear, transparent water and milky, translucent water. The dishes were positioned so that the lower half of their surface reflected specularly incident diffuse ambient light, while the upper half was in shadow. The light reflected from the lower half of the oil surface is almost totally polarized with horizontal direction of polarization. The top,

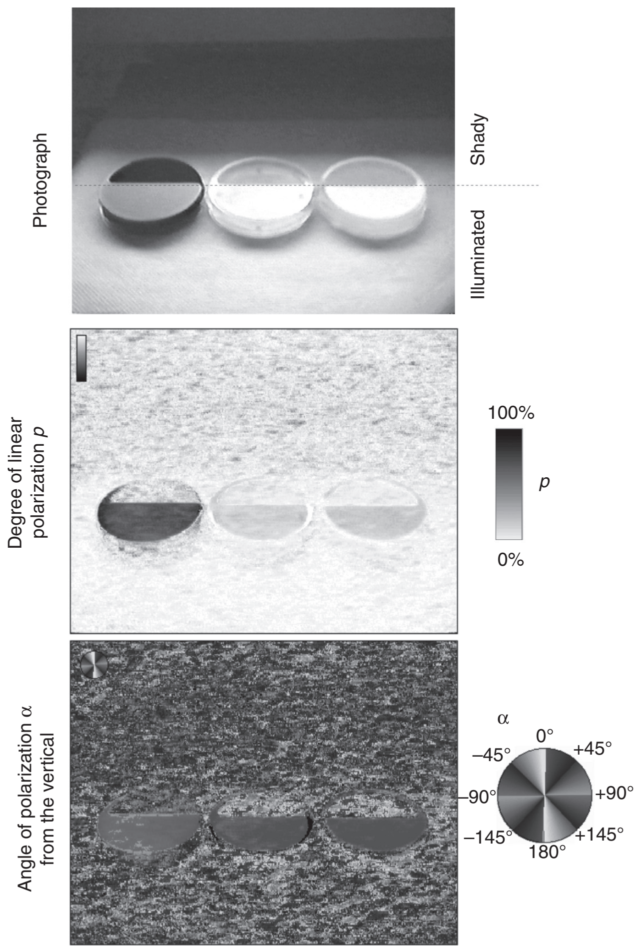

Fig. 11.6. Reflection–polarization characteristics of Petri dishes filled with black crude oil (left), clear water (middle) and milky water (right) measured by imaging polarimetry at 450 nm. The top half of the dishes is in shadow, the bottom half is illuminated by unpolarized diffuse light from an overcast sky. Viewing direction is –35° relative to the horizontal.

shaded half of the oil surface reflects little and almost unpolarized ambient light with horizontal direction of polarization. The top, shaded half of the water surfaces return mainly refracted light, which is scattered and reflected from the subsurface layer of water, while the bottom half returns a mixture of refracted and surface-reflected light. The specular surface reflection dominates in the bottom half of the water-filled dishes and has polarization characteristics similar to those of the oil surface (high p with horizontal direction of polarization). In the top shaded half of the water surfaces, however, the returned light is vertically polarized because of refraction at the water surface. Refraction polarization also reduces the net p in the bottom half of the water surface.

The water-filled dishes in Fig. 11.6 demonstrate well that light emanating from water is vertically polarized whenever the refracted light dominates, and horizontally polarized when surface-reflected light dominates. A similar effect cannot occur in an oil pond, because all the penetrating light is absorbed by the dark oil. The direction of polarization of light reflected from a flat oil surface is therefore always horizontal. The larger the p and the smaller the deviation from horizontal in the direction of polarization of reflected light, the more attractive the surface is to polarotactic aquatic insects. Consequently, dark oil can be even more attractive to polarotactic aquatic insects than bright water. Thus, for polarotactic aquatic insects, oil lakes appear to be exaggerated water surfaces acting as a supernormal, horizontally polarized stimulus.

Some ancient natural asphalt seeps in the Earth's history have acted as massive animal traps and their fossil remains are important in palaeontology. Examples include the Rancho La Brea tar pits in Los Angeles (Akersten *et al.*, 1983) and the asphalt seeps at Starunia in Western Ukraine (Angus, 1973). In Rancho La Brea, 95% of the entrapped animal species are insects, mainly aquatic ones. Most of the insect fossil remains found in Starunia are water beetles of the genus *Helophorus*.

A general view in palaeontology is that animals might have stumbled accidentally across tar seeps, which may have been camouflaged by dust or leaves (Angus, 1973; Akersten *et al.*, 1983). Alternatively, these asphalt seeps may have been covered by rain-water from time to time, thus attracted animals that then sank into the underlying tar, became entrapped and fossilized. Another possible scenario (Horváth and Zeil, 1996) is that polarotactic aquatic insects were deceived by and attracted to the tar pits, even in the absence of water, by the horizontal polarization of light reflected from the tar surface and mimicking a supernormally attractive body of water.

