Epigaeic Diptera Brachycera from the coastal sand dunes of National Park Thy, Denmark

Epigæiske fluer (Diptera Brachycera) fra klitterne i Nationalpark Thy

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Abstract

In 2013-2014 flies (Diptera Brachycera exclusive Calyptratae) active on the sand surface (epigaeic) were collected in pitfall traps in yellow and grey coastal sand dunes in National Park Thy, Denmark. A total of 15,670 flies of 227 species representing 31 families were captured. Sphaeroceridae, Dolichopodidae, and Chloropidae were particularly speciesrich, contributing 61, 30 and 25 species, respectively. Twenty species were new to the Danish fauna (Appendix). Phoridae made up c. 40% of the flies captured, while Dolichopodidae and Chloropidae contributed c. 14% and c. 9% of the total catch. The species collected in yellow and grey dunes were ranked according to frequency. The ten most frequent species in yellow and grey dunes contributed c. 73% and c. 87% of the total fauna, respectively. Several species captured were few in number, e.g. 51 species and 46 species trapped in yellow and grey dunes, respectively, were singletons. The species composition and number of flies recorded from the two types of dune differed distinctly. The difference is further underlined by the indices of similarity (QS, Sørensen). The highest similarities were found between sites situated within yellow dunes or grey dunes, whereas the similarities between all combinations of sites in yellow and grey dunes were lower. The seasonal activity patterns of predominant brachycerans are outlined. The catch of flies in the traps reflects a versatile fly activity on the sand surface, e.g. in relation to hatching, feeding, oviposition or other necessities of life. Presumably, some fly species were actually attracted by the smell from the multitude of dead animals accumulated in the pitfall traps. Based on information in the literature the flies of the coastal dunes were grouped according to the trophic level of the larvae (Appendix). The most numerous trophic group is the saprophages, followed by zoophages and phytophages, while mycetophages, microphages and parasitoids each totals less than 2%.

Sammenfatning

I 2013-2014 blev 15.670 fluer (Diptera Brachycera; eksklusiv Calyptratae), der var aktive på sandoverfladen (epigæiske), fanget i faldfælder i hvid og grå klit i Nationalpark Thy. I alt 227 arter fra 31 fluefamilier var repræsenteret. Familierne Sphaeroceridae, Dolichopodidae og Chloropidae med henholdsvis 61, 30 og 25 arter omfattede tilsammen ca. halvdelen af alle arterne. Tyve arter er nye for den danske fauna (Appendix). På individplan dominerede Phoridae (ca. 40%) efterfulgt af Dolichopodidae (ca. 14%) og Sphaeroceridae (ca. 13%). De 10 hyppigste arter i hvid og grå klit udgjorde henholdsvis ca. 73% og 87% af det indsamlede materiale. Et stort antal arter forekom kun i meget lavt antal, bl.a. var 51 arter fra hvid klit og 46 fra grå klit kun repræsenteret ved enkeltindivider. Artssammensætningen og individtallet i hvid og grå klit var tydeligt forskellig (Appendix). Forskellen i faunaen i de to klittyper blev yderligere understreget af Sørensens similaritetsindeks. Fluefaunaens sæsonaktivitet var forskellig i hvid og grå klit. Nogle hyppige fluearters bidrag til sæsonaktiviteten vises, f. eks. dominerer to phoridearter flueaktiviteten fra sidst i september. Fangsten af fluer i faldfælderne afspejler en alsidig flueaktivitet på sandoverfladen, f. eks. i forbindelse med klækning, byttesøgning og æglægning, men i nogle tilfælde givet også tiltrækning til fælderne på grund af lugten fra de mange døde dyr akkumuleret i fælderne. Baseret på litteraturoplysninger blev fluerne i fælderne grupperet i henhold til larvernes trofiske niveau. Saprofage arter var talrigest repræsenteret efterfulgt af zoofager og fytofager medens mycetofager, mikrofager og parasitoider kun udgjorde en meget beskeden andel af den samlede fluefangst. De vigtigste arter i de forskellige trofiske grupper udpeges, f. eks. er mange sphaerocerider og phorider saprofager.

Introduction

Coastal sand dunes are habitats of a species-rich dipterous fauna, for instance almost 750 species of Diptera were recorded from coastal sand dunes and the littoral zone in Denmark, Norway and Sweden (Ardö, 1957), and in 2013-2014, 112 species of Diptera Nematocera were collected in pitfall traps in yellow and grey sand dunes in National Park Thy, Denmark (Nielsen *et al.*, 2016). A comprehensive catch of Diptera Brachycera from the latter traps forms the basis of the present study on the species diversity and phenology of epigaeic brachycerans of coastal sand dunes.

Study area and methods

National Park Thy situated at the north-western corner of Jutland, Denmark (Fig. 1) borders c. 50 km of the North Sea coast. The national park includes a range of natural and man-made habitats, all established on shifting sand. Yellow dunes constitute the outer formation from the maritime sand high beach and 20-200 m inland, forming a nearly continuous band of habitats. To the east of this is a mosaic of inland habitats: heathlands, meadows and marshes. Scattered groups of older dune hills allow development of grey dune vegetation, mainly found on south-facing hill slopes and in wind breaks. In the lower parts and depressions the heathland turns into oligotrophic marshes and shallow pools.

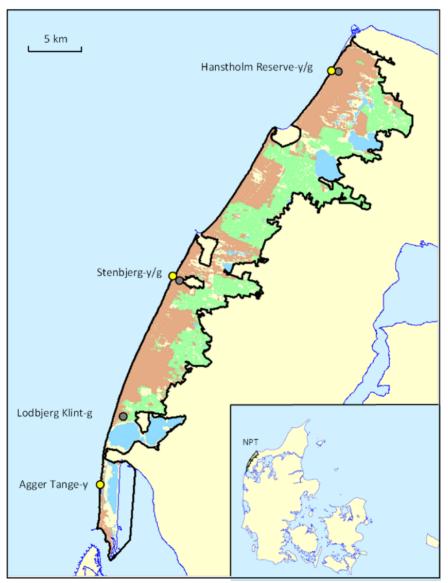


Fig. 1. Map of National Park Thy, showing the sampling sites referred to. Inset: the geographical position of National Park Thy (NPT) in Denmark. Locality name added -y indicates yellow dune (yellow dots) and added -g grey dune (grey dots). Colouration inside Park (surrounded by heavy line): brown colour=dune and heathland; light yellow=meadow and grassland, green=coniferous plantations, blue= lake, lighter blue=fjord.

