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

Epigæiske myg (Diptera, Nematocera) fra klitterne i National Park Thy.

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Abstract

From March 2013 to April 2014 Diptera Nematocera were collected in pitfall traps in yellow and grey sand dunes in the National Park Thy, Denmark. A total of 5997 nematocerans were trapped, comprising 15 families and 112 species. Sciaridae, Mycetophilidae and Scatopsidae were particularly species-rich, contributing 38, 15 and 10 species, respectively. Two sciarid species are new to science (to be described elsewhere) and 27 species of nematocerans are new to the Danish fauna. A total of 75 and 77 species of nematocerans were recorded from yellow and grey dunes, respectively. Sciarids made up about 73% of all specimens. The ten most frequent species trapped in yellow and grey dunes contributed 81% and 75% of the catch, respectively, while a considerable number of species only occurred in low or very low number, e.g. 27 species from yellow dunes and 30 from grey dunes were singletons. A clear difference between the fauna of yellow and grey dune sites is revealed by means of the Sörensen similarity index , Cluster Analysis, and Detrended Correspondence Analysis. In both dune habitats the seasonal epigaeic activity of nematocerans proceeded in two distinct waves, viz. in early and late summer. A low winter activity owing to trichocerids was observed. The microhabitat associations and trophic relations of the larvae of the species recorded are presented. The larvae of roughly 70% of the species trapped in the dunes are associated with soil, litter layer or other sorts of plant debris being phytosaprophages, which applies to e.g. Sciaridae, Tipulidae, Trichoceridae and Bibionidae. Further, some nematocerans recorded are associated with macrofungi or dead wood, others with aquatic or semi-aquatic habitats. The most abundant and notable nematoceran species are commented on. The species recorded do not constitute a specific dune fauna, as all species are previously listed from other types of habitat, e.g. about a fifth are ubiquists. The results reflect a considerable diversity of habitats within the dune landscape, in particular in the grey dunes.

Sammendrag

Fra marts 2013 til april 2014 blev 5997 myg, der var aktive på jordoverfladen (epigæiske), fanget i faldfælder i hvid og grå klit. Ialt 112 arter tilhørende 15 myggefamilier var repræsenteret. Sørgemyg (Sciaridae), svampemyg (Mycetophilidae) og gødningsmyg (Scatopsidae) var artsrigest med henholdsvis 38, 15 og 10 arter. Af de fundne arter var 27 nye for den danske fauna, heriblandt 2 sørgemyg, der er ubeskrevne og vil blive beskrevet i anden sammenhæng. På individplan dominerede sørgemyg (73%). De 10 hyppigste arter i hvid og grå klit udgjorde henholdsvis 81% og 75% af materialet, mens et stort antal arter kun forekom i meget lavt antal, f. eks. var 27 arter fra hvid klit og 30 arter fra grå klit kun repræsenteret ved enkeltindivider. En tydelig forskel på faunaen i de to klittyper kunne påvises v. hj. af Sørensens similaritetsindeks, Cluster-analyse og DCA. Myggeaktiviteten på klitoverfladen i både hvid og grå klit forløb i to adskilte bølger, en i forsommeren og en i eftersommeren. Vinteraktiviteten var lav og skyldtes især vintermyg. De

fundne arters habitattilknytning og trofiske placering er præsenteret i et appendix. Hos omkring 70% (især sørgemyg, stankelben, vintermyg og hårmyg) er larverne nedbrydere af dødt plantemateriale (phytosaprophager) og knyttet til jordbunden og døde plantedele. Hos andre arter lever larverne i storsvampe og nogle få er knyttet til akvatiske og semiakvatiske habitater. De hyppigste eller mest bemærkelsesværdige arter er nærmere omtalt. Artssammensætningen i materialet fra klitarealerne repræsenterer ikke en særlig klitfauna, alle arter er tidligere fundet på andre habitattyper, f. eks er en femtedel allestedsnærværende. Resultatet afspejler i stedet en betydelig diversitet af habitater i klitlandskabet, især i den grå klit.

