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When do beetles and bugs fly? A unified scheme for describing seasonal flight behaviour of highly dispersing primary aquatic insects

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When do beetles and bugs fly? A unified scheme for describing seasonal flight behaviour of highly dispersing primary aquatic insects

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Keywords: flight behaviour, seasonal patterns, year-long dispersal, polarotaxis, Coleoptera, Heteroptera

Introduction

Overwintering, mating and deposition of eggs in suitable aquatic habitats are instinctive goals for aquatic insects (Bohonak & Jenkins 2003). To be in the most suitable habitat in each period of their life cycle, aquatic beetles and bugs shuttle among these habitats by flight according to their 'colonization cycle' denoted by Fernando & Galbraith (1973). Flight is not the only but the most effective way of dispersal (Bilton et al. 2001) and be an important prerequisite of survival in both individual and population level (Landin 1980). Indirectly, dispersal flight is important from conservation biological (Eyre 2006), and evolutionary points of view (Wagner & Liebherr 1992). Thus, understanding this kind of dispersal behaviour of aquatic insects is an old goal for ecologists.

The phenomenon of the dispersal flight, as a result of complex processes is driven and influenced by many biotic and abiotic factors: e.g. elevation of the sun which determines the polarotactic detectability of water surfaces (Csabai et al. 2006), air temperature (Weigelhofer et al. 1992), water temperature (Popham 1953, Pajunen & Jansson 1969), wind speed (Pajunen & Jansson 1969, Csabai & Boda 2005), rain, reproductive status (Boda & Csabai 2009a), density (Yee et al. 2009, Pajunen & Pajunen 2003), actual state and changing of the original habitat (food sources, decrease of the water level, amount of predators, etc.) as noted by Nilsson & Svensson 1992, Ohba & Takagi 2005, Yee et al. 2009, for example. Almost all of these factors are continuously changing in time; many of them are changing between well defined thresholds through different seasons. All of the environmental factors together have a well defined seasonal rhythm, and it clearly defines the possibilities and needs of dispersal flight, so they must have a seasonal rhythm, too. If this is so, the most useful approach to describe the year-long changes of dispersal flight would be a season-based one.

Many authors have investigated the flight of aquatic beetles and bugs and the literature is rich with useful information and data about the seasonal changes of aerial dispersal. Some authors tried to describe the changes of the dispersal behaviour during longer periods than one season (Thomas 1938, Leston & Gardner 1953, Brown 1954, Fernando 1958, Richard 1958, Young 1966, Pajunen & Jansson 1969, Benedek & Jászai 1972, Fernando & Galbraith 1973, Landin 1980, Bagge 1982, Van der Eijk 1987, Behr 1990, Weigelhofer et al. 1992, Nilsson 1997, Lundkvist et al. 2002, Miguélez & Valladares 2008), while others noted only some clearly visible peaks of dispersal activity (Popham 1964, Williams 1987, Davy-Bowker 2002) or just noted that the dispersal flight occurred in warmer days without strong wind (Richardson 1907, Macan 1939, Poisson et al. 1957). Generally, the objects of these investigations are restricted to only a few species. Moreover, most of the former studies were conducted by using light traps (e.g. Benedek & Jászai 1972, Zalom et al. 1980, Weigelhofer et al. 1992), but in these cases only the evening and the night flight are observable, which is important but only a short part of the daily flying period. In colder seasons of the year (spring and autumn) no dispersal activity could be observed during night flights mainly due to the lower evening and night air temperature, although the dispersal flight can be remarkable during daytime in these seasons too (Csabai et al. 2012). Applying the light-trap method we cannot draw reasonable conclusions about the rhythm of the year-long dispersal flight. There are some methods, which might be proper to follow up year-long dispersal behaviour such as mark-recapture methods (Pajunen & Jansson 1969, Davy-Bowker 2002, Pajunen & Pajunen 2003), water filled trays, tanks or pools (Fernando & Galbraith 1973, Behr 1990, Lundkvist et al. 2002, Boix et al. 2011), but these techniques require huge sampling efforts to studying dispersal flight throughout the year. Strictly because of the above mentioned shortcomings just some of these papers (Pajunen & Jansson 1969, Fernando & Galbraith 1973, Landin 1980, Behr 1990, Nilsson 1997, Lundkvist et al. 2002, Miguélez & Valladares 2008) treated and tried to describe the real seasonal rhythm of dispersal flight. Additional dispersal-based studies focused not on seasonal dispersal activity but on other strongly specified questions, which are only marginally affected by seasonal dispersal flight.

Summarized, many details of the seasonal dispersal flight of certain species have become known thanks to former studies conducted by variously applied methods. However these data were episodic and no one has yet tried to integrate the accumulated knowledge into a comprehensive scheme.

The aim of our work was to describe the dispersal flight activity of a wide spectrum of aquatic insects all day long on every week during a whole year period. We hypothesized that species (or group of species) can be characterized by different yearly rhythms of dispersal flight. Based on the annual flight data of a wide spectrum of species we proposed here a new unified scheme with seasonal approach for classification and description of seasonal dispersal flight. Finally, in spite of the methodological incongruence, we tried to insert the previously published results into the scheme.

Material and methods

Study site: Our study area was in north-eastern Hungary, in the territory of Hortobágy National Park, in the area of the Egyek-Pusztakócs Marsh System, at the shore of Hagymás-basin marsh (47°33'29” N, 20°55'29” E; 10 km ×10 km UTM grid code: DT 96). It lies in a semiarid-semihumid climatic region, where average yearly air temperature is 9.8–9.9 °C. Average yearly precipitation is 520–550 mm, and most of that falls in spring and autumn. The area of the Hagymás-basin was approximately 0.3 km^2 with depth up to 80 cm. The marsh was characterized by various and extremely patchy vegetation, and consequently by rich and diverse aquatic beetle and bug assemblages (Csabai et al. 2005). During the sampling period the water level of the marsh was more or less permanent, because of the continuous water supply from floods and rainfalls.

Theoretical basis of the sampling method: Almost all aquatic insects are capable of detecting polarised light (Horváth & Varjú 2004, Kriska et al. 2007, Horváth et al. 2011). Aquatic beetles and bugs can also find new habitats by means of the horizontal polarization of light reflected from the water surface (Schwind 1991). Shiny surfaces (e.g. car bonnets, black plastic sheets used in agriculture, vertical glass surfaces) – from which the direction and the degree of the polarized light is similar to that of the light reflected from water surfaces – may confuse polarotactic water insects, since they detect them as horizontally polarizing water surfaces (Horváth 1995). Therefore aquatic insects can be trapped by using these artificial surfaces (Bernáth et al. 2001).