Plastic sheets

Horváth et al. (1998), Wildermuth (1998), Kriska *et al.* (1998, 2006a), Bernáth *et al.* (2001) and Csabai *et al.* (2006) performed multiple-choice experiments with polarotactic aquatic insects in the field using white and black plastic (polyethylene) sheets laid on the ground in different wetlands (Fig. 11.7). Such plastic sheets are commonly used in agriculture. The black plastic sheet reflects horizontally polarized light with high degrees of linear polarization p, while the white

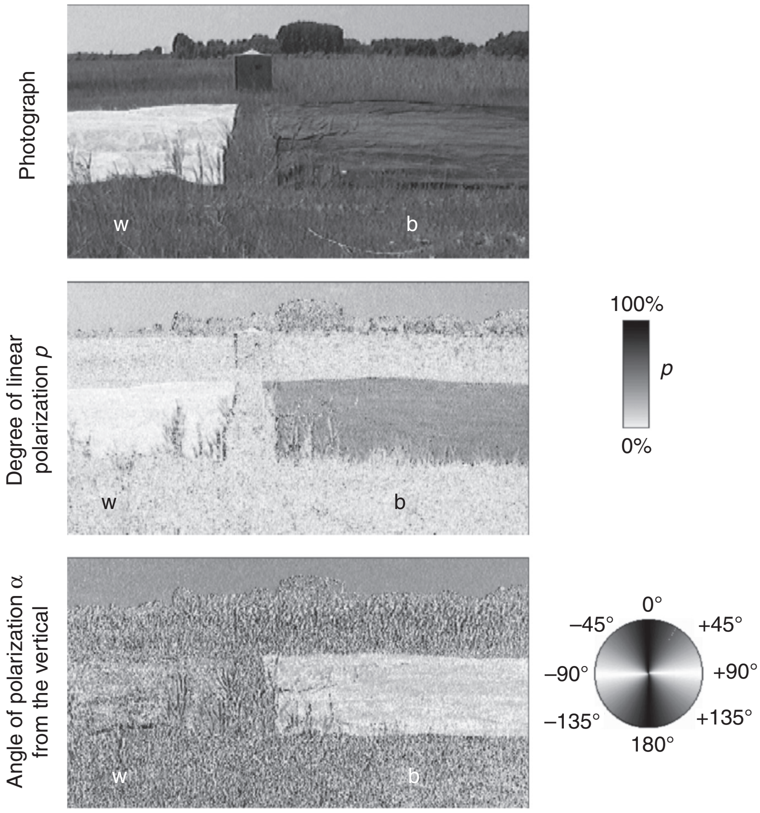

Fig. 11.7. Reflection–polarization patterns of a shiny white (left, w) and black (right, b) plastic sheet laid on the ground and measured by imaging polarimetry at 450 nm, under a clear sky at sunset. The viewing direction of the camera was −30° from the horizontal and perpendicular to the solar meridian.

plastic sheet reflects vertically or obliquely polarized light with very low p (Fig. 11.7). Thus, the light reflected from a horizontal shiny black plastic sheet acts as a supernormally polarized stimulus for polarotactic water-seeking insects, as in the case of a black oil surface.

Bernáth *et al*. (2001) reported on the behaviour of great diving beetles *Dytiscus marginalis* on horizontal shiny dry black plastic sheets at sunset. The water beetles landed on the plastic sheet, touched and probed the surface, then flew up from the plastic and looked for another place. After landing again, the beetles tried to swim, crawl or creep on the smooth plastic surface. After about 30 min, the beetles were exhausted and unable to fly away, despite repeated attempts. Within an hour the beetles perished. This behaviour demonstrates how dangerous horizontally polarizing black plastic sheets can be for polarotactic aquatic insects.

Horizontal black plastic sheets attract aquatic insects, but white plastic sheets are totally unattractive (Horváth *et al*., 1998; Wildermuth, 1998; Kriska *et al*., 1998, 2006a; Bernáth *et al*., 2001; Csabai *et al*., 2006). The reasons for this are the reflection–polarization characteristics of the plastic surfaces (Fig. 11.7) and the polarotactic behaviour of aquatic insects. All aquatic insects behaved in a similar way on the black plastic sheet: landing, flying up, touching, crawling, egg-laying, copulating, reproductive activity and, finally, all of them dried out and perished. Dragonflies were also attracted to the black plastic sheet, but they did not perish. These experiments and observations show that horizontal shiny black plastic sheets can act as an ecological trap, by attracting and deceiving polarotactic aquatic insects due to the highly and horizontally polarized reflected light, while white plastic sheets are unattractive because the reflected light is weakly or not horizontally polarized.

Asphalt roads

Puschnig (1926) and Fraser (1936) reported that the dragonflies *Ophiogomphus forcipatus, Ictinogomphus ferox*, *Macromia magnifica* and several species of *Chlorogomphus* patrolled along asphalt roads instead of rivers and showed a typical water-touching behaviour above the asphalt surface. Kriska *et al*. (1998) witnessed a similar behaviour in mayflies swarming above dry asphalt roads. They observed that, near sunset, individuals of the mayfly species *Ephemera danica*, *Ecdyonurus venosus*, *Epeorus silvicola*, *Baetis rhodani*, *Rhithrogena semicolorata* and *Haproleptoides confusa* swarmed, mated above and landed on dry asphalt roads, shiny black plastic sheets and windscreens and roofs of cars close to their emergence sites (mountain streams). After copulation, the female mayflies laid their eggs on the dry asphalt surface instead of the water surface. The mayflies showed the same behaviour above the asphalt roads and black plastic sheets as at water surfaces. These observations, especially the egg-laying, suggest that the mayflies were apparently deceived by and attracted to the asphalt and plastic surfaces. Previous descriptions of mayfly swarming, mating and egg-laying behaviour have largely ignored or misinterpreted this phenomenon, suggesting that asphalt roads were acting as swarm markers, or that oviposition was due to the shiny surface of wet roads resembling streams (Ladócsy, 1930; Savolainen, 1978).

