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Dispersing diving beetles (Dytiscidae) in agricultural and urban landscapes in south-eastern Sweden

Elisabeth Lundkvist*, Jan Landin & Fredrik Karlsson

*Department of Biology, Linköping University, SE-581 83 Linköping, Sweden (*e-mail: elilu@ifm.liu.se)*

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Flying dytiscids were trapped in an agricultural landscape with wetlands in different successional stages and in two urban landscapes with young wetlands. We compared the faunas in air and in water. *Hydroporus* and *Agabus* were the most frequently trapped genera in air. Most species were trapped near water in the agricultural landscape; species characteristic of later successional stages were common in air and dominated in water. In the urban landscapes, species were mainly trapped far from water and species known to colonise new waters were common in air and in the youngest waters. Overall, females and immature adults were more common in flight catches during April–July than during August–October. Our results indicate that urbanisation would result in a less diverse fauna, but may lead to an assemblage dominated by species that are infrequent in agricultural landscapes. To obtain a rich wetland insect fauna, a wide range of wetland types is required at the landscape scale.

Introduction

Diving beetles (Dytiscidae) inhabit both temporary and permanent habitats and are among the first large invertebrate predators to arrive in newly formed wetlands (Layton & Voshell 1991). They are generally good fliers and can disperse over distances of several kilometres, allowing them to utilise resources fragmented both in space and time (Bilton 1994). However, some species within the family lack flight ability due to reduction or absence of wings or wing muscles (Jackson 1952, 1956a, 1956b). The evolution of flightlessness is strongly linked to stable continuous habitats (Southwood 1962, Wagner & Liebherr 1992) and migration is more prominent in the fauna of temporary habitats than permanent ones. However, Hamilton and

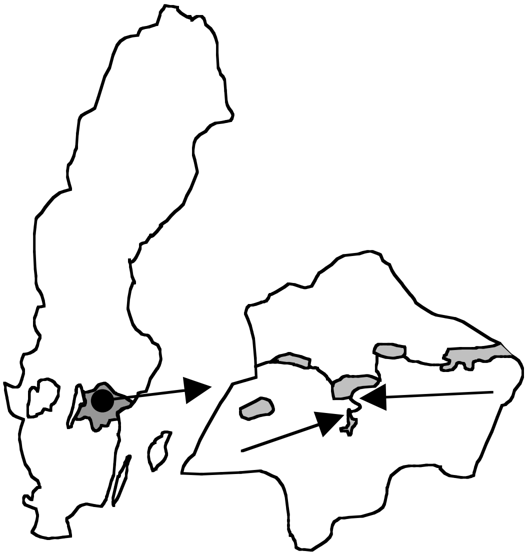

Fig. 1. The map shows the county of Östergötland in south-eastern Sweden. The arrows denote the landscapes where diving beetles were trapped in 1996–1999; the upper arrow shows the location of Nykvarn (58°25´N, 15°38´E) and the Wetland Park (58°23´N, 15°35´E), the lower arrow shows Stavsätter (58°18´N, 15°40´E). The grey areas in the county map are large lakes.

May (1977) argued that migration is important even in uniform and stable habitats. Permanent habitats have more diving beetle species lacking flight ability and most species in temporary habitats are good and ready fliers (Jackson 1952, 1956, Southwood 1962).

The colonisation of waters by flying dytiscids is restricted to the spring, summer and early autumn months in temperate latitudes (Williams 1987) often with two peaks, the highest in spring and a lower one in autumn. Daily flights are initiated by heat and peak around sunset (Nilsson 1997). Dytiscids in temporary waters avoid drought by aestivating and/or hibernating as eggs, larvae or adults in the dry basin, or by completing their life cycle before drying occurs (Wiggins *et al.* 1980). In the later case, adults of the next generation migrate to, and over-winter, in permanent habitats. Such emigration, from a drying wetland, can be initiated by water loss (Velasco & Millan 1998).

Most dytiscid dispersal flights should be migratory rather than trivial (Southwood 1962, Dingle 1996) and mainly serve to colonise new habitats. However, migration of dytiscids in relation to the landscape and different types of waters is not well studied. Nilsson and Svensson (1995) have studied immigration rates into waters in clearings and forests, and Behr (1990) studied immigration into artificial ponds, but almost all other studies concerning flight examine the flight ability of different species, flight periodicity etc. (e.g., Jackson 1952, 1956, Southwood 1962, Bilton 1994, Nilsson 1997).

In this study, we investigate flying dytiscids in three landscapes; one agricultural landscape with many wetlands and two urban landscapes with newly constructed wetlands. We assume that the regional species pool is common to all landscapes, as the maximum distance between areas is about 20 kilometres. Our hypotheses are (1) that more species should fly in the agricultural landscape than in the urban ones, as there are more types of waters represented, and in different successional stages. (2) Fewer and also other species should fly in the urban landscapes. Species typical for early stages in the succession should be more common in the urban landscapes than in the agricultural landscape. Generally, in disturbed environments large proportions of the species are migratory. We therefore expect to find a larger proportion of migratory species in the urban landscapes than in the agricultural landscape. We also study (3) the phenology of flight by different species, and characteristics of flying specimens, if young specimens or any sex are over-represented, and (4) if species composition differs between air and water, and how this is related to environmental parameters.

