

A 'polarisation sun-dial' dictates the optimal time of day for dispersal by flying aquatic insects

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SUMMARY

1. Daily changes in the flight activity of aquatic insects have been investigated in only a few water beetles and bugs. The diel flight periodicity of aquatic insects and the environmental factors governing it are poorly understood.

2. We found that primary aquatic insects belonging to 99 taxa (78 Coleoptera, 21 Heteroptera) fly predominantly in mid-morning, and/or around noon and/or at nightfall. There appears to be at least four different types of diurnal flight activity rhythm in aquatic insects, characterised by peak(s): (i) in mid-morning; (ii) in the evening; (iii) both in mid-morning and the evening; (iv) around noon and again in the evening. These activity maxima are quite general and cannot be explained exclusively by daily fluctuations of air temperature, humidity, wind speed and risks of predation, which are all somewhat stochastic.

3. We found experimental evidence that the proportion (%) $P(\theta)$ of reflecting surfaces detectable polarotactically as 'water' is always maximal at the lowest (dawn and dusk) and highest (noon) angles of solar elevation (θ) for dark reflectors while $P(\theta)$ is maximal at dawn and dusk (low solar elevations) for bright reflectors under clear or partly cloudy skies.

4. From the temporal coincidence between peaks in the diel flight activity of primary aquatic insects and the polarotactic detectability $P(\theta)$ of water surfaces we conclude 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–polarisation patterns, combined with an appropriate air temperature, clearly explain why polarotactic aquatic insects disperse to new habitats in mid-morning, and/or around noon and/or at dusk. We call this phenomenon the 'polarisation sun-dial' of dispersing aquatic insects.

Keywords: aquatic insect dispersal, detection of water, diel flight activity, polarisation vision, positive polarotaxis

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Introduction

Although it is well known that most aquatic insects can fly (Jackson, 1952, 1956, 1973; Fichtner, 1972; Kirby & Foster, 1991; Bilton, 1994), their seasonal and diel flight activity (Fernando, 1958; Popham, 1964; Pajunen

& Jansson, 1969; Fernando & Galbraith, 1973; Landin, 1980; Behr, 1990, 1993; Zalom, Grigarick & Way, 1990) and the influence on flight of environmental variables (Landin, 1968; Landin & Stark, 1973; Landin & Vepsäläinen, 1977; Nilsson & Svensson, 1992; Weigelhofer, Weissmair & Waringer, 1992; Bernáth, Gál & Horváth, 2004; Csabai & Boda, 2005) have been studied only sporadically. Most of our knowledge about the dispersal of aquatic insects originates from light-trapping at night (e.g. Tshernyishev, 1961; Nowinszky, 2003), in which insect phototaxis dominates. However, daily changes in the flight activity of aquatic insects cannot be assessed by 24-h light trapping, because the attraction of light traps to insects is considerably reduced by day due to the higher ambient light intensity. While suction traps may be of use for monitoring small, weakly flying insects, assessment of the diel pattern of a wide range of aquatic insects needs a method that is similarly efficient by day and night.

Both primary (where both adults and larvae are aquatic) and secondary (where only the larvae live in water) aquatic insects recognise their habitat by means of the horizontal linear polarisation of light reflected from the water surface (Schwind, 1991, 1995; Horváth & Varjú, 2003). The higher the degree of linear polarisation of reflected light, the more attractive is a reflecting surface to aquatic insects. Thus, a horizontal shiny black plastic sheet is an ideal trap for aquatic insects, because it always polarises the reflected light strongly and horizontally (Horváth & Varjú, 2003). Indeed, we observed in the field that in mid-morning, near noon and at dusk the rattling noise caused by thousands of primary aquatic insects crashing into such shiny black plastic sheets created the impression of an intense 'rain' of aquatic insects.

Using such traps, we explored the diel flight activity patterns of primary aquatic insects and assessed the most important factors governing their daily activity rhythm. We report here the major peaks in flight activity of almost one hundred (99) taxa of primary aquatic insects and their environmental correlates.

Methods

The biological part of our research was performed in the Hungarian Hortobágy National Park, on the shore of Hagymás Basin marsh (47°33'29" N, 20°55'29" E;

10 km × 10 km UTM grid code: DT 96) that is characterised by a patchy vegetation with a rich and diverse aquatic insect community. The area of the Hagymás Basin is 0.3 km² and the depth of water ranges between 25 and 60 cm. Aquatic insects were sampled using five different, colourless, horizontal test surfaces laid onto the ground: (i) aluminium foil; (ii) shiny white plastic sheet; (iii) shiny black plastic sheet; (iv) matt white cloth; and (v) matt black cloth. Each test surface had an area of 9 m × 3 m. One of each of the test surfaces was placed 25 m from the shoreline of the water and 10 m from each other. They were pinned to the ground with tent-pegs and their order was changed randomly.

The sampling was carried out between 10 March and 7 July 2000, when there were hourly captures continuously for 24 h every week from 08:00 hours Friday to 08:00 hours Saturday (local summer time = UTC + 2), giving a total of 18 sampling days over 18 weeks. During this 4-month period the exact time of sunrise (from 04:50 hours to 07:01 hours), noon (from 12:47 hours to 12:41 hours) and sunset (from 18:33 hours to 20:33 hours) shifted, and this is represented by grey bands in Figs 1 & 2. At sunrise and sunset the sun is placed at the horizon with an angle of solar elevation $\theta = 0^\circ$. During our 4-month sampling period the solar elevation angle θ_{\max} at noon changed from 38° to 67°. This angular shift of culmination is represented by a grey band in Figs 3 & 4.