The collections were concentrated on yellow and grey dune habitats. Yellow dunes (Fig. 2) are continuously reshaped by shifting sand and covered by rather homogenous grass vegetation, mostly marram (*Ammophila arenaria*) in some places mixed with red fescue (*Festuca rubra*). While the composition of the vegetation is rather uniform, its density varies a great deal. Exposed parts of the dunes are covered with sand blown in from the beach forming areas with scarce, low vegetation and a free sand surface. In less exposed areas and in depressions the marram vegetation becomes dense with accumulation of litter. The grey dune habitats (Fig. 3) occur on older dune hills for a stretch of a few hundred meters to a few kilometres inland. The vegetation is scarce but much more diverse than on the yellow dunes, often forming a mosaic of bare ground and patches of marram, sand sedge (*Carex arenaria*), various herbs or low carpets of moss or lichens.



Fig. 2-3. Left: Close-up of yellow dune surface at Agger Tange-y. Tussocks of marram (*Ammophila arenaria*) and bare sand. Photo Lise Brunberg Nielsen. Right: Close-up of grey dune surface at Lodbjerg Klint-g. Bare sandy surface with scattered *Ammophila arenaria* and *Corynephorus canescens* tussocks, lichens and beginning encroachment of *Calluna vulgaris* and *Empetrum nigrum*. Photo Søren Toft.

The material of the present investigation came from 6 localities within the national park (Fig. 1). Since some of the localities share locality name, they are added -y and -g for yellow and grey dune localities. Three localities are situated in yellow dunes near (5-10 m) the slope to the beach. To the east, two of them (Hanstholm Reserve-y and Stenbjerg-y) are neighbouring grey dunes and dune heaths, whereas the third locality (Agger Tange-y) is adjacent to salt marshes and lagoons at Krik Vig (Fig. 1). Another three localities are situated in grey dunes, two of them (Hanstholm Reserve-g and Stenbjerg-g) about 200 m to the east of a yellow dune locality, at Hanstholm Reserve with a road in-between. The third grey dune locality (Lodbjerg Klint-q) is situated about 380 m from the nearest yellow dune site. All localities are at altitudes of 5-30 m above sea level. Twenty traps were employed at each locality. At all sites the traps were placed in lines parallel to the coast with a distance of 5 m between them. They were sampled throughout a full year (March 2013-April 2014). At the yellow dune sites 10 traps were situated in exposed positions in low and scarce marram vegetation. A considerable proportion of the ground was bare sand, which became increasingly covered with beach pea (Lathyrus japonicus ssp. maritimus) during the growing season. The other 10 traps were placed in more mature, dense marram vegetation with accumulation of marram litter on the ground. For further details, see Nielsen et al. (2016).

The traps consisted of double plastic beakers, 8.5 cm in diameter and 11 cm deep, covered by a wooden roof. A concentrated salt solution with detergent was used as preservative. The traps were emptied twice per month. In the laboratory the preservative was exchanged to 70% alcohol. The sampling design and running of the traps were managed by ST and the flies were identified by LBN and BON. Literature used for identification of the most important flies is

presented in the list of references. Regarding *Megaselia longicostalis* (Phoridae) males were identified on hypopygial structures visible in stereo microscope; identification of females, however, requires preparation of microscopic slides. Ten females were identified by means of the key in Disney (1999). Of the remaining females, 91% were tentatively also referred to *M. longicostalis* in accordance with the proportion of *M. longicostalis* males among all *Megaselia* males.

Results

Numbers of species and individuals

From early March 2013 to early April 2014 a total of 15,670 flies (Diptera Brachycera excl. Calyptratae) representing 31 families and 227 species were trapped in 6 localities within the national park (Table 1): in yellow dunes at Agger Tange-y, Stenbjerg-y and Hanstholm Reserve-y (n=10,413, 184 species) and grey dunes at Lodbjerg klint-g, Stenbjerg-g and Hanstholm Reserve-g (n=5,257, 122 species); 105 species were captured exclusively in yellow dunes, 43 species only in grey dunes, while 79 species were recorded from both dune habitats. The highest number of individuals (3,835) was recorded in traps at Stenbjerg-y and the lowest number (912) at Stenbjerg-g. The highest number of species (136) was collected in traps at Hanstholm Reserve-y, and the lowest number (62) at Stenbjerg-g.

The families Sphaeroceridae, Dolichopodidae and Chloropidae were particularly species-rich, contributing 61 species (26.9 %), 30 species (13.2 %) and 25 species (11.0%), respectively, or a total of 51.1 % (Table 1). According to Fauna Europaea (2017) twenty of the fly species trapped are new to the Danish fauna (Appendix).

Phoridae made up 40.3% of all individuals captured; Dolichopodidae contributed 14.3%, Sphaeroceridae 13.3% and Chloropidae 9.5%, viz. in all 77.4% of the total catch. The species collected in yellow and grey dunes were ranked according to frequency (Fig. 4). A minority of species was very frequent, the ten most frequent species in yellow and grey dunes contributed 73.1% and 87.3% of the totals, respectively (Table 2). Several species captured were few in number, e.g. 51 species and 46 species trapped in yellow and grey dunes, respectively, were singletons.

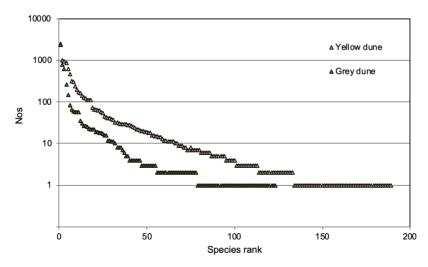


Fig. 4. All brachyceran species collected in pitfall traps in yellow and grey dunes in National Park Thy, 2013-2014 ranked according to frequency.

Table 1. Brachyceran families caught in pitfall traps in sand dunes of National Park Thy, Denmark, 2013-2014. Total numbers of species, numbers of species in yellow and grey dunes, as well as numbers of species shared by yellow and grey dunes.