Methods

Study areas

The study was conducted near the city of Linköping in south-eastern Sweden (Fig. 1). Stavsätter, the agricultural landscape, is situated ca. 20 km south of Linköping. It is dominated by arable fields, deciduous woods, spruce plantations, and pastures with scattered oaks. There are many new and old wetlands constructed for waterfowl and other wildlife. These wetlands are of different sizes and are found mainly in open, cattle-grazed or recently abandoned pastures. The urban landscapes are located in Linköping. The first, referred to as "Nykvarn", is situated near the wastewater treatment plant, where six wetlands were constructed in 1993 in an attempt to reduce nutrients, mainly nitrogen. The wetlands are rectangular and have a simple shape with steep sides. Tall plants such as *Typha* and *Phragmites* dominate the macrophytes. The surroundings are open and exposed. The other urban landscape, the "Wetland Park", is situated in the Linköping University campus area. The park was constructed in 1998 and there are 20 wetlands ranging from 1 to 2000 m^2. Wetlands were filled for the first time in winter 1998–1999. The only vegetation present was sparsely planted *Carex* tufts in one of the largest basins. Buildings and lawns dominate the surroundings. Nykvarn and the Wetland Park are ca. 5 km apart.

Flight traps

Diving beetles were caught by flight traps. These were constructed after Fernando (1958) and Landin (1980). They consist of a wooden frame with a glass pane, placed horizontally on the ground. The glass pane measures 100 × 60 cm and leans gently downwards to a container filled with water and detergent. The traps reflect polarised ultraviolet light, which is the main optical cue for water-living insects searching for suitable habitats (Schwind 1991, Horváth 1995, Nilsson 1997, Carron & Becze-Deak 1999). Flying beetles land on the pane, and crawl towards the container. In total, 16 traps were placed in the three study areas, near and far (N = Near, F = Far) from water in open sun exposed (O = Open) environments. In the agricultural landscape traps were placed both in open and forested (S = Shaded) environments (Table 1). Two traps were placed at each site.

The study was conducted during 1998 and 1999 at Stavsätter and Nykvarn and during 1999 at the Wetland Park. We trapped from early May to mid October in 1998 and from early April to mid October in 1999. Traps were emptied at least once a week, and new water and detergent were added. During warm weather, traps were emptied more often. Dytiscids were put in 80% ethanol and identified in the laboratory. Nomenclature follows that of Nilsson and Holmen (1995).

Diving beetles in water

Diving beetle faunas were sampled with activity traps, described by Lundkvist *et al.* (2001). The traps were placed horizontally on the bottom, near the shoreline and in different microhabitats.

At Stavsätter, we trapped in a wetland adjacent to the flight traps at Stavsätter NO. This wetland is ca. 5000 m^2, constructed for waterfowl (in 1983), and is nutrient rich with dense macrophytes and submersed vegetation. We used

Table 1. Locations and surrounding landscape where flying dytiscids were trapped during 1998–1999. All sites are situated near the city of Linköping, south-eastern Sweden. F and N mean that traps are situated near or far from water. O and S mean that traps are situated in open or shaded environments.

Location of flight traps, two at each site	Distance from water (m)	Landscape type	Surrounding environment
Stavsätter NO	1	Agricultural	Open
Stavsätter FO	420	Agricultural	Open
Stavsätter NS	7	Agricultural	Wooded
Stavsätter FS	380	Agricultural	Wooded
Nykvarn NO	1	Urban	Open
Nykvarn FO	150	Urban	Open
Wetland Park NO	2	Urban	Open
Wetland Park FO	250	Urban	Partly wooded

10 traps and trapped during 1996–1998. At Nykvarn, assemblages were trapped in the wetlands for nutrient retention described above. We used 20 traps, (five traps in four of the six wetlands) and trapping was done during 1998–1999. At the Wetland Park, trapping was done during 1999. Here, the water levels fluctuated, and some of the smallest waters frequently dried up. Therefore, different numbers of traps were used during the year but at least 12 traps were used and as a maximum 37 traps. In all areas, we trapped from April–October, with comparable trapping intensities. The traps were emptied every 2–4 days during warm weather and every 5–7 days during periods with lower temperatures. Beetles were processed as described above.

Analyses

We studied species richness and composition in air and compared with compositions in water. Flying individuals were examined if they showed signs of being recently hatched. They were classified as immature adults or mature adults depending on abdomen colour (light in immatures and dark in matures) and elytra softness (soft in immatures and hard in matures). We calculated sex ratios in the total material and also for the most frequently caught species, to see if we could confirm the oogenesis flight syndrome (Johnson 1969). In that case, immature female adults would be more common in the flight catches in the early season, before egg laying occurs. We studied phenology of the common species to see when the main flight periods occurred and to see if sex or immature/mature ratios differed between species.

Similarity in species composition between sites was calculated for 1999 only, since data from the Wetland Park only were available from 1999. Between-year similarity was calculated for Stavsätter and Nykvarn. We used Sørensen's index and Morisita-Horn's index for quantitative data (Magurran 1988, Baev & Penev 1995). Sørensen's index varies from 0–1 (no species in common–all species in common). Morisita-Horn's index also varies from 0–1 (no species in common–all species are in common and exactly the same numbers of individuals per species).

We made a direct gradient analysis (Canonical Correspondence Analysis, CCA) of flight catches using Canoco 4 (ter Braak & Smilauer 1998). Variables used in the CCA were landscape type (urban or agriculture), distance from water, vegetation complexity near the flight traps, year of sampling (1998 or 1999), and air temperature. Distance was measured as metres from nearest water edge, and values were log transformed ($x + 1$). Vegetation complexity was measured qualitatively on two scales. First we classified complexity within a metre from the traps and sites were ranked according to their diversity in vegetation, both species number and physical

Table 2. Number of dytiscid species and individuals trapped in flight traps during 1998–1999 near Linköping, south-eastern Sweden. *Hydroporus* and *Agabus* were the most frequently genera trapped. F, N = trap situated far or near water. O, S = trap situated in open or shaded environment.