Aquatic insects landing on the test surfaces were captured with aspirators (small species) or nets (large species) and preserved in 70% ethanol for later identification. Insects were attracted exclusively by the shiny black plastic (see Results). After landing, they stayed on the black plastic for various periods, when we could capture them. In the morning and evening, when the plastic was cool, the insects stayed for at least 5–15 min, when they tried to swim; they could not fly off due to the low temperature. In the forenoon and afternoon, when the plastic was hot, smaller (<20 mm) insects died in a few seconds due to dehydration. Larger (>20 mm) insects (e.g. *Dytiscus* species) could fly off, but were conspicuous and were easily seen and captured.

The polarimetric part of our research was performed near Kunfehértó in Hungary (46°23'N, 19°24'E). Using 180° field-of-view imaging polarimetry, we measured the reflection–polarisation

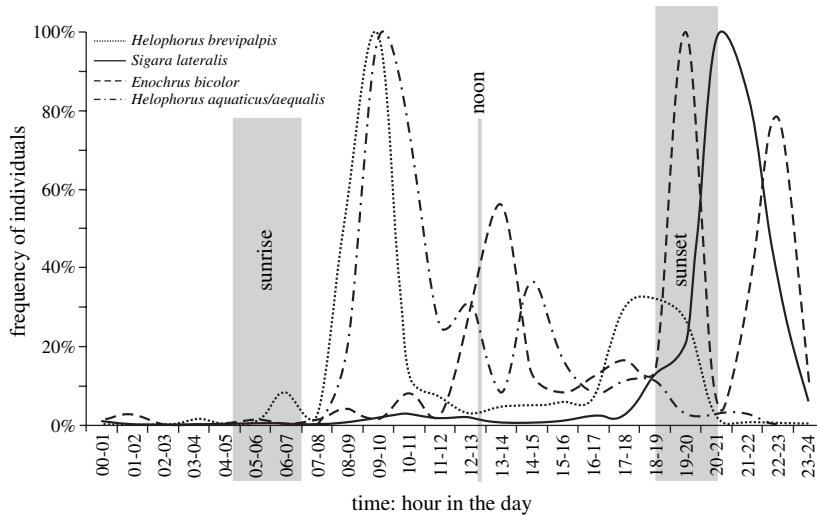


Fig. 1 Four different typical daily rhythms of dispersal by aquatic insects. Frequency of *Helophorus brevipalpis*, *Sigara lateralis*, *Enochrus bicolor* and *Helophorus aquaticus/aequalis* landed *en masse* on the horizontal shiny black plastic sheet as a function of the hour in the day (local summer time = UTC + 2). Frequency is calculated as the total number N of insects captured in any 1 h, summed over the 18 sampling days, divided by the maximum N_{max} . The temporal shifts of sunrise (from 04:50 hours to 07:01 hours), noon (from 12:47 hours to 12:41 hours) and sunset (from 18:33 hours to 20:33 hours) from the beginning to the end of our 4-month monitoring of aquatic insects are marked by grey bands.

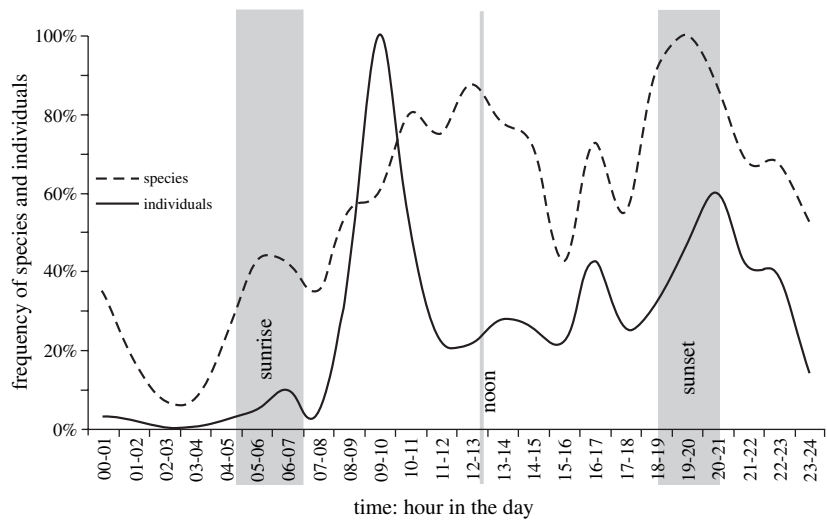


Fig. 2 Frequency of species (dashed) and individuals (continuous) of dispersing aquatic insects landed *en masse* on the horizontal shiny black plastic sheet as a function of the hour in the day. Other conventions as in Fig. 1.

patterns of two horizontal reflectors in the red (650 nm), green (550 nm) and blue (450 nm) spectral ranges as a function of the solar elevation angle θ from sunrise to an hour after sunset. This was done under clear and partly cloudy skies on 17 and 18 July 2002. Further details of our polarimetric method are given by Bernáth *et al.* (2004), who also describe reflection-polarisation patterns of 'black' and 'grey' reflectors as a function of solar elevation. These reflectors were composed of a 1 m × 1 m horizontal glass pane

underlain by a matt cloth. This cloth was either black or grey, imitating a 'dark' and 'bright' waterbody respectively. Dark waterbodies reflect a small amount of light, because they are deep, and/or their water contains dark suspended particles and/or their bed is dark (Bernáth *et al.*, 2002). On the other hand, bright waterbodies reflect a large amount of light, because their water contains bright suspended particles, and/or their water is clear and shallow and the bed is bright (Bernáth *et al.*, 2002).