Sampling period, method and elaboration: In the light of climatic and meteorological conditions in Hungary and their effects on the seasonal flight activity and phenology of primary aquatic insects (e.g. Boda & Csabai 2009a, 2009b), samples were taken altogether on 30 sampling weeks, from 14th week (beginning of April) until 43rd week (end of October) in 2005. Aquatic insects were collected for 24 hours on every week separated hourly. Sampling began every Wednesday at 8 a.m. (Local summer time: UTC + 2), regardless of weather conditions and was carried out until the next morning (8 a.m.). Aquatic insects were trapped on three black agricultural plastic sheets (foils) laid onto the ground, all of them were 9 m × 3 m in size. During the sampling period several such plastic sheets were used, their order was changed randomly. These test surfaces were placed 40 m apart from each other, and 30 m from the water margin. Using insect aspirators, water bugs and beetles that landed on the test surfaces were collected continuously by manual sampling. Individuals from the test surfaces were put into separate bottles hourly, which were labeled by the code of the surface and the time and date of collection. Collected animals were preserved in 70% ethanol. Beetles were identified under stereomicroscope in the laboratory using keys and descriptions by Csabai (2000) and Csabai et al. (2002). Aquatic bugs were identified using keys by Jansson (1986), Savage (1989) and Soós et al. (2009). *Dryops* spp., *Hydrochus* spp. and *Helophorus* spp. taxa were identified only to genus level.

Evaluation: Despite the hourly separated samples, daily pooled data were used during evaluation. There were no significant differences among the catch efficiencies of the sheets (Csabai et al. 2012), hence the data originating from the three sheets were grouped together in the evaluation. Those sampling days, when the weather conditions (strong wind and rain) inhibited or extremely decreased the dispersal flight – 16th, 18th and

23rd weeks – were ignored and excluded from the evaluation. There were two notable altering dates in the composition of the flying assemblage [numbers of individuals of each species (see details in Csabai et al. 2012)]. The first such date was on the 21st week, and another one was in the 35th week. These two dates show high coincidence with the turning points of the seasons. Hence, seasonal approach with two stages was used to analyze the data and define the main dispersal periods. The characteristic of dispersal flight in case of a given species can be assessed as proportion of the maximal dispersal flight activity. Hence, the comparison will be relevant in cases of various regions and in cases of certain species by the help of this percentile approach. Maximal dispersal activity of species can be observed solely in one season, with a global peak of activity. This global peak with maximal number of individuals was regarded as 100 % of the dispersal activity and further activity peaks were expressed as a percentage of this global peak. Besides the maximal dispersal peak, there might be lower but clearly visible peak(s) of flight activity in another season or seasons. If these additional peaks reached at least 20% of the maximal flight activity, it was considered as a significant local peak. Namely, the season of the maximal dispersal activity with the global peak may define the 'seasonal dispersal main pattern'; moreover local peak(s) of dispersal activity or its absence may correspond to the 'seasonal dispersal sub-pattern'. Relations of the local peaks to each other were not taken into consideration in the sub-pattern stage because of their high variability and less importance. Thereby, spring (SP), summer (SU) and autumn (AU) main patterns and related sub-patterns are evolved (Table 1 and 2). The naming process follows the evaluation stages as three-code signs. Namely, the code written in capital letters means the abbreviation of the main pattern (SP, SU or AU), the other codes with small letters refers to the sub-patterns (sp, su, au). The order of the codes follows the natural order of seasons. For example, sp-SU-au means that the highest flight activity peak can be found during summer and additional local peaks are visible during spring and autumn, of which either local peak can be higher or lower. '0' code was used when one or both of the additional local peaks were absent such as in the following cases for example: 0-SU-0 means maximal activity in summer and no significant dispersal flight during spring and autumn; sp-0-AU means maximal activity in autumn and local peak(s) can be found only in spring, but not during summer; or SP-0-au means highest dispersal activity in spring, no notable flight in summer but local peak(s) present during autumn. All possible combinations of patterns and sub-patterns according to the seasons with a short description of each combination were summarized in Table 2. All of the common species can be placed into one combination of the patterns and sub-patterns with no doubt, but below 100 captured individuals, the flight dynamics might be formed by coincidental occurrences, hence dispersal patterns of these less common species were assigned as questionable. To prove the soundness of the scheme based on the percentile approach we used non-metric multidimensional scaling (NMDS) ordination with Euclidean distances. Dispersal characteristics of all common species were included in the analyses; as variables the percentage share of dispersal peaks were used. On the scattergram, species of each main pattern were denoted by convex hulls, while sub-patterns were signed with different symbols.

Results

45 433 specimens belonging to 90 taxa of water beetles (40 200 individuals, 69 taxa) and bugs (5 233 individuals, 21 taxa) were captured (Table 1). The collected species are common inhabitants of both temporary and permanent waters and they are generally good fliers (Savage 1989, Nilsson & Holmen 1995). Dispersal flight of aquatic insects was observed from April till October with various numbers of individuals and species (Figure 1).

Generally, the species showed different activity in the seasons (Table 1). Based on the two stages seasonal approach, we observed all of the three possible main patterns and 10 sub-patterns of the 12 possible ones (Figure 2 A-I). All possible and realized combinations of patterns and sub-patterns according to the seasons were listed in Table 2. Based on the captured numbers of individuals, 22 species were regarded as common species (n>100) and in these cases the classification could be done without doubt. The dispersal pattern/sub-pattern could be assigned with relatively high certainty to 23 species (10<n<100), but the classification was still questionable. Further 45 species cannot be classified to any seasonal pattern because of the small numbers of individuals (n<10). 29 of 45 more common species flew during all of the three seasons, 14 species occurred in two seasons only, while two were noticed only in one season (Table 1).

More than half, 24 of 45 more common species flew according to the summer (SU) main pattern; it was the most popular season for flight. There were no species – except some with extreme low numbers of individuals (n<10) – which did not fly in summer. 17 species followed the spring (SP) and only four species followed the autumn (AU) main-patterns. Within the spring main pattern (SP), the most frequent sub-patterns were the SP-0-0 and SP-su-0 sub-patterns, both followed by 8 species. There was only one species which flew according to SP-0-au sub-pattern. Within the summer main pattern (SU), the 0-SU-0 sub-pattern was preferred the most (16 species), but 2-2 species flew according to the 0-SU-au sub-pattern and the sp-SU-au sub-pattern. Although, sp-SU-0 sub-pattern had 4 follower species, but all of them were less common species (10<n<100), so in these cases the classifications were questionable. Among the three species, which flew *en masse* in autumn, one followed the 0-0-AU sub-pattern, one the sp-0-AU sub-pattern, and one the 0-su-AU sub-pattern; moreover the later one has further follower species with lower number of individuals.