	Sand dunes	s Yellow dunes	Grey dunes	Shared species
Agromyzidae	1	0	1	0
Anthomyzidae	4	3	1	0
Asilidae	2	0	2	0
Bombyliidae	1	0	1	0
Carnidae	1	0	1	0
Chamaemyiidae	3	1	3	1
Chloropidae	25	15	18	8
Diastatidae	1	1	0	0
Dolichopodidae	30	27	12	9
Drosophilidae	7	7	2	2
Dryomyzidae	1	1	0	0
Empididae	6	5	1	0
Ephydridae	14	10	8	4
Heleomyzidae	10	8	8	6
Heterocheilidae	1	1	0	0
Hybotidae	6	5	4	3
Lonchopteridae	2	2	0	0
Micropezidae	1	1	1	1
Opomyzidae	5	5	1	1
Phoridae	17	15	12	10
Pipunculidae	1	1	0	0
Platystomatidae	1	1	1	1
Psilidae	1	1	0	0
Rhagionidae	3	3	2	2
Sciomyzidae	6	4	2	0
Sepsidae	4	4	1	1
Sphaeroceridae	61	59	31	29
Syrphidae	5	2	4	1
Tephritidae	2	0	2	0
Therevidae	3	1	2	0
Trixoscelidae	2	1	1	0
Totals	227	184	122	79
Exclusively in yellow dunes		105		
Exclusively in grey dunes			43	

Table 2. The ten most abundant Diptera Brachycera caught in pitfall traps in yellow and grey dunes of National Park Thy, 2013-2014.

Yellow dunes (-y)	Nos.	Relative abun- dance	Grey dunes (-g)	Nos.	Relative abun- dance
Megaselia longicostalis	2,575	0.247	Triphleba trinervis	2,408	0.458
Dolichopus acuticornis	1,015	0.098	Medetera micacea	810	0.154
Platypalpus strigifrons	978	0.094	Megaselia longicostalis	636	0.121
Scaptomyza pallida	890	0.086	Suillia similis	261	0.050
Conioscinella zetterstedti	626	0.060	Conioscinella zetterstedti	152	0.029
Copromyza stercoraria	464	0.045	Thaumatomyia hallandica	86	0.016
Spelobia clunipes	316	0.030	Copromyza stercoraria	65	0.012
Aphanotrigonum nigripes	302	0.029	Platypalpus strigifrons	60	0.011
Geomyza tripunctata	244	0.023	Oscinella frit	58	0.011
Psilopa bornholmi	201	0.019	Dolichopus migrans	58	0.011
	7,611	0.731		4,594	0.873

The brachyceran fauna of yellow and grey dunes.

The numbers of brachyceran species and individuals recorded from yellow and grey dunes differed distinctly. This difference was further underlined by the indices of similarity (QS, Sørensen, 1948) (Fig. 5). The highest similarities were found between sites situated within yellow dunes (QS=61-68%, mean 65%) or within grey dunes (QS=57-63%, mean 60%), whereas the similarities between all combinations of sites in yellow and grey dunes were lower (QS=38-47%, mean 43%).

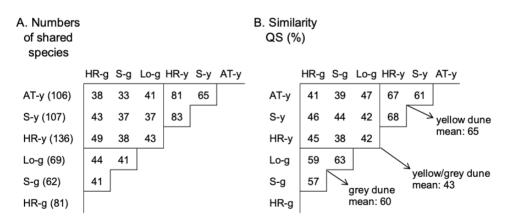


Fig. 5. Comparison of the sampling sites at yellow (-y) and grey (-g) dunes in National Park Thy 2013-2014. **A.** Number of species at each site (in parenthesis) and number of shared species of all binary combinations of sites. **B.** Quotient of similarity (QS, Sørensen) of the same combinations and the mean of QS values within and between yellow and grey dunes.

The seasonal activity of epigaeic Diptera Brachycera

The seasonal activity patterns of Brachycera in the yellow and grey dune sites were different (Fig. 6 and 7). In the yellow dunes (Fig. 6), the activity was initiated in March, rising to a distinct peak in late July owing to the increasing numbers of *Conioscinella zetterstedti* and *Aphanotrigonum nigripes* (Chloropidae) and *Dolichopus acuticornis* (Dolichopodidae). In addition, *Psilopa bornholmi* (Ephydridae) and *Platypalpus strigifrons* (Hybotidae) also contributed to the maximum. A subsequent declining activity was primarily a result of decreasing numbers of chloropids and dolichopodids, whereas phorids, hybotids (*Platypalpus strigifrons*) and many species of Sphaeroceridae were still active. From late September onwards phorids dominated, the vast majority belonging to one species, *Megaselia longicostalis*, which was active all the season. In the grey dunes (Fig. 7), however, the activity started as late as ultimo May and rose to a weak summer peak dominated by dolichopodids (especially *Medetera micacea*) and several species of chloropids. A distinct peak in the last months of the year was mainly due to very high abundances of *Triphleba trinervis* (Phoridae), but also *Megaselia longicostalis* contributed.

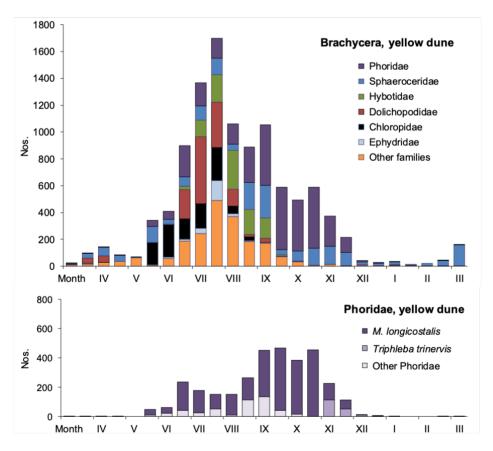


Fig. 6. Seasonal activity of epigaeic brachycerans at yellow dunes of National Park Thy, March 2013-April 2014. Above sum of activity of all families, below the activity of phorid species. Females of *Megaselia* are tentatively referred to species according to proportions of identified males.

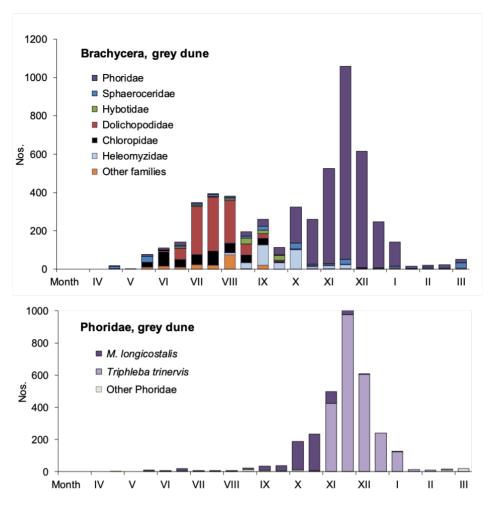


Fig. 7. Seasonal activity of epigaeic brachycerans at grey dunes of National Park Thy, March 2013-April 2014. Above sum of activity of all families, below the activity of phorid species. Females of *Megaselia* are tentatively referred to species according to proportions of identified males.