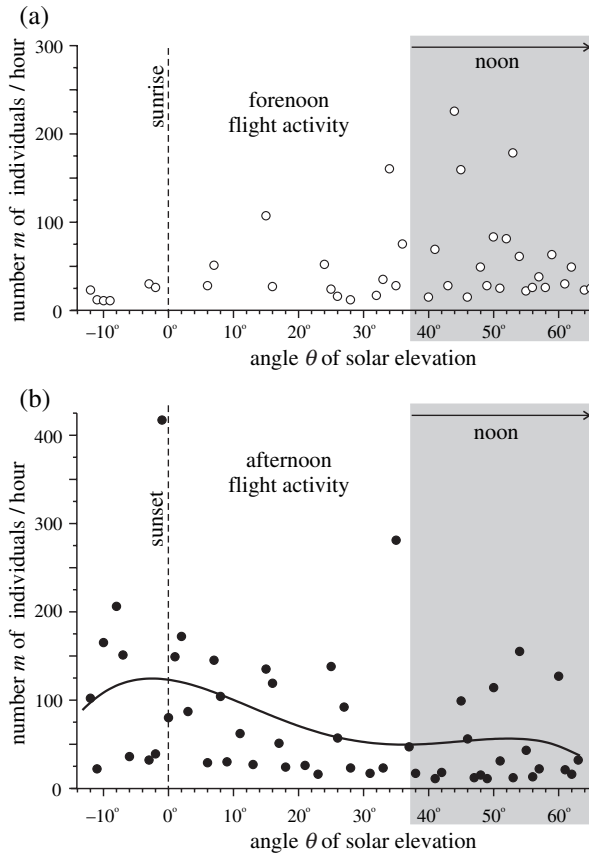


Fig. 3 Number m of aquatic insects per hour landing on the shiny black plastic sheet in the forenoon (a) and afternoon (b) as a function of the angle θ of solar elevation. $m = N/t$, where N is the total number of individuals caught during the total sampling time t (measured in hour) when the solar elevation was between θ and $\theta + \Delta\theta$ ($\Delta\theta = 1^\circ$) in the whole sampling period (18 days). The angular shift of solar culmination (noon) from the beginning to the end of our 4-month monitoring of aquatic insects is marked by grey bands, where horizontal arrows show the shift direction. The polynomial in (b) was fitted to the data points for the afternoon ($r^2 = 0.169$; $SD = 68.329$; $n = 74$; $P = 0.012$) period by means of the method of least squares.

Polarotactic aquatic insects trying to find water are attracted to any surface, if the degree of linear polarisation d of reflected light is higher than the threshold d_{tr} of polarisation sensitivity, and if the deviation $\Delta\alpha$ of the angle of polarisation of reflected light from the horizontal is smaller than a threshold $\Delta\alpha_{tr}$ in that part of the spectrum in which the polarisation of reflected light is perceived (Horváth & Varjú, 2003). Thus, a hypothetical polarotactic insect in flight over the centre of our test surfaces (black and grey reflectors) was assumed to mistake for water those areas of the reflectors from which skylight is

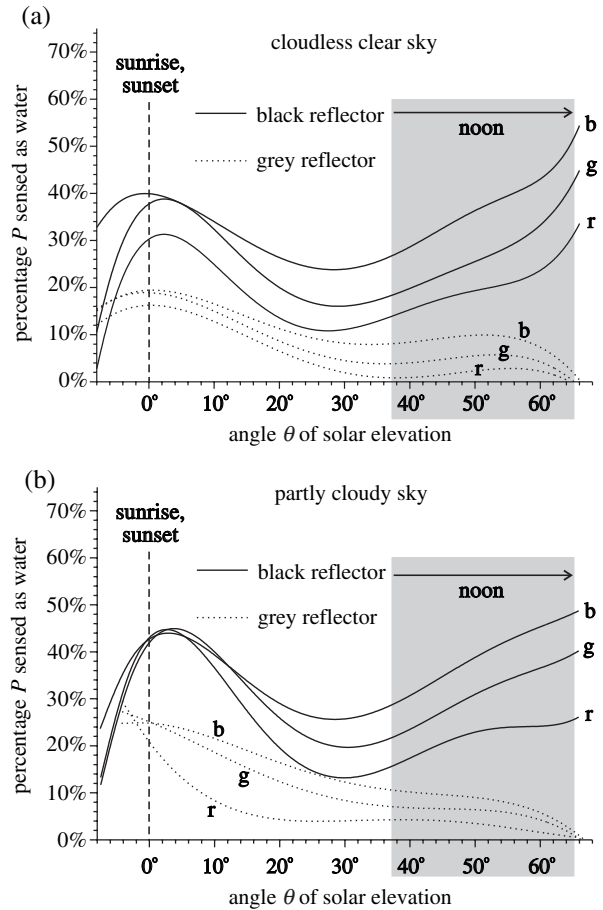


Fig. 4 Polarotactic detectability P , i.e. the percentage (%) of black (continuous) and grey (dashed) horizontal reflectors that would be sensed as water by water-seeking polarotactic aquatic insects as a function of the solar elevation angle θ in the blue (b, 450 nm), green (g, 550 nm) and red (r, 650 nm) parts of the spectrum under clear (a) and partly cloudy (b) sky. The angular shift of solar culmination (noon) from the beginning to the end of our 4-month monitoring of aquatic insects is marked by grey bands, where horizontal arrows show the shift direction.

