Correspondence Between Larval Development and Adult Residence Habitats of Dolichopodid Flies (Diptera, Empidoidea: Dolichopodidae) in a Heterogeneous Mosaic of Seacoast Grassland Habitats

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VILKS K. 2007. CORRESPONDENCE BETWEEN LARVAL DEVELOPMENT AND ADULT RESIDENCE HABITATS OF DOLICHOPODID FLIES (DIPTERA, EMPIDOIDEA: DOLICHOPODIDAE) IN A HETEROGENEOUS MOSAIC OF SEACOAST GRASSLAND HABITATS. – *Latvijas entomologs*, 44: 109-118.

Abstract: Spatial distribution of dolichopodid adults and larvae was investigated in a heterogeneous mosaic of seacoast habitats in the Lake Engure Nature Park (Latvia) in July 2006. The patchy coastal landscape was dominated by dry dune grasslands, wet seacoast grasslands and reed beds. Larval development habitats were determined by using soil emergence traps, while the flight activity of adult flies was examined by yellow water traps. In total, 30 dolichopodid species were recorded. The most abundant species were *Dolichopus nubilus*, *D. notatus*, *Teuchophorus spinigerellus*, *Sympucnus pulicarius*, *Dolichopus acuticornis*, *D. pennatus*, *D. plumipes* and *Sciapus maritimus*. There were much higher species richness and abundance for adult flies flying above the ground in comparison with those species emerging from soils. In general, dolichopodids were more abundant in humid habitats. Flying adult dolichopodids concentrated in reed beds, while their emergence activity, representing larval development habitats, was significantly higher in wet seacoast grasslands. Thus, habitats of larval development did not correspond to adult residence habitats. The article discusses several alternative explanations for such spatial distribution of different development stages. Behavioural aspects seem to be the most important for the habitat selection of adult flies. In conclusion, this study shows that dolichopodid flies may require a highly heterogeneous environment during their life cycle.

Key words: Adult flight activity, Diptera, Dolichopodidae, Empidoidea, larval development, Latvia, migration, seacoast.

Introduction

There is no doubt, that insects are the most species-rich animal group in any terrestrial environment (Steffan-Dewenter, Tscharntke 2002), and that they make up most of the biodiversity in the world (Speight et al. 1999). Dipterans have been recorded as one of the largest insect order (Speight et al. 1999, Frouz 1999), and they clearly dominate in a wide range of terrestrial habitats (Melecis et al. 1999), representing an important component of soil and grass-dwelling faunas (Frouz 1999).

Despite of this, dipterans still belong to the least investigated animals, mainly due to taxonomical and methodological difficulties (Frouz 1999, Hövemeyer 2000). Furthermore, the majority of ecological studies related to dipterans considers the adult stage only, and thus obtains only simplified knowledge on the actual diversity and distribution of different species (Frouz 1999). There is an urgent need to improve our knowledge on the spatial distribution of different development stages of dipterans in the context of biodiversity research and bioindication. If dipteran species depend on different habitats during their life cycle, this should take into account planning the conservation of endangered and rare dipteran species or communities. Further, species showing multi-habitat use should indicate fine-scale habitat or landscape heterogeneity and could be used as bioindicators of habitat quality and diversity.

The subject of the present study is dolichopodid flies occurring in a highly complex seacoast landscape. Dolichopodids represent a diverse and species-rich dipteran group worldwide (Grichanov 2006), and heterogeneous mosaic of clearly different coastal habitats was used as a model ecosystem, allowing studying small-scale distribution of species.

There are two main aims for the present study: to determine dolichopodid larval development sites (1), and to try to answer the question, weather dolichopodid larval development habitats correspond with habitats preferred by the adult flies (2).

Methods
Study area

This study was performed in the territory of the Lake Engure Nature Park (Western Latvia) near the village Mērsrags. Two sampling plots (plot A: 57°19.481´N, 23°08.249´E and plot B: 57°19.461´N, 23°08.265´E) (~30x30 m) were selected within a heterogeneous mosaic of coastal habitats composed of patches of dry dune grasslands and wet seacoast grasslands as well reed beds in the depressions of microrelief (Fig.1).