The first interpretation, however, cannot be applied to the observed egg-laying on asphalt roads because, normally, mayflies oviposit on to the water surface and not on to marker objects. The second interpretation cannot explain why egg-laying by Ephemeroptera frequently occurs also on totally dry asphalt surfaces.

Using imaging polarimetry, Kriska *et al*. (1998) showed that asphalt surfaces lit by skylight near sunset (when the investigated mayflies swarm), mimic a highly and horizontally polarizing water surface (Fig. 11.8). The polarization direction of sunlight reflected from sunlit asphalt roads is always perpendicular to the plane of reflection determined by the observer, the sun and the point observed. Thus, the direction of polarization of asphalt-reflected sunlight is usually tilted relative to the horizon, but it is always horizontal if the observer looks toward the solar or antisolar meridian because the plane of reflection is vertical. If the asphalt road

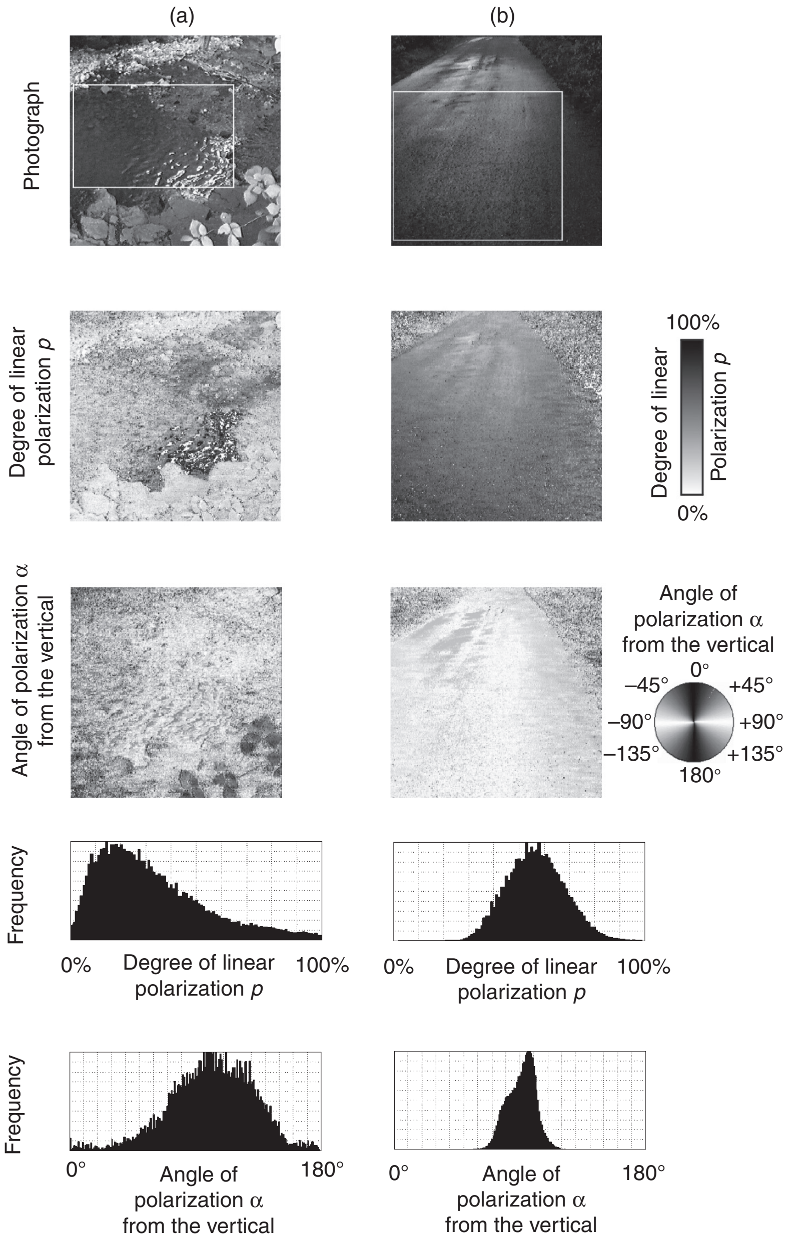

Fig. 11.8. Reflection–polarization characteristics of a reach of a mountain creek (A) and a section of an asphalt road (B) measured in the blue (450 nm) part of the spectrum. The creek was shadowed by trees and, through the foliage, the sky light illuminated the water surface from above right. The dry asphalt road was illuminated by the direct light from the setting sun under a clear sky, and the camera viewed towards the solar meridian. For both scenes, the optical axis of the polarimeter was –30° with respect to the horizontal. The frequencies (in arbitrary units) of p and α were calculated for the rectangular windows in the photographs.

is diffusely illuminated by light from the sky (i.e. no direct sun), the reflected light is always horizontally polarized due to the extended sky, which illuminates the road from all possible directions. Kriska *et al.* (1998) also concluded that the darker and smoother the asphalt, the greater is its attractiveness to water-seeking polarotactic mayflies. Thus, the highly, and at sunset always, horizontally polarizing asphalt roads with a relatively homogeneous distribution of p and α (Fig. 11.8B), can be much more attractive to polarotactic mayflies than the water surface of their emergence site (Fig. 11.8A). Roads also may be attractive because the sky above them is usually visible, providing the males with an ideally homogeneous and bright background for the visual recognition of flying females. At sunset, asphalt may also have a slightly higher temperature than the surrounding areas.

