16 Multiple-Choice Experiments on Dragonfly Polarotaxis: Dragonflies Find Crude Oil Visually More Attractive than Water

Kennedy (1917) gave an account of many individuals of the dragonfly *Anax junius* having been killed as a result of mistaking an open surface of crude oil for water. Puschnig (1926), Fraser (1936) and Whitehouse (1941) reported that 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. Kennedy (1938) cited cases in which dragonflies were attracted to pools of petroleum. Horváth and Zeil (1996) reported that dragonflies were deceived, attracted and trapped in large numbers by crude oil lakes in the desert of Kuwait. Horváth et al. (1998a) observed the same behaviour of dragonflies at a waste oil lake in Budapest (Fig. 16.1).

Such examples demonstrate that dragonflies[1] respond to shiny black oil or dark grey asphalt surfaces, and also that their response is elicited by particular misleading cues. Horváth and Zeil (1996) suggested that the reason why crude oil deceive, lure and trap insects on a large scale might be that an oil surface looks like an "exaggerated", strongly horizontally polarizing water surface, making oil visually more attractive than water to water-loving insects, the visual system of which is sensitive to the polarization of reflected light.

Horváth et al. (1998a) tested and supported this hypothesis in multiple-choice field experiments with dragonflies. They compared the numbers of dragonflies being caught in water, crude oil (Fig. 16.2) and salad-oil (Fig. 16.3) traps with different reflection-polarizational characteristics. They demonstrated that polarotaxis is the most important mechanism which guides dragonflies during their habitat choice and oviposition site selection, and this is the reason why dragonflies can be deceived by and attracted to crude and waste oil, tar or asphalt (Kennedy 1917, 1938; Puschnig 1926; Fraser 1936; Whitehouse 1941; Angus 1973; Akersten et al. 1983; Horváth and Zeil 1996; Kowalski 1999).

In the first choice experiment of Horváth et al. (1998a), two matt aluminium trays of 0.5 m^2 area were filled with water respectively black crude oil. They were placed on a large field about 500 m away from a small lake. Matt aluminium trays

[1] Dragonflies: all members of Odonata, including both Anisoptera and Zygoptera; the latter commonly known as damselflies.

were chosen to mimic the bright grey colour of the ground of the alkaline field. The bottom of the water-filled tray was covered by a thin layer of grey, sandy soil to imitate the typical bottom of alkaline puddles in the biotope. In order to trap all insects that touched the water, the common ecological method of catching and monitoring insects was used (Southwood 1966): the surface tension of water was reduced with a detergent. In a pilot-experiment it was proven that both crude oil and detergent-treated water were efficient insect traps. Any insect that touched either surface was entrapped at once. These traps were left in the field for two weeks and checked every day. The dragonflies trapped by the trays were collected and identified. The distance between the traps was 0.5 meter. The position and orientation of the trays was changed randomly. The evaporated crude oil and water were continuously replenished. The reflection-polarizational characteristics of the traps were measured by video polarimetry (Horváth and Varjú 1997) on a typical sunny day under a clear sky.

We can see in Table 16.1 that male dragonflies were trapped about twice as frequently as females, and black crude oil was significantly more attractive than water on a light grey background. This observation constitutes the experimental evidence for the hypothesis put forward by Horváth and Zeil (1996). The light reflected from the oil had a degree of linear polarization p = 33% with horizontal E-vector (Table 16.1, Fig. 16.2). The light reflected from the water had p = 4% with vertical E-vector, since a slightly greater amount of light with vertical polarization came from the bottom than horizontally polarized light from the water surface. Although the reflection-polarizational characteristics of the trays depend on the angle of view, solar zenith angle and meteorological conditions, Fig. 16.2 demonstrates well the fact that crude oil is a more effective polarizer than water with a bright bottom, even relatively far away from the Brewster angle (57^o from the vertical for crude oil and 53^o for water). Thus, the light reflected from crude oil is a supernormally polarized stimulus for water seeking dragonflies.