reflected with the following two criteria: (i) degree of linear polarisation $d > d_{tr} = 5\%$; and (ii) deviation of the angle of polarisation $|\alpha - 90^\circ| < \Delta\alpha_{tr} = 5^\circ$. We introduce the quantity 'percentage (%) P of a reflecting surface sensed as water', which is the angular proportion P of all viewing directions (relative to the angular extension of 2π steradians of the whole lower hemisphere of the field of view of the hypothesised insect) for which both criteria are satisfied. In other words, P gives the relative proportion of the entire ventral field of view in which the reflecting surfaces would be sensed polarotactically as water. The higher the P -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. Thus, for the sake of simplicity, P is thereafter called 'polarotactic detectability'. P is actually a physical description of our test surfaces obtained from polarimetric measurements and is used to predict the perception of the insect subjects. Further details of the determination of the $P(\theta)$ curves in Fig. 4 (where θ is the solar elevation angle) can be found in Bernáth *et al.* (2004).

It would be very difficult to prove that polarotaxy in aquatic insects allows horizontally polarising reflectors to be 'seen as water' (even when they are not). Thus, a more guarded form of expression would be that horizontally polarising surfaces are 'attractive to water-seeking polarotactic aquatic insects as if they were water'. Instead of this long, but correct formulation, in this work we preferred the following simpler term: horizontally polarising surfaces are 'sensed polarotactically as water'.

Results

All the aquatic insects observed by us landed exclusively on the strongly and horizontally polarising shiny black plastic sheet, and avoided the other, non-polarising (matt black and matt white cloths, aluminium foil, shiny white plastic sheet) horizontal test surfaces (Csabai *et al.*, 2003, 2004). This practically proves that they are polarotactic: they detect water by polarotaxis, i.e. by the horizontal polarisation of reflected light, as do aquatic insects in general (Schwind, 1991, 1995; Horváth & Varjú, 2003). From the shiny black plastic sheet we collected 78 Coleoptera and 21 Heteroptera taxa (Table 1). We observed four different, species-specific types of daily rhythm of the aquatic insect dispersal (Fig. 1, Table 1):

1 The daily activity has one striking maximum in mid-morning, which gradually decreases to a minimum in the early evening. This type of dispersal is typical for the closely related species *Helophorus aquaticus/aequalis* (Fig. 1) and *Helophorus liguricus*, for example.

2 There are two peaks in daily activity, a major maximum in mid-morning and a minor peak at nightfall. *Helochares obscurus*, *Rhantus suturalis* and *Helophorus brevipalpis* (Fig. 1), for instance, possess such a pattern of activity.

Table 1 Aquatic Coleoptera and Heteroptera taxa captured on the horizontal shiny black plastic sheet

Coleoptera (78)
Haliplidae (5)
<i>Halipilus fluviatilis</i> (Aubé, 1836)
<i>Halipilus heydeni</i> (Wehncke, 1875)
<i>Halipilus immaculatus</i> (Gerhardt, 1877)
<i>Halipilus ruficollis</i> (De Geer, 1774)
<i>Peltodytes caesus</i> (Duftschmid, 1805) E
Dytiscidae (29)
<i>Cybister lateralimarginalis</i> (De Geer, 1774)
<i>Dytiscus circumflexus</i> (Fabricius, 1801)
<i>Dytiscus marginalis</i> (Linnaeus, 1758)
<i>Graphoderus austriacus</i> (Sturm, 1835)
<i>Acilius canaliculatus</i> (Nicolai, 1822)
<i>Hydaticus transversalis</i> (Pontoppidan, 1763)
<i>Hydaticus seminiger</i> (De Geer, 1774)
<i>Agabus bipustulatus</i> (Linnaeus, 1767)
<i>Agabus labiatus</i> (Brahm, 1790)
<i>Agabus uliginosus</i> (Linnaeus, 1761)
<i>Ilybius ater</i> (De Geer, 1774)
<i>Ilybius subaeneus</i> (Erichson, 1837)
<i>Rhantus frontalis</i> (Marsham, 1802)
<i>Rhantus suturalis</i> (MacLeay, 1825) ME
<i>Colymbetes fuscus</i> (Linnaeus, 1758)
<i>Laccophilus minutus</i> (Linnaeus, 1758) E
<i>Bidessus nasutus</i> (Sharp, 1887)
<i>Bidessus unistriatus</i> (Goeze, 1777)
<i>Hydroglyphus geminus</i> (Fabricius, 1792) E
<i>Graptodytes bilineatus</i> (Sturm, 1835)
<i>Hydroporus angustatus</i> (Sturm, 1835)
<i>Hydroporus fuscipennis</i> (Schaum, 1868)
<i>Hydroporus palustris</i> (Linnaeus, 1761)
<i>Hydroporus planus</i> (Fabricius, 1781)
<i>Porhydrus obliquesignatus</i> (Bielz, 1852)
<i>Hygrotus decoratus</i> (Gyllenhal, 1818)
<i>Hygrotus impressopunctatus</i> (Schaller, 1783)
<i>Hygrotus inaequalis</i> (Fabricius, 1776)
<i>Hygrotus parallellogrammus</i> (Ahrens, 1812)
Noteridae (1)
<i>Noterus clavicornis</i> (De Geer, 1774)
Hydrochidae (4)
<i>Hydrochus angustatus</i> (Germar, 1824)
<i>Hydrochus crenatus</i> (Fabricius, 1792)
<i>Hydrochus elongatus</i> (Schaller, 1783)
<i>Hydrochus flavipennis</i> (Küster, 1852)
Helophoridae (10)
<i>Helophorus aquaticus</i> (Linnaeus, 1758) M
<i>Helophorus aequalis</i> (Thomson, 1868) M
<i>Helophorus brevipalpis</i> (Bedel, 1881) ME
<i>Helophorus granularis</i> (Linnaeus, 1761) NE
<i>Helophorus liguricus</i> (Angus, 1970) M
<i>Helophorus longitarsis</i> (Wollaston, 1864)
<i>Helophorus micans</i> (Faldermann, 1835)
<i>Helophorus minutus</i> group
<i>Helophorus montenegrinus</i> (Kuwert, 1885) NE
<i>Helophorus nubilus</i> (Fabricius, 1776)
<i>Helophorus redtenbacheri</i> (Kuwert, 1885)