Car paintwork and gravestones

Aquatic insects frequently land on red cars (Jäch, 1997; Nilsson, 1997; van Vondel, 1998; Kriska *et al*., 1998; Bernáth *et al*., 2001), which has been explained by the shiny appearance or the red colour of the car body (Jäch, 1997; Nilsson, 1997), or considered enigmatic (van Vondel, 1998). Dragonflies swarm above cars and oviposit on car bodies, sometimes causing damage to their coatings (Wyniger, 1955; Svihla, 1961; Watson, 1992; Wildermuth, 1998; Stevani *et al*., 2000, Bernáth *et al*., 2001, Günther, 2003; Torralba Burrial and Ocharan, 2003; Wildermuth and Horváth, 2005). Kriska *et al*. (2006a) found that horizontal red and black plastic sheets were equally highly attractive to aquatic insects (30 Coleoptera and seven Heteroptera taxa), while yellow and white ones did not attract insects. In the blue and green spectral ranges, the light reflected from red and black car roofs, bonnets and boots is highly and nearly horizontally polarized (Fig. 11.9A,C), which is very attractive to polarotactic aquatic insects. On the other hand, the horizontal surfaces of yellow and white cars reflect weakly and not always horizontally polarized light (Fig. 11.9B,D), which is unattractive to aquatic insects. Owing to depolarization by diffuse reflection, very dirty cars reflect light with much lower degrees of polarization than recently washed or waxed shiny cars. Thus, the most environmentally friendly car is white and dirty.

Recently, Horváth *et al*. (2007) observed that the dragonfly species *Sympetrum flaveolum*, *S. striolatum*, *S. sanguineum*, *S. meridionale* and *S. danae* were attracted by polished black gravestones in a Hungarian cemetery without any water body. These dragonflies showed the same behaviour to that which they display in the presence of water: (i) they perched persistently in the immediate vicinity of the chosen gravestones and defended their perch against other dragonflies; (ii) flying individuals repeatedly touched the horizontal surface of the shiny black tombstones with the ventral side of their body; and (iii) pairs in tandem position frequently circled above black gravestones. Tombstones preferred by these dragonflies had an area of at least 0.5 m^2 with an almost horizontal, polished, black surface, the sky was open above them, and there was at least one perch in the immediate vicinity.

The horizontal parts of black gravestones reflect highly and horizontally polarized light and, consequently, are attractive to polarotactic dragonflies