During the evaluation we revealed that there might be two more sub-patterns theoretically (Table 2). In spite of that, we could not find species which flew in spring like SP-su-au sub-pattern and in autumn as sp-su-AU sub-pattern. Namely, there were no species in our study which flew *en masse* during all the three seasons and the maximal dispersal activity was in spring or autumn. Based on the theoretical background of the scheme, the realness of the hypothetic sub-patterns are highly presumptive. Even if these sub-patterns were considered theoretical, we treated them as genuine parts of the scheme.

Based on the NMDS ordination, the dispersal flight characteristics in case of the common species were truly different in pattern and sub-pattern levels, the scattergram clearly shows that species were classified to different patterns and sub-patterns were highly separated each other (Figure 3). The species formed three well-separated groups according to the main patterns, the sub-patterns also separated well within these groups.

Discussion

It is notable, that aquatic insects achieve dispersal flight in any period of the year, but its extent and duration have remained poorly understood in the majority of primary aquatic insect species. We used an adequate new sampling method (Csabai et al. 2006, 2012) to follow up the seasonal changes of dispersal flight. A unified scheme was established based on seasonal dispersal activity of 45 species to assess the types of seasonal dispersal behaviour. In the first stage spring, summer and autumn seasonal dispersal main patterns were observed. In general, we found that there are no periods from the beginning of April till the end of October, when aquatic insects are not rising into the air. Most of the species flew in maximal number of individuals in summer. This is highly consistent with the results of all former studies (Table 3), but we revealed that there are several species which flew ‘*en masse*’ in spring and autumn. Dispersal flight in spring and autumn were mentioned in former publications, but rarely assigned as maximal peaks of activity. The optimal flying periods are shorter in spring and autumn than summer because of the rainfall and the lower air temperature (Csabai et al. 2012). In spite of this, a lot of species show maximal dispersal activity during either of these colder periods. In the second stage we described 12 sub-patterns all together. The common marsh dwelling species utilized nine of them in Hungary; hence these are treated as realized sub-patterns. One further sub-pattern exists with only some species and low numbers, so the presence of this sub-pattern can be not clearly revealed in our region. There are two more sub-patterns (SP-su-au, sp-su-AU) marked as theoretical sub-patterns which were not realized during our sampling period and/or among these marsh-dwelling species in Hungary. Naturally, there might be followers for these sub-patterns at different habitats and/or in different geographical areas.

General conclusions about the dispersal or concrete seasonal peaks of dispersal flights were described by many authors using various sampling methods. But only those dispersal-based studies pointed out the seasonal changes of dispersal flight, in which the sampling periods covered three seasons and the sampling frequency was strictly regular (Table 3). Based on these papers, the first period of dispersal flight might occur during April and May. Generally, both the mass and maximal dispersal flights were observed in the summer months. From September to the end of October only a low number of individuals were collected. Respectively, several exact seasonal flight periods and peaks of dispersal activity were mentioned by these authors, but the differences between the extents of peaks were never taken into consideration. Without the assessment of the relationship among the peaks it is hard to draw exact conclusions about the seasonal changes of dispersal behaviour. We are not only considering the extent of the peaks, but this is also the basis of the scheme. Despite that our scheme was established based on a Hungarian pilot study, the classification is widely and generally applicable to characterize the seasonal dispersal flight of primary aquatic insects. To demonstrate this, we selected some former studies in which the sampling periods were more than seven months (covering three seasons) and reported high numbers of collected individuals, moreover the changes of the dispersal activity are traceable and the applied method is adequate to study the seasonal dispersal rhythm (Table 4). Six of these seven studies investigated the seasonal flight periods of aquatic beetles, whereas only one paper dealt with this kind of activity of aquatic bugs. Reviewing these studies well-defined seasonal dispersal description can be found in cases of 19 species. Unfortunately there are only three aquatic beetle species which were common both among results of these studies and in our checklist and further three aquatic beetle species were common among the cited papers (Table 4). In the case of these species, strong differences in the seasonal patterns could have been caused by a few factors.

1. *Geographic differences:* In case of *Anacaena limbata*, Fernando & Galbraith (1973) mentioned an SU main pattern with various sub-patterns (sp-SU-0 or sp-SU-au) in Canada, but we observed this species as a typical spring flyer (SP-0-0). Both classifications are based on many data (more than 500 individuals), hence the classifications are not questionable. The spring dispersal period was observed in the dispersal behaviour in both regions. The climate of the Canada might have formed the various seasonal dispersal behaviours, and suppressed the spring dispersal to the sub-pattern level. Similar mechanisms might have formed the pattern and sub-patterns of *Agabus bipustulatus*. According to Behr (1990) and Lundkvist et al. (2002), *A. bipustulatus* had two active

periods during the year. The first period was in summer months and the second was during October. In Germany (Behr 1990), the maximal activity was observed in summer with a feasible peak in autumn (0-SU-0 or 0-SU-au), while in Sweden (Lundkvist et al. 2002) the species had 0-su-AU sub-pattern. Most probably, the same effect might be seen according to the changes of the altitude. Unfortunately, there are no results about this phenomenon in case of aquatic insects, but it is clearly shown in case of terrestrial insects (e.g. Holuša et al. 2006).

2. *Number of individuals collected:* For example, *Hydroporus planus* flew according to SP-su-0 sub-pattern in Hungary, but there are no great difference in the seasonal dispersal percentages in spring and summer (spring: 51,6%, summer: 41,9%; Table 1). In Germany, Behr (1990) described this species as a typical summer flyer (0-SU-0), while Lundkvist et al. (2002) in Sweden described two different flight behaviors (0-SU-0 and 0-SU-au). These differences might be caused by the differences among the collected number of individuals (Behr: 86 ind., Lundkvist et al.: almost 500 ind., this study: 31 ind.). Our classification might be influenced by the coincidental occurrences because of the smaller number of collected individuals and the almost equal dispersal percentage during two seasons. If three individuals did not fly in the last sampling day of spring, but did in the first sampling day in summer, the main pattern and the sub-pattern could be the same as Behr (1990) and Lundkvist et al. (2002) described. Similar reasons could explain *Hydroglyphus geminus* being described as 0-SU-0 or 0-SU-au sub-pattern in Spain based on only 72 specimens (Miguélez & Valladares 2008), while in Hungary this species had 0-su-AU sub-pattern with no doubt (1926 ind.). These cases strongly support our statement that classification can be done without doubt when the number of individuals are high enough (n>100), otherwise the patterns must be considered as questionable.