Discussion

A catch of 227 species of brachyceran flies recorded in pitfall traps in the coastal sand dunes reflects a versatile fly activity on the sand surface. The brachyceran species trapped represent a variety of life histories and ecological associations. Without doubt many of the trapped flies actually hatched from sand, debris or vegetation in the neighbourhood of the traps, being detained when scuttling along on the surface searching for prey, oviposition sites, mates, or other necessities of life. Some fly species were, however, attracted by the smell from the multitude of dead animals accumulated in the pitfall traps. In addition some species with reduced wings, e.g. *Conioscinella zetterstedti* (Chloropidae) are supposed to be particularly frequent in the pitfall traps.

Based on information in the literature the fly species recorded in the sand dunes were grouped according to larval trophic level (Appendix). The saprophages is the most species-rich group (115 species), second is the zoophages (62 species) and third the phytophages with 30 species. Microphages, parasitoids and mycetophages count 9, 8 and 3 species respectively.

The trophic distribution in yellow and grey dunes is almost the same (Fig. 8) (χ^2 =1.2062, df=5, p=0.9443, i.e. no significant difference).

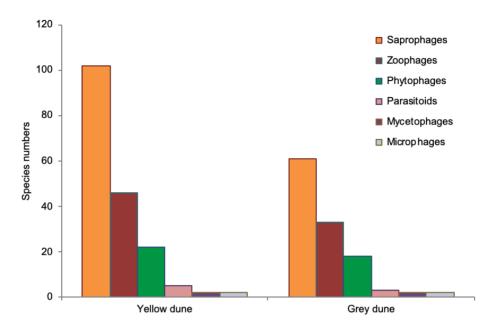


Fig. 8. Trophic distribution of epigaeic brachyceran species in yellow and grey dunes of National Park Thy, 2013-2014.

Saprophages

The saprophagous larvae exploit plant debris (phytosaprophages) or animal debris (zoosaprophages), however many saprophagous species are apparently polysaprophages, ingesting all disintegrating material available. Saprophagy is particularly common among Sphaeroceridae and Phoridae. In the yellow dunes a single phorid species, Megaselia longicostalis accounted for 37% (N=2,575) of all saprophages. It was also numerous in pitfall traps run in moorland in northern England (Disney 1994). According to Lundbeck (1912) M. longicostalis was common in forest litter in Denmark. In the yellow dunes accumulated litter in and around marram tussocks is presumably the larval habitat. M. longicostalis was also rather common at grey dune sites (N=636) where another phorid species Triphleba trinervis was more prominent (N=2,408 or 66% of all saprophages). It was predominant in the samples from November-February (Fig. 7). Winter activity of this species was also recorded by Soszyńska & Durska (2002), who found a high activity at temperatures down to -4 °C even on snow. During December-February the outer third of the wings were shredded or lost in nearly all individuals (Fig. 9), the flight ability being impeded. The larval food is apparently not known, but presumably it consists of dung and carrion as in some other Triphleba species (Durska, 2003).

Two saprophagous chloropids, *Conioscinella zetterstedti* and *Aphanotrigonum nigripes* were numerous in the yellow dunes (N=626 and 302, respectively). The former is also recorded from other dry habitats (Nartshuk & Andersson, 2013; Nielsen, 2014). In the dunes *C. zetterstedti* is associated with marram and lyme grass (*Leymus arenarius*); the larvae are found in the marram tussocks, probably nourishing on accumulated withered plant material (Nartshuk & Andersson, 2013). The wings of the adults are reduced to various degrees; most

females have strap-like wings with few veins, whereas the wings of males are more or less shortened. Therefore, the adults are not flying, but they run and jump on the sand surface (Ardö, 1957). In the yellow dunes it was significantly more numerous in the front line of traps (in rather open marram vegetation) than in the second line of traps in more dense vegetation (N=454 and 172, t-test: t=4.2813, p<0.005). The difference in abundance might be due to a difference in wind exposure influencing the activity – and risk of being trapped. The second chloropid (*A. nigripes*) is recorded from *Leymus* and *Puccinellia*, but is also bred from stems of cereals (Nartshuk & Andersson, 2013). Previously rather few specimens have been recorded, but in the actual investigation 252 specimens were trapped at the yellow dune site Stenbjerg-y. *A. nigripes* has rather short wings; it probably rarely flies, but runs on the sand surface. The larval food is presumably decaying plant material present in the marram tussocks.



Fig. 9. The winter active phorid *Triphleba trinervis* from grey dunes of National Park Thy, 2013-2014. The outer third of the wings is shredded and lost. Photo Lise Brunberg Nielsen.

Almost all sphaerocerid flies are saprophages, breeding in a variety of decaying, organic matter, e.g. dung, carrion, litter, or grass brought into the runs and nests of small mammals. Usually the adults stay near or on the larval food (Roháček, 1982). In the actual investigation 59 species were caught in yellow dunes, 31 in grey dunes. A total of 35 spaerocerid species were represented by less than 10 individuals, and only 9 species counted more than 50 specimens. A distribution like that may reflect that many species are rather specialized, and that the preferred breeding media are sparse in the dunes. Most numerous were two ubiquitous species, *Copromyza stercoraria* (N=529) and *Spelobia clunipes* (N=338); both have wide food preferences, are widespread, and apparently polyvoltine – in addition adults are active all the year (Roháček 1982).

Zoophages

Most larvae of Hybotidae and Empididae are probably soil-living predators feeding on worms and insect larvae. In the sand dunes the hybotid *Platypalpus strigifrons* (N=1,038) was a predominant fly, making up 27.7% of all zoophages. It was trapped at all six localities, but most specimens derived from yellow dunes, in particular at Agger Tange-y and Stenbjerg-y. *P. strigifrons* is a typical coastal species found on ground vegetation in sandy dunes. It is very common on the coasts of Denmark (Chvála, 1975), for instance it is also recorded from dunes in Thy (Ardö, 1957). The sex-ratio in the actual catches from the national park is remarkably skewed: 10♂♂/1,028♀♀. In some common species of *Platypalpus* the male sex is rare or unknown and in some species geographical parthenogenesis has been found (Chvála, 1975).