In the first choice experiment of Horváth et al. (1998a), the bottom of water was much lighter than the black crude oil, like in the desert of Kuwait, where there occurred bright sand-bottomed water ponds and dark brown or black crude oil lakes and ponds (Horváth and Zeil 1996). Horváth et al. (1998a) performed also a second multiple-choice experiment: Five white plastic trays were filled with transparent, slightly yellowish salad-oil. The bottom of four traps was covered by shiny plastic sheets with different grey shades ranging from black, through dark and light grey to white. The bottom of the fifth trap was a shiny aluminium foil. In this experiment differences of the trapping efficiency of the salad-oil filled in five traps were surely not due to smell. We can see in Table 16.2 and Fig. 16.3 that the relative radiance I gradually increased while p gradually decreased from the black trap (S5) through the dark (S3) and light (S6) grey to the white trap (S4). The aluminium trap possessed a relatively high p = 20.2%, but because shiny aluminium surfaces reflect the linearly polarized light with practically no change (Horváth and Pomozi 1997), the reflection-polarizational characteristics of this trap was very variable depending on the solar zenith angle. Apart from the white and aluminium traps, the direction of polarization of the light reflected from the traps was always horizontal. The E-vector of reflected light was more or less vertical for the white and very variable for the aluminium trap.

Although the black trap reflected about twice so highly polarized light (p = 69.6%) as the dark grey trap (p = 33.7%), there was no significant difference between the number of dragonflies trapped by them. The light grey and white traps with low p trapped significantly fewer dragonflies and the aluminium trap with very variable polarization was the least attractive. Males were trapped again much more frequently than females.

In full sunshine, the black crude oil and the salad-oil in the black-bottomed tray heated up considerably, maximum of about 70°C, unlike the water and the salad-oil in the white- and aluminium-bottomed trays, the temperature of which followed the temperature of the surroundings, maximum of ca. 35°C. Similarly to Horváth et al. (1998a), Wildermuth (1993) also observed that dragonflies (*Aeshna juncea*) do not land when the test surface composed of black plastic sheet or cloth heated up too much in full sunshine.

To exclude the role of temperature and radiance of the surfaces in the choice of dragonflies, Horváth et al. (1998a) performed a third experiment. They laid six odourless sheets measuring 1 m × 1 m covered by different materials, non-transparent black, grey and white shiny plastic sheets, shiny aluminium foil, matt black and white cloths with the same temperature and with different reflection-polarizational characteristics on the ground (Fig. 16.4). In the experiments the surfaces were positioned along a rectangle, and their order was changed randomly. The response of flying dragonflies to these test surfaces was studied by visual observation. The following main behaviour types were differentiated:

- air fight, hovering and protection of the territory against intruders;
- surface touching;
- settling down;
- egg-laying.

The relative frequency of these behaviour types have been counted and compared, and the reflection-polarization patterns of the test surfaces were recorded (Table 16.3, Fig. 16.4).

The number of egg-laying was very low (Table 16.3), thus one cannot draw any firm conclusion considering the oviposition. Egg-laying occurred only on the shiny surfaces. Settling down occurred also only sporadically, but significantly more often than egg-laying. For settling down the brighter test surfaces, matt white cloth, shiny white plastic, shiny aluminium with low p were preferred independently of their shiny or matt appearance and of the angle of polarization of reflected light. This reaction recalls the settling down behaviour onto the matt light grey ground observed frequently in the study site. This behaviour is apparently different from the water-seeking behaviour, because dragonflies never settle down directly onto the water surface. According to Corbet (1999), settling down to a brighter surface may serve thermoregulation or simply resting. Many dragonfly species must warm their thorax to a temperature well above the ambient temperature before they can fly, and they do this by behavioural and physiological means. Behavioural warming occurs as basking in sunlight, sometimes gaining additional heat by sitting on hot rocks or the ground (Corbet 1999).