Reed beds and less frequently adjacent lower situated grasslands were regularly overflooded during high level of seawater. Dry dune grasslands were formed by scarce vegetation dominated by *Festuca rubra, Leymus arenarius* and *Achilea millefolium* and by dense layer of mosses, however some patches of bare sandy ground were also present. A dense vegetation of *Juncus gerardii*, *Lathyrus palustris*, *Galium palustre* dominated wet seacoast grasslands and *Elytrigia repens,* and patches of dense grass litter were frequently present in this habitat. Both dry and wet grasslands were slowly overgrown with common reed *Phragmites australis*, as habitat management in the investigated site has not been carried out for at least ten years. Reed beds were strongly dominated by a tall vegetation of common reeds, although *Galium palustre* was also relatively abundant.

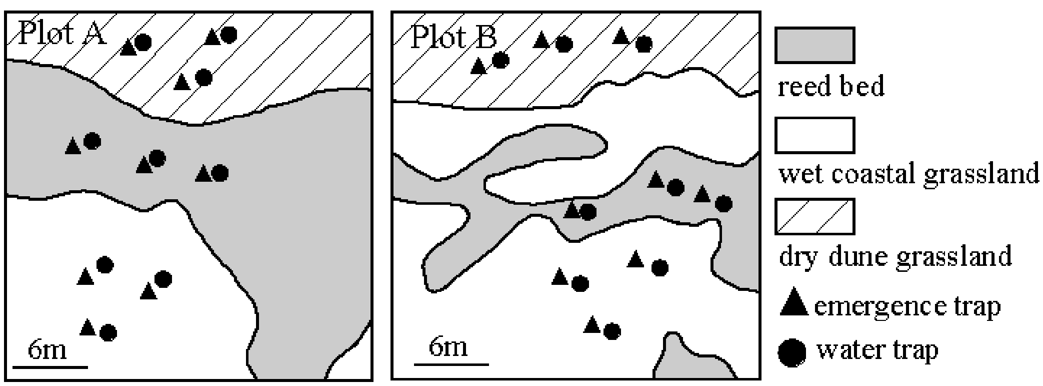

Figure 1. Scheme of the investigated sampling plots situated in a heterogeneous mosaic of three coastal habitats in the Lake Engure Nature Park (Western Latvia) and location of emergence and water traps.

Sampling and identification

Aerial activity of flying adult dolichopodids was registrated by using yellow water traps (diameter 12 cm, depth 6 cm), which have been previously recorded as an excellent method for the investigation of dipteran communities (Pollet, Grootaert 1999, De Bruyn et al. 2001). All water traps were filled at two-thirds with a 4% formaldehyde solution to which a few drops of detergent was added in order to decrease surface tension. Water traps were placed on the ground or 5-10 cm above ground attached to piles of wood within inundated reed beds as such locations allow to collect the highest numbers of dolichopodid species as shown by Pollet and Grootaert (1994). In dense vegetation, the surrounding plants were cut off at distance of 10 cm around the water traps.

Larval distribution pattern was assessed using soil emergence traps (basal area 0.25 m^2, height 50 cm), which registrate freshly emerged adults of dolichopodids from soils in such a way allowing to detect their breeding sites. Prior to placing of the emergence traps, all vegetation in the basal area of traps was cut off. In order to obtain an effective isolation, lower margins of emergence traps were digged in the soil at the deep of 10 cm. Sampling bottles at the tips of emergence traps were filled with a 4% formaledhyde solution to which a few drops of detergent was added. In each habitat type, six water traps and six emergence traps were installed. Traps were placed with a minimum distance of 5 m from each other.

Dolichopodids were collected in July of 2006. This period of season was selected, while, according to my previous investigations (unpublished data), the majority of species shows the highest adult activity in July. The materials from traps were emptied two times per investigation period.

In the laboratory, dolichopodids were sorted and stored in 70% alcohol. Identification was performed by means of the keys compiled by Grichanov (2006), Meuffels and Grootaert (1990), Negrobov and Stackelberg (1969) and Pollet (1990, 1996). Nomenclature follows Grichanov (2006). The materials of the sampled dolichopodids are deposited within the collection of the Faculty of Biology of the Latvian University (Rīga).

Data analysis

Non-parametric Kruskal-Wallis H test was performed for testing differences in species richness and abundance among investigated habitats. If significant differences were found, non-parametric Mann-Whitney U test was used then for the pairwise comparisons of variables. Differences in the proportions were examined using the χ^2-test (Sokal, Rohlf 1995). Detailed analyses for individual species were performed for those species only, representing 30 or more individuals in the total catch. All statistical analyses were performed using SPSS 15.0 for Microsoft Windows® software.