Dolichopus acuticornis and Medetera micacea (Dolichopodidae) were the most prominent dolichopodids in yellow and grey dunes, respectively. Both species are seemingly associated with coastal dune habitats. D. acuticornis (N=1,015) was numerous at all three sites in the yellow dune. It was recorded from coastal localities in Denmark by Lundbeck (1912) and previously collected from marram dunes and dune heathland in Thy by Ardö (1957). In Norway Jonassen (1985) found the species between dunes on a dry sandy beach, Pollet & Grootaert (1996) recorded a high abundance in the coastal dunes in Belgium, and Vilks (2007) trapped numerous specimens in water traps in reed beds close to dune grassland in Latvia. The larval habitat is not known, but the high abundance exclusively in the yellow dunes strongly indicates some association with this habitat; Vilks (2007), however, collected four specimens in emergence traps placed in dune grassland, which is comparable to grey dunes. In the grey dunes in Thy, another dolichopodid, Medetera micacea was very abundant (N=810) particularly at Lodbjerg Klint-g. Apparently, it is not previously recorded from sand dunes in Denmark; however Lundbeck (1912) mentions other coast-near habitats. In the Belgian coastal dunes M. micacea was abundant in dune grassland and in a dune slack (Pollet & Grootaert, 1996).

The larvae of Chamaemyiidae feed on scale insects (Coccoidea) and other Homoptera. *Chamaemyia flavipalpis* should be sought on sandy coasts (Smith, 1989) and is restricted to the dune ridge, where it is active especially on the outer side amongst *Elymus* and marram. It is previously recorded from Thy (Ardö, 1957). Sciomyzidae were represented by six species (12 specimens). Sciomyzid flies are commonly found in marshes and other damp habitats; the larvae are predators (or parasitoids) of pulmonate snails or pea mussels (Rozkošný, 1984). *Pherbellia cinerella* and *P. ventralis* have been collected in wet dune slacks (Beaver, 1972). Finally, some larger predatory flies with predatory, soil-living larvae (viz. Asiliidae, Rhagionidae and Therevidae) were also caught in the dunes, although none of them is typical for dune habitats.

Phytophages

In the material from the sand dunes of the national park about 14% of all species – but only 5% of the total number – are phytophagous feeding on living plant tissues. Phytophagy is particularly common among Chloropidae, Opomyzidae and Psilidae, but also a few species of Drosophilidae feed on living plants. Several stemboring and herbivorous chloropids were present in low numbers in the dunes, one of them (*Meromyza pratorum* (N=53)) is specifically associated with marram. The larvae damage shoots of marram (Huiskes, 1979); the adults are efficient flyers and occurred at all six study sites in the national park. Five species of Opomyzidae were caught in the yellow dunes all of them stem boring in grasses. *Geomyza tripunctata* (N=244), which was the commonest, is widespread in Denmark and found in almost every grassy habitat, the larvae feeding in stems of several species of grass. *G.*

apicalis (N=124) is mainly recorded from coastal habitats, e.g. grazed marsh, reeds and dunes (Drake, 1993).

One species of Micropezidae, *Micropeza corrigiolata* (N=41) was trapped at all three localities in the yellow dunes and also at a single site in grey dunes (Hanstholm Reserve-g). The larva eats the root nodules of legumes growing on bare sand, e.g. in fore dunes, dry beach margins and sand pits with sparse vegetation (Kahanpää, 2006). In the actual case the most likely host plant is beach pea (*Lathyrus japonicus*), since almost all *M. corrigiolata* were caught in traps situated in the most exposed and open marram vegetation, where beach pea gradually covered the bare sand during the summer. *Chamaepsila buccata* (Psilidae, N=25) was collected at Stenbjerg-y and Hanstholm Reserve-y. In Denmark it is mainly distributed in Jutland and chiefly recorded from localities near the coast (Lyneborg, 1964). The larvae have been found in the roots of red clover and may damage the host plant. The species was also observed in the East Frisian Islands along the north-western coast of Germany (Tschirnhaus, 2008). *Scaptomyza graminum* (Drosophilidae) was primarily trapped in yellow dunes (N=65) and previously recorded from Thy (Klitmöller, Ardö, 1957). It is a leaf-miner of various herbs, e.g. Caryophyllaceae and Leguminosae (Bächli & Burla, 1985).

A number of other trophic relations are observed in brachyceran larvae of the dunes, for instance microphages feeding on small organisms and particles and mycetophages nourishing on sporophores of fungi. They are, however, scarce in the present material, making up <5% of all species (Fig. 8). Microphagy is particularly found in larvae of Ephydridae, for instance in 5 species of *Scatella* and possibly also in *Psilopa bornholmi* (N=200), which is recorded from marshy habitats (Parvu, 2004, 2005). The larvae of *Scatella* (and those of three *Thoracochaeta*-species (Sphaeroceridae)) are surface scrapers. In Heleomyzidae the larvae of the subfamily Suillinae, which is represented by three species, mostly develop in fresh fungi (Smith, 1989). This probably also applies to *Suillia similis* (N=267), the predominant heleomyzid species trapped in the dunes in Thy.

Parasites / parasitoids.

This trophic group includes only a few species belonging to the families Bombylidae and Pipunculidae. Bombyliids are parasites on larvae and/or pupae of Lepidoptera, Hymenoptera and other insects. A single specimen of *Phtiria pulicaria* was collected at Lodbjerg Klint-g. It is a sand dune species, which has been reared from *Scrobipalpula psilella* (Gelechidae, Lepidoptera). A specimen of *Cephalops varipes* (Pipunculidae) was collected in the yellow dunes at Agger Tange-y. The larvae of *Cephalops* are endoparasites of Delphacidae (Homoptera).

Most of the brachyceran species caught in the dunes of the national park are ubiquists also occurring in many other habitats, e.g. woodland, grassland and wetland. Their presence in the dunes presumably mainly owes to the range of their preferred microhabitats and food resources, e.g. plants, dung, carrion, algae, nests of small mammals and Hymenoptera. This group includes most species of Sphaeroceridae and Phoridae. Other species are recorded from open, dry areas in general (Appendix: marked X), occurring in dry grassland, heathland, sandy soils, road verges etc. They may also find suitable conditions in the coastal dune habitats of the national park, for instance the anthomyzid *Stiphrosoma sabulosum*. Furthermore a few species whose larvae live in wet habitats (and which almost exclusively are trapped at Agger Tange-y), e.g. *Anagnota bicolor* (Anthomyzidae), *Campsicnemus armatus* (Dolichopodidae) and *Psilopa bornholmi* (Ephydridae), have presumably been spread in the adult stage from the wet hinterland, viz. the salt marshes at Krik Vig (Fig. 1). Of

the remaining species a few are purely coastal (Appendix: marked C), feeding and breeding in the littoral wrack zone but caught in the traps at the dune sites, e.g. five species of *Scatella* (Ephydridae) and three of *Thoracochaeta* (Sphaeroceridae).