Another problem based on numbers of individuals can be arisen during applying our evaluation method, if the sampling intensity was highly uneven among the seasons. If numbers of samples are the same from every season, the activity pattern and coding can undoubtedly considered to be real and appropriate. However, if the numbers of samples from each season are different, it is recommended to introduce a restriction for assessing the seasonal flight activity. Our suggestion that it could be done based on the percentage shares of the samples and numbers of individuals among the seasons. If the percentage distribution of the samples (sampling days) are, for example, spring: 20% - summer: 60% - autumn: 20 %, the activity pattern can be considered as real and acceptable if the percentage share of the number of individuals of a certain species reach or exceed the share of the samples for that season when the maximum activity peak can be visible (main pattern). So if the global activity peak could be seen in spring and local peaks were observed in summer, the seasonal activity pattern would be SP-su-0; but it can be considered to be real and acceptable if more than 20% of the individuals were caught during spring. If the maximal peak was observed in summer and there were additional peaks in spring (sp-SU-0), the pattern can be correct if at least the 60% of the individuals were captured in summer. If this criterion is not satisfied the stated pattern should be regarded as questionable, even if it is based on high number of individuals. In our study the percentage distribution of the samples (sampling days) among the seasons was 7 (23,33%) - 13 (43,33%) - 10 (33,33%), respectively. Based on this, all common species met the criterion and produced significantly higher proportion (Table 1) than the share of samples in that season when the maximal dispersal peak was manifested.

3. *Taxonomic resolution: Helophorus brevipalpis* were mentioned by Landin (1980) from Sweden and by Miguélez & Valladares (2008) from Spain as a summer species, but whereas Miguélez & Valladares (2008) described a local peak in spring (sp-SU-0), Landin (1980) found it only in summer (0-SU-0). Landin & Stark (1973) previously mentioned that *H. brevipalpis* occurs in September in Sweden, but they only followed dispersal flight during a short period. In the present study, *Helophorus* individuals were identified only to genus level, and flew *'en masse'* in summer, but further local peaks can be seen in the other seasons. Further analyses with better taxonomic resolution are needed before making conclusions about these comparisons for *H. brevipalpis.*

4. *Unidentified reasons: Hydroporus incognitus* were described as 0-SU-au species in Sweden by Nilsson (1997), with high numbers of individuals in September. In Germany, Behr (1990) described *H. incognitus* as a typical summer species (0-SU-0). The flight is pre-reproductive in Sweden and directly following the breeding season in Germany (Nilsson 1997). Later, in Sweden also, Lundkvist et al. (2002) found 0-SU-au sub-pattern during the first sampling year, but in the second year the local peak occurred in spring (sp-SU-0). In both years, the local peaks were near to the global peak. Based on this, the explanation of Nilsson might be reconsidered. In fact, *H. incognitus* has a very high dispersal activity throughout the year where it is found.

In summary, we described the results of a mensurative experiment, established a frame scheme and inserted all previously known results into the frames. Our scheme is likely in accordance with the natural phenomenon. Namely, there might be several main periods of dispersal flight based on likely reasons of why the aquatic insects arise to the air. The 'colonization cycle' – habitat selection for different purposes during life cycle – determines the main periods of dispersal flight, and it can be further divided based on the purpose of the flight - breeding-, hibernation-, aestivation- and feeding-flight as noted by Fernando & Galbraith (1973). In Europe, the breeding flight generally occurs in spring and early summer. In summer, the purposes of the dispersal flight are to find suitable habitat for feeding or aestivation. In this period the starting of dispersal flight is primary influenced by the condition of habitats and stochastic ecological conditions as noted by Popham (1964). In autumn, most of the species are looking for a suitable habitat for overwintering (Fernando & Galbraith 1973). Whatever is the reason, the phenology features and the environmental factors (e.g. rainfall, water loss, increased water and air temperature, high predation pressure, food shortage) together affect the realized flying periods. It follows that these periods are species and geographically dependent. The turning point of the seasons might be different based on the latitude. If this is so, the dispersal behaviour of a given species might be different in different geographical areas, as Pajunen & Jansson (1969), Benedek & Jászai (1972), Lundkvist et al. (2002) and Boda & Csabai (2009a) previously mentioned.

All the data from previous studies about the dispersal flight originated from the temperate zone of Europe and North America; the scheme is useable in these regions yet. Naturally, winter season may play a significant role in forming seasonal dispersal flight in warmer climates, for example the south part of the Mediterranean, subtropical or tropical territories of other continents. Thus, a winter main pattern (WI) and its sub-patterns likely would appear in the scheme and the sub-pattern level might be widened in the future in cases of all other main patterns. The scheme is appropriate for including in new patterns and can be expanded to accommodate future investigations.

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Legends of Figures

Figure 1 Dispersal activity during the whole sampling period. (A) total number of collected individuals, (B) total number of species. The grey arrows show the sampling days, when the weather conditions inhibited the dispersal.

Figure 2 Seasonal dispersal patterns and realized sub-patterns based on the dispersal dynamics of a typical species highlighted in bold. The species included the same pattern and sub-pattern displayed in the diagram, too. (A-C) Spring main pattern (SP), framed up with green (A): Spring sub-pattern (SP-0-0), (B): Spring-summer sub-pattern (SP-su-0), (C): Spring-autumn sub-pattern (SP-0-au). (D-F) Summer main pattern (SU), framed up with red (D): Summer sub-pattern (0-SU-0), (E): Summer-autumn sub-pattern (0-SU-au), (F): Summer-spring-autumn sub-pattern (sp-SU-au). (G-I) Autumn main pattern (AU), framed up with grey (G): Autumn sub-pattern (0-0-AU), (H): Autumn-summer sub-pattern (0-su-AU), (I): Autumn-spring sub-pattern (sp-0-AU). 20% of the maximal flight activity was shown by the broken lines as the boundary of the sub-pattern level. The species highlighted in bold are represented in pictures.

Figure 3 The differentiation of the dispersal flight behaviour in pattern and sub-pattern levels using non-metric multidimensional scaling (NMDS, final stress = 0.0239).