Table 1 (Continued)

Hydrophilidae (26)
<i>Coelostoma orbiculare</i> (Fabricius, 1775)
<i>Hydrobius fuscipes</i> (Linnaeus, 1758)
<i>Limnoxenus niger</i> (Zschach, 1788)
<i>Chaetarthria seminulum</i> (Herbst, 1797)
<i>Anacaena limbata</i> (Fabricius, 1792)
<i>Anacaena lutescens</i> (Stephens, 1829)
<i>Laccobius bipunctatus</i> (Fabricius, 1792)
<i>Laccobius minutus</i> (Linnaeus, 1758)
<i>Enochrus affinis</i> (Thunberg, 1794) E
<i>Enochrus bicolor</i> (Fabricius, 1792) NE
<i>Enochrus coarctatus</i> (Gredler, 1863)
<i>Enochrus fuscipennis</i> (Thomson, 1878)
<i>Enochrus melanocephalus</i> (Olivier, 1792)
<i>Enochrus ochropterus</i> (Marshall, 1802)
<i>Enochrus quadripunctatus</i> (Herbst, 1797) E
<i>Enochrus testaceus</i> (Fabricius, 1801)
<i>Helochaeres lividus</i> (Forster, 1771)
<i>Helochaeres obscurus</i> (O.F.Müller, 1776) ME
<i>Cymbiodyta marginella</i> (Fabricius, 1792) E
<i>Hydrochara caraboides</i> (Linnaeus, 1758)
<i>Hydrochara dichroma</i> (Fairmaire, 1892)
<i>Hydrochara flavipes</i> (Steven, 1808)
<i>Berosus frontifoveatus</i> (Kuwert, 1890) E
<i>Berosus luridus</i> (Linnaeus, 1761)
<i>Berosus signaticollis</i> (Charpentier, 1825)
<i>Berosus spinosus</i> (Steven, 1808)
Dryopidae (1)
<i>Dryops luridus</i> (Erichson, 1847)
Hydraenidae (2)
<i>Limnebius</i> sp.
<i>Ochthebius</i> sp.
Heteroptera (21)
Gerridae (2)
<i>Gerris argentatus</i> (Schummel, 1832)
<i>Gerris odontogaster</i> (Zetterstedt, 1828)
Mesoveliidae (1)
<i>Mesovelia furcata</i> (Mulsant et Rey, 1852)
Hebridae (1)
<i>Hebrus pusillus</i> (Fallén, 1807)
Corixidae (14)
<i>Micronecta</i> sp.
<i>Cymatia coleoptrata</i> (Fabricius, 1776)
<i>Cymatia rogenhoferi</i> (Fieber, 1864)
<i>Callicorixa praeusta</i> (Fieber, 1848)
<i>Corixa punctata</i> (Illiger, 1807)
<i>Hesperocorixa linnaei</i> (Fieber, 1848) E
<i>Paracorixa concinna</i> (Fieber, 1848)
<i>Sigara falleni</i> (Fieber, 1848)
<i>Sigara lateralis</i> (Leach, 1817) E
<i>Sigara limitata</i> (Fieber, 1848)
<i>Sigara nigrolineata</i> (Fieber, 1848)
<i>Sigara striata</i> (Linnaeus, 1775)
<i>Sigara</i> sp.
Corixinae
Naucoridae (1)
<i>Ilyocoris cimicoides</i> (Linnaeus, 1758)

Table 1 (Continued)

Notonectidae (1)
<i>Notonecta glauca</i> (Linnaeus, 1758)
Pleidae (1)
<i>Plea minutissima</i> (Leach, 1817) NE

The abbreviation of the activity rhythm type is given after the name of those species, the numbers of which were not smaller than 50; M, one major activity peak in mid-morning; E, one major activity peak in the evening; ME, a major maximum in mid-morning and a minor peak in the evening; NE, a minor maximum at noon or in the early afternoon and a major maximum in the evening.

3 The daily rhythm has a minor, brief maximum around noon or in the early afternoon, and a major, more prolonged maximum in the evening, which is occasionally split into a few peaks. This type is characteristic of, e.g. *Enochrus bicolor* (Fig. 1), *Helophorus montenegrinus* and *Helophorus granularis*.

4 There is only one peak in daily flight activity, in the early/late evening from 18 to 22 h. This is typical for *Berosus frontifoveatus*, *Cymbiodyta marginella*, *Enochrus quadripunctatus*, *Enochrus affinis*, *Hesperocorixa linnaei*, *Hydroglyphus geminus*, *Peltodytes caesus* and *Sigara lateralis* (Fig. 1), for example.