Results

Dolichopodid emergence from soils

In total, 13 species with 87 individuals were caught with soil emergence traps (Table 1). Despite of low numbers of emerging individuals, the calculated mean abundance per area was quite high, at least in the patches of wet meadows (37 ind./m^2). *Dolichopus nubilus* (39%), *Teuchophorus spinigerellus* (14%), *Achalcus vaillanti* (8%), *Dolichopus plumipes* (8%) and *D. popularis* (7%) were the most abundant species.

Table 1. Summary of dolichopodid species collected with water traps and emergence traps in a heterogeneous mosaic of three coastal habitats in July of 2006. Abbreviations: I – reed beds, II - wet seacoast grasslands, III – dry dune grasslands.

Species	Water traps				Emergence traps			
	I	II	III	Total	I	II	III	Total
Achalcus vaillanti BRUNHES, 1987	3	3	0	6	2	5	0	7
Campsicnemus scambus (FALLÉN, 1823)	0	0	0	0	3	0	0	3
Chrysotus cilipes MEIGEN, 1824	3	9	4	16	0	1	0	1
Chrysotus femoratus ZETTERSTEDT, 1843	0	1	0	1	0	0	0	0
Chrysotus gramineus (FALLÉN, 1823)	1	0	0	1	0	0	0	0
Chrysotus pulchellus KOWARZ, 1874	0	0	1	1	0	0	0	0
Dolichopus acuticornis WIEDEMANN, 1817	90	1	6	97	0	0	4	4
Dolichopus claviger STANNIUS, 1831	0	1	0	1	0	0	0	0
Dolichopus diadema HALIDAY, 1832	2	1	4	7	0	0	0	0
Dolichopus latipennis FALLÉN, 1823	2	2	0	4	0	0	0	0
Dolichopus nitidus FALLÉN, 1823	3	0	2	5	0	2	0	2
Dolichopus notatus STAEGER, 1842	232	12	4	248	0	0	0	0
Dolichopus nubilus MEIGEN, 1824	138	62	75	275	7	27	0	34

To be continued

Continuation of Table 1

Dolichopus pennatus MEIGEN, 1824	47	30	5	82	0	4	0	4
Dolichopus plumipes (SCOPOLI, 1763)	25	25	10	60	2	4	1	7
Dolichopus popularis WIEDEMANN, 1817	4	3	0	7	6	0	0	6
Dolichopus sabinus HALIDAY, 1838	0	1	1	2	0	0	0	0
Dolichopus simplex MEIGEN, 1824	6	4	2	12	0	0	0	0
Dolichopus ungulatus (LINNAEUS, 1758)	3	0	2	5	0	0	0	0
Hercostomus aerosus (FALLÉN, 1823)	3	3	1	7	0	0	0	0
Hercostomus assimilis (STAEGER, 1842)	1	0	0	1	0	0	0	0
Hercostomus chalybeus (WIEDEMANN, 1817)	2	1	0	3	0	0	0	0
Hercostomus chrysozygos (WIEDEMANN, 1817)	1	5	1	7	0	0	0	0
Medetera plumbella MEIGEN, 1824	0	0	7	7	0	0	1	1
Rhaphium riparium (MEIGEN, 1824)	4	0	7	11	0	0	0	0
Sciapus lobipes (MEIGEN, 1824)	2	0	0	2	0	0	2	2
Sciapus maritimus BECKER, 1918	20	1	16	37	0	0	4	4
Sympucnus pulicarius (FALLÉN, 1823)	83	10	22	115	0	0	0	0
Syntormon pallipes (FABRICIUS, 1794)	2	0	3	5	0	0	0	0
Teuchophorus spinigerellus (ZETTERSTEDT, 1843)	153	25	12	190	0	12	0	12
Total number of individuals	830	200	185	1215	20	55	12	87
Number of species	24	20	20	29	5	7	5	13

The highest numbers of emerging flies was observed in wet meadows and decreased both in reed beds and dry meadows (Kruskal-Wallis test: H=9.31, df=2, p<0.05) (Fig. 2A). Total species richness was found approximately similar in all investigated habitats (Table 1), although there were significant higher species richness per trap in wet meadows in comparison with the other habitats (Kruskal-Wallis test: H=7.25, df=2, p<0.05) (Fig. 3A).