Introduction

Coastal sand dunes are habitats of a species-rich insect fauna, particularly regarding Coleoptera, Hymenoptera and Diptera (e.g. Krogerus, 1932; Ranwell, 1972; McLachlan, 1991). First of all the dipterous fauna is very rich (Cogan, 1978), thus Ardö (1957) recorded nearly 750 species of Diptera from coastal sand dunes and the littoral zone in Denmark, Norway and Sweden. Apparently no specific studies on the nematocerous fauna of dunes have been carried out, however, in three previous studies on the arthropod fauna of dunes some species of Diptera Nematocera are listed, viz. 18 species (Finland, Krogerus, 1932), 13 (Ardö, 1957), and 4 (Terschelling, The Netherlands, Van Heerdt & Bruyns, 1960). The three studies are based on different sampling methods, mainly sweeping and hand sorting of sample plots. As pointed out by Hövemeyer (2000) the catch composition and the species richness of a given habitat are influenced by several factors, including sample methods employed and sampling effort. Several species of Diptera Nematocera are epigaeic and at least temporarily active on the soil surface, among others the species-rich and abundant Sciaridae. This family is not at all represented in the species lists of Krogerus (1932), Ardö, (1957) and van Heerdt & Bruyns (1960), and no doubt other groups of epigaeic nematocerans are also missed. Still, epigaeic nematocerans are often abundant in pitfall traps. In 2013–2014 the surface active fauna of several dune habitats in National Park Thy, Denmark, was recorded by means of pitfall traps (Toft, in prep), and a comprehensive catch of Diptera Nematocera from these collections forms the basis for the present study on species diversity and phenology of nematocerans of coastal sand dunes.

Study area and methods

National Park Thy is situated at the north-western corner of Jutland, Denmark (Fig. 1), bordering c. 50 km of the North Sea coast. The national park includes a range of natural and man-made habitats, all established on sand blown in by the prevailing westerly wind. Yellow dunes constitute the

Fig. 1. Map of National Park Thy showing sampling sites, 2013–2014 (yellow dots: yellow dune sites; grey dots: grey dune sites). Inset: the geographical position of National Park Thy (NPT) in Denmark. Colouration on the map (inside park border = black line): brown= dune and heathland; light yellow= meadow and grassland; green= coniferous plantation; blue= lake; light blue= fjord.

outer formation from the beach and 20–200 m inland, where they form a nearly continuous band of habitat along the coast. Behind this (i.e. to the east) is a mosaic of habitats: heathlands, meadows and marshes cover the flat low-lying areas, while scattered groups of older dune hills allow development of grey dune vegetation which can be found mainly on the south-facing hill slopes and in wind breaks. They occur from a few hundred meters to a few kilometers inland. Parts of the dune hills and heathlands are covered by low *Pinus mugo* plantations. In the lower parts and depressions the heathland turns into oligotrophic marshes and shallow ponds.

The collections taking place in 2013–14 were concentrated on the yellow and grey dune habitats. Yellow dunes (Fig. 2A) 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 sandy surface. In less exposed areas and in depressions, the marram vegetation becomes dense with accumulation of litter. The grey dune habitat is very different (Fig. 2B). It occurs on older dune hills a few hundred meters to a few kilometers inland. The vegetation is scarce but much more diverse than on the yellow dunes and often forms a mosaic of bare ground and patches of *Ammophila arenaria*, *Carex arenaria*, various herbs, or low carpets of moss or lichens. In the present investigation the grey dune sites were situated on south-facing dune slopes with poor vegetation cover, and in windbreaks in various stages of vegetation recovery (from bare sand to complete cover of mosses and lichens), but dwarf-shrub (heathland) patches were avoided.