Location of trap	Number of species	Number of individuals	Most frequent species*	Percentage *Hydroporus*	Percentage *Agabus*
Stavsätter NO	29	676	*H. incognitus* (65)	86	3
Stavsätter FO	16	428	*H. incognitus* (38)	81	17
Stavsätter NS	3	5	*H. incognitus* (60)	60	40
Stavsätter FS	4	6	*H. incognitus* (50)	67	33
Nykvarn NO	15	60	*H. planus* (35)	57	3**
Nykvarn FO	19	370	*H. planus* (69)	83	9
Wetland Park NO	4	18	*H. planus* (56)	56	28
Wetland Park FO	11	90	*H. planus* (40)	89	8

* Percentage of total individuals

** At Nykvarn NO, *Hydroglyphus* was the second most common genus and made up 20% of the material.

structure of the plants. Then we classified complexity within ten metres from the traps, where we estimated different heights and diversity of elements (grass, shrubs and trees). Ranking the complexity gave values from 1–8 where 1 was the least complex and 8 the most complex. We used an average of the two rankings in the ordination analysis.

As dytiscid flight, at least partly, is initiated by heat, the maximum day temperature should be important. However, the threshold temperature for flight is poorly known, and probably differs among species. We calculated average daily maximum temperatures since last trap emptying, i.e. an average of maximum day temperatures during 4–7 days. Measurements were done at a weather station 3.5 km west of the Wetland Park (SMHI 1996–1999). Temperatures used in the ordination are based on when dytiscids occurred and hence, observations when no dytiscids were found are not included in the analysis. Therefore, temperatures used in the ordination are rarely below 15 °C.

A Monte Carlo permutation test ($N = 1000$) was performed to evaluate the strength of the species-environment relationship. To evaluate the relative importance of the variables, and to what extent they explain unique variation in the species data, we conducted variation partitioning, including only the variation that was explained by our environmental variables, as suggested by Økland (1999).

Results

Richness and composition of faunas

In total we flight trapped 42 species and 1653 individuals; most species and individuals near water in the agricultural landscape and least in shaded environments (Table 2). Shaded environments were excluded from further analyses, since numbers were too low to allow meaningful analyses, only 11 individuals being trapped. In the two urban landscapes, more species and individuals were trapped far from water than near. At Stavsätter, *Hydroporus incognitus* dominated the material. It made up 54% of the total catch (Table 2), but *Hydroporus planus* and *Agabus bipustulatus* were also common. *H. planus* made up 64% of total individuals at Nykvarn and 43% at the Wetland Park.

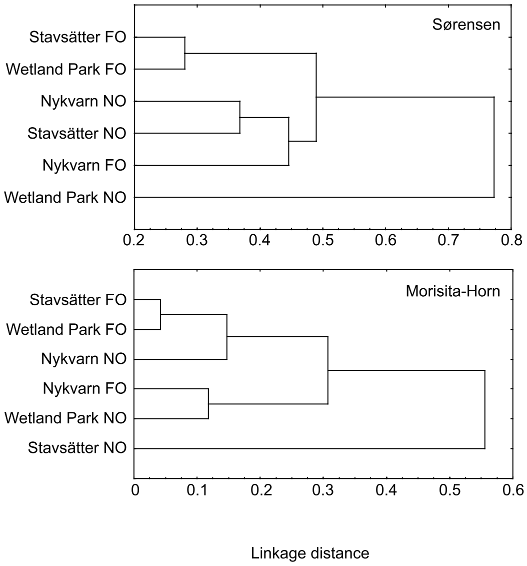

Fig. 2. Similarities in diving beetle faunas trapped in flight traps during 1999. Note that small numbers mean similar faunas. Sørensen's qualitative index is based on the number of species in common for the different traps. Morisita-Horn's quantitative index is based on number of species and individuals and gives a measure on structural similarity. F, N = trap situated far or near water; O, S = trap situated in open or shaded environment.

The most similar catches, measured qualitatively and quantitatively, were made far from water in two different landscapes (Fig. 2). At the Wetland Park NO only four species were trapped, and hence the composition measured by Sørensen's index differed much from the others (Fig. 2, upper panel). When comparing quantitative data (Morisita-Horn's index), the pattern partly differs, the most divergent wetland being Stavsätter NO, which had most species and individuals. The Wetland Park NO had a similar structure to Nykvarn FO with *H. planus* and *A. bipustulatus* as dominant species, which explains why those two constitute a cluster (Fig. 2, lower panel).

At Stavsätter, species composition in flight traps was similar between years (Sørensen = 0.755), and structure of assemblages even more so (Morisita-Horn = 0.976). At Nykvarn, species composition differed between years (Sørensen = 0.5) and the Morisita index was lower between years (0.81) than at Stavsätter.

Species compositions of faunas in water and air at Stavsätter were relatively similar, but the structures of faunas differed substantially (Table 3). At Nykvarn, the same pattern was found, but similarity in species composition was lower. At Wetland Park the opposite pattern was found. Similarity in species composition was low but the structures of faunas were more similar.

