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

Gábor Horváth, Balázs Bernáth, Gergely Molnár
Department of Biological Physics, Eötvös University, H-1088 Budapest, Puskin u. 5-7, Hungary

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In 1917 Kennedy [1] gave an account of many dragonflies having been killed as a result of mistaking an open surface of crude oil for water. Puschnig [2], Fraser [3], and Whitehouse [4] reported that dragonflies patrolled along asphalt roads instead of rivers and showed a typical water-touching behaviour above the asphalt surface. Kennedy [5] cited instances in which dragonflies were attracted to pools of petroleum. Recently Horváth and Zeil [6] reported that dragonflies were deceived by, attracted to, and trapped in large numbers by the crude oil lakes in the desert of Kuwait. Most recently we have observed the same behavior of dragonflies at the waste oil lake in Budapest (Fig. 1).

Such examples serve to show that dragonflies – by which we mean all members of Odonata including both Anisoptera and Zygoptera (commonly known as damselflies) – respond to shiny black oil or dark grey asphalt surfaces, and also that their response is elicited by particular misleading cues. On the basis of the earlier results of Schwind [7–9], Horváth and Zeil [6] suggested that the reason why crude oil deceive, lure, and trap insects on a large scale is that an oil surface resembles an "exaggerated," strongly horizontally polarized water surface, making oil visually more attractive than water to water-loving insects, the visual system of which is sensitive to polarized reflected light.

This hypothesis could not, however, be confirmed by comparative studies on the dragonflies entrapped by oil and water ponds. In multiple-choice experiments we have now tested and supported this hypothesis. We compared the numbers of dragonflies being caught in crude oil, salad oil, and water traps with different reflection-polarization characteristics, and furthermore observed the behaviour of dragonflies at the shiny black surface of the open-air waste oil reservoir in Budapest. We demonstrate in this work that polarotaxis is the most important mechanism which guides dragonflies during their habitat choice and oviposition site selection, and that this is the reason why dragonflies can be deceived by and attracted to crude and waste oil, tar, or asphalt [1–6, 10–12].

In the first choice experiment two matt aluminum trays of 0.5 m^2 area were filled with water and black crude oil, respectively. They were placed on a large field about 500 m from a small lake in the vicinity of the village Kunfehértó in the southern part of the Hungarian Great Plain from August 3 to 20, 1995. We chose matt aluminum trays to mimic the bright grey colour of the ground of the sodic field. The bottom of the water-filled tray was covered by a thin layer of grey, sandy soil to imitate the typical bottom of sodic puddles in the biotope. In order to trap all insects that touched the water we used the common ecological method of catching and monitoring insects [13]; the surface tension of water was reduced with a detergent. A pilot experiment lasting 3 days demonstrated that both crude oil and detergent-treated water are efficient insect traps: any insect that touched either surface was entrapped at once.

These traps were left in the field for 2 weeks and checked every day: the dragonflies trapped by the trays were collected and conserved in denaturated alcohol for later identification. The distance between the traps was always 0.5 m. The position and orientation of the trays was changed randomly. The evaporated crude oil and detergent-treated water were continuously replenished. The reflection-polarization characteristics of the traps were measured by video polarimetry (for details of the method see [14]) at the study site on a typical sunny day under clear sky.

As seen in Table 1, male dragonflies were trapped by the two trays about twice as frequently as females, and that black crude oil in competition with water on a light grey background was significantly more attractive to dragonflies. This observation constitutes the experimental evidence for the hypothesis put forward by Horváth and Zeil [6]. The crude-oil-filled tray had a much higher degree of polarization (33%) with a horizontal E-vector (Table 1, Fig. 2). In contrast to

Table 1. Row 1: 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. Rows 2–4: The relative brightness, degree of polarization and direction of polarization of light reflected from the trays and measured by video polarimetry in the blue spectral range ($\lambda = 470$ nm) from a direction of view of 70° with respect to the vertical. The trays are designated by S1 and S2 as in Fig. 2

	crude-oil-filled tray S1	water-filled trays S2
number of trapped dragonflies	50 = 16 F + 34 M	2 = 2 M
relative brightness	20%	100%
degree of polarization	33%	4%
direction of polarization	horizontal	vertical