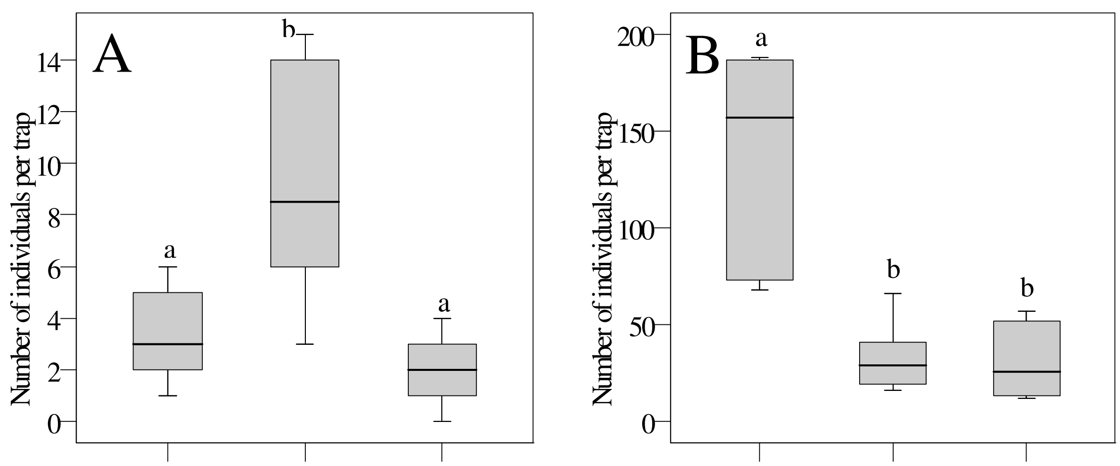

Figure 2. Boxplots (median, quartiles and min/max values) for the abundance of dolichopodid flies emerged from soils (A) and flying above the ground (B) in a mosaic of three coastal habitats in July 2006. Kruskal-Wallis H test shows significant (p<0.05) differences in abundance among habitats. Pairwise comparisons were carried out using Mann-Whitney U test; different letters above the bars indicate significant (p<0.05) differences. Abbreviations: I – reed bed, II – wet coastal grassland, III – dry dune grassland.

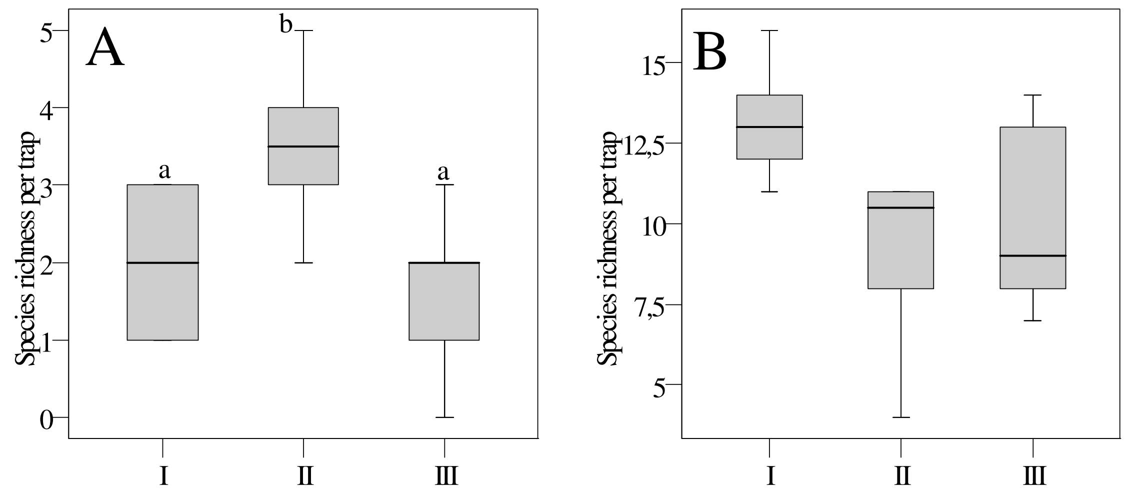

Figure 3. Boxplots (median, quartiles and min/max values) for the species richness of dolichopodid flies emerged from soils (A) and flying above the ground (B) in a mosaic of three coastal habitats in July 2006. Kruskal-Wallis H test shows significant ($p<0.05$) differences in species richness among habitats for emerging dolichopodids only. Pairwise comparisons were carried out using Mann-Whitney U test; different letters above the bars indicate significant ($p<0.05$) differences. Abbreviations: I – reed bed, II – wet coastal grassland, III – dry dune grassland.