At Stavsätter, the flight catch was dominated by *Hydroporus* species while several other genera were the most abundant in water: *Rhantus, Hydaticus, Hygrotus, Ilybius, Acilius* and *Dytiscus* (*see* Appendix). Only 3.4% of the water material from Stavsätter were *Hydroporus*. At Nykvarn, *Hydroporus* also dominated while *Rhantus, Ilybius, Acilius, Hygrotus* and *Dytiscus* dominated in the water. Only 1% of the water material was *Hydroporus*. At the Wetland Park up to 86% of the flight material were *Hydroporus* and here they also were abundant in water catches (30.6%). Together with *Hydroglyphus, Agabus* and *Hygrotus* they constituted the most abundant genera at the Wetland Park.

Flight periodicity, sexes and immatures

Flight periodicity was more distinct in 1999 than in 1998 (Fig. 3). In 1998 more specimens flew in May than during the rest of the year, but there is also a small maximum at the end of July–beginning of August. In 1999 there were two main periods of migration, the first period from June–middle of August and then another in September. Total numbers trapped were more than twice as many in 1999 (1178) as in 1998 (475). The distinct periodicity entirely depends on a few common species: *H. incognitus*, *H. planus* and *A. bipustulatus*. *H. planus* mostly flew in June–July while *H. incognitus* were frequently found from May until September. *A. bipustulatus* had no distinct flight periodicity.

Sex ratio (females/males) in the whole flight catch throughout the year was 1.1 both in 1998 and 1999, i.e. a small predominance of females. The sex ratios differed substantially between the main flight periods, April–July and August–October, but only for 1999 (Fig. 4). Of the most frequently caught species, *H. planus* females were more common (Fig. 5). *H. incognitus* and *A. bipustulatus* showed no clear tendency of any sex being more common than the other did.

Immature specimens of six species were found in the flight catches; *Hydroporus planus, H. incognitus, H. striola*, *H. nigrita, H. discretus* and *H. tristis* (Table 4). Of the six, only *H. planus* and *H. nigrita* had large proportions of young specimens at all sites. Young *Hydroporus planus* individuals were mainly found in June and the beginning of July. Immature specimens of the other species were later, with maximum numbers in July and the beginning of August (Fig. 6).

Environmental factors affecting the flight

The environmental variables included in the CCA explained much of the variation. The eigenvalues of axes 1–3 were 0.34, 0.10, and 0.10, respectively. The relationship between species and the whole set of environmental variables was highly significant (*p* = 0.005). Landscape type was important for the species distribution pattern (Fig. 7) as well as distance from water, and vegetation complexity near the traps. These variables were separated on the first two axes. Species that were typical and common in catches

Table 3. Faunal similarities between flight catches and water catches of diving beetles. Read as three matrices. The first figure is Sørensen's index for qualitative data and second figure is Morisita-Horn's index for quantitative data. F, N = trap situated far or near water, respectively. O, S = trap situated in open or shaded environment, respectively.

	Stavsätter water		Nykvarn water		Wetland Park water
Stavsätter NO	0.53/0.05	Nykvarn NO	0.41/0.21	Wetland Park NO	0.19/0.70
Stavsätter FO	0.31/0.03	Nykvarn FO	0.38/0.05	Wetland Park FO	0.33/0.58

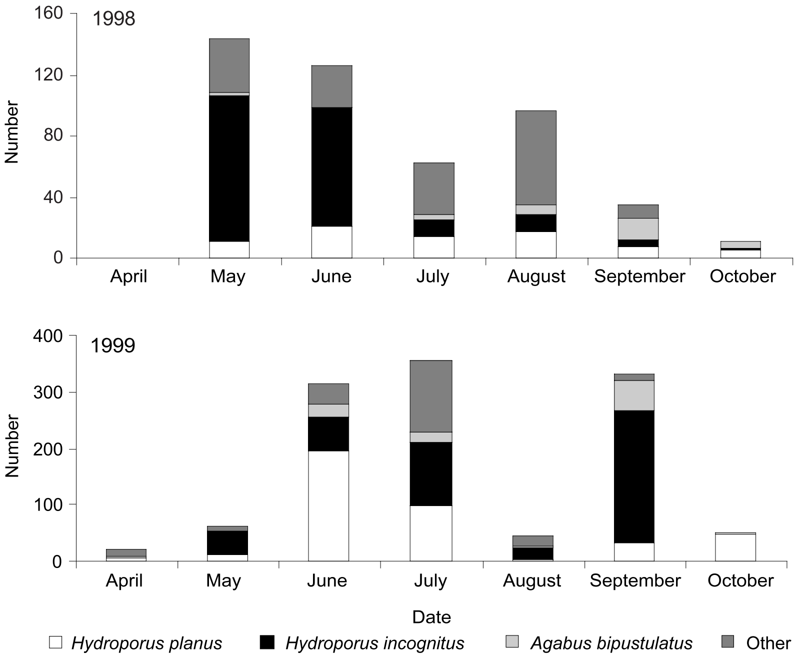

Fig. 3. Flight periodicity of diving beetles trapped in flight traps during 1998 and 1999. The dominating species are indicated.

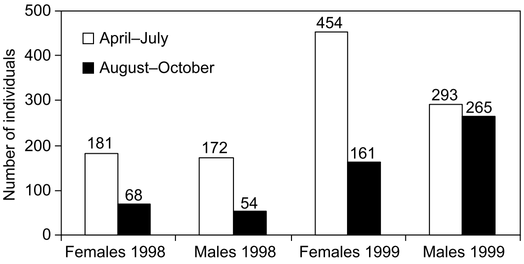

Fig. 4. Numbers of females and males in flight catches (all species summed) during the two flight periods April–July and August–October 1998 and 1999.