Figure

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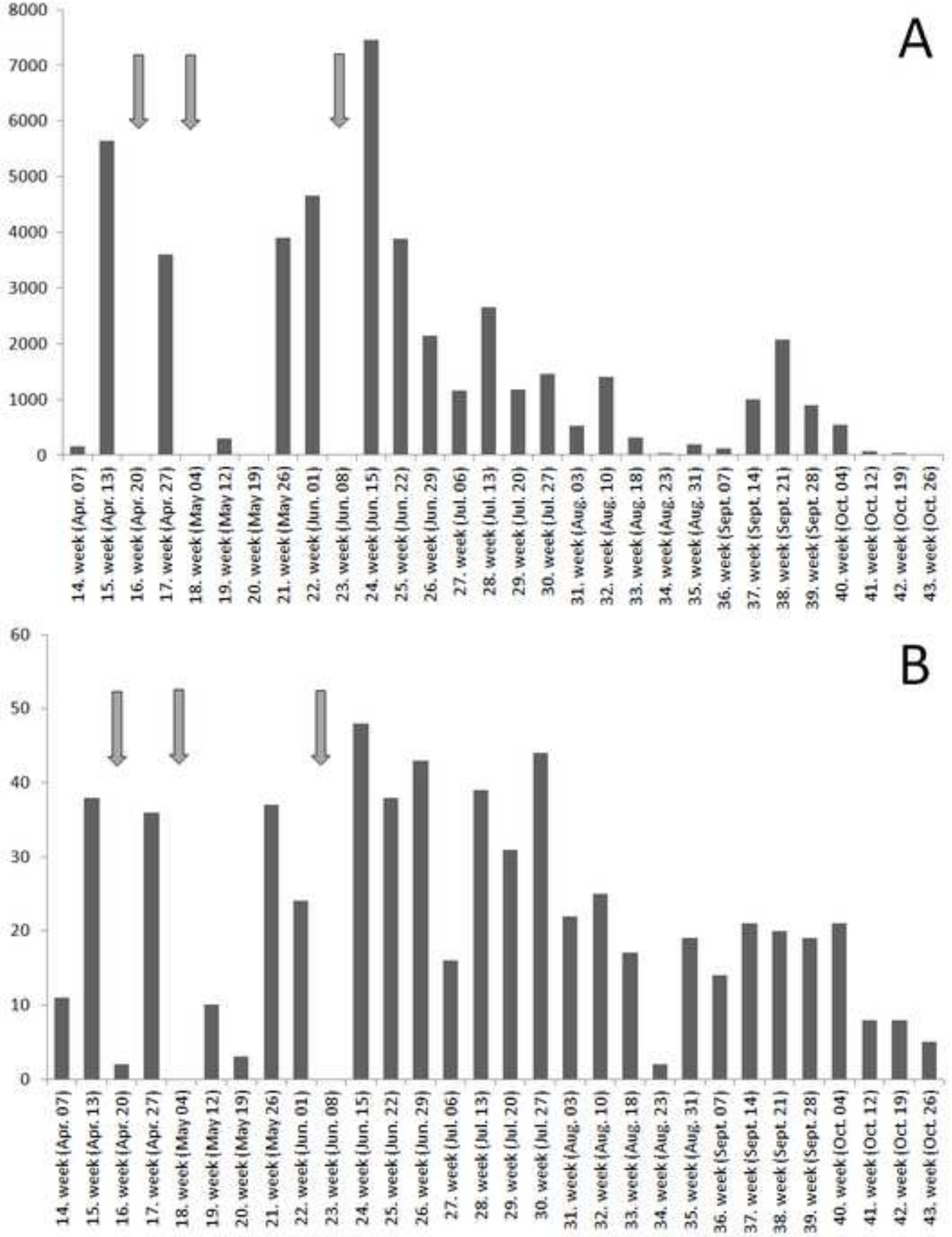
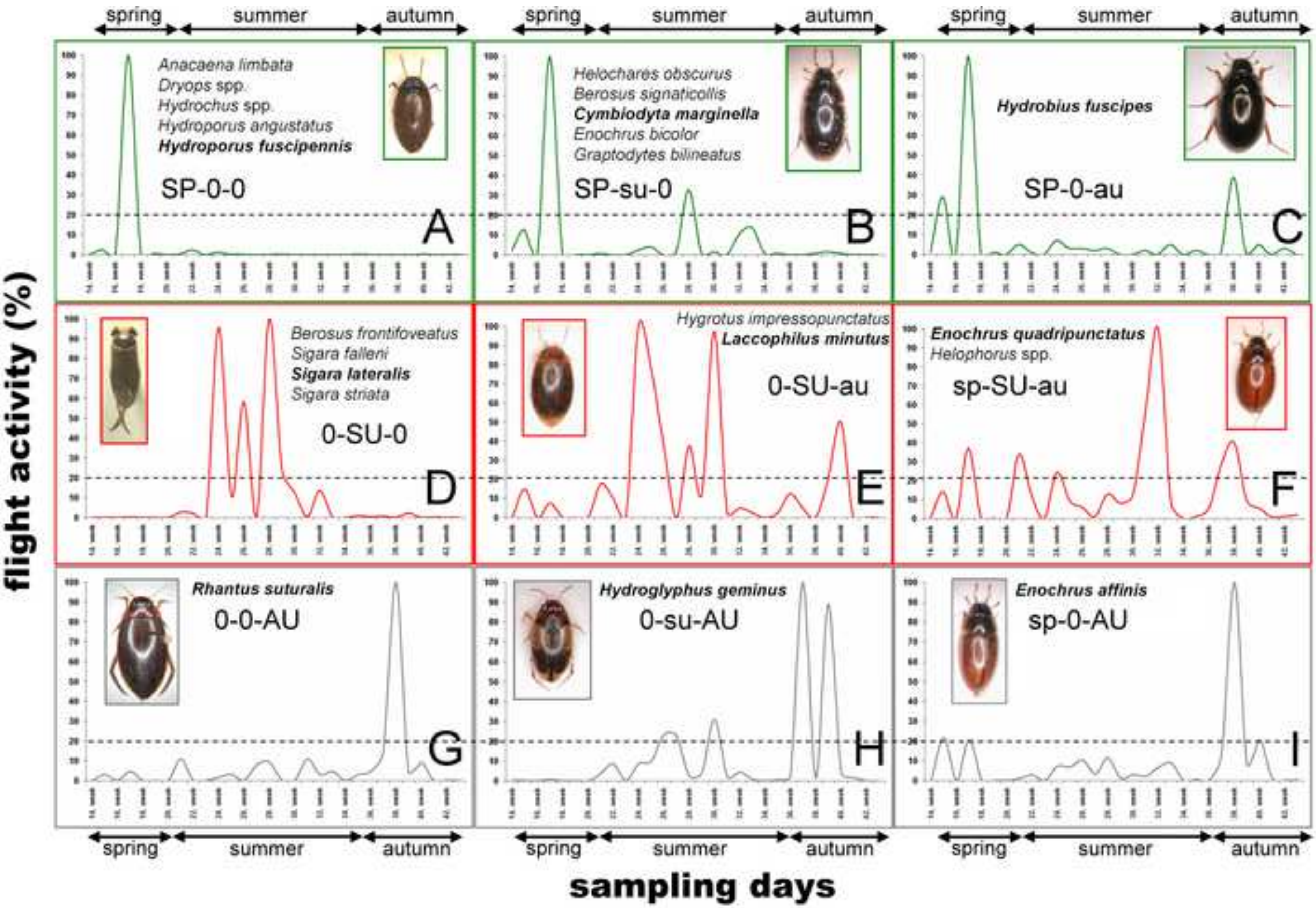
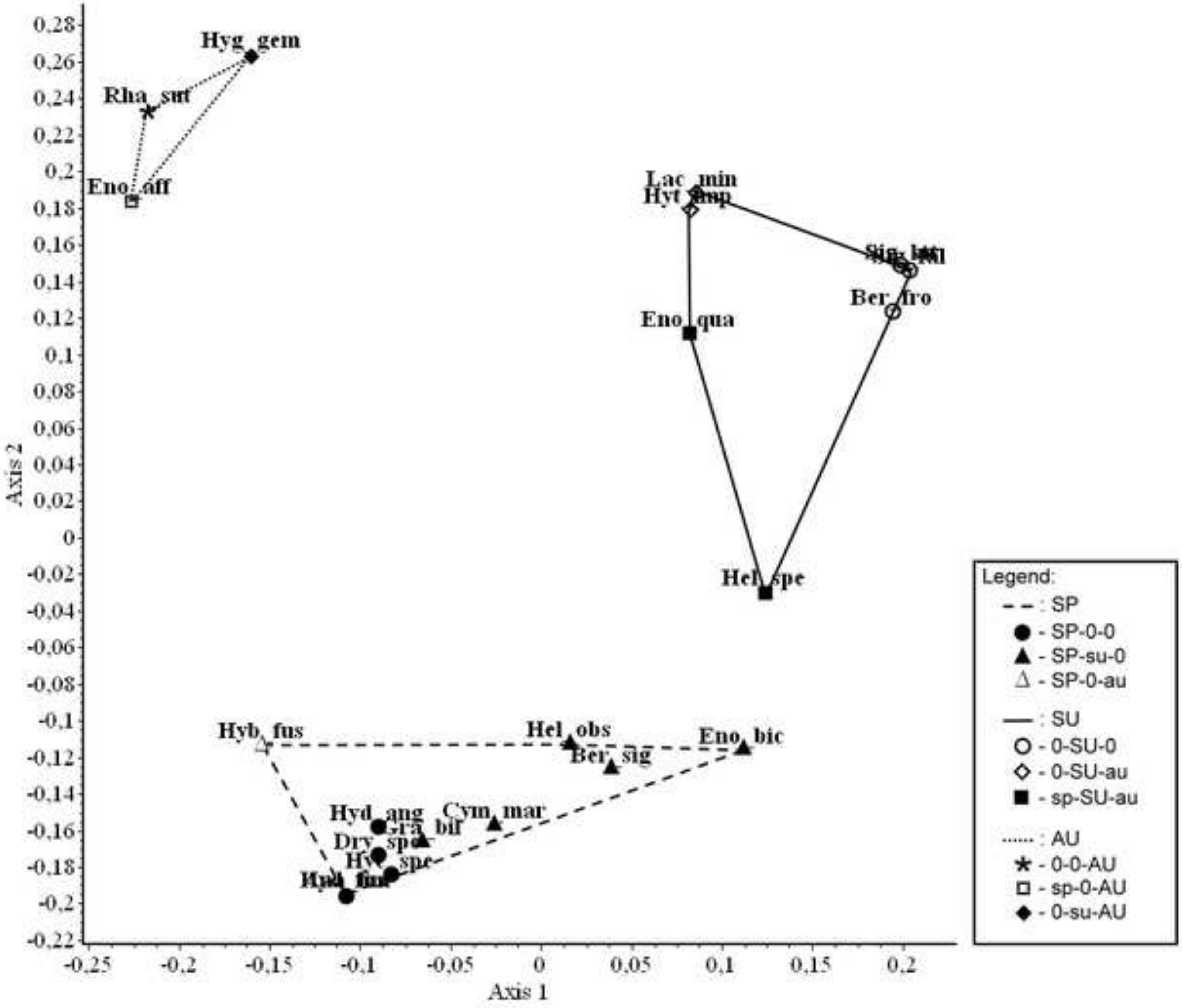