Fig. 2 shows the frequencies of species and individuals of dispersing primary aquatic insects landing *en masse* on our horizontal shiny black plastic sheet as a function of the hour in the day. Here, frequency means the total number N of insects captured in any one particular hour summed over the 18 sampling days, divided by the maximum N_{\max} . Two major peaks occurred in the frequency of individuals: the first in mid-morning between 09:00 hours and 10:00 hours, and the second at dusk between 20:00 hours and 21:00 hours. There were also two secondary peaks in the afternoon (13:00–14:00 hours and 16:00–17:00 hours). Late at night and before dawn the flight activity was minimal. The frequency of species was highest at sunset (19:00–20:00 hours) and noon (12:00–13:00 hours), and had a secondary peak at sunrise (05:00–06:00 hours).

Fig. 3 represents the number m of aquatic insects trapped per hour on the shiny black plastic sheet as a function of the solar elevation angle θ in the morning and in the afternoon. Here $m = N/t$, where N is the total number of individuals caught during the total sampling time t (measured in hour) when the solar elevation was between θ and $\theta + \Delta\theta$ ($\Delta\theta = 1^\circ$) in the

whole sampling period (18 days). The numbers of insects trapped at different solar elevations θ during the collection period were strongly influenced by air temperature, wind speed and rain. The polynomial fitted to the data for the afternoon was significant ($r^2 = 0.169$; $SD = 68.329$; $n = 74$; $P = 0.012$). Maxima of the polynomial indicates that aquatic insects flew predominantly around noon, when θ is the highest (Fig. 3b), and around sunset when θ is the lowest (Fig. 3b). The polynomial fitted to the forenoon data points was not significant ($r^2 = 0.079$; $SD = 93.979$; $n = 67$; $P = 0.272$). The air temperature was mostly too low for flight at sunrise. Thus, the first maximum flight activity, expected on the basis of the maximal polarotactic detectability P of water surfaces at sunrise, was not evident (Fig. 3a & 4). The other expected maximum at high solar elevations was clearly observable (Fig. 3a).

Fig. 4 displays the percentage P (polarotactic detectability given in %) of the black and grey horizontal reflectors (imitating dark and bright waterbodies) that would be sensed as water by our hypothetical polarotactic aquatic insect (see Methods) as a function of the solar elevation angle θ , measured in the blue, green and red parts of the spectrum, under clear and partly cloudy skies. The shorter the wavelength, the higher the polarotactic detectability P . Independently of the wavelength and the weather conditions (clear or partly cloudy), P is maximal at the lowest θ (sunrise and sunset) as well as at the highest θ (noon) for the black reflector (dark waters), while P is maximal at the lowest θ (sunrise and sunset) for the grey reflector (bright waters).

Discussion

Our understanding of factors governing the flight of primary aquatic insects in nature is still poor. Much data on the flight of aquatic insects comes from light trap studies, which do not adequately reflect natural behaviour. Therefore, we monitored their flight by use of a trap consisting of a strongly and horizontally polarising shiny black plastic sheet, which is as attractive to polarotactic aquatic insects as is a natural dark water surface. Our hypothesis was that the diel flight activity pattern of aquatic insects is governed predominantly by the polarotactic detectability $P(\theta)$ of water surfaces depending on the solar elevation angle θ . This hypothesis was supported by the experimental data presented here.

Many polarotactic aquatic insects fly most actively at dusk and/or in mid-morning. Many other insects are non-polarotactic and are not associated with water, and some of them may also disperse at low solar elevations, in the evening and morning (e.g. Danthanarayana, 1986). In the case of such insects the daily change of the polarotactic detectability P of water surfaces is irrelevant, and their flight activity patterns may be governed by other environmental factors, such as the air temperature, air humidity, wind velocity and predation risks, for example.

The exact pattern of the daily flight activity of aquatic insects is species dependent (Fig. 1) and is probably governed partly by air temperature, relative humidity and wind velocity. However, these environmental factors strongly depend on the weather: generally, the higher the air temperature, the lower the humidity. Thus, humidity is usually low at noon and in the early afternoon, when air temperature is generally maximal, while humidity is generally high in the morning and at nightfall, when air temperature is usually low. As higher humidity is advantageous for flying aquatic insects, due to the reduced risks of dehydration, dawn and dusk are optimal for flight. However, peak flight activity was observed around noon and in the afternoon (Figs 1 & 2) when low humidity is very disadvantageous, as is the high risk of visual predation (e.g. by birds and dragonflies). Dawn and dusk offer a lower risk of visual predation, although the risk of predation from echolocating bats is usually high. High wind speeds (*c.* $>6 \text{ km h}^{-1}$) strongly influence the flight activity of aquatic insects, while below a certain (probably species dependent) wind speed threshold (*c.* $<6 \text{ km h}^{-1}$) the flight of water beetles and bugs was not influenced (Csabai & Boda, 2005). Around noon the wind speed is usually much greater than that after dusk and before dawn due to thermal convection currents in the air at night (Landin & Stark, 1973). Therefore, flying at noon and in the afternoon in wind is more disadvantageous to aquatic insects than flying at dawn and dusk in still air. However, as a high air temperature is necessary for the efficient functioning of insect flight muscles, flying near dawn is disadvantageous due to the usually lowest air temperature.

It is clear from the above that the three daily maxima in the flight activity of aquatic insects observed in mid-morning, around noon and around nightfall cannot be explained on the basis of daily

variations in air temperature, humidity, wind speed and/or risk of predation. Daily changes in these environmental factors are rather stochastic, due to the chaotic weather fluctuations.