Fig. 1. The shiny, strongly horizontally polarized, water-imitating surface of the waste oil lake in Budapest (A) has deceived, attracted and trapped this specimen of the dragonfly *Anax imperator* (B), and this copulating pair of *Sympetrum sanguineum* (C, *left*) on a sunny day in September 1997. Unfortunately, every year thousands of dragonflies are killed in this way by this open-air oil reservoir. The waste oil lake in Budapest acts as a huge insect trap, as the crude oil lakes in the desert of Kuwait [6], the ancient asphalt seeps in Rancho La Brea (Los Angeles), and the Pleistocene tar pits in Starunia (western Ukraine) [10–12]. *Right* (C) the carcass of a pigeon can also be seen, which was trapped by the oil

this, the water-filled tray had only a very low degree of polarization (4%), and its direction of polarization was vertical from this direction of view. The reason for this is that a slightly greater amount of light with vertical polarization came from the bright-bottomed water than the amount of the surface-reflected, horizontally polarized light (see [6]). Of course, this does not mean at all that water bodies would always be vertically polarized. Figure 2 demonstrates the phenomenon: a water body reflects vertically polarized light with a low degree of polarization when the amount of light coming from water (due to reflection from the bottom or back-scattering from suspended particles) is greater than the amount of light reflected by the surface [9]. Water bodies generally reflect horizontally polarized light with a high degree of polarization at the Brewster angle, and this is the reason why the vision of insects associated with water evolved to deal with horizontal polarization [7–9].

The dry soil and the sporadic vegetation in the surroundings of the trays had a very low degree of polarization due to the diffuse reflection and scattering of light, and the alignment of the reflected E-vector changed randomly in space. Although the reflection-polarization characteristics of the trays depend on the angle of view, the sun's zenith distance, and meteorological conditions, Fig. 2 demonstrates well the fact that crude oil is a more effective polarizing reflector than water with a bright bottom, even