Surface touching was the second more frequent behaviour type observed at the test surfaces. This is a reaction, which is typical above water surfaces when dragonflies inspect the surface to select the optimal oviposition site. The shiny black plastic sheet with the highest degree (p = 73.5%) of horizontal polarization was the most attractive (46.3%). The shiny grey plastic sheet with a much lower degree (p = 9.1%) of horizontal polarization was less attractive (25.6%). Since the direction of polarization was not horizontal, the matt white and black cloths, independently of their low or high p, and the shiny aluminium were practically unattractive.

The most frequently observed types of behaviour were the air fight, hovering and protection. These are typical again only above water surfaces. Males frequently hover in their territories, or when they search for females elsewhere. Hovering serves to advertise the presence of a male in his territory. Females also hover when they inspect oviposition sites (Corbet 1999). Both females and males inspect the surface, or males protect their territory during air fights against intruders. Considering these aerial territorial behaviours, the shiny black plastic sheet was again the most attractive (40.1%). The shiny grey plastic sheet was less attractive (21.2%). The matt white and black cloths furthermore the shiny aluminium were practically unattractive. The shiny white plastic sheet was only slightly attractive (17.3%). Hence, for air fight, hovering and protection the relative attractiveness of the different test surfaces was similar to that obtained for the surface touching behaviour. These reactions demonstrate that the higher the degree of horizontal polarization, the greater is its attractiveness to dragonflies.

Analysing Table 16.3, we can establish that the radiance I does not play an important role in the choice of surfaces. The dragonflies were attracted predominantly to the shiny black plastic sheet, and the very dark matt black and too bright white and aluminium surfaces were unattractive. The preferred shiny black plastic sheet reflected highly and horizontally polarized light. The matt test surfaces scattered light diffusely due to their roughness, and the reflected light was practically unpolarized. Thus, the strong reflection polarization of light remains as the only explanation for the fact that dragonflies preferred exclusively the black plastic surface. This conclusion is in agreement with the results of Wildermuth and Spinner (1991) and Wildermuth (1993, 1998).

Since the smell of the salad-oil traps was the same and the test surfaces used in the third choice experiment were odourless, one can conclude that olfaction is not relevant for detection of water by dragonflies. Because the temperature of the black shiny plastic and matt cloth, like the temperature of the white plastic and cloth, were approximately the same, the dragonflies trapped by the crude oil and salad-oil traps were presumably not be attracted by the heat, that is, the temperature was not relevant in their choice. It can also be established, that the radiance of reflected light did not play an important role in their choice, as otherwise either the darkest matt black cloth, the white cloth, or the brightest aluminium would have been the most attractive.

To confirm that strongly polarized reflected light is very attractive to water-seeking dragonflies, Horváth et al. (1998a) performed a fourth field experiment. One half (0.2 m^2) of a shiny aluminium test surface was covered by a common linearly polarizing filter, while the other half was uncovered. The two halves were separated by a narrow matt black cloth, which was unattractive. The polarizing filter was neutral grey with a transmissivity of 80% in the visible range of the spectrum and absorbed entirely UV light. The number of the different behaviour types above the two different halves of the aluminium test surface have been counted and compared. The results are presented in Table 16.4.

The light reflected from the filter-covered half of the aluminium was totally linearly polarized (p = 100%) in the visible spectral range and its E-vector was horizontal for dragonflies flying from the proper directions towards the filter. Since the uncovered half of the aluminium was only slightly polarized and its E-vector was generally not horizontal, there was a strong polarization contrast between the two halves. The number of egg-laying and settling down was very low on both halves (2:1 and 6:3, respectively). About 60% of the most frequent reactions, the air fight and hovering, happened above the polarizing filter, which thus was not significantly more attractive than the aluminium surface. The reason for this is that the territories of the observed small dragonflies are usually less than 1 m^2 (Corbet 1999). Thus, both halves of the aluminium belonged to their territory. About 86% of the surface touching, the second most frequent reaction, happened on the polarizing filter. This difference is highly significant and demonstrates that both males and females select strongly horizontally polarizing surfaces as habitats and oviposition sites.