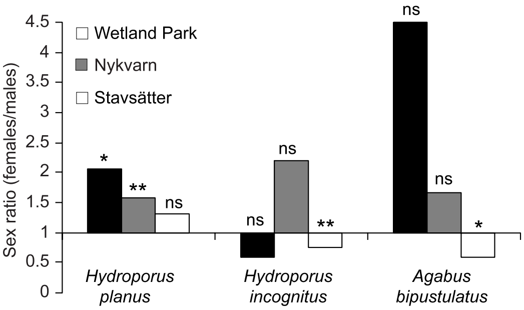

Fig. 5. Sex ratios of the three commonest species in the flight traps in three different landscapes. The material is from 1999, the two flight periods pooled. The sex ratio differs significantly from 1, * = $p < 0.05$, ** = $p < 0.01$. ns = no significant difference from 1 (chi-square test).

in urban landscapes were *Hydroglyphus pusillus, Colymbetes fuscus, and H. planus* (Fig. 7), the later two were common far from water. Most of the common species (species with 5 or more individuals are included in Fig. 7) were typically trapped in complex habitats near water. Stavsätter NO largely affects the pattern as it was the most species-rich site. Temperature, year, and day of sampling were less important for species distribution, and were distinguished on the third and fourth axes (data not shown).

Variation partitioning confirmed that landscape type was an important variable (Table 5). It explained 15% of the explainable variation (*F*), however, the intersection term was substantial i.e. the landscape and complexity gradients probably covary to some extent as they both lie mainly along axis 1. Distance (*C*) and complexity (*D*) also had large intersection terms. Year explained 15% of the variation (*B*), and the intersection was low, hence year explained unique variation. Day (*A*) and temperature (*E*) explain variation only a little.

Discussion

Why do *Hydroporus* dominate the flight catches? The traps are relatively small and it could be that they selectively attract small species. Nilsson (1997) also found *Hydroporus* to be the most common genus in the air. However, we do not know that the species caught in traps or on other surfaces are the most common in air. Quantitative methods like net sampling suggested by Dingle (1996) or suction traps (Johnson 1969) are needed to confirm species' abundance in air. Except for the Wetland Park, the body size structure we found in water was almost the opposite of the flight traps. In the water catches intermediate sized species dominated and only a small fraction were small species. However, this could partly be explained by the trapping method in water, which is biased towards larger individuals (Hilsenhoff & Tracy 1985, Hilsenhoff 1987, 1991). However, Nilsson and Söderberg (1996) did not find that traps caught larger species than sweep nets, but they caught other species and the common species differed between the two samples. These methodological questions of course influence the conclusions that can be drawn.

Diving beetle flight in different landscapes

There were large differences in wetland numbers and types between the landscapes, which can explain not only the larger species number we flight trapped at Stavsätter, but also the different species compositions and structures of flight catches. The amount of water is less in the urban landscapes and their wetlands are more isolated from each other than at Stavsätter. Their wetlands are also of recent origin, while several successional stages are available in the agricultural landscape. Also, the urban landscapes are more open while woods are common in the agricultural landscape. These differences were reflected in the species composition, e.g. the dominating flight trapped species at Stavsätter, *H. incognitus*, prefers small ponds with detritus while *H. planus*, that dominates in the urban landscapes, prefers unshaded waters with mineral substrate (Nilsson & Holmen 1995). Our hypothesis that more species would be found in the agricultural landscape was supported, and also that we found other species in the urban landscape.

The traps in shaded environments did not catch many specimens. Nevertheless, small waters in forests, of the same size as the trap, often do contain many dytiscids (Nilsson 1984, Nilsson & Svensson 1994, 1995). There are several possible reasons for our result. First, the reflection in the glass panes might have been too weak, since during the months of May and June a lot of pollen and debris fell on the panes. This coincides with the main flight period (May–July) and can partly explain why few specimens landed on the traps. Second, the colonisation rate might be slower in shaded environments, as the waters are hard to find from the air as shown by Nilsson and Svensson (1995). Their artificial pools in forests were more slowly colonised than similar pools in clearings. They also tested two pool sizes and only the larger pools (1.6 m^2) were colonised. Nevertheless, the specimens we trapped in shade were trapped both before and after the trees were leafing, which suggests that the dytiscids

Table 4. Number of immature *Hydroporus* adults in flight catches from Stavsätter, Nykvarn and the Wetland Park, near Linköping south-eastern Sweden. First figure is the percentage of young individuals, second figure in parenthesis is the total number of individuals, both immature and mature adults.

	H. planus	*H. incognitus*	*H. striola*	*H. nigrita*	*H. discretus*	*H. tristis*
Stavsätter 1998	33 (27)	4 (193)	80 (31)	81 (27)	100 (1)	86 (21)
Stavsätter 1999	31 (123)	10 (412)	90 (31)	73 (22)	100 (5)	0 (6)
Nykvarn 1998	22 (50)	0 (8)	0 (5)	20 (5)	0 (2)	0 (8)
Nykvarn 1999	55 (225)	35 (23)	100 (1)	75 (4)	–	–
Wetland Park 1999	39 (46)	3 (32)	0 (1)	50 (6)	50 (2)	0 (1)

are able to detect reflections through dense foliage. The size of the traps cannot explain the low numbers in shaded areas as we trapped many individuals in the traps in open areas.