Dolichopus plumipes emerged from soils in all habitats, but other species showed a more specific emergence pattern, and the majority of species (77%) were registrated by soil eclectors in a single habitat only. *D. acuticornis*, *Medetera plumbella*, *Sciapus lobipes* and *S. maritimus* were recorded only in dry meadows, *Dolichopus popularis* and *Campsicnemus scambus* were registrated in reed beds only, and *Chrysotus cilipes*, *Dolichopus nitidus*, *D. pennatus* and *Teuchophorus spinigerellus* were specific for wet meadows. Detailed analysis of emergence pattern for individual species was possible to conduct only for the most abundant species *Dolichopus nubilus*, which showed similar emergence patterns as in the case of total dolichopodid numbers (Kruskal-Wallis test: $H=13.13$, $df=2$, $p<0.01$). The abundance of other species was too low to compare the distribution of adults emerging from soils among different habitats.

Flight activity of adult dolichopodids

In total, 29 dolichopodid species with 1215 individuals were sampled with yellow water traps (Table 1). *Dolichopus nubilus* (23%), *D. notatus* (20%), *Teuchophorus spinigerellus* (16%), *Sympucnus pulicarius* (9%) and *Dolichopus acuticornis* (8%) were the most abundant species.

Adult dolichopodids preferred clearly reed beds and the abundance of individuals flying above the ground decreased gradually from wet to dry habitats (Kruskal-Wallis test: $H=11.57$, $df=2$, $p<0.05$) (Fig. 2B). In contrast to the emerging dolichopodids, species richness of adult dolichopodids flying above ground was not significantly different among investigated habitats (Kruskal-Wallis test: $H=4.53$, $df=2$, $p>0.05$), although slightly larger values were recorded for samples from reedmarsh habitat (Fig. 3B).

Table 2 gives a summary on differences in abundance pattern of adult flies flying above the ground for abundant dolichopodid species, which were represented at least with 30 individuals in the total catch. All species except *Dolichopus plumipes* showed significant differences in abundance among investigated habitats. Adult flies of *Dolichopus nubilus, D. notatus, Teuchophorus spinigerellus, Dolichopus acuticornis, Sympucnus pulicarius* were most abundant in reedmarshes, *Dolichopus pennatus* was less abundant in dry meadows respectively *Sciapus maritimus* less abundant in wet meadows in comparison with the other two habitats.

Emergence activity versus flight activity

The proportion of collected dolichopodids among habitat types was significantly different for adult flies flying in the vegetation layer and flies emerging from soils and thus representing larval development sites (χ^2 = 116.3, df=2, p<0.01).

Discussion

Dolichopodid communities studied were dominated by species, which according to the literature data can be considered as typical for coastal habitats. Among most abundant species, *Dolichopus nubilus* has been called halophilous (Dyte 1959, Emeis 1964, Meyer and Heydemann 1990), *D. notatus* has been recorded from coastal marshlands (Falc, Crossley 2005), *D. acuticornis* and *Sciapus maritimus* have been found in coastal dunes (Ardö 1957, Emeis 1964, Pollet, Grootaert 1996). Further, among less abundant species there are also other species such as *Dolichopus diadema, D. latipennis, D. sabinus, Rhaphium riparium* and *Syntormon pallipes*, which frequently inhabit coastal habitats (Ardö 1957, Emeis 1964, Meyer, Heydemann 1990, Pollet 1992, Crossley 1996, Falc, Crossley 2005).

Table 2. Differences in abundance (mean value per trap ± SE) of adult dolichopodids of dominant species (n>30 individuals in total collection) catched by yellow water traps in a heterogeneous mosaic of three coastal habitats in July 2006. Differences among habitats were tested using Kruskal-Wallis test. Residence habitat of adult dolichopodids flying above the ground was evaluated with pairwise comparisons performed using Mann-Whitney U test (values with different letters are significantly (p<0.05) different in this test). Abbreviations: I – reed bed, II – wet coastal grassland, III – dry dune grassland.