One can conclude that dragonflies detect water by means of polarotaxis, like many other water insects (Schwind 1985b, 1991, 1995). The spectral range in which this water detection functions in dragonflies is still unknown. Some dragonflies have UV receptors looking downwards (Corbet 1999) which respond perhaps to the polarization of UV light reflected from water. In the choice experiments of Horváth et al. (1998a) chiefly males were trapped. Wildermuth and Spinner (1991) and Wildermuth (1993) have also observed that female dragonflies visited black, shiny plastic sheets and natural oviposition sites less frequently. This can be explained by the operational sex ratio at breeding sites which is strongly biased towards males, because females spend much time elsewhere (Corbet 1999).

The first experiment of Horváth et al. (1998a) with the crude-oil- and water-filled trays closely mimicked the "natural" situation in the desert of Kuwait from late autumn to late spring, when some of the oil lakes were partially covered by sand and rain water (Horváth and Zeil 1996). Then water-seeking dragonflies had to choose between the dark crude oil ponds and the bright sand-bottomed water bodies. The crude or waste oil lakes in nature as well as the crude-oil- and salad-oil-filled trays in the choice experiments of Horváth et al. (1998a) entrapped the dragonflies when the males or females performed a water-touching manoeuvre or when the females tried to deposit their eggs. Monitoring the waste oil lake in Budapest (Fig. 16.1), Horváth et al. (1998a) could observe that the dragonflies exhibited the complete repertoire of behavioural elements which belong to reproduction including site defence and oviposition. These dragonflies behaved at the strongly horizontally polarizing shiny black surface of the waste oil lake very much like at natural water surfaces or above water-imitating dummies as reported by Wildermuth and Spinner (1991) and Wildermuth (1993, 1998).

Muller (1937) observed the females of *Orthetrum* dragonflies laying eggs on a shiny cement floor and *Copera marginipes* made repeated egg-laying movements in a dirty seam on a shiny black bench. Wyniger (1955) has reported on the egg-laying of *Libellula depressa* onto a glass pane of a greenhouse. Neville (1960) experienced that mature individuals of *Pantala flavescens* performed sexual behaviour and oviposition movements over shiny roofs of tents. Kennedy (1938) reported on instances in which dragonflies were attracted to shiny roofs of automobiles. These authors experienced that the dragonflies performed sexual behaviour and oviposition movements over these shiny surfaces. Noordwijk (1980) found that the flight activity of dragonflies above shiny plastic sheets (2 m × 3 m) laid on *Sphagnum* bog was significantly higher than above control plots without plastic.

Fränzel (1985) laid out transparent plastic sheets at the edge of a creek and observed that both female and male dragonflies *Cordulegaster bidentatus* were attracted to the plastic, and the females performed oviposition movements while males patrolled predominantly over those plastic pieces which covered dark regions of the ground. These authors, however, did not recognize the important role of polarotaxis in the habitat choice or in the deceiving by different artificial shiny black surfaces.

Using different breeding site dummies in multiple-choice experiments, Wildermuth and Spinner (1991) and Wildermuth (1993) found that a shiny black plastic sheet was highly attractive to both sexes of *Somatochlora arctica* and *Aeshna juncea*, and they exhibited the complete repertoire of behavioural elements which belong to reproduction including site defence and oviposition. Matt white or black tulle and cotton cloths, even when covered with glass splinters proved to be completely unattractive, and when glass splinters providing a great number of reflecting light spots were added to a black shiny plastic sheet no enhancement of the responses was recorded (Wildermuth and Spinner 1991; Wildermuth 1993). According to Steiner (1948), matt black paper had almost no effect on *Leucorrhinia dubia*, and Wildermuth and Spinner (1991) noticed similar weak reactions towards matt black cotton also by *Somatochlora alpestris*.