Sampling was done at 16 localities distributed over the national park. Of these, 8 were in yellow dunes and 8 in grey dunes. Three yellow and three grey dune sites (Table 1) were sampled throughout a full year (7 March 2013 to 18 April 2014) with 20 traps at each site; they are termed “main study sites”. At the yellow dune sites, 10 traps were situated on exposed spots with recent sand shifting, i.e. the marram vegetation was low and scarce and a considerable proportion of the ground was bare sand; however, the bare sandy areas 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 no recent sand shifting and with subsequent accumulation of marram litter on the ground. No systematic habitat difference existed between the grey dune trap sites. Five yellow dune and five grey dune sites were each sampled by 10 traps

operating for one month in spring (mid May–mid June), one month in summer (mid July–mid August), one month in early autumn (mid September–mid October), and one month in late autumn/winter (mid November–mid December); these are termed “supplementary study sites”. All localities were at altitudes of 5–30 m above sea level. For an overview of the sampling localities, see Fig. 1 and Table 1.

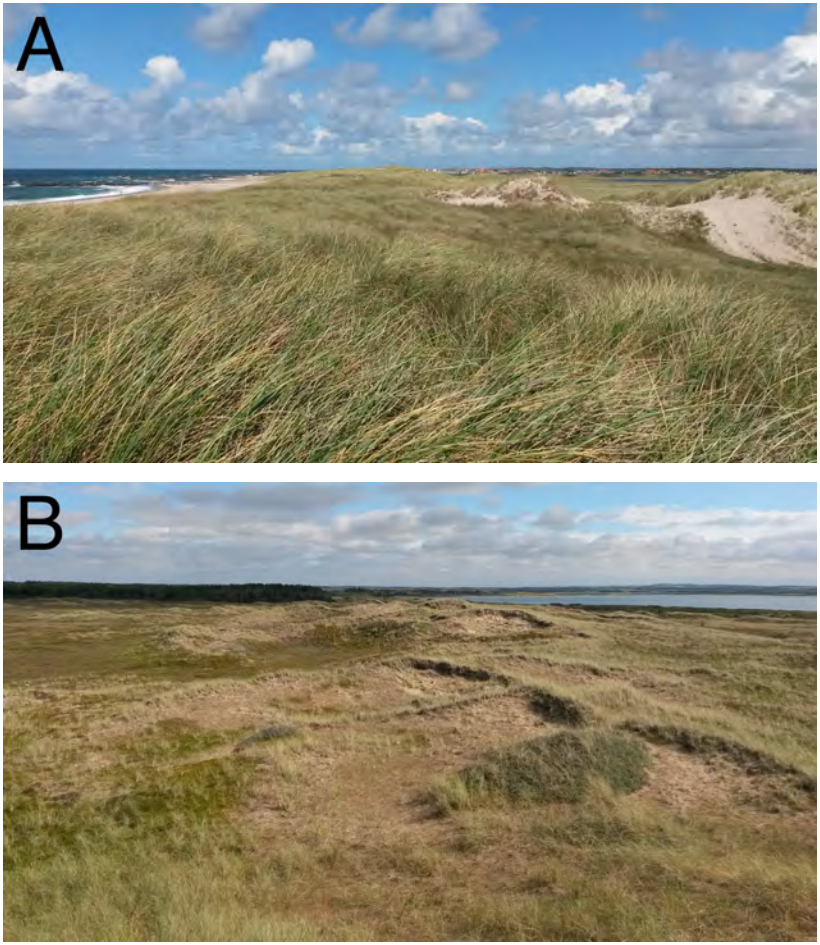

Fig. 1A-B. (A) Yellow dunes at Agger Tange. (B) Grey dunes at Lodbjerg Klint. Photos Søren Toft.

In several cases yellow and grey dune sites were chosen as pairs, i.e. they were at the same location with the grey dune site situated a few hundred meters inland of the yellow dune site. Since they share the locality name,

throughout the paper we distinguish them by adding -y or -g to the locality name, e.g. Hanstholm Reserve-y and Hanstholm Reserve-g (or HR-y and HR-g) for the yellow and grey dune site, respectively.