Species	Kruskal-Wallis test (H statistic, p value)	I	II	III	Adult residence habitat
Dolichopus acuticornis	H=8.55, p<0.05	15.0±3.5 (a)	0.2±0.2 (b)	1.0±0.6 (b)	I
Dolichopus notatus	H=12.64, p<0.01	38.7±10.8 (a)	2.0±0.7 (b)	0.7±0.4 (b)	I
Dolichopus nubilus	H=6.71, p<0.05	23.0±2.8 (a)	10.3±2.5 (b)	12.5±3.8 (b)	I
Dolichopus pennatus	H=8.58, p<0.05	7.8±1.7 (a)	5.0±1.4 (a)	0.8±0.5 (b)	I,II
Dolichopus plumipes	H=4.71, n.s.	4.2±1.4	4.2±0.7	1.7±0.7	I,II,III
Sciapus maritimus	H=11.16, p<0.01	3.3±0.8 (a)	0.2±0.2 (b)	2.7±0.8 (a)	I,III
Sympucnus pulicarius	H=9.02, p<0.05	13.8±3.7 (a)	1.7±0.9 (b)	3.7±2.0 (b)	I
Teuchophorus spinigerellus	H=9.83, p<0.01	25.5±6.8 (a)	4.2±1.4 (b)	2.0±0.8 (b)	I

The present study shows that dolichopodids both adults and larvae were observed mainly in reed beds and wet grasslands in comparison with dry dune grasslands. This statement agrees with literature data that the majority of dolichopodid species can be characterized as more or less hygrophilous (Dyte 1959, Emeis 1964, Meyer, Heydemann 1990, Pollet, Grootaert 1991, Pollet et al. 1992, Bährmann 1993, Pollet, Grootaert 1999, Pollet et al. 2003). Pollet and Grootaert (1996) investigated dolichopodids in a dune landscape along the Belgian coast and have also found that species diversity and abundance increased from dry to humid sites. However, there are some xerophilous species such as *Medetera plumbella* and *Sciapus wiedemanni*, which prefer dry dune habitats (Pollet, Grootaert 1996). I have also found that dolichopodids of species *Medetera plumbella* and both *Sciapus* species emerged from soils in dry dune grasslands, although a remarkable part of adult *S. maritimus* was observed in an adjacent reed bed. These findings support conclusion, previously obtained by Pollet and Grootaert (1999), that dolichopodids are ecologically diverse group of dipterans, occurring in every terrestrial or semi-terrestrial habitat.

The current knowledge on dolichopodid ecology has been based to a great extent on the studies on adult flies, and there is only a limited number of literature data on larval development habitats. Dyte (1959) has reported that larvae of many species occur in mud, humid soil, leaf litter and in other various substrata near ponds and streams. Dolichopodids may emerge also from stagnant or running water (Caspers, Wagner 1982, Negrobov, Silina 1987, Grichanov 1999, Reeves et al. 2003). However, this is contradicted by Meyer and Speth (1995), Hedström (1997) and Meyer and Filipinski (1998) who argumented that the majority of dolichopodids, catched by swimming emergence traps, are actually terrestrial species attracted to water for mating or feeding, and thus trapped by the emergence traps. Meyer (2006) has demonstrated that dolichopodid larvae develop in great numbers in soils of wet meadows. Similarly, I have also found that the majority of dolichopodids emerged from wet grasslands, which can be characterized by intermediate moisture comparing to other investigated habitats. It is somewhat surprisingly that emergence from reed beds was lower than in grasslands. Dyte (1959) and Sommer (1978) showed that preimaginal stages of some dolichopodid species have adaptations to periodically inundated environment such as elongated respiratory horns of pupae of *Machaerium maritimae*. This implies that reed beds could be also a suitable habitat for the development of larvae. Probably, some dolichopodid species may be true ecotone species with their larvae developing at direct margins of ponds or reed beds, and thus not catched in this study.

There were much higher numbers of dolichopodid individuals and species flying above the ground in comparison with those emerging from soils. Further, two dominant species observed as adult flies, namely *Dolichopus notatus* and *Sympucnus pulicarius*, were not found emerging from soils in any of investigated habitat. The most probably, both are immigrated species from adjacent habitats. Alternative explanations could be: 1) that some dolichopodid species originated from ecotone habitats, not studied in this investigation or 2) that individuals of some species emerged before the study. Delettre et al. (1998) obtained similar results in the investigations on empidid flies and concluded that part of species originated from habitats not sampled in their study.