Tables

Table 16.1. Row 2: The total number and sex (F: female, M: male) of dragonflies (*Sympetrum vulgatum, Ischnura pumilio, Enallagma cyathigerum*) trapped by the crude-oil- and water-filled trays during the first choice experiment of Horváth et al. (1998a). Rows 3-5: The relative radiance *I*, degree of linear polarization *p* and direction of polarization of light reflected from the trays and measured by video polarimetry at 450 nm from a direction of view of 70° relative to the vertical. (After Table 1 of Horváth et al. 1998a, p. 292).

	crude oil-filled tray S1	**water-filled tray S2**
number of trapped dragonflies	16 F + 34 M	2 M
relative radiance *I*	20%	100%
degree of linear polarization *p*	33%	4%
direction of polarization	horizontal	vertical

Table 16.2. Row 2: The total number (J: juvenile) and sex (F: female, M: male) of dragonflies (Ischnura elegans, Erythromma viridulum, Lestes macrostigma, Enallagma cyathigerum, Orthetrum cancellatum, Libellula quadrimaculata, Sympetrum sanguineum) trapped by the salad-oil-filled trays during the multiple-choice experiment of Horváth et al. (1998a). Rows 3-5: The relative radiance I, degree of linear polarization p and direction of polarization of light reflected from the trays and measured by video polarimetry at 450 nm from a direction of view of 70° from the vertical. The trays are designated by S3-S7 as in Fig. 16.3. (After Table 2 of Horváth et al. 1998a, p. 294).

	black tray S5	**dark grey tray S3**	**light grey tray S6**	**white tray S4**	**aluminium tray S7**
number of trapped dragonflies	8 F (5 J) + 62 M (7 J)	12 F (3 J) + 63 M (9 J)	11 F (7 J) + 32 M (3 J)	7 F (5 J) + 21 M (2 J)	5 F (4 J) + 10 M (2 J)
relative radiance *I*	22.1%	35.6%	52.4%	100%	42.3% (variable)
degree of linear polarization *p*	69.6%	33.7%	10.3%	4.6%	20.2% (variable)
E-vector direction	horizontal	horizontal	horizontal	vertical	horizontal (variable)

Table 16.3. The total number and the frequencies relative to the total number of a given reaction counted above all six test surfaces of the different behaviour types of dragonflies (*Ischnura elegans, Erythromma vividulum, Lestes macrostigma, Enallagma cyathiqerum, Orthetrum cancellatum, Sympetrum sanquimum*) in the choice experiment, repeated 11 times. The relative radiance *I*, degree of linear polarization *p* and angle of polarization with respect to the vertical of the light reflected from the test surfaces and measured by video polarimetry at 470 nm from a direction of view of 70° relative to the vertical.

behaviour type	**shiny black plastic S8**	**shiny grey plastic S9**	**matt white cloth S13**	**shiny white plastic S11**	**matt black cloth S12**	**shiny aluminium S10**
air fight, hovering, protection	922 (40.1%)	486 (21.2%)	189 (8.2%)	397 (17.3%)	91 (4.0%)	212 (9.2%)
surface touching	343 (46.3%)	190 (25.6%)	22 (3%)	120 (16.2%)	13 (1.8%)	53 (7.1%)
settling down	5 (6.3%)	9 (11.4%)	30 (38%)	20 (25.3%)	1 (1.3%)	14 (17.7%)
egg-laying	4 (20%)	8 (40%)	0	4 (20%)	0	4 (20%)
relative radiance *I*	52.9%	63.5%	99.7%	100%	22.2%	78.8% variable
degree of polarization	73.5%	9.1%	3.4%	2.8%	21.5%	7.0% variable
angle of polarization	90° horizontal	90° horizontal	51.3° variable	0° vertical	51.6° variable	80.3° variable