The two most similar flight catches were far from water in two different landscapes (Fig. 2). This indicates that species fly long distances, probably searching for suitable habitats, and that the potential species pool therefore is large. But for reasons of which we are not certain, the species' environmental demands are not fulfilled, and they do not automatically colonise waters just because they are in the neighbourhood. Factors we have not studied may be important, for example, a species or specimens reaching water may accept or reject it as a habitat, and until we find larvae we can not say that waters are colonised.

Our hypothesis that a larger proportion of the species pool should be migrating in urban landscapes could not be supported. On the contrary, a higher proportion of the local species pool was migrating in the agricultural landscape, as the species composition in air and in water was most similar there. The lower similarities in species composition between flight catches and water catches in the urban landscape again indicate that species fly long distances and that the species in air therefore not necessarily originate from the species pool in adjacent waters. This also reflects the differences between the landscapes, the agricultural landscape had more types of waters and therefore a larger species pool in water than had the urban landscapes.

The composition of the faunas in air and in water apparently differed both at Stavsätter and Nykvarn (Table 3). The dominating genera in water were rare in the air and vice versa. Again, the pattern changed at the Wetland Park, where the structures were similar in spite of the fact that the species compositions were highly different. The same species dominated both in air and water (*H. planus*). It may be typical for newly constructed wetlands that early colonisers (opportunists) also dominate the water. Species that are good flyers and have the ability of migrating long distances should also be the earliest colonisers. Gradually they should diminish in abundance or in proportion as other, slower species, colonise the water. This is in concordance with our results, and also with the result of Lockwood *et al.* (1997). They modelled community assembling and found that faunas in frequently invaded systems were highly ephemeral and that the species composition changed all the time, as opposed to systems with lower colonisation rates where the initial species composition never changed.

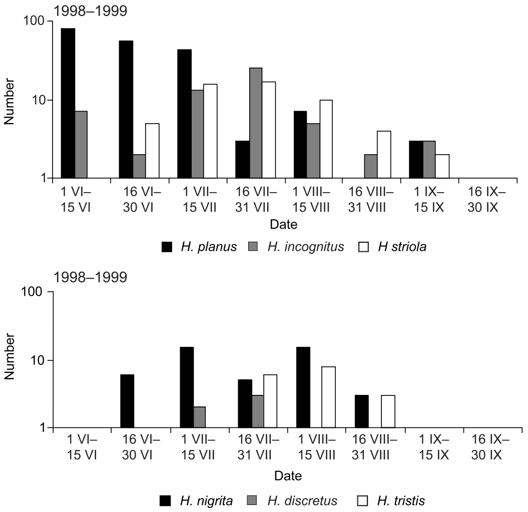

Fig. 6. Numbers of young individuals of six species of diving beetles, observe that three species are displayed in the upper diagram and that the other three are displayed in the lower diagram. The beetles were trapped in flight traps during 1998 and 1999 south of Linköping, south-eastern Sweden.

Environmental factors affecting flight and immigration of diving beetles

Agricultural or urban landscape seems to be important for the fauna we trapped. The urban landscape with low complexity attracts a few species. The agricultural landscape with characters as complex vegetation and short distances between wetlands attracts far more species. We cannot fully distinguish between the three variables landscape type, distance from water, and complexity, even in the variation partitioning (Table 5); we can only say that they together are important factors. Vegetation complexity near the traps should reflect the species' habitat demands, and since more of the species we

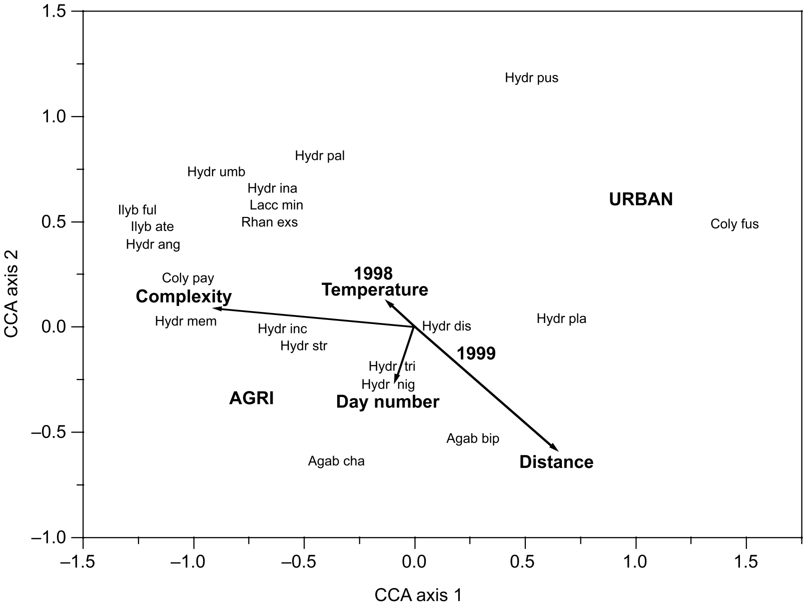

Fig. 7. Canonical Correspondence Analysis of diving beetles trapped in flight traps during 1998–1999. The most important variables are landscape type, distance from water and vegetational complexity near the traps. Species with fewer than 5 individuals are not included in the analysis. Full species names are given in the Appendix.

trapped are bound to waters with vegetation than without (Nilsson & Holmen 1995) the result was expected. Distances between wetlands or "islands" are foundations in ecology and flying dytiscids are indeed sensitive to large distances even if flight abilities are poorly known. The landscape types in our study are not fully described by complexity and distance. The matrix between wetlands differ in more respects; buildings, roads, wind exposure etc. Some of these variables are likely to affect a flying fauna. However, it is doubtful to include all these variables in a CCA.