The present study shows that spatial distribution of dolichopodid larvae and adults does not correspond well with each other. Both the highest abundance as well as the highest species richness of emerging dolichopodids from soils were found in wet grasslands. Thus, larval development was observed mainly in this habitat. On the other hand, adult flies preferred clearly reed beds. The most abundant species *Dolichopus nubilus* showed just the same pattern of spatial distribution. Although there were not enough data for a detailed quantitative analysis for other seven most abundant species, it is clearly visible, that observed occurrences of emerging flies were located in habitats others than those preferred by flying adults. *D. plumipes* was an exception, because both larvae and adult flies were recorded from all investigated habitats. Further, occurrences of emergence of some other numerous species, such as *Teuchophorus spinigerellus* and *Dolichopus acuticornis*, were located in habitats with significantly lower abundance of adult flies in comparison with the other habitats investigated. This implies that dolichopodids migrated at small-scale distances through a mosaic of different seacoast habitats from patches of wet meadows to reed beds, where concentration of adult flies occurred. It remains unclear, however, whether these migrations are a specific feature of species life cycle or simply a response to changes in their environment, for example, in variable inundation or soil moisture regime at certain places in different years. It should take also a note, that this study considered only dolichopodid emergence in July, although catches of adults flying above ground may include individuals which emerged earlier in the season. Thus, this study was unable to detect spatial pattern of species if a remarkable part of dolichopodids emerged before the period of investigations. My previous research (unpublished data) in this area, however, showed that abundance of adult dolichopodids increased only in July, which means that emergence is also restricted to this period.

In literature, there are only few other studies comparing the spatial distribution of larval and adult dolichopodids. Frequently, it is assumed that adult flies are found in close proximity to the larval development sites (Corpus 1980 after Reeves et al. 2003). The reason for this is that adults oviposit in the direct vicinity of their emerging sites (Frouz, Paoletti 2000). There should not be a necessity for dispersion or migration to other sites, if larval development in certain habitat was successful. Frouz and Paoletti (2000) investigated various dipterans in an agricultural landscape in the northern Italy and have found that the distribution of dolichopodid larvae and adults correspond well with each other. At the same time, they mentioned that dolichopodids developed in various habitats but concentrated in a single one as adult flies. Results of present study are similar to those obtained by Delettre et al. (1992, 1999), who studied empidid flies in a mosaic landscape near an oligotrophic pond in France and have found that empidids use different habitats during their life-cycle. They concluded that reproduction sites and space used by adults differed for the dominant empidid species, because empidids emerged mainly from heathland in comparison to adult residence near pond banks. Similarly, the present study also shows that adult dolichopodids are distributed in more humid places than their larvae.

Delettre et al. (1992) reported that behaviour of empidid flies is the reason for migration of adult flies. Empidids show specific behaviour expressions, and each of them requires different environmental resources (Delettre et al. 1992). There are also published data on the complex behaviour of dolichopodid flies, including mating, feeding, migration and oviposition (Frouz, Olejníček 1999). Dolichopodids search for soft-bodied arthropods and annellids (Ulrich 2004) on soil surface, on the surface of lower vegetation (Frouz, Olejníček 1999) or use surface of pools and ponds as their hunting ground (Hedström 1997). As many chironomid and culicid larvae and adults are common in humid places, this may increase attractiveness of such habitats for adult dolichopodids (Frouz, Olejníček 1999). Further, courtship and mating behaviour of dolichopodids occur also, at least partly, on the ground and involves visual communication between flies (Zimmer et al. 2003). Thus, adult dolichopodids require free space for feeding and sexual behaviour, and reed beds with bare soil and sparse vegetation may be more suitable as adult residence sites in comparison with wet grasslands, characterized by dense vegetation and well developed litter layer.

In conclusion, the results of the present study show that distribution of dolichopodid larvae and adults was different among various habitats in a patchy seacoast landscape. This indicates, that dolichopodids may use different habitats for different behaviour expressions during their life-cycle, although further more detailed investigations are still necessary. As dolichopodids require seemingly highly heterogeneous environment during their life-cycle, they can be used probably as an tool for the fine-scale assessment of habitat heterogeneity and diversity. Further, this study illustrates that abundance data in invertebrate studies should be carefully evaluated, as habitats with the highest numbers of species or individuals may not always represent the best ones, which conforms with all specific requirements of species.

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