Table 16.4. Rows 2-5: The total number of the different behaviour types of dragonflies (*Ischnura elegans, Erythromma viridulum, Lestes macrostigma, Enallagma cyathigerum, Orthetrum cancellatum, Sympetrum sanguineum*) above the two test surfaces in the fourth choice experiment repeated five times. Rows 7-9: The relative radiance, degree of linear polarization and angle of polarization with respect to the vertical of the light reflected from the test surfaces and measured by video polarimetry at 450 nm from a direction of view of 70° relative to the vertical. (After Table 3 of Horváth et al. 1998a, p. 296).

1	**behaviour type**	**polarizing filter on shiny aluminium**	**shiny aluminium**
2	air fight and hovering	412 (59.6%)	279 (40.4%)
3	surface touching	115 (85.8%)	19 (14.2%)
4	settling down	6	3
5	egg-laying	2	1
6	**optical characteristics**		
7	relative radiance *I*	40%	100%
8	degree of polarization *p*	100%	30% (variable)
9	angle of polarization α	90° (horizontal)	65° (variable)

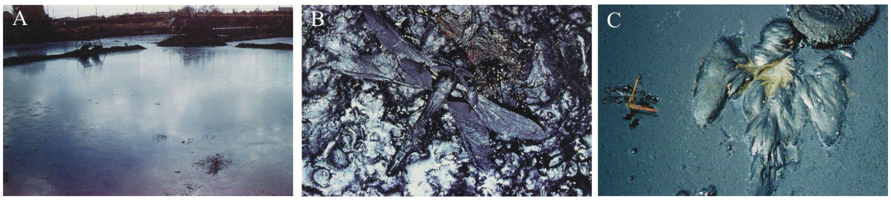

Fig. 16.1. The shiny, strongly horizontally polarizing, water-imitating surface of the waste oil lake in Budapest (A) has deceived, attracted and trapped a dragonfly *Anax imperator* (B) and a copulating pair of *Sympetrum sanguineum* (C, left hand side).