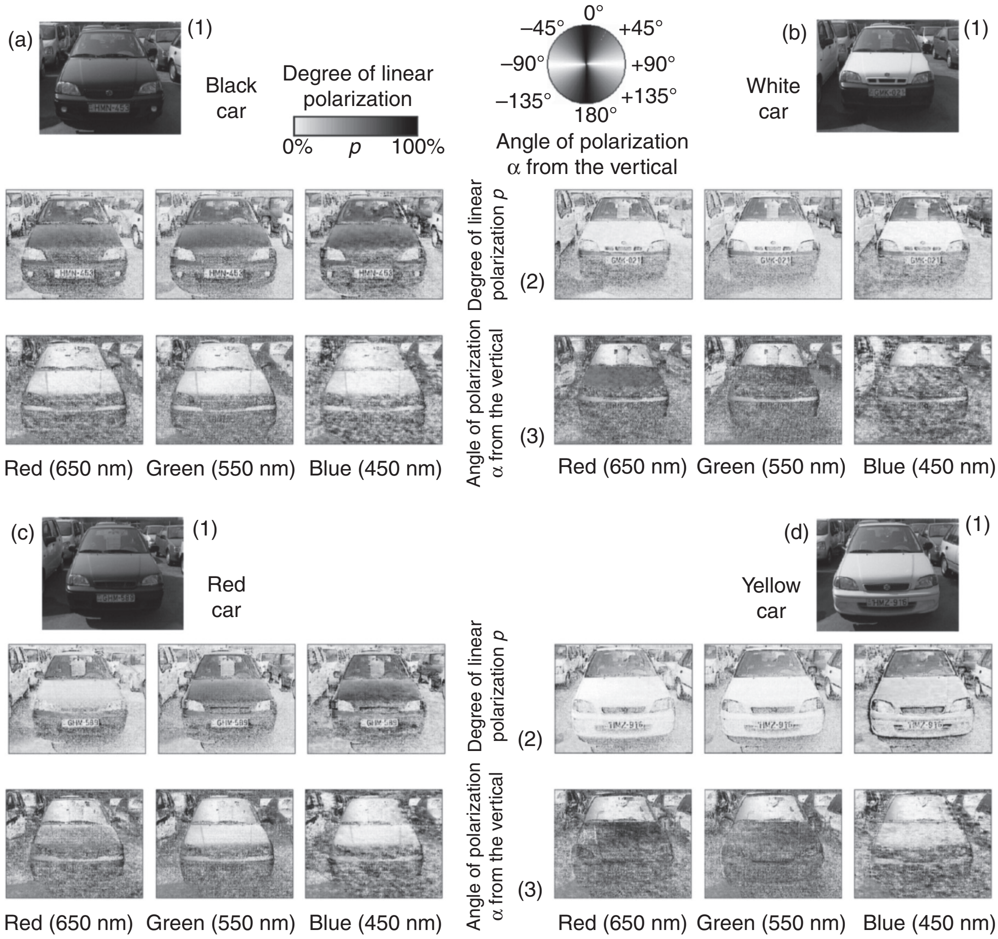

Fig. 11.9. Reflection–polarization patterns of a black (A), white (B), red (C) and yellow (D) car measured in the red (650 nm), green (550 nm) and blue (450 nm) parts of the spectrum under a clear sky at a solar zenith angle of 55°. The cars were illuminated from the left hand side by the sun, the long axis of the cars and the viewing direction of the polarimeter were perpendicular to the solar meridian, the angle of elevation of the optical axis of the polarimeter was –20°.

(Horváth *et al*., 2007). Gravestones with matt, bright or non-horizontal surfaces reflect light with low degrees of linear polarization or with non-horizontal direction of polarization, and thus are unattractive to polarotactic dragonflies. In double-choice field experiments, Horváth *et al*. (2007) showed that the dragonflies attracted to shiny black tombstones possess positive polarotaxis and therefore, under natural conditions, detect water by means of the horizontally polarized reflected light. The positive polarotaxis and the reflection–polarization characteristics of black gravestones explain why the observed *Sympetrum* dragonflies were attracted to black tombstones.

Reflecting Surfaces that do Not Attract Polarotactic Aquatic Insects

The previous section discusses several different artificial shiny surfaces that attract polarotactic aquatic insects, because they reflect highly and horizontally polarized light. Some reflecting surfaces, however, do not attract aquatic insects, even though they are horizontal and sometimes highly polarizing. In this section two such surfaces are considered.

Why are aquatic insects not attracted by mirages?

On sunny days, mirages may appear on sunlit roads and hot plains: there appears to be a pool of shiny water in the distance, which dissolves on approach. The sky, landmarks and objects are mirrored in this 'pool', which deceives human observers. Can mirages also deceive polarotactic aquatic insects? To answer this question, Horváth *et al*. (1997) measured and compared the polarization characteristics of a mirage and a water surface in Tunisia. The light reflected from the sandy bottom of the desert is only weakly polarized. The skylight is partially polarized with various direction of polarization. As the light from the sky and the sky's mirage has the same degree p and angle α of linear polarization, there is no polarization difference between the sky and its mirage. On the other hand, there can be large differences in the intensity, as well as in p and α, of light from the sky and the water surface: the light reflected from the water surface is usually horizontally polarized and, near to the Brewster angle, its p is high, while both p and α of skylight change spatiotemporally.

Hence, there are significant differences between the polarization characteristics of water-imitating mirages and real water surfaces: flat water surfaces reflect usually horizontally polarized light, while undulating water surfaces reflect light with directions of polarization perpendicular to the plane of reflection. The p of reflected light depends upon the direction of view and the undulation of the water surface. If the water is far away from the observer, p is relatively low due to the grazing direction of view. If the horizon is defined by the border between the water surface and the sky, there is, in general, a high polarization difference between water and sky in both p and α. This is because skylight reflected from water surfaces gets repolarized (Fig. 11.10A). On the other hand, in the desert landscape there are no differences in intensity, p and α between the sky and its mirage. Mirages are not usual reflections, but are formed by gradual refraction and a total reflection of light (Fig. 11.10B): The nearer to the ground, the warmer the air and the smaller its index of refraction. Thus, the direction of grazing rays of light gradually changes to such an extent that the rays do not reach the ground, but after total reflection, they are deflected upward (Fig. 11.10B). This gradual deflection provides an observer with the same impression as mirroring does. Such gradual refractions and total reflection of light do not change the state of polarization.

Mirages may imitate water surfaces only for animals whose visual system is polarization-blind, but sensitive to intensity and colour differences (Horváth

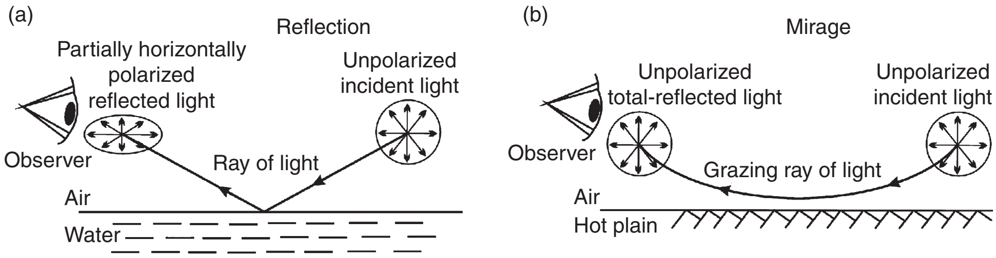

Fig. 11.10. (A) Unpolarized light becomes partially horizontally linearly polarized when reflected from the water surface. (B) Formation of a mirage above a hot plain, where the air temperature decreases and the refractive index of air increases exponentially with height above ground. The resulting gradual refraction and total reflection do not alter the polarization of light. Double-headed arrows represent the directions of polarization.

et al., 1997). Polarization-sensitive aquatic insects, however, can detect the polarization of mirage-reflected light. As this polarization differs considerably from that of water-reflected light (Fig. 11.10), they are not attracted to mirages.