Table 1. List of trapping sites (from north to south, Fig. 1), their geographical position, number of traps operated, and trapping period. At some localities traps were operated in habitat pairs, i.e. the grey dune site was placed a few hundred meters inland of the yellow dune site. Trapping period was either whole year (March 2013–April 2014) or partial (one month in spring, summer, autumn and half a month in winter 2013). Habitat abbreviations: y= yellow dune; g= grey dune.

Locality	Abbr.	No. traps/ site	Trapping period	Position	
				Yellow dunes (y)	Grey dunes (g)
Hanstholm Reserve (north)	HR-y/g	20	Whole year	57°04'48"N, 8°33'03"E	57°04'51"N, 8°33'22"E
Hanstholm Reserve South	HS-y/g	10	Partial	57°03'42"N, 8°31'38"E	57°03'32"N, 8°31'57"E
Klitmøller	Kl-y/g	10	Partial	57°01'24"N, 8°27'20"E	57°01'04"N, 8°28'10"E
Graves Bakker	GB-g	10	Partial		56°59'47"N, 8°30'17"E
Bøgsted Rende	BR-y	10	Partial	56°58'43"N, 8°24'15"E	
Nr. Vorupør	NV-g	10	Partial		56°57'19"N, 8°24'06"E
Stenbjerg	St-y/g	20	Whole year	56°55'36"N, 8°20'04"E	56°55'31"N, 8°20'17"E
Lyngby	Ly-y/g	10	Partial	56°52'36"N, 8°17'22"E	56°52'37"N, 8°17'31"E
Lodbjerg Klint	Lo-y	10	Partial	56°48'47"N, 8°14'49"E	
Lodbjerg Klint	Lo-g	20	Whole year		56°48'38"N, 8°15'07"E
Agger Tange	AT-y	20	Whole year	56°46'13"N, 8°13'46"E	

Some sites differed from the typical of their vegetation type in one or more respects that might influence what species could be found. This was particularly the case with the grey dune site Graves Bakker which was situated further inland (c. 4.5 km) than the others; it was surrounded on all sides by coniferous plantation and the dune itself had been covered by *Pinus silvestris* until 2008; stumps of the trees still prevailed over the site. At Stenbjerg-g, the heathland and grassland vegetation in the depressions adjacent to the dunes where the traps were situated, had been burned two years before the study. Whereas the hinterland of most yellow dune sites is heathland with grey dunes, Agger Tange is adjacent to the lagoons and salt marshes within the Agger-embankment at Krik Vig (Fig. 1). At the North Sea side the coast was protected by several groynes along the spit. Stenbjerg-y had several large patches of the invasive shrub *Rosa rugosa* near traps 11–20; all traps were placed outside these patches, however. Similarly, the Lyngby-y site had patches of *Hippophaë rhamnoides*. At a distance of c. 200 m from the Klitmøller-y site, a low *Pinus mugo* plantation had been burned in March 2013, i.e. just before sampling started, with the black skeletons of the trees still remaining.

At all sites the traps were placed in lines parallel to the coast with a distance of 5 m between them. Some of the yellow dune trap lines were situated near

(0.5–5 m) the bluff towards the beach. A gale on 5 December 2013 (named "Bodil") washed away two of the supplementary yellow dune trapping sites, Bøgsted Rende and Lyngby. This happened in the middle of the second half of the late autumn/winter trapping period of the supplementary study sites; therefore, data from this trapping period had to be omitted from the locality comparisons.

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 and the traps were emptied twice per month. After collection of the samples, the preservative was exchanged to 70% alcohol. Identification of the Nematocera was done by LBN (Sciaridae) and BON (other taxa). A low number of gall-inducing Cecidomyiinae were not included. The material is deposited at the Natural History Museum, Aarhus.