Figure


spring
summer
autumn
Anacaena limbata
Dryops spp.
Hydrochus spp.
Hydroporus angustatus
Hydroporus fuscipennis
SP-0-0
A
Helochares obscurus
Berosus signaticollis
Cymbiodyta marginella
Enochrus bicolor
Graptodytes bilineatus
SP-su-0
B
Hydrobius fuscipes
SP-0-au
C
Berosus frontifoveatus
Sigara falleni
Sigara lateralis
Sigara striata
0-SU-0
D
Hygrotus impressopunctatus
Laccophilus minutus
0-SU-au
E
Enochrus quadripunctatus
Helophorus spp.
sp-SU-au
F
Rhantus suturalis
0-0-AU
G
Hydroglyphus geminus
0-su-AU
H
Enochrus affinis
sp-0-AU
I
flight activity (%)
sampling days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Legend:
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△ - SP-0-au
— : SU
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◇ - 0-SU-au
■ - sp-SU-au
...... : AU
★ - 0-0-AU
□ - sp-0-AU
◆ - 0-su-AU

Table 1 Checklist of the collected taxa, percentage distribution of seasonal dispersal activity, total numbers of individuals and seasonal dispersal flight patterns / sub-patterns followed by each species (N_{total}: numbers of captured individuals during the whole sampling period; *: patterns and sub-patterns are questionable; Abbreviations of the pattern codes as in Figure 2.)