Why do highly polarizing black burnt stubble-fields not attract aquatic insects?

As polarotactic aquatic insects can be attracted to dark oil surfaces, black or dark grey asphalt roads, black plastic sheets, black or dark-coloured car-bodies and black tombstones, one might assume that all 'black anthropogenic products', involving artificial surfaces that reflect light with high and horizontal polarization, can deceive and lure polarotactic aquatic insects. A typical and frequent black anthropogenic products is a burnt stubble-field (Fig. 11.11A,B). The black ash layer formed by the burning reflects highly polarized light due to the Umow effect (Umow, 1905; Können, 1985): the darker a surface, the higher the degree of linear polarization p of reflected light.

Black ash might be expected to attract polarotactic aquatic insects in large numbers, but Kriska *et al*. (2006b) showed that this is not the case. They monitored numerous highly polarizing black burnt stubble-fields, but never found aquatic insects or their carcasses in the ash, although flying polarotactic aquatic insects were abundant in the area, which was shown by attracting them to horizontal black plastic sheets close to burnt stubble-fields. From this, Kriska *et al*. (2006b) concluded that black burnt stubble-fields are unattractive to polarotactic aquatic insects, despite the high p of reflected light. To explain this, they measured the reflection–polarization characteristics of burnt stubble-fields at three different directions of view relative to the solar meridian (Fig. 11.11C). They established that: (i) p of light reflected from the black ash is high; (ii) p increases with the darkness of the ash; (iii) the direction of polarization of reflected light is nearly horizontal only towards the solar meridian (SM) and antisolar meridian (ASM), and it is tilted in other directions of view; (iv) the standard deviation of both the degree and the direction of polarization of reflected light is large.