Data analysis

The main sites were compared by summing the full-year catches, whereas comparisons of all sites were restricted to the summed catches of the seven trapping periods which were common to main and supplementary sites. The fauna of the main sites was compared by means of a simple binary index of similarity, QS (Sørensen, 1948) which is based only on the number of shared species in relation to the total species number of the two sites. Species represented only by females are included.

As the females of many species could not be identified, community analysis at the species level was based only on males. In order to secure identical sampling effort for all sites, traps 1–10 and 11–20 of the main localities were treated as separate sites (named e.g. HR-ya and HR-yb, respectively, for the two trap series at Hanstholm Reserve-y). For every site the catches of each species were summed over all trapping periods. The resulting matrix (81 species * 22 sites) was subjected to Cluster Analysis based on Bray-Curtis similarities (performed in Primer 6 (Clarke & Gorley, 2006)). A Detrended Correspondence Analysis (DCA) was performed in Canoco5 (ter Braak & Smilauer, 2012) using a yellow/grey dune classification of the sites as factor. DCA was chosen because the species composition data had a gradient length of 5.6 SD.

Results

Numbers of species and individuals

From March 2013 to April 2014 a total of 5997 nematocerans were trapped in 8 localities in yellow dunes and 8 in grey dunes in the national park. The

catch comprised fifteen families and 112 species (Appendix). Sciaridae, Mycetophilidae and Scatopsidae were particularly species-rich contributing 38 (33.9%), 15 (13.4%) and 10 (8.9%) species, respectively, or a total of 56% of all species (Fig. 3A). Two sciarid species are new to science (to be described elsewhere by Kai Heller, Quickborn, Germany). According to Fauna Europaea 2013, 27 species of the nematocerans collected are new to the Danish fauna, viz. Sciaridae: 19, Scatopsidae: 4, Mycetophilidae: 3, and Ceratopogonidae: 1.

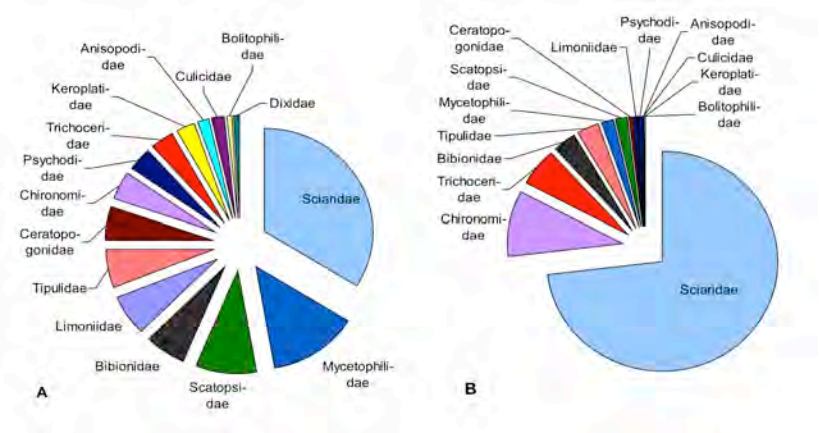

Fig. 3A-B. The total nematoceran catch in dunes, National Park Thy, 2013–2014. The contribution of nematoceran families to the number of species (A) and individuals (B). Totals: 112 species, 5997 individuals.

Sciarids made up 72.9% of all individuals captured out of which a little over half were females. Generally female sciarids cannot be identified to species level. Chironomidae contributed 9.8%, Trichoceridae 5.5%, Bibionidae 3.4% and Tipulidae 3.1%, or in all –including sciarids– 95% of the total catch (Fig. 3B). From yellow and grey dunes 75 and 77 species were recorded, respectively, 35 species were captured exclusively in yellow dunes and 37 species in grey dunes, while 40 species were present in both dune habitats. The species collected in yellow and grey dunes were ranked according to frequency (Fig. 4). A minority of species were very frequent; the ten most frequent species in yellow and grey dunes contributed 81% and 75% of the total, respectively, whereas a considerable number of species were characterized by a low or very low number, e.g. 27 species from yellow dunes and 30 species from grey dunes were singletons.