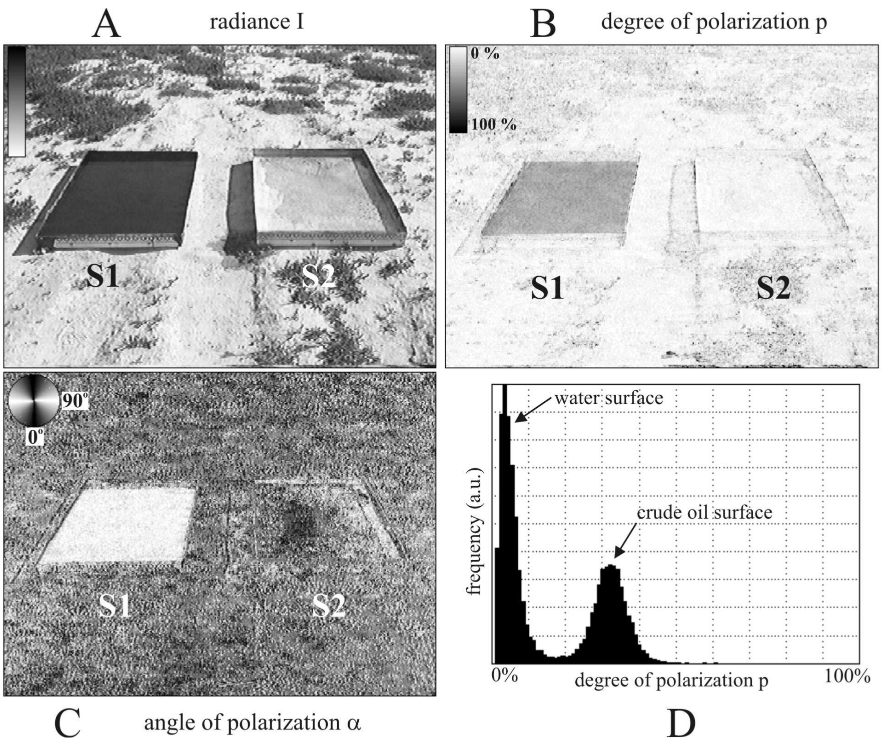

Fig. 16.2. The reflection-polarizational characteristics of the two trays used by Horváth et al. (1998a) in the first choice experiment, filled with black crude oil (S1) and detergent-treated water (S2) measured by video polarimetry at 450 nm under a clear sky. A: Distribution of the radiance *I*. B: Pattern of the degree of linear polarization *p*. C: Pattern of the angle of polarization α. (Black: vertical E-vector, white: horizontal E-vector). D: Histogram of *p* calculated for the surface area of the two trays. The left (p = 4%) and right (p = 33%) peak of the distribution corresponds to the water and crude oil surface, respectively. Viewing direction was 70° from the vertical and at a right angle to the solar meridian. (After Fig. 2 of Horváth et al. 1998a, p. 294).