The differences in species composition between years could reflect the rate of successional changes in the landscapes, but probably more how dytiscid population dynamics respond to different weather situations. Temperature was substantially lower in 1998 than in 1999 (SMHI 1996–1999), but explained only little in the ordination. The short temperature gradient probably means that many of the species trapped have a flight threshold near 15 °C, as we hardly trapped any species below that temperature. However, the variation in temperatures probably are larger than our data indicate, since they were

Table 5. Variation partitioning of variables used in a Canonical Correspondence Analysis of catches of flying diving beetles. Day = time of year when sampling was done, Year = 1998 or 1999, Distance = distance (m) from water where traps were placed, Complexity = diversity and structure of vegetation near the traps, Temperature = average daily maximum temperatures since last sampling occasion, Landscape = agricultural or urban.

Variable tested vs. covariables	Variance uniquely explained by tested variable	Variance uniquely explained by covariables	Intersection, variation jointly explained by variable and covariables
Day (*A*) vs. *B*–*F*	6	92	1
Year (*B*) vs. *A*, *C*–*F*	15	84	1
Distance (*C*) vs. *A*–*B*, *D*–*F*	10	68	22
Complexity (*D*) vs. *A*–*C*, *E*–*F*	8	54	37
Temperature (*E*) vs. *A*–*D*, *F*	4	93	3
Landscape (*F*) vs. *A*–*E*	15	57	28

measured at a weather station and do not reflect the exact air temperatures where the beetles took off.

The precipitation was much higher during the summer months in 1998 than in 1999, and rain probably prevents dytiscids from flying, although the effect of rain on the flight of insects is poorly known (Johnson 1969). Sunny or cloudy weather may not be important as long as the temperature is high enough, since clouds do not affect the reflected polarised light pattern in the traps (Carron & Becze-Deak 1999).

The species composition did not change much between years but the number of individuals trapped was higher in 1999 than in 1998, which probably reflects the warmer and drier weather. Day of sampling was not important in the ordination and this means that phenological differences between species were relatively small, or inconsistent within or between seasons as suggested by the data in Fig. 3.

Flight ability and colonising ability

The overall sex ratio in the whole flight material was heavily weighted towards females during April–July 1999 (Fig. 4). The number of immature adults was largest during this period too (Fig. 6). These observations indicate that dytiscid flight generally may confirm the idea of an oogenesis flight syndrome (Johnson 1969) characterising migrating species. An oogenesis flight syndrome implies that females migrate from their birthplaces before reproduction. Therefore they are efficient colonisers. However, conclusions must be cautious since immatures were only found in six species.

H. planus has several traits that make it a good example of a migrating and colonising species. It is common in the air and seems to be an excellent flyer (Jackson 1952), it shows a clear flight periodicity with more females (colonisers) during the spring and early summer at the Wetland Park and at Nykvarn (Fig. 5). The high proportion of immatures (Table 4 and Fig. 6) is also an argument for being a good migrant and coloniser. *H. planus* was trapped at all distances from water but in a higher proportion far from water, i.e. it has the potential of flying long distances. *H. incognitus* and *A. bipustulatus* are also known to be good fliers, and just as in *H. planus*, their wing muscles and wings are well developed (Jackson 1952). Of the other species known to be good fliers only *H. nigrita* and *H. striola* were common in the flight catches (*see* Appendix) and they also had high proportions of immature adults (Table 4).

Urbanisation and succession

Urbanisation and landscape exploitations are common processes. Our result may indicate how wetland faunas change when an agricultural landscape gradually turns into an urban area. We have shown that different species dominate in the air and in the water, depending on the landscape structure, and the consequence of this is that the potential colonisers are not the same in the three landscapes, in spite of a common regional species pool. *H. planus*, an early coloniser that prefers bare inorganic substrates dominates the Wetland Park, both in water and in air. If the succession proceeds, more vegetation is established in the water and in the surroundings and this is reflected in the aerial species pool, which is larger at Nykvarn than at the Wetland Park. In the most heterogeneous landscape of the three, at Stavsätter, the species pool is largest and here the dominating species in the flight catches, *H. incognitus*, is not typical for newly constructed wetlands, but instead typical for waters with rich macrophyte vegetation or much debris.

Therefore urbanisation would imply a species poorer fauna, but other species than in agricultural landscapes. Accordingly, to obtain a rich wetland insect fauna as exemplified by diving beetles, it seems necessary to take into account more than single wetlands or ponds. A series of wetlands in different environments and successional stages should be recommended on a landscape scale.

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Appendix. The total number of dytiscids trapped in flight traps during 1998–1999 and in water during 1996–1999, near Linköping, south-eastern Sweden. Stavsätter is an agricultural landscape, while Nykvarn and the Wetland Parks are urban landscapes. The first column contains the available information on the species' flight capacity where 0 = cannot fly, because of absence or reduction of flight muscles of wings, 1 = sometimes lack flight muscles sometimes have flight muscles, 2 = good fliers with well-developed flight muscles, X = poor information. Information of flight capacity from Jackson (1952, 1956a, 1956b), Bilton (1994), and Nilsson (1997).