Our data lead us to suggest that one of the most important factors is the polarotactic detectability $P(\theta)$ of waterbodies, while air temperature, humidity, wind and predation risks are secondary. We emphasise that sufficiently high $P(\theta)$ -values are a prerequisite for the polarotactic detection of water by dispersing aquatic insects: if $P(\theta)$ is too low, it is not worth flying, because the surface of waterbodies cannot be polarotactically detected, despite other secondary advantages (such as low wind velocity, for example). Note that for dark waters (simulated by the black reflector), the maxima of $P(\theta)$ at the highest and lowest solar elevations θ (Fig. 4) coincide with the two maxima in the daily flight activity (at the highest θ near noon and at the lowest θ around sunset; Fig. 3). On the other hand, for bright waters (imitated by the grey reflector), the maximum of $P(\theta)$ at the lowest θ (Fig. 4) coincides with the activity maximum of aquatic insects (at the lowest θ near sunset; Fig. 3). The first temporal peak in dispersal is in mid-morning rather than at sunrise, when the solar elevation θ is minimal (zero) and the polarotactic detectability $P(\theta)$ of waters is maximal. The reason for this is that the air temperature must increase from its minimum at dawn so that the insects can fly. Thus, the flight maximum in mid-morning (09:00–10:00 hours, Figs 1 & 2) is a compromise between simultaneous maximisation of polarotactic detectability and air temperature.

Our results raise the following questions: What is the biological (ecological) significance of the four different patterns of daily activity of aquatic insects? What induces aquatic insects to leave their habitats *en masse* with species-specific dynamics, in spite of the great aerial danger of predation and dehydration? Food shortage, or weather dependent, stochastic changes in the environment cannot account for the observed diel flight activity patterns of aquatic insects. It is more probable that the daily activity is driven by species-dependent reproduction and colonisation, which significantly enhance the success of reproduction and survival.

We conclude that mid-morning and nightfall are two optimal periods of the day for aquatic insects to disperse, due to the high (morning) or maximum

(nightfall) polarotactic detectability $P(\theta)$ of dark and bright waters (Fig. 4) and because air temperature is usually sufficient. Around noon/early afternoon is a further optimal period for dispersal by insects that are looking for dark waters, because then the polarotactic detectability $P(\theta)$ of dark waterbodies is always maximal (Fig. 4), as usually is air temperature. This explains the third activity maximum of certain aquatic insects around noon.

These three optimal periods for dispersal by polarotactic aquatic insects, governed by the reflection–polarisation pattern of the water surface, can be easily and reliably identified on the basis of the solar elevation θ , even under the water where neither air temperature nor wind velocity can be perceived. This phenomenon can be called a ‘polarisation sun-dial’ for dispersing aquatic insects. Our findings put the ecology of dispersal by aquatic insects in a new context, because we have demonstrated that the daily flight activity of aquatic insects is highly likely to be optically governed. Although the polarotactic detection of water by aquatic insects is well established (Schwind, 1991, 1995; Horváth & Varjú, 2003), we have shown here experimentally that, beyond air temperature, the daily flight activity of aquatic insects is most closely associated with the polarotactic detectability $P(\theta)$ of water.

We need to note that natural waterbodies can be considered as ‘bright’ or ‘dark’ only in a restricted range of the wavelength λ . This wavelength range can be wide (e.g. from 400 to 750 nm) or narrow (e.g. from 500 to 600 nm). The former look bright or dark, while the latter have some colour (e.g. greenish due to a dense growth of phytoplankton) for the human eye. As a consequence, in the latter case the polarotactic detectability $P(\lambda)$ can alter significantly with wavelength. This phenomenon may determine the spectral regions in which aquatic insects detect aquatic habitats of different types (Schwind, 1995).

As the polarotactic detectability $P(\theta)$ is determined by the time-dependent angle of solar elevation θ , the duration of optimal periods for dispersal should change with latitude. Near to the Equator, morning and evening periods of high $P(\theta)$ are much shorter, due to the rapid rise and set of the sun. The consequence of this could be an intense, but short flight activity period of polarotactic aquatic insects at dusk and dawn because suitable temporal interval is brief. When $P(\theta)$ is high also around noon, the air

temperature near to the Equator is so high that aquatic insects might not fly at all.

Near to the Arctic Circle the daily variation in the angle of solar elevation is moderate, the consequence of which is a moderate change in air temperature and in the polarotactic detectability $P(\theta)$ of water. Thus one might expect that the daily activity peaks of polarotactic aquatic insects may be less evident. A test of these predictions would be an interesting task in the future.

An interesting effect occurs far beyond the Arctic Circle, where the sun does not set for half a year: as the solar elevation angle θ changes between about 10° and 40° for several weeks, the polarotactic detectability $P(\theta)$ of waters remains low for several weeks (Fig. 4). This means that even dark waterbodies (typical in the boreal coniferous forests of these arctic areas where water is often stained brown by humic substances, for example) remain polarotactically poorly detectable for long periods.