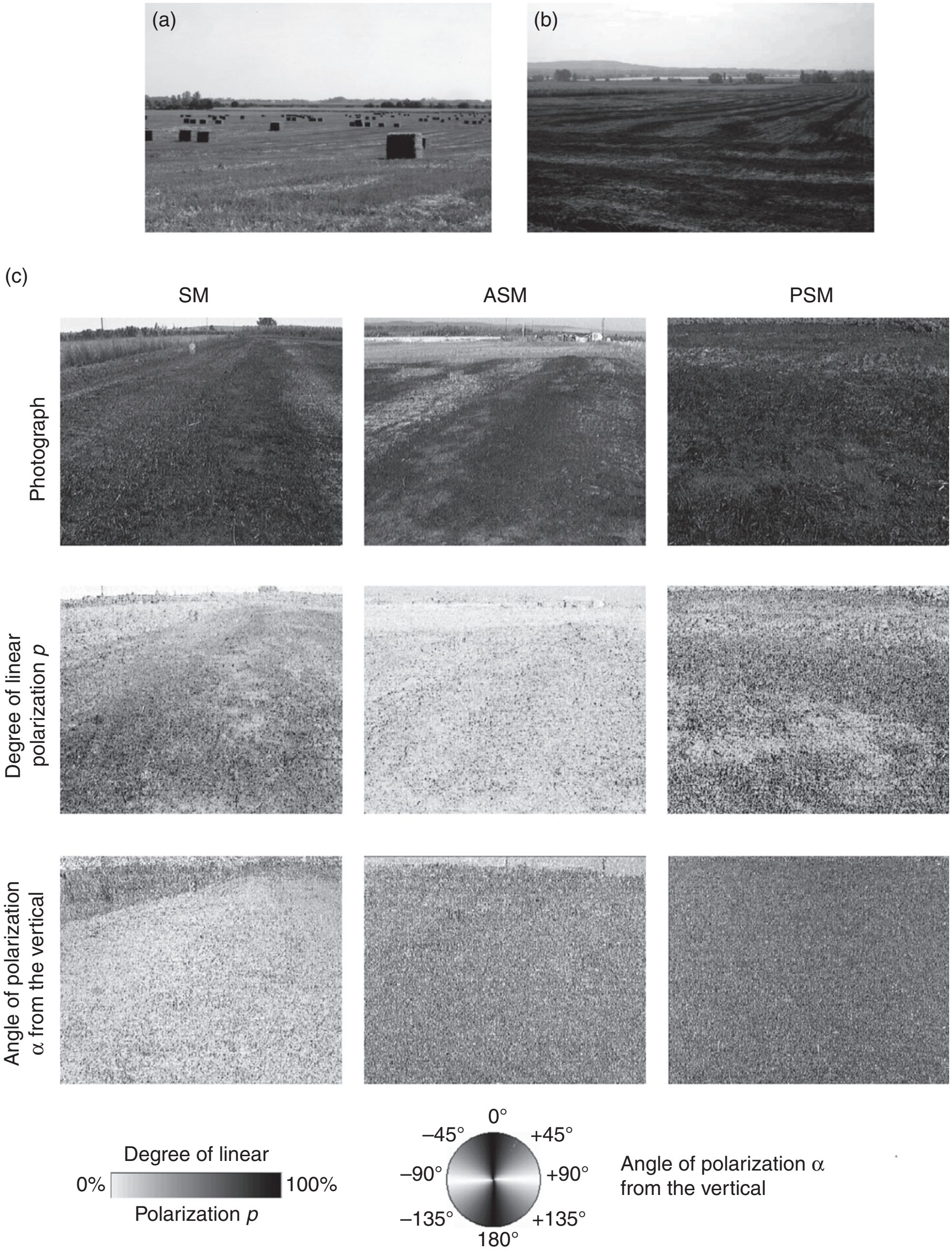

Fig. 11.11. A Hungarian stubble-field prior to (A) and after burning (B). (C) Photographs and polarization patterns of the burnt stubble-field measured under a clear sky in sunshine in the green (550 nm) part of the spectrum, when the direction of view of the polarimeter was towards the solar meridian (SM), antisolar meridian (ASM) and perpendicular to the solar meridian (PSM). The elevation angle of the optical axis of the polarimeter was –30° from the horizontal.

The latter two characteristics explain why burnt-up stubble-fields are unattractive to aquatic insects: burnt stubble-fields can be attractive only from directions of view towards the SM and ASM, where the light reflected from stubble-fields is horizontally polarized, on average. From other directions of view, burnt stubble-fields cannot be attractive, because the direction of polarization of reflected light is not horizontal.

The ash layer is a rough surface due to the random orientation of the charred stalks of plant material. One characteristic of rough surfaces is that the polarization direction of reflected light is always perpendicular to the plane of reflection (Können, 1985; Horváth and Varjú, 2003). In the case of sunlit, burnt stubble-fields, the plane of reflection passes through the observer, the sun and the point of the ash observed. This plane of reflection is vertical towards both the SM and ASM, and it is tilted for other directions of view. This explains why the average direction of polarization of light reflected from burnt stubble-fields is nearly horizontal towards the SM and ASM, and it is tilted in all other directions of view (Fig. 11.11C). These results may be important in the study of the wider environmental effects of postharvest burning.

Unexpected Aspects of Polarization Vision in Aquatic Insects

Polarotaxis in a mayfly that never leaves the water surface

Mayflies develop as larvae in water. After emergence they swarm and mate while on the wing, then lay eggs into the water. According to Brodskiy (1973), mayflies can be sorted into three groups based on their swarming site: group 1, species swarming immediately over water and never moving away horizontally from the water surface; group 2, species swarming over the littoral, but maintaining visual contact with the water; group 3, species swarming far from the water (<500–1000 m) and without visual contact with its surface. Kriska *et al*. (1998) showed that the mayfly species *Ephemera danica*, *Ecdyonurus venosus*, *Epeorus silvicola*, *Baetis rhodani*, *Rhithrogena semicolorata* and *Haproleptoides confusa* detect water by means of the horizontally polarized light reflected from the water surface. These six mayfly species belong to groups 2 and 3 *sensu* Brodskiy (1973). Species in group 1 do not require polarotaxis as they do not leave the water, but are mayflies in this group polarotactic?

The Tisza mayfly, *Palingenia longicauda* is a typical representative of group 1. It swarms exclusively over the surface of its name-giving river, the Tisza (Andrikovics and Turcsányi, 2001) (Fig. 11.12A), although there has been a report of an anomalous swarming of Tisza mayflies above a wet asphalt surface (Ladócsy, 1930). During swarming, Tisza mayflies fly immediately above the river in such a way that their cerci frequently touch the water or sweep its surface (Fig. 11.12B), using their tactile organs and hygroreceptors of their cerci and wings to detect water (Fink and Andrikovics, 1997) as well as by the intensity of light reflected from the water surface. They never swarm under windy conditions, when they could drift to the riparian vegetation. Hence, it is not obvious that Tisza mayflies need or possess positive polarotaxis.