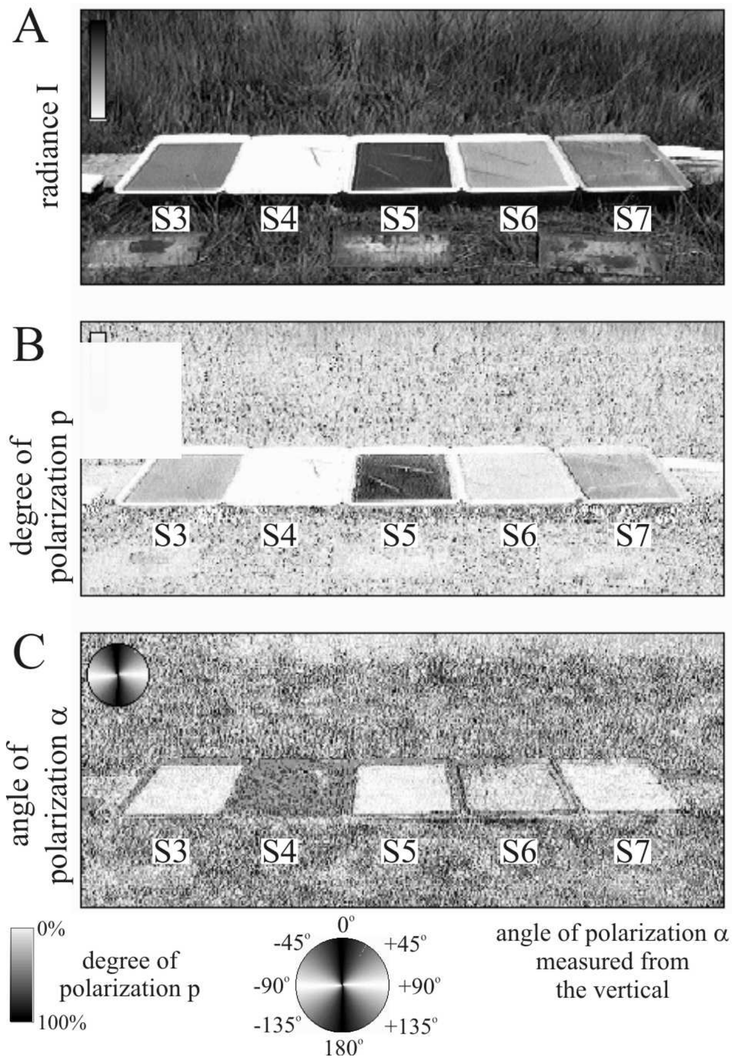

Fig. 16.3. The reflection-polarizational characteristics of the salad-oil-filled traps used by Horváth et al. (1998a) in the multiple-choice experiment measured by video polarimetry at 450 nm from a direction of view of 70° with respect to the vertical and at a right angle to the solar meridian under a clear sky. The bottom of the salad-oil-filled trays were covered by dark grey (S3), white (S4), black (S5), light grey (S6) plastic sheets and aluminium foil (S7). The trays were positioned farther away from each other during the experiment than seen here. They are placed in this picture as close as possible in order to image them at the same time. A: Distribution of the radiance *I*. B: Pattern of the degree of linear polarization *p*. C: Pattern of the angle of polarization α from the vertical. (After Fig. 3 of Horváth et al. 1998a, p. 295).

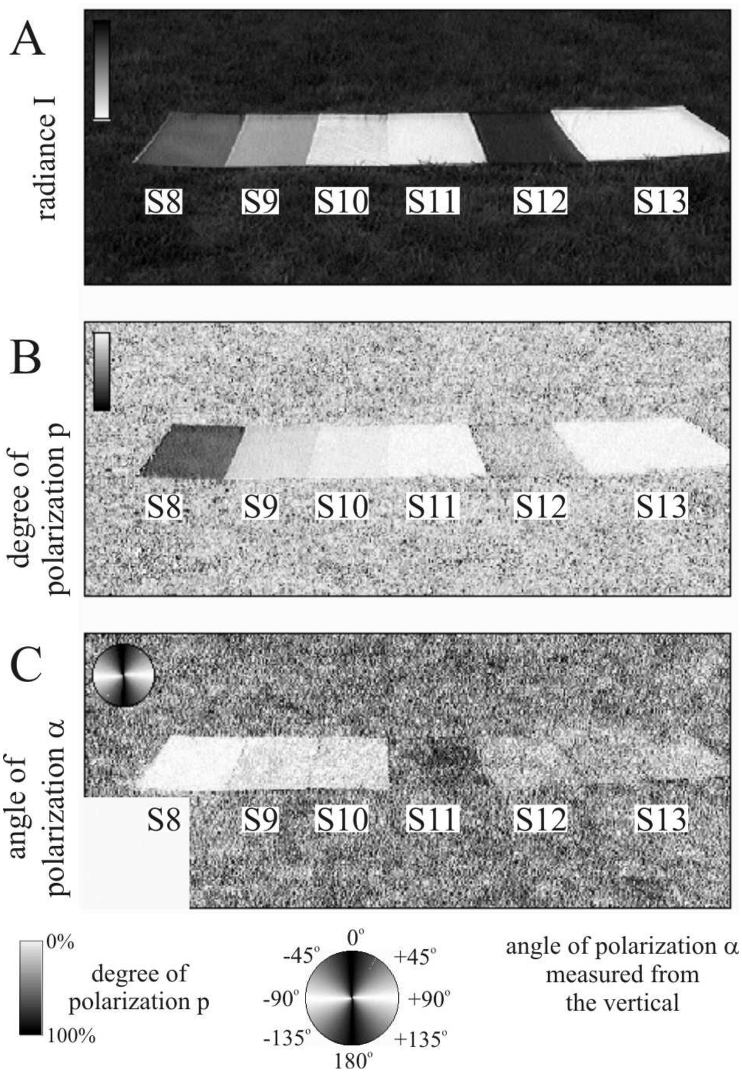

Fig. 16.4. The reflection-polarizational characteristics of the different test surfaces used in the third experiment by Horváth et al. (1998a) and measured by video polarimetry at 450 nm under a clear sky from a direction of view of 70° with respect to the vertical at a right angle to the solar meridian. The test surfaces were shiny black plastic sheet (S8), shiny grey plastic sheet (S9), shiny aluminium foil (S10), shiny white plastic sheet (S11), matt black cloth (S12) and matt white cloth (S13). These test surfaces were positioned farther away from each other during the experiment than seen here. They are placed here as close as possible in order to image them at the same time.