Taxon	Spring % (14-20. week)	Summer % (21-33. week)	Autumn % (34-43. week)	N_{total}	Patterns and sub-patterns
Helophorus spp.	17,8	76,4	5,8	24590	sp-SU-au
Sigara lateralis (Leach, 1817)	0	98,6	1,4	3375	0-SU-0
Enochrus quadripunctatus (Herbst, 1797)	12,3	66,1	21,6	3243	sp-SU-au
Helochares obscurus (O.F. Müller, 1776)	49,8	44,7	5,5	2478	SP-su-0
Enochrus affinis (Thunberg, 1794)	17	25,8	57,2	1937	sp-0-AU
Hydroglyphus geminus (Fabricius, 1792)	0,3	37,7	61,9	1926	0-su-AU
Sigara falleni (Fieber, 1848)	0,1	99,8	0,1	1446	0-SU-0
Hydroporus fuscipennis Schaum, 1868	84,9	15	0,1	1387	SP-0-0
Berosus frontifoveatus Kuwert, 1888	5,2	93,8	1	730	0-SU-0
Hydrochus spp.	87,2	12,8	0	697	SP-0-0
Anacaena limbata (Fabricius, 1792)	92,5	6,6	0,9	548	SP-0-0
Enochrus bicolor (Fabricius, 1792)	27,7	71,8	0,5	365	SP-su-0
Hygrotus impressopuctatus (Schaller, 1783)	5,3	65,1	29,5	281	0-SU-au
Graptodytes bilineatus (Sturm, 1835)	71,4	27,4	1,2	248	SP-su-0
Cymbiodyta marginella (Fabricius, 1792)	61,3	36,2	2,6	235	SP-su-0
Hydrobius fuscipes (Linnaeus, 1758)	58,5	19,2	22,3	224	SP-0-au
Sigara striata (Linnaeus, 1775)	0	98,6	1,4	219	0-SU-0
Laccophilus minutus (Linnaeus, 1758)	4,4	78	17,6	205	0-SU-au
Dryops spp.	81,3	14,1	4,7	128	SP-0-0
Rhantus suturalis (MacLeay, 1825)	4	26,4	69,6	125	0-0-AU
Hydroporus angustatus Sturm, 1835	70,4	22,6	7	115	SP-0-0
Berosus signaticollis (Charpentier, 1825)	34,9	61,5	3,7	109	SP-su-0
Enochrus coarctatus (Gredler, 1863)	54,8	29,8	15,5	84	*SP-su-0
Hesperocorixa linnaei (Fieber, 1848)	6,3	93,8	0	64	*0-SU-0
Agabus uliginosus (Linnaeus, 1761)	81,7	16,7	1,7	60	*SP-0-0
Enochrus testaceus (Fabricius, 1801)	32,1	67,9	0	53	*0-SU-0
Sigara nigrolineata (Fieber, 1848)	0,0	97,6	2,4	41	*0-SU-0
Hydrochara flavipes (Steven, 1808)	31,6	55,3	13,2	38	*sp-SU-0
Hygrotus inaequalis (Fabricius, 1776)	3,0	72,7	24,2	33	*0-SU-0
Hydroporus planus (Fabricius, 1781)	51,6	41,9	6,5	31	*SP-su-0
Liopterus haemorrhoidalis (Fabricius, 1787)	83,9	16,1	0	31	*SP-0-0
Hydrochara caraboides (Linnaeus, 1758)	76,7	13,3	10,0	30	*SP-0-0
Limnoxenus niger Zschach, 1788	60,0	40,0	0	25	*SP-su-0
Colymbetes fuscus (Linnaeus, 1758)	0	100,0	0	24	*0-SU-0
Gerris odontogaster (Zetterstedt, 1828)	20,8	58,3	20,8	24	*0-SU-0
Graphoderus austriacus (Sturm, 1834)	18,2	72,7	9,1	22	*0-SU-0
Berosus luridus (Linnaeus, 1761)	50,0	50,0	0	20	*sp-SU-0
Haliplus ruficollis De Geer, 1774)	5,3	94,7	0	19	*0-SU-0
Enochrus melanocephalus (Olivier, 1792)	23,5	70,6	5,9	17	*0-SU-0
Callicorixa praeusta (Fieber, 1848)	6,3	93,8	0	16	*0-SU-0
Peltodytes caesus (Duftschmid, 1805)	43,8	53,2	0	16	*sp-SU-0

Porhydrus obliquesignatus (Bielz, 1852)	6,7	80,0	13,3	15	*0-SU-0
Paracorixa concinna (Fieber, 1848)	0,0	100,0	0	14	*0-SU-0
Bidessus nasutus Sharp, 1887	23,1	76,9	0	13	*0-SU-0
Agabus labiatus (Brahm, 1790)	58,3	41,7	0	12	*SP-0-0
Hydaticus grammicus (Germar, 1830)	8,3	33,3	58,3	12	*0-su-AU

Further species with low **number of captured individuals**: **(9)** *Coelostoma orbiculare* (Fabricius, 1775), **(8)** *Enochrus fuscipennis* (Thomson, 1878), **(7)** *Gerris argentatus* Schummel, 1832, *Hydrochara dichroma* (Fairmaire, 1892), **(6)** *Cymatia rogenhoferi* (Fieber, 1864), **(4)** *Gyrinus substriatus* Stephens, 1829, *Hebrus pusillus* (Fallén, 1807), *Hydaticus seminiger* (De Geer, 1774), *Hydroporus palustris* (Linnaeus, 1761), *Notonecta glauca* Linnaeus, 1758, **(3)** *Acilius canaliculatus* (Nicolai, 1822), *Colymbetes striatus* (Linnaeus, 1758), *Corixa punctata* Illiger, 1807, *Rhantus frontalis* (Marsham, 1802), **(2)** *Acilius sulcatus* (Linnaeus, 1758), *Corixa affinis* Leach, 1817, *Graphoderus cinereus* (Linnaeus, 1758), *Gyrinus paykulli* Ochs, 1927, *Haliplus immaculatus* Gerhardt, 1877, *Hydrophilus aterrimus* (Eschscholtz, 1822), *Hygrotus parallellogrammus* (Ahrens, 1812), *Ilyocoris cimicoides* (Linnaeus, 1758), *Porhydrus lineatus* (Fabricius, 1775), **(1)** *Cymatia coleoptrata* (Fabricius, 1776), *Dytiscus circumflexus* Fabricius, 1801, *Enochrus ochropterus* (Marsham, 1802), *Gerris lacustris* (Linnaeus, 1758), *Graptodytes granularis* (Linnaeus, 1767), *Graptodytes pictus* (Fabricius, 1787), *Haliplus heydeni* Wehncke, 1875, *Hesperocorixa sahlbergi* (Fieber, 1848), *Hygrotus confluens* (Fabricius, 1787), *Hyphydrus ovatus* (Linnaeus, 1761), *Ilybius ater* (DeGeer, 1774), *Ilybius quadriguttatus* (Lacordaire, 1835), *Laccobius bipunctatus* (Fabricius, 1792), *Laccobius minutus* (Linnaeus, 1758), *Noterus clavicornis* (De Geer, 1774), *Noterus crassicornis* (O.F. Müller, 1776), *Plea minutissima* (Leach, 1817, *Rhantus bistriatus* (Bergsträsser, 1778), *Sigara assimilis* (Fieber, 1848), *Sigara limitata* (Fieber, 1848), *Spercheus emarginatus* (Schaller, 1783)

Table 2 All possible and realized combinations of patterns and sub-patterns according to the seasons with a short description of each combination. Abbreviations of the pattern codes as in Figure 2.