Flight capacity	Species	Stavsätter		Nykvarn		Wetland Park	
		1998–1999 flight	1996–1998 water	1998–1999 flight	1997–1998 water	1999 flight	1999 water
X	*Hydroglyphus pusillus* (F.)	4	–	23	–	3	437
X	*Hygrotus decoratus* (Gyll.)	1	23	–	–	–	
1	*H. inaequalis* (F.)	14	499	5	44	–	26
X	*H. versicolor* (Schall.)	–	1	–	–	–	58
X	*H. impressopunctatus* (Schall.)	1	24	–	13	–	1
2	*H. confluens* (F.)	1	–	2	1	–	227
X	*H. nigrolineatus* (Stev.)	–	–	–	–	–	5
1	*Hyphydrus ovatus* (L.)	–	152	–	1	–	1
2	*Hydroporus nigrita* (F.)	49	–	9	–	6	2
1	*H. discretus* Fairm. & Bris.	5	–	3	–	2	
2	*H. pubescens* (Gyll.)	–	–	2	–	–	
X	*H. fuscipennis* Schaum	–	–	1	–	–	
2	*H. planus* (F.)	150	4	275	3	46	568
0	*H. obscurus* Sturm	–	–	–	–	–	1
1	*H. erythrocephalus* (L.)	1	16	1	–	–	3
X	*H. scalesianus* Steph.	1	1	–	–	–	
2	*H. angustatus* Sturm	9	23	–	2	–	7
1	*H. glabriusculus* Aubé	–	1	–	–	–	
1	*H. umbrosus* (Gyll.)	4	5	1	–	–	1
1	*H. tristis* (Payk.)	27	14	8	–	1	3
1	*H. gyllenhalii* Schiöd.	–	4	–	–	1	1
X	*H. notatus* Sturm	–	1	1	–	–	
2	*H. incognitus* Shp	604	20	31	–	32	8
1	*H. striola* (Gyll.)	61	25	7	1	1	5
1	*H. palustris* (L.)	8	20	2	–	–	1
X	*H. neglectus* Schaum	1	1	–	–	1	

Continued

Appendix. Continued.

Flight capacity	Species	Stavsätter		Nykvarn		Wetland Park	
		1998–1999 flight	1996–1998 water	1998–1999 flight	1997–1998 water	1999 flight	1999 water
1	*H. memnonius* Nic.	10	–	–	–	–	
X	*Porhydrus lineatus* (F.)	–	4	–	1	–	17
X	*Graptodytes granularis* (L.)	–	1	–	–	–	
X	*Suphrodytes dorsalis* (F.)	–	20	–	1	–	1
X	*Scarodytes halensis* (F.)	2	–	–	–	2	43
X	*Agabus striolatus* (Gyll.)	–	1	–	–	–	
2	*A. chalconatus* (Panz.)	5	–	–	–	1	
X	*A. subtilis* Er.	–	1	–	–	–	
X	*A. unguicularis* (Thoms.)	–	5	–	–	–	
0	*A. paludosus* (F.)	–	1	–	–	–	
2	*A. melanarius* Aubé	1	–	–	–	–	
2	*A. bipustulatus* (L.)	88	18	32	–	11	212
2	*A. nebulosus* (Forst.)	–	–	–	–	–	89
1	*A. sturmii* (Gyll.)	–	69	–	13	1	5
0	*A. congener* (Thunb.)	3	–	1	–	–	
X	*A. fuscipennis* (Payk.)	–	1	–	–	–	
1	*A. uliginosus* (L.)	–	–	3	–	–	
2	*Ilybius subaeneus* (Er.)	–	53	4	65	–	
2	*I. ater* (De G.)	5	224	–	13	–	
X	*I. guttiger* (Gyll.)	1	8	–	4	–	1
X	*I. quadriguttatus* (Lac.)	–	79	–	28	–	2
X	*I. similis* Thoms.	–	11	–	–	–	
2	*I. aenescens* Thoms.	–	1	–	4	–	
2	*I. fuliginosus* (F.)	8	25	–	–	–	27
0	*I. fenestratus* (F.)	–	58	–	1	–	
X	*Rhantus grapii* (Gyll.)	–	96	–	5	–	
X	*Rhantus suturalis* (MacL.)	1	–	1	17	–	33
X	*R. frontalis* (Marsh.)	1	479	33	–	–	62
X	*R. suturellus* (Harr.)	–	2	–	1	–	
2	*R. exsoletus* (Forst.)	16	676	2	21	–	18
2	*Colymbetes fuscus* (L.)	–	–	10	21	–	18
X	*C. striatus* (L.)	1	26	–	6	–	4
X	*C. paykulli* Er.	16	81	–	1	–	10

2	*Laccophilus minutus* (L.)	11	75	3	5	–	48
X	*Hydaticus seminiger* (De G.)	–	293	–	29	–	2
X	*H. transversalis* (Pontopp.)	–	225	–	3	–	
X	*H. aruspex* Clark	–	6	–	–	–	
2	*Graphoderus cinereus* (L.)	–	46	–	3	–	
X	*G. zonatus* (Hoppe)	–	132	–	2	–	
X	*G. bilineatus* (De G.)	–	1	–	–	–	
X	*Acilius canaliculatus* (Nic.)	4	174	–	132	–	3
2	*A. sulcatus* (L.)	–	72	–	12	–	
2	*Dytiscus marginalis* L.	1	30	–	18	–	5
X	*D. circumcinctus* Ahr.	–	119	–	25	–	4
0	*D. lapponicus* Gyll.	–	7	–	–	–	
	Number of species	34	54	24	33	13	38
	Number of individuals	1115	3954	430	580	108	1959