At least 38 species are, however, repeatedly recorded from coastal dune habitats in many countries (Appendix: marked CD, XD or D). Seemingly, they are associated with dunes or dune grassland. In the national park they were often trapped in large numbers. For instance the chloropids *Conioscinella zetterstedti* and *Meromyza pratorum*, which are associated with marram, and the Dolichopodids *Dolichopus acuticornis* and *Medetera micacea*. Whereas the Diptera Nematocera recorded from pitfall traps in National Park Thy were considered not to represent a specific dune fauna (Nielsen *et al.*, 2016), the brachyceran fauna actually includes several species characteristic for the coastal dune habitat.

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Litterature

(+) only used for identification of the flies; [Ref. no.] see Appendix.

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Appendix. List of brachyceran species trapped in pitfall traps in sand dunes of National Park Thy, Denmark, 2013-2014. +New to the Danish fauna (ref: Fauna Europaea version 2017.06). Larval trophic groups: mi=microphage, my=mycetophage, par=parasitoid, ph=phytophage, s=saprophage, z=zoophage. References refer to [Ref. no.] in list of references.

	Num	bers	Larval	Dry ()	(), coastal (C)
	Yellow dunes	Grey dunes	Larval trophic group	and dune (D) habitats recorded [references]	
Agromyzidae					
Cerodontha denticornis (Panzer, 1806)		1	ph		
Anthomyzidae					
+ Anagnota bicolor (Meigen, 1838)	74		s		
Anthomyza gracilis Fallén, 1823		1	s		
+ Anthomyza socculata (Zetterstedt, 1847)	1		s		
Stiphrosoma sabulosum (Haliday, 1837)	30		s	Х	[1,4,17]
Asilidae					
Dysmachus trigonus (Meigen, 1804)		1	z	XD	[4,6,12]
Pamponerus germanicus (Linnaeus, 1758)		1	z	D	[3,6]
Bombyliidae					
Phthiria pulicaria (Mikan, 1796)		1	par	XD	[3,4,6]
Carnidae					
Meoneura vagans (Fallén, 1823)		4	s		
Chamaemyiidae					
Chamaemyia aridella (Fallén, 1823)		3	z	D	[1]
Chamaemyia flavipalpis (Haliday 1838)	3	11	z	XD	[1,12]
Chamaemyia herbarum (Robineau-Desvoidy, 1830)		12	z	XD	[12]
Chloropidae					
Aphanotrigonum nigripes (Zetterstedt, 1848)	302	5	s	CD	[14,15,19,2
Calamoncosis aprica (Meigen, 1830)		1	ph		
Cetema cereris (Fallén 1820)	14		ph		
Chlorops calceatus Meigen, 1830	1		ph		
Conioscinella frontella (Fallén, 1820)	1		ph		
Conioscinella mimula Collin, 1946	1		ph		
Conioscinella sordidella (Zetterstedt, 1848)	11		ph		
Conioscinella zetterstedti Andersson, 1966	626	152	s	XD	[1,3,14,15]
Elachiptera diastema Collin, 1946		1	s		
Incertella albipalpis (Meigen, 1830)	43	1	ph		
Lasiambia brevibucca (Duda, 1933)		1	s		
Lasiambia palposa (Fallén, 1820)		26	z	D	[3,15]
Meromyza palposa Fedoseeva, 1960		4	ph		
Meromyza pratorum Meigen, 1830	18	35	ph	XD	[1,9,14]

	Num	bers		Dry (X), coastal (C)
	Yellow dunes	Grey dunes	Larval trophic group	and habita	dune (D) ts recorded ferences]
Meromyza triangulina Fedoseeva, 1960	2		ph		
Meromyza sp (♀♀)	5	4	ph		
Oscinella frit (Linnaeus, 1758)	8	58	ph		
Oscinella hortensis Collin, 1946	5	2	ph		
Oscinella nigerrima (Macquart, 1835)		1	ph		
Oscinella pusilla (Meigen, 1830)	18		ph		
Oscinella vastator (Curtis, 1845)	21	4	ph		
Oscinimorpha minutissima (Strobl, 1900)		4	s		
Parectecephala longicornis (Fallén, 1820)		1	ph	XD	[14,21]
Thaumatomyia glabra (Meigen, 1830)		1	z		
Thaumatomyia hallandica Andersson 1966		86	z	XD	[14,15,22
Tricimba cincta (Meigen, 1830)	1	22	s		
iastatidae					
Diastata fuscula (Fallén, 1823)	1		s		
olichopodidae					
Campsicnemus armatus (Zetterstedt, 1849)	145	1	z	С	[13,19]
Campsicnemus curvipes (Fallén, 1823)	5		z		
Campsicnemus loripes (Haliday, 1832)	13	1	z		
Campsicnemus picticornis (Zetterstedt, 1843)	1		z		
Campsicnemus pumilio (Zetterstedt, 1843)		7	z		
Campsicnemus scambus (Fallén, 1823	28	2	z		
Chrysotus neglectus (Wiedemann, 1817)	1		z		
Dolichopus acuticornis Wiedemann, 1817	1,015		z	CD	[16,20]
Dolichopus brevipennis Meigen, 1824	2		z		
Dolichopus festivus Haliday, 1832		3	z		
Dolichopus longicornis Stannius, 1831	5		z	Χ	[13]
Dolichopus melanopus Meigen, 1824	1		z		
Dolichopus migrans Zetterstedt, 1843	14	58	z	XD	[1,16]
Dolichopus plumipes (Scopoli, 1763)	22	1	z	CD	[3,20]
Dolichopus rupestris Haliday, 1833	2		z		
Dolichopus trivialis Haliday, 1832	1		z		
Dolichopus vitripennis Meigen, 1824	1		z		
Gymnopternus angustifrons (Staeger, 1842)	1		z		
Hercostomus praeceps Loew, 1869	6		z		
Hydrophorus albiceps Frey, 1915	1		z		
Medetera jacula (Fallén, 1823)	1	4	z		
Medetera micacea Loew, 1857	1	810	z	XD	[13,16]
Medetera petrophiloides Parent, 1925	1		z		
Medetera plumbella Meigen, 1824	7	1	z	XD	[16]