		main pattern (global peak in dispersal activity)		
		spring The maximum seasonal activity is in spring	summer The maximum seasonal activity is in summer	autumn The maximum seasonal activity is in autumn
sub-pattern (>20% of total dispersal activity)	none no local peaks in other seasons	SP-0-0	0-SU-0	0-0-AU
	spring there is/are local peak(s) of flight activity in spring	▨	sp-SU-0*	sp-0-AU
	summer there is/are local peak(s) of flight activity in summer.	SP-su-0	▨	0-su-AU
	autumn there is/are local peak(s) of flight activity in autumn	SP-0-au	0-SU-au	▨
	spring-summer there are local peaks of flight activity both in spring and summer	▨	▨	sp-su-AU**
	spring-autumn there are local peaks of flight activity both in spring and autumn	▨	sp-SU-au	▨
	summer-autumn there are local peaks of flight activity both in summer and autumn	SP-su-au**	▨	▨

Cells filled with grey are not possible pattern combinations.
*This pattern combination was followed up by only some species which were captured in quite small numbers of individuals, so it was not shown on Figure 2.
** Follower species for this pattern combination were not found in our study.

Table 3 Summary of published dispersal based studies in which (i) the sampling periods were more than seven months, (ii) the sampling frequency were regular, and (iii) original investigations that provided seasonal dispersal flight conclusions.

Author(s)	Taxa	Method	Territory	Sampling period	General conclusion about the mass dispersal period(s)
Bagge (1982)	Corixidae	light-trap	Finland	from May to October	from July to August
Behr (1990)	*Hydroporus* spp.	artificial habitat	Germany	from April to December	from June to August
Benedek & Juhász (1972)	Corixidae	light-trap	Hungary	from March to November	June and September
Brown (1954)	Corixidae	light trap	Great Britain	throughout the year*	spring and early summer
Fernando (1958)	Corixidae	light reflecting glass trap	Great Britain	from March to October	spring and from June to August
Fernando & Galbraith (1973)	aquatic Coleoptera	artificial habitat	Canada	from April to October	from July to August
Landin (1980)	Helophoridae	light reflecting glass trap	Sweden	from March to November	from June to August
Leston & Gardner (1953)	Corixidae	light-trap	Great Britain	from May to August	July
Lundkvist et al. (2002)	Dytiscidae	light reflecting glass trap	Sweden	from April to mid October	from May to September
Miguélez & Valladares (2008)	aquatic Coleoptera	Moericke trap	Spain	from March to November	April to October
Nilsson (1997)	*Hydroporus* spp.	red car roofs	Sweden	from May to early October	from June to September
Pajunen & Jansson (1969)	Corixidae	capture-mark-recapture	Finland	from May to October	early spring and late autumn
Richard (1958)	Corixidae	light trap	Great Britain	from April to mid October	April and from August to September
Thomas (1938)	Corixidae	light-trap	Great Britain	throughout the year*	summer
Van der Eijk (1987)	*Gyrinus marinus*	capture-mark-recapture	Netherland	from April to December	from April to October
Weigelhofer et al. (1992)	Corixidae	light-trap	Austria	from February to March (next year)	from June to September
Young (1966)	Corixidae	direct observation	Great Britain	from February to October	from March to June

*data originated from continuous use of light-traps

Table 4 Review and classification of formerly published results using the scheme. The table shows only those articles, which conform to the requirements of comparability given in Table 3

Taxa	Seasonal flight pattern	References	Territory
Classification of the common species, which have more descriptions for seasonal dispersal flight in previous papers			
Coleoptera			
Dytiscidae			
Agabus bipustulatus (Linnaeus, 1767)	0-SU-0	Behr (1990)	Germany
	0-SU-au	Behr (1990)	Germany
	0-su-AU	Lundkvist et al. (2002)	Sweden
Hydroglyphus geminus (Fabricius, 1792)	0-SU-0*	Miguélez & Valladares (2008)	Spain
	0-SU-au*	Miguélez & Valladares (2008)	Spain
	0-su-AU	present study	Hungary
Hydroporus incognitus Sharp, 1869	sp-SU-0	Lundkvist et al. (2002)	Sweden
	0-SU-au	Lundkvist et al. (2002)	Sweden
	0-SU-0	Behr (1990)	Germany
	0-SU-au	Nilsson (1997)	Sweden
Hydroporus planus (Fabricius, 1781)	SP-su-0	present study	Hungary
	0-SU-0	Behr (1990)	Germany
	0-SU-0	Lundkvist et al. (2002)	Sweden
	0-SU-au	Lundkvist et al. (2002)	Sweden
Helophoridae			
Helophorus brevipalpis Bedel, 1881	sp-SU-0	Miguélez & Valladares (2008)	Spain
	0-SU-0	Landin (1980)	Sweden
Hydrophilidae			
Anacaena limbata (Fabricius, 1792)	SP-0-0	present study	Hungary
	sp-SU-0	Fernando & Gailbraith (1973)	Canada
	sp-SU-au	Fernando & Gailbraith (1973)	Canada
Classification of the species, which have only one description for seasonal dispersal flight in previous papers			
Coleoptera			
Dytiscidae			
Hydroporus morio Aubé, 1838	0-Su-au	Nilsson (1997)	Sweden
Hydroporus neglectus Schaum, 1845	0-SU-0	Behr (1990)	Germany
Hydroporus nigrita (Fabricius, 1792)	0-SU-0	Nilsson (1997)	Sweden
Hydroporus piceus Stephens, 1828	0-SU-au*	Behr (1990)	Germany
Hydroporus pubescens (Gyllenhal, 1808)	sp-0-AU*	Miguélez & Valladares (2008)	Spain
Hydroporus tristis (Paykull, 1798)	0-SU-0	Behr (1990)	Germany
Helophoridae			
Helophorus aequalis Thomson, 1868	0-SU-0	Behr (1990)	Germany
Helophorus alternans Gené, 1836	SP-0-0*	Miguélez & Valladares (2008)	Spain
Helophorus orientalis Motschulsky, 1860	0-SU-0	Fernando & Gailbraith (1973)	Canada
	0-SU-au	Fernando & Gailbraith (1973)	Canada
Helophorus strigifrons Thomson, 1868	SP-0-0	Landin (1980)	Sweden
Hydrophilidae			
Anacaena lutescens (Stephens, 1829)	0-SU-0	Behr (1990)	Germany
Heteroptera			
Corixidae			
Arctocorisa carinata (Sahlberg, 1819)	0-su-AU	Pajunen & Jansson (1969)	Finland
Callicorixa producta (Reuter, 1880)	0-su-AU	Pajunen & Jansson (1969)	Finland

*due to the low number of individuals captured the classification is questionable (10<n<100)