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References

- Behr H. (1990) Untersuchungen zum Flug- und Immigrationsverhalten von Wasserkäfern der Gattung *Hydroporus* Claiv. (Col.: Dytiscidae). *Drosera*, **90**, 77–94.
- Behr H. (1993) Wiederfangergebnisse aus Markierungsexperimenten an fünf in einem Moorgewässer koexistierenden *Hydroporus*-Arten (Coleoptera; Dytiscidae: Imagines). *Zoologisches Jahrbuch der Systematik*, **120**, 201–214.
- Bernáth B., Szedenics G., Wildermuth H. & Horváth G. (2002) How can dragonflies discern bright and dark waters from a distance? The degree of polarization of reflected light as a possible cue for dragonfly habitat selection. *Freshwater Biology*, **47**, 1707–1719.
- Bernáth B., Gál J. & Horváth G. (2004) Why is it worth flying at dusk for aquatic insects? Polarotactic water detection is easiest at low solar elevations. *Journal of Experimental Biology*, **207**, 755–765.
- Bilton D. (1994) The flight apparatus and flying ability of *Hydroporus glabriusculus* (Coleoptera, Dytiscidae), with a brief review of structural modifications in flightless beetles. *Entomologisk Tidskrift*, **115**, 23–32.
- Csabai Z. & Boda P. (2005) Effect of the wind speed on the migration activity of aquatic insects (Coleoptera, Heteroptera). *Acta Biologica Debrecina Supplementum Oecologica Hungarica*, **13**, 37–42.
- Csabai Z., Gidó Zs., Móra A., Boda P., Dévai Gy., Király A., Szilágyi K. & Varju T. (2003) Migration activity patterns of aquatic beetles and aquatic bugs (Coleoptera, Heteroptera) I. Changing of the number of individuals and species richness. *Journal of the Hungarian Hydrological Society*, **83**, 29–32.
- Csabai Z., Gidó Zs., Boda P. & Móra A. (2004) Migration activity patterns of aquatic beetles and aquatic bugs (Coleoptera, Heteroptera) III. Seasonal and daily migration of selected species. *Journal of the Hungarian Hydrological Society*, **84**, 28–30.
- Danthanarayana W. (ed.) (1986) *Insect Flight: Dispersal and Migration*. Springer, Berlin, Heidelberg, New York.
- Fernando C.H. (1958) The colonization of small freshwater habitats by aquatic insects. 1. General discussion, methods and colonization by the aquatic Coleoptera. *Ceylon Journal of Science*, **1**, 117–154.
- Fernando C.H. & Galbraith D. (1973) Seasonality and dynamics of aquatic insects colonizing small habitats. *Verhandlungen des Internationalen Vereins der Limnologie*, **18**, 1564–1575.
- Fichtner E. (1972) Flugvermögen und Lichtfang und Wasserkäfern (Nachtrag). *Entomologische Nachrichten*, **16**, 47–50.
- Horváth G. & Varjú D. (2003) *Polarized Light in Animal Vision – Polarization Patterns in Nature*. Springer, Heidelberg, Berlin, New York.
- Jackson D.J. (1952) Observations on the capacity for flight of water beetles. *Proceedings of the Royal Entomological Society of London*, **27**, 57–70.
- Jackson D.J. (1956) Observations on flying and flightless water beetles. *Journal of the Linnaean Society of London*, **43**, 18–42.
- Jackson D.J. (1973) The influence of flight capacity on the distribution of aquatic Coleoptera in Fife and Kinross-shire. *Entomologist's Gazette*, **24**, 247–293.
- Kirby P. & Foster G.N. (1991) *Agabus uliginosus* takes off. *Balfour-Browne Club Newsletters*, **49**, 8–9.
- Landin J. (1968) Weather and diurnal periodicity of flight by *Helophorus brevipalpis* Bedel (Col. Hydrophilidae). *Opuscula Entomologica*, **33**, 28–36.
- Landin J. (1980) Habitats, life histories, migration and dispersal by flight of two water-beetles *Helophorus*

- brevipalpis* and *H. strigifrons* (Hydrophilidae). *Holarctic Ecology*, **3**, 190–201.
- Landin J. & Stark E. (1973) On flight thresholds for temperature and wind velocity, 24-hour flight periodicity and migration of the water beetle *Helophorus brevipalpis*. *ZOON (Journal of Zoology of the Uppsala University), Supplement*, **1**, 105–114.
- Landin J. & Vepsäläinen K. (1977) Spring dispersal flights of pond-skaters, *Gerris* spp. (Heteroptera). *Oikos*, **29**, 156–160.
- Nilsson A.N. & Svensson B.W. (1992) Taking off in cold blood – *Dytiscus marginalis* flying at 6.4 °C. *Balfour-Browne Club Newsletters*, **50**, 1–2.
- Nowinszky L. (2003) *The Handbook of Light Trapping*. Savaria University Press, Szombathely, Hungary.
- Pajunen V.I. & Jansson A. (1969) Dispersal of the rock pool corixids *Arctocoris carinata* (Sahlb.) and *Callicorixa producta* (Reut.) (Heteroptera, Corixidae). *Annales Zoologici Fennici*, **6**, 391–427.
- Popham E.J. (1964) The migration of aquatic bugs with special reference to the Corixidae (Hemiptera Heteroptera). *Archiv für Hydrobiologie*, **60**, 450–496.
- Schwind R. (1991) Polarization vision in water insects and insects living on a moist substrate. *Journal of Comparative Physiology A*, **169**, 531–540.
- Schwind R. (1995) Spectral regions in which aquatic insects see reflected polarized light. *Journal of Comparative Physiology A*, **177**, 439–448.
- Tshernyishev W.B. (1961) The time of flight of different insects to light. *Zoologicheskij Zhurnal*, **40**, 1009–1018.
- Weigelhofer G., Weissmair W. & Waringer J. (1992) Night migration activity and the influence of meteorological parameters on light-trapping for aquatic Heteroptera. *Zoologischer Anzeiger*, **229**, 209–218.
- Zalom F.G., Grigarick A.A. & Way M.O. (1990) Diel flight periodicities of some Dytiscidae (Coleoptera) associated with California rice paddies. *Ecological Entomology*, **5**, 183–187.

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