		Num	bers	Larval trophic group	Dry (X), coastal (C		
		Yellow dunes	Grey dunes		and habita	dune (D) ts recorded erences]	
1	Medetera truncorum Meigen, 1824	19	23	z	XD	[16]	
5	Sciapus platypterus (Fabricius, 1805)	1		z			
5	Sciapus wiedemanni (Fallén, 1823)	30		z			
5	Sympycnus aeneicoxa (Meigen, 1824)	1		z			
5	Sympycnus desoutteri Parent, 1925	7		z			
+ 7	Thrypticus pollinosus Verrall, 1912		1	ph			
Oros	ophilidae						
L	Drosophila funebris (Fabricius, 1787)	5		s			
L	Drosophila subobscura Collin, 1936	1		s			
L	Drosophila transversa Fallén, 1823	1		s			
L	Lordiphosa andalusiaca (Strobl, 1906)	3		s			
5	Scaptomyza flava (Fallén, 1823)	1		ph			
5	Scaptomyza graminum (Fallén, 1823)	65	2	ph	CD	[1,19,23]	
5	Scaptomyza pallida (Zetterstedt, 1847)	890	17	s	CD	[23]	
Oryo	myzidae						
+ /	Pseudoneuroctena senilis (Zetterstedt, 1838)	1		s			
Empi	didae						
L	Dolichocephala guttata (Haliday, 1833)	1		z			
L	Empis opaca Meigen, 1804	1		z			
E	Empis stercorea Linnaeus, 1761	2		z			
ı	Phyllodromia melanocephala (Fabricius, 1794)		1	z	С	[13]	
ı	Rhamphomyia maculipennis Zetterstedt, 1842	12		z			
ı	Rhamphomyia simplex Zetterstedt, 1849	29		z			
phy	dridae						
,	Axysta cesta (Haliday, 1833)	2		s	С	[5]	
(Coenia palustris (Fallén, 1823)	4		s	С	[19]	
L	Ephydra riparia Fallén, 1813		1	s	С	[5,19]	
ı	Hydrellia griseola (Fallén, 1813)		1	s			
L	Lamproscatella sibilans (Haliday, 1833)		3	s			
L	Limnellia quadrata (Fallén, 1813)	1		s			
I	Philotelma nigripenne (Meigen, 1830)	10		s			
I	Philygria punctatonervosa (Fallén, 1813)	1		s			
I	Psilopa bornholmi Becker, 1926	200		mi?			
5	Scatella paludum (Meigen, 1830)	9	8	mi	С	[5,19]	
5	Scatella silacea Loew, 1860	1	1	mi	С	[5,11]	
5	Scatella stagnalis (Fallén, 1813)		2	mi	С	[5,11,19]	
5	Scatella subguttata (Meigen, 1830)	1	2	mi	С	[5,11,19]	
	Scatella tenuicosta Collin, 1930	15	10	mi			

	Num	bers	Larval trophic group	Drv (X), coastal (C)
	Yellow dunes	Grey dunes		and dune (D) habitats recorded [references]	
Heleomyzidae					
Eccoptomera longiseta Loew, 1862	2	3	s		
+ Gymnomus caesius (Meigen, 1830)		1	s		
Oecothea fenestralis (Fallén, 1820)	16	1	s	D	[23]
Oecothea praecox Loew, 1862	9	2	s		
Schroederella iners (Meigen, 1830)	1	16	s		
Scoliocentra confusa (Wahlgren, 1918)	2		s		
Suillia atricornis (Meigen, 1830)	1		my		
Suillia humilis (Meigen, 1830)		16	my		
Suillia similis (Meigen, 1838)	6	261	my		
+ Tephrochlaena halterata (Meigen, 1830)	1	18	s		
Heterocheilidae					
Heterocheila buccata (Fallén, 1820)	11		mi	CD	[1,4,19,23
Hybotidae					
Hybos culiciformis (Fabricius, 1775)		2	z		
Platypalpus nigritarsis (Fallén, 1816)	11	18	z	Х	[13]
Platypalpus strigifrons (Zetterstedt, 1849)	978	60	z	XD	[1,13,16]
Tachydromia umbrarum Haliday, 1833	2		z		
Tachypeza nubila (Meigen, 1804)	4	19	z		
Tachypeza truncorum (Fallén, 1815)	1		z		
Lonchopteridae					
Lonchoptera lutea Panzer, 1809	40		s	D	[1]
Lonchoptera tristis Meigen, 1824	1		s		
Micropezidae					
Micropeza corrigiolata (Linnaeus, 1767)	40	1	ph	XD	[1,10]
Opomyzidae					
Geomyza apicalis (Meigen, 1830)	124		ph	CX	[1,7]
Geomyza balachowskyi Mesnil, 1934	1		ph		
Geomyza tripunctata Fallén, 1823	244	1	ph		
Opomyza florum (Fabricius, 1794)	3		ph		
Opomyza germinationis (Linnaeus, 1758)	1		ph		
Pipunculidae					
Cephalops varipes (Meigen, 1824)	1		par		
Platystomatidae					
Rivellia syngenesiae (Fabricius, 1781)	1	2	?		

		Num	bers	Larval	Dry (X)	, coastal (C)
		Yellow	Grey dunes	Larval trophic group	and dune (D) habitats recorded [references]	
	Aenigmatias lubbockii (Verrall, 1877)		2	z		
	Anevrina curvinervis (Becker, 1901)	2	2	s		
	Anevrina thoracica (Meigen, 1804)	30	3	s		
	Anevrina urbana (Meigen, 1830)		1	s		
	Borophaga femorata (Meigen, 1830)	3		s		
	Conicera floricola Schmitz, 1938	6	1	s		
+	Diplonevra funebris (Meigen, 1830)	111	6	z		
	Megaselia sp (♀♀)	1,774	368	s		
	Megaselia longicostalis (Wood, 1912)	976	286	s		
	Megaselia nigriceps (Loew, 1866)	12	2	s		
	Megaselia pleuralis (Wood, 1909)	43	12	s		
	Megaselia ruficornis (Meigen, 1830)	48	1	s		
	Megaselia sordescens (Schmitz, 1927)	4		s		
	Triphleba intermedia (Malloch, 1908)	3		s		
+	Triphleba nudipalpis (Becker, 1901)	1		z		
	Triphleba opaca (Meigen, 1830)	3	31	s		
	Triphleba papillata (Wingate, 1906)	5		s		
	Triphleba trinervis (Becker, 1901)	171	2,408	s		
Psi	lidae					
	Chamaepsila buccata Fallén, 1826)	25		ph	CD	[23]
Rha	agionidae					
	Rhagio lineola Fabricius, 1794	5	1	z		
	Rhagio scolopaceus (Linnaeus, 1758)	8	3	z	D	[12]
	Rhagio tringarius (Linnaeus, 1758)	1		z		
Sci	omyzidae					
	Coremacera marginata (Fabricius, 1775)	2		par		
	Limnia paludicola Elberg, 1965		1	par		
	Pherbellia cinerella (Fallén, 1820)	2		par	D	[4]
+	Pherbellia griseicollis (Becker, 1900)	3		par		
	Pherbellia ventralis (Fallén, 1820)	2		par		
	Trypetoptera punctulata (Scopoli, 1763)		2	par		
Sep	osidae			· · ·		
·	Sepsis cynipsea (Linnaeus, 1758)	3	2	s	CD	[1,19,22]
	Sepsis fulgens Meigen, 1826	2		s	CD	[19,22]
	Sepsis punctum (Fabricius, 1794)	1		s	CD	[19,22]
	Themira putris (Linnaeus, 1758)	1		s	CD	[19,22]