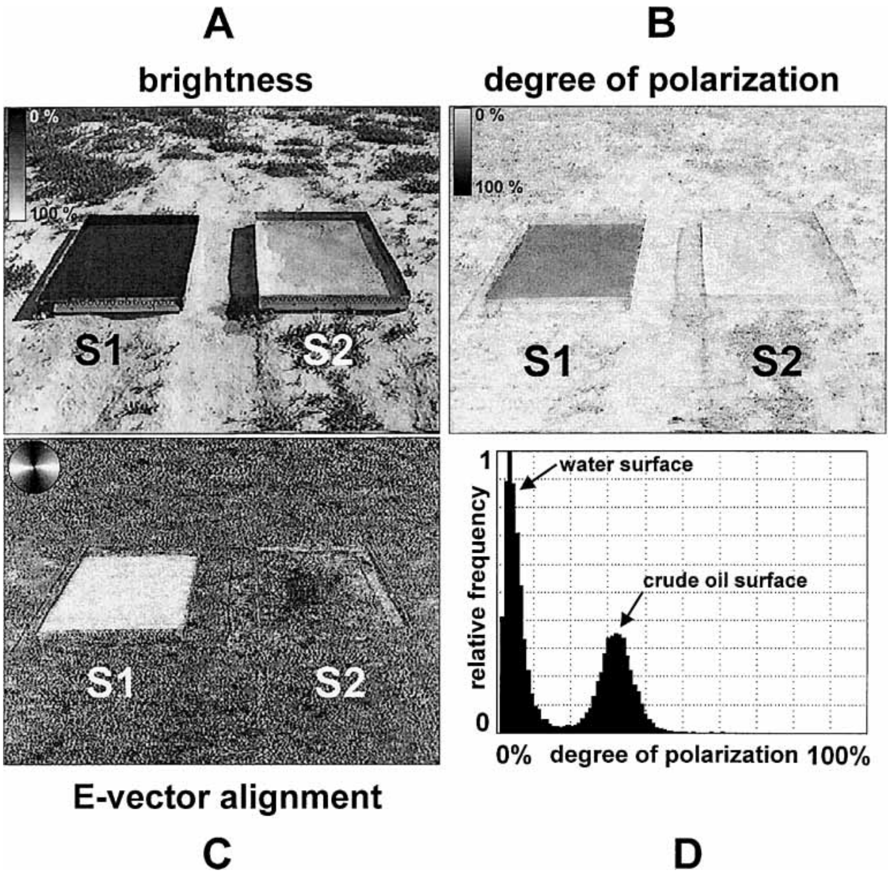

Fig. 2. The reflection-polarization characteristics of the two trays used in the first choice experiment and filled with black crude oil (S1) and detergent-treated water (S2) measured by video polarimetry under a clear sky. *Insets*, grey-level codes for brightness, degree of polarization, and E-vector alignment. A) Distribution of the brightness I in the scene (*black*, I = 0%, *white*, I = 100%). B) Degree of polarization d (*white*, $d = 0\%$; *black*, $d = 100\%$). C) Direction of polarization (*black*, vertical E-vector; *white*, horizontal E-vector). D) Histogram of the degree of polarization calculated for the surface area of the two trays. The left (4%) and right (33%) peaks of the distribution correspond to the water and crude oil surface, respectively. Viewing direction was 70°, measured from the vertical and at a right angle to the solar meridian (to avoid the strong reflection of direct sunlight)

relatively far away from the Brewster angle (57° from the vertical for crude oil and 53° for water). Thus crude oil is a supernormally polarized stimulus for water seeking dragonflies possessing polarization vision [15, 16].

In our first choice experiment the bottom of water was much lighter than the black crude oil, as in the desert of Kuwait where there occur bright sand-bottomed water ponds and dark brown or black crude oil lakes and ponds [6]. Because the smell of crude oil differs from the odour of detergent-treated water, and also because we could not be entirely certain that the trapping efficiency of the crude oil was exactly the same as that of the detergent-treated water, we performed a second multiple-choice experiment between 20 July and 8 August 1997 on the same study site as earlier. We applied the method of ecologists, who use coloured dishes filled with colourless transparent fluid to test colour preferences of insects [17]: Five white plastic trays were filled with transparent, slightly yellowish salad oil. The bottom of four traps was covered by shiny plastic foils with various 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 the smell and the trapping efficiency of the salad oil were the same for all five traps.

We can see in Table 2 and Fig. 3 that the relative brightness gradually increased while the degree of polariza-

Table 2. Row 1: The total number and sex (F: female, M: male) of dragonflies (*Ischnura elegans, Erythromma viridulum, Lestes macrostigma, Enallagma cyathigerum, Orthetrum cancellatum, Libellula quadrimaculata, Sympetrum sangineum*) trapped by the salad-oil-filled trays during the second choice experiment. Rows 2–4: The relative brightness, degree of polarization and direction of polarization of light reflected from the trays and measured by video polarimetry in the blue spectral range ($\lambda = 470$ nm) from a direction of view of 70° with respect to the vertical. The trays are designated by S3–S7 as in Fig. 3

	black tray S5	dark grey tray S3	light grey tray S6	white tray S4	aluminium tray S7
number of trapped dragonflies	70 = 8 F + 62 M	75 = 12 F + 63 M	43 = 11 F + 32 M	28 = 7 F + 21 M	15 = 5 F + 10 M
relative brightness	22.1%	35.6%	52.4%	100%	42.3% (variable!)
degree of polarization	69.6%	33.7%	10.3%	4.6%	20.2% (variable!)
direction of polarization	horizontal	horizontal	horizontal	vertical	horizontal (variable!)