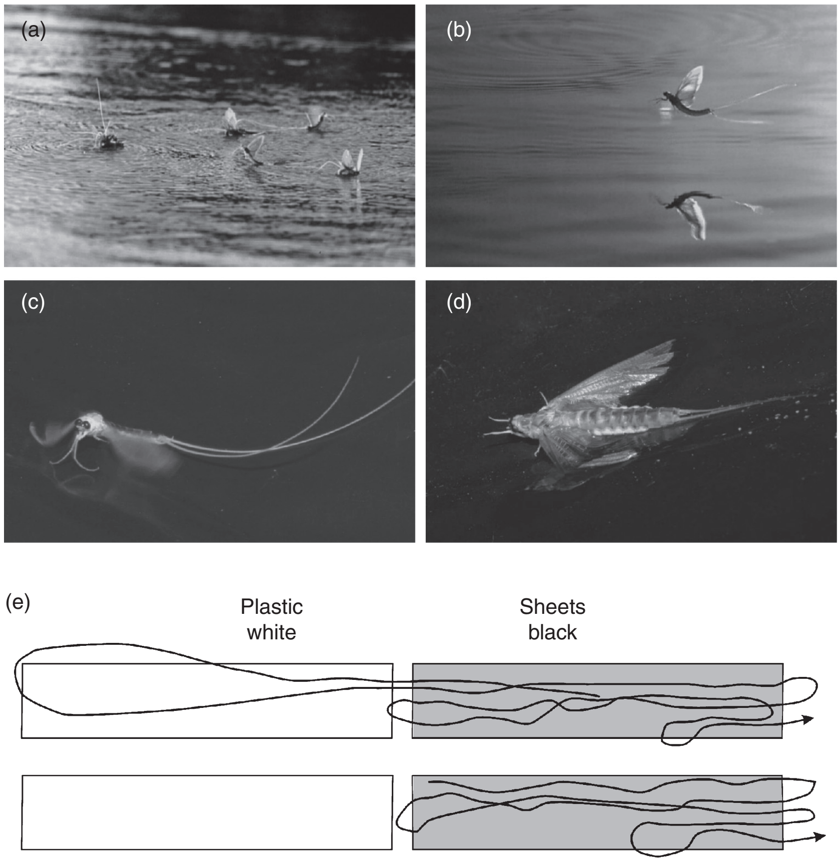

Fig. 11.12. (A,B) *Palingenia longicauda* mayflies swarm immediately above the river surface (photographs by Sándor Zsila). (C) A male *P. longicauda* flying immediately above a horizontal shiny black plastic sheet. (D) A female *P. longicauda* laying eggs on to a black plastic sheet. (E) Two typical trajectories of male *P. longicauda* mayflies released and flying immediately above shiny black and white plastic sheets laid on to the shore of the river Tisza, from which the water surface was not visible.

To reveal whether *P. longicauda* is, or is not polarotactic, Kriska *et al*. (2007) performed multiple-choice field experiments during the very short (only a few days) swarming period of Tisza mayflies. They showed that *P. longicauda* has positive polarotaxis, but this can be observed only under unnatural conditions (Fig. 11.12C,D), e.g. when animals are displaced from the water and released above artificial test surfaces (shiny black and transparent white plastic sheets, aluminium foil, matt black and white cloths). Only the shiny black and the transparent white plastic sheets influenced the flight of Tisza mayflies, and the black plastic sheet was preferred against the white one (Fig. 11.12E). The flying mayflies followed the black and white plastic sheets and turned back several times at the edges.

The demonstration of polarotactic water detection in a species that does not need it to locate water bodies would suggest that polarization-based water detection is an ancient, conservative ability among Ephemeroptera.

Polarotaxis in tabanid flies

The tabanid flies (Diptera: Tabanidae) are spread worldwide. Adult tabanids feed on nectar and pollen, and the females usually feed also on the blood of domestic animals and humans (Hall *et al*., 1998), which aids the development of their eggs, and are vectors of animal and human diseases and parasites (Foil, 1989). Understanding how tabanids locate their terrestrial mating and egg-laying sites would be very useful for control measures. Several different traps have been designed to catch tabanids (Malaise, 1937; Moore *et al*., 1996). According to Allan *et al*. (1987), the haematophagous female tabanids can find their host animals by odour, heat and visual cues. The optical cues relevant in the search for rendezvous and oviposition sites of tabanids are poorly understood. It is generally accepted that size, shape, motion, brightness and colour are factors that influence the attraction of tabanids (Thorsteinson *et al*., 1965).

In double-choice field experiments, Kriska *et al*. (2006, unpublished results) discovered positive polarotaxis in both males and females of numerous tabanid species (e.g. *Haematopota pluvialis*, *Heptatoma pellucens*, *Hybomitra ciureai*, *H. solstitialis*, *H. ucrainica*, *Tabanus bovinus*, *T. bromius*, *T. sudeticus*, *T. tergestinus*). The adults of all these tabanids are terrestrial, but lay eggs on the lower side of leaves of marsh plants overhanging the water where, after hatching, the larvae drop into the water where they develop. Kriska *et al*. (2006, unpublished results) proposed that, in these tabanids, the first step in the search for potential terrestrial mating and egg-laying sites happens indirectly by means of the detection of horizontally polarized light reflected from the surface of waters, on the shore of which appropriate plants for oviposition may occur.

The existence of polarotaxis in tabanids is surprising for two reasons. (i) Although the larvae develop in water, the adults do not lay their eggs directly into water. Attraction by horizontally polarized light has been found only in aquatic insects that oviposit directly into water (Schwind, 1991; Wildermuth, 1998; Horváth *et al*., 1998; Kriska *et al*. 1998, 2006a, 2007; Horváth and Varjú, 2003; Csabai *et al*., 2006). Positive polarotaxis has been described previously only in connection with the direct visual detection of water or moist substrata. (ii) Tabanids belong to the order Diptera, and no other dipteran species have been found to exhibit similar polarotaxis.

The discovery of polarotaxis in tabanids makes it possible to develop new, optically luring traps that are more efficient than the existing traps based on attraction by the brightness or colour of reflected light. The polarotaxis in male and female tabanids offers a new method for trapping both sexes. On the basis of this, the design of some new types of tabanid trap by the authors of this work is in progress.

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