Sphaeroceridae

		Num	Numbers		Dry (X), coastal (C)		
		Yellow dunes	Grey dunes	Larval trophic group	and dune (D) habitats recorded [references]		
+	Alloborborus pallifrons (Fallén, 1820)	2		s			
	Apteromyia claviventris (Strobl, 1909)	3	2	s			
	Chaetopodella scutellaris (Haliday, 1836)	39	3	s			
	Coproica acutangula (Zetterstedt, 1847)	3		s	D	[1]	
	Coproica ferruginea (Stenhammar, 1855)	16	4	s			
	Coproica hirticula Collin, 1956	1		s			
	Coproica lugubris (Haliday, 1836)	28	1	s			
	Coproica pusio (Zetterstedt, 1847)	5		s			
	Coproica vagans (Haliday, 1833)	66	5	s	CD	[1]	
	Copromyza equina Fallén, 1820	7	1	s			
	Copromyza nigrina (Gimmerthal, 1847)	15	1	s			
	Copromyza stercoraria (Meigen, 1830)	464	65	s			
	Crumomyia fimetaria (Meigen, 1830)	1		s			
	Crumomyia nitida (Meigen, 1830)	12		s			
	Crumomyia notabilis (Collin, 1902)	112	56	s			
	Crumomyia pedestris (Meigen, 1830)	7		s			
+	Herniosina bequaerti (Villeneuve, 1917)	1	2	s			
	Ischiolepta nitida (Duda, 1920)	26		s			
	Ischiolepta pusilla (Fallén, 1820)	33		s			
+	Ischiolepta vaporariorum (Haliday, 1836)	2		s			
	Leptocera caenosa (Rondani, 1880)	5	1	s			
	Leptocera finalis (Collin, 1956)	46		s			
	Leptocera fontinalis (Fallén, 1826)	37		s			
	Leptocera nigra Olivier, 1813	4	1	s			
	Leptocera oldenbergi (Duda, 1918)	1		s			
	Lotophila atra (Meigen, 1830)	56	2	s			
+	Minilimosina baculum Marshall, 1985	1	1	s			
	Minilimosina fungicola (Haliday, 1836)		1	s			
+	Minilimosina gemella Roháček, 1983	4		s			
	Minilimosina parvula (Stenhammar, 1855)		1	s			
	Minilimosina vitripennis (Zetterstedt, 1847)	6	1	s			
	Opacifrons coxata (Stenhammar, 1855)	63	2	s			
+	Opalimosina collini (Richards, 1929)	1		s			
	Opalimosina liliputana (Rondani, 1880)	1		s			
	Paralimosina fucata (Rondani, 1880)	7	25	s			
	Pseudocollinella humida (Haliday, 1836)	20	2	s	С	[19]	
	Pullimosina heteroneura (Haliday, 1836)	163	1	s			
	Pullimosina meijeri (Duda1918)	1		s			
_	Pullimosina pullula (Zetterstedt, 1847)	22	3	s			

		Num	bers		Drv (X), coastal (C
		Yellow dunes	Grey dunes	Larval trophic group	and dune (D) habitats recorded [references]	
P	Pteremis fenestralis (Fallén, 1820)	54		s		
F	Rachispoda breviceps (Stenhammar, 1855)	2		s		
F	Rachispoda fuscipennis (Haliday, 1833)	20	3	s	С	[19]
+ F	Rachispoda intermedia (Duda, 1918)	3		s		
F	Rachispoda limosa (Fallén, 1820)	1	1	s		
F	Rachispoda lutosa (Stenhammer, 1855)	9	2	s		
S	Spelobia clunipes (Meigen, 1830)	316	22	s		
S	Spelobia luteilabris (Rondani, 1880)	31	1	s		
S	Spelobia nana (Rondani, 1880)	4	22	s		
S	Spelobia ochripes (Meigen, 1830)	3		s		
S	Spelobia palmata (Richards, 1927)	2		s		
S	Spelobia pseudosetaria (Duda, 1918)	7	2	s		
S	Spelobia rufilabris (Stenhammar, 1855)	4		s		
S	Spelobia talparum (Richards, 1927)	64	8	s		
S	Sphaerocera curvipes Latreille, 1805	3		s		
+ S	pinilimosina brevicostata (Duda, 1918)	1		s		
Т	elomerina pseudoleucoptera (Duda, 1924)	6		s		
Т	elomerina flavipes (Meigen, 1830)	2		s		
Т	horacochaeta brachystoma (Stenhammar, 1855)	10	1	mi	С	[4,8,18]
T	horacochaeta seticosta (Spuler, 1925)	6		mi	С	[8,18]
Т	horacochaeta zosterae (Haliday, 1833)	7		mi	С	[1,4,8,18
+ <i>T</i>	rachyopella bovilla Collin, 1954	8		s		
Syrph	idae					
C	Cheilosia praecox (Zetterstedt, 1843)		1	ph		
Е	pisyrphus balteatus (De Geer, 1776)		12	z		
Е	umerus sabulonum (Fallén, 1817)		2	z	D	[3]
Е	Supeodes corollae (Fabricius, 1794)	19	8	z	D	[19]
S	caeva pyrastri (Linnaeus, 1758)	2		z		
Tephr	itidae					
C	Campiglossa loewiana (Hendel, 1927)		1	ph		
٨	loeeta pupillata (Fallén, 1814)		2	ph		
There	vidae					
D	Dialineura analis (Linnaeus, 1761)	24		z	D	[3,4,6]
	Thereva bipunctata Meigen, 1820		11	z	D	[6,12]
	Thereva cinifera Meigen, 1830		1	z	-	[-,]
	scelidae					
Т	rixoscelis frontalis (Fallén, 1823)	2		s	D	[1]
	rixoscelis marginella (Fallén, 1823)	_	19	s	D	[3]

	Numbers			Dry (X), coastal (C)
	Yellow dunes	Grey dunes	Larval trophic group	and dune (D) habitats recorded [references]
227 species	10,413	5,257		