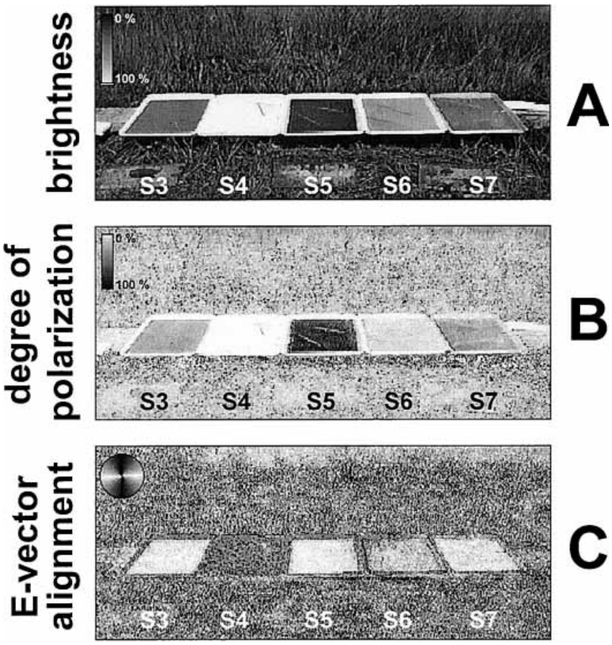

Fig. 3. The reflection-polarization characteristics of the salad oil traps used in the second choice experiment measured by video polarimetry from a direction of view of 70° with respect to the vertical and at a right angle to the solar meridian under a clear sky. The bottoms of the salad-oil-filled trays were covered by dark grey (S3), white (S4), black (S5), light grey (S6), and aluminium (S7) foil. 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, however, in order to image them at the same time. A) Distribution of the brightness I in the scene (*black*, I = 0%; *white*, I = 100%). B) The pattern of the degree of polarization d (*white*, $d = 0\%$; *black*, $d = 100\%$). C) The pattern of the direction of polarization (*black*, vertical E-vector; *white*, horizontal E-vector). *Insets*, grey-level codes for brightness, degree of polarization, and E-vector alignment

tion gradually decreased from the black trap (S5) through the dark (S3) and light (S6) grey to the white trap (S4). The video-polarimetric measurement showed that the aluminium trap possessed a relatively high degree of polarization (20.2%), but because shiny aluminium surfaces reflect the polarization of light with practically no change [18], the reflection-polarization characteristics of this trap was very variable depending on the zenith distance of the sun. Apart from the white and aluminium traps the direction of polarization of the light reflected from the traps was always horizontal. The reflected E-vector was more or less vertical for the white trap and very variable for the aluminium one.

Although the black trap reflected about twice as much polarized light ($d = 69.6\%$) as the dark grey trap ($d = 33.7\%$), there is not any significant difference between the number of dragonflies trapped by them. The light grey and white traps with low degrees of polarization trapped significantly fewer dragonflies and the aluminium trap with very variable polarization was the least attractive to dragonflies. Males were trapped again much more frequently than females.

To exclude the role of temperature and brightness of the surfaces in the choice we compared the reactions (air fight and hovering, surface touching, settling down, egg laying) of dragonflies to 1 m^2 test surfaces composed of odourless black and white shiny plastic foils and matt cloths with the same temperature. In agreement with the results of Wildermuth and Spinner [19] and Wildermuth [20, 21], we observed in this third multiple-choice experiment that independently of brightness, matt surfaces were totally unattractive to dragonflies; only the shiny black plastic foil was highly attractive. Since the smell of the salad oil traps was the same, and the test surfaces used in the third choice experiment were odourless, we conclude that olfaction is not relevant for detection of water by dragonflies. Because the temperature of the black shiny plastic and matt cloth (as 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 attracted by the heat, that is, the temperature was not relevant in their choice. We can also conclude that the intensity of reflected light did not play an important role in the choice of dragonflies, as otherwise either the darkest matt black cloth, the white cloth, or the brightest aluminium would have been the most attractive.

The dragonflies preferred predominantly the shiny black plastic; the very dark (matt black) and very bright (white and aluminium) surfaces were unattractive. The shiny black plastic reflects highly and polarizes light horizontally while the matt (rough) test surfaces scatter light diffusely; thus the reflected light is practically unpolarized, and furthermore its E-vector differs from the horizontal. The only explanation for the observed behaviour of dragonflies is therefore that the attractiveness of the traps was controlled by the polarization of reflected light: the higher the degree of horizontal polarization, the greater is the attractiveness to adult dragonflies. However, above a certain threshold of polarization the traps (S5 and S3) were equally attractive.

To confirm that strongly polarized reflected light is very attractive to water-seeking dragonflies we performed a fourth choice experiment. One half (0.2 m^2) of a shiny aluminium test surface was covered by a common linearly polarizing filter (Göttingen Farbfilter), while the other half was uncovered. The two halves were separated by a narrow matt black cloth which was unattractive to dragonflies. The polarizing filter was neutral grey. We counted and compared the number of the different behaviour types of dragonflies above the two different halves of the aluminium test surface. The results are presented in Table 3.

Table 3. Rows 1–4: The total number (relative frequency) 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 5–7: The relative brightness, degree of polarization and direction of polarization (with respect to the vertical) of the light reflected from the test surfaces and measured by video polarimetry in the blue spectral range ($\lambda = 470$ nm) from a direction of view of 70° with respect to the vertical

behaviour type	polarizing filter on shiny aluminium	shiny aluminium
air fight and hovering	412 (59.6%)	279 (40.4%)
surface touching	115 (85.8%)	19 (14.2%)
settling down	6	3
egg-laying	2	1
relative brightness	40%	100%
degree of polarization	100%	30% (variable!)
direction of polarization	90° (horizontal)	65° (variable!)

The light reflected from the filter-covered half of the aluminium was totally polarized ($d = 100\%$) 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 frequency 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, occurred above the polarizing filter, which thus was not significantly more attractive than the aluminium surface. About 86% of the surface touching, the second most frequent reaction, occurred on the polarizing filter. This difference is highly significant and demonstrates that both male and female dragonflies select strongly (horizontally) polarized surfaces as habitats and oviposition sites.

We conclude that dragonflies detect water by means of polarotaxis, as is the case with many water insects [7–9, 22, 23]. The spectral range in which this water detection functions is still unknown. In our choice experiments chiefly male dragonflies were trapped. Wildermuth and Spinner [19] and Wildermuth [20] also observed that female dragonflies visited black, shiny plastic foils and natural oviposition sites less frequently. This can be explained by the operational sex ratio at breeding sites, which is strongly biased towards males [24].

Our first choice experiment with the crude-oil- and water-filled trays closely mimics the "natural" situation in the desert of Kuwait from late autumn to late spring, when some of the oil lakes are partially covered by sand and rain water [6]; then water-seeking dragonflies must decide 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 our choice experiments entrapped the dragonflies when the males or females performed a water-touching manoeuvre for closer inspection of the surface or when the females tried to deposit their eggs. Monitoring the waste oil lake in Budapest (Fig. 1), we observed that the dragonflies exhibited the complete repertoire of behavioural elements which belong to reproduction, including site defense and oviposition. These dragonflies behaved at the strongly horizontally polarized shiny black surface of the waste oil lake very much as at natural water surfaces and above water-imitating dummies as reported by Wildermuth and Spinner [19] and Wildermuth [20, 21].

Our results are in accordance with the earlier results of other researchers. Muller [25], Kennedy [5], Wyniger [26], and Neville [27], for example, reported on instances in which dragonflies were attracted to shiny cement floors, black benches, roofs of automobiles and tents, and glass panes. These authors observed dragonflies to show sexual behaviour and oviposition movements over these shiny surfaces. Noordwijk [28] found that the flight activity of dragonflies above shining plastic sheets laid on Sphagnum bog was significantly higher than above control plots without plastic. Fränzel [29] laid out transparent plastic foils at the edge of a creek and observed that both female and male dragonflies were attracted to the plastic, and that the females showed 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 of dragonflies by different artificial shiny black surfaces. Recently Schwind [7–9] demonstrated that a glass pane underlined by a black paper was far more attractive to flying water insects than any other reflecting surfaces with different polarization and spectral characteristics. He showed that the higher the degree of polarization of reflected light, the more attractive is a given surface to water insects and insects living on moist substrata.

Since dragonflies are protected animals in many countries, it is difficult to carry out experiments on them. In our first two choice experiments we therefore minimized the area of the oil- and water-filled traps and the duration of study in order to restrict the number of killed insects to a minimum. The individuals of the entrapped dragonflies belonged to very abundant species in Hungary, and we performed the third and fourth choice experiment with the use of non-dangerous test surfaces. We conclude that due to its huge surface area the waste oil lake in Budapest must kill many more dragonflies every week than the total number of dragonflies trapped in our first and second choice experiment. Our results are in accordance with the results of Wildermuth [21] and call the attention of environment protection experts to the need to eliminate such open-air oil, tar, or bitumen reservoirs in order to avoid the killing of water insects, especially the protected dragonflies.

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Dragonflies Recognize the Water of Rendezvous and Oviposition Sites by Horizontally Polarized Light: A Behavioural Field Test

Hansruedi Wildermuth
Haltbergstrasse 43, CH-8630 Rüti, Switzerland

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As larvae, dragonflies and damselfies (Odonata) are aquatic. After emergence, during the aerial stage of their life cycle, the individuals scatter and congregate later at or near the species-specific oviposition site. For habitat selection to be successful, appropriate responses must be developed in both sexes, being directed towards mating in males, and towards mating and oviposition in females [1]. Accordingly one seeks to identify the cues that enable dragonflies to recognize their rendezvous and oviposition sites.

Odonatologists have repeatedly reported sexual behaviour and oviposition of species that lay eggs while in flight over roofs of automobiles, smooth cement floors and horizontally aligned panes [2–6]. Obviously, shiny surfaces and water, by virtue of their reflectivity, elicit the same behavioural responses. Dark crude oil surfaces prove even more attractive than water [7, 8].