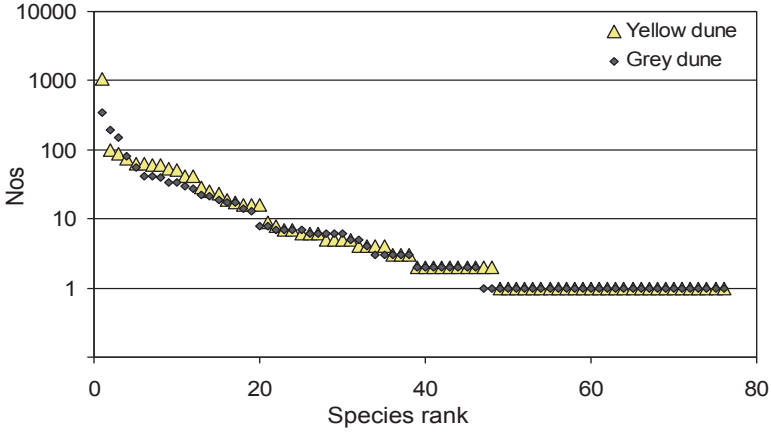

Fig. 4. All nematoceran species caught in yellow and grey dunes in National Park Thy, 2013–2014, ranked according to frequency.

The study sites in yellow and grey dunes

In the main study sites in yellow dunes the traps at Hanstholm Reserve-y caught the highest number of species (44, Table 2), but the lowest number of individuals (541). The corresponding numbers from Stenbjerg-y and Agger Tange-y were 23 species / 870 individuals and 28 species / 825 individuals, respectively. The species composition of the three sites offer several points of resemblance, but some differences catch the eye: the chironomid *Telmatogeton japonicus* is only recorded from Agger Tange, and another chironomid, *Chironomus plumosus* and the sciarid *Bradysia normalis* are with a few exceptions also limited to this site where also a considerable number of the scatopsid *Reichertella geniculata* were found. Among nematocerous flies from Hanstholm Reserve-y three species are notable: The sciarid *Corynoptera* sp. *a* (not described), the bibionid *Bibio longipes* and the moth fly *Philosepedon humeralis* (Psychodidae).

In the five supplementary sites in yellow dunes (Lodbjerg Klint-y, Lyngby-y, Bøgsted Rende-y, Klitmøller-y and Hanstholm Reserve South-y) the species composition is very similar to that of the main sites. The highest number of the sciarid *Bradysia angustoocularis* were trapped at Bøgsted Rende-y in a line of traps placed near the edge of the dune ridge. During a period of four weeks (16.5–14.6.2013) the number of *B. angustoocularis* caught per trap averaged 40, while the corresponding numbers for the traps at Agger Tange-y and Stenbjerg-y were 8 and 16, respectively. At Lyngby-y the traps were

placed in a similar exposed position, however, at this site *B. angustoocularis* was practically absent. The scatopsid *Reichertella geniculata* and the moth fly *Philosepedon humeralis* were most abundant at Hanstholm Reserve South-y.

The main study sites in the grey dunes (Lodbjerg Klint-g, Stenbjerg-g and Hanstholm Reserve-g) were situated 400 m, 260 m and 220 m, respectively, east of yellow dune areas. The number of nematoceran species in the three sites is the same, viz. 38, 37 and 38, respectively (Table 2), while Lodbjerg Klint is richer in individuals (902) than are Stenbjerg (673) and Hanstholm Reserve (476). The main habitat of the chironomid *Bryophaenocladius flexidens* and the sciarid *Bradysia* sp. *a* (not described) is Lodbjerg Klint, while the sciarid *Corynoptera subparvula* is abundant at Stenbjerg and Hanstholm Reserve, but absent at Lodbjerg Klint. Further, *Bradysia angustoocularis*, which is very abundant (N= 1078) in yellow dunes, is also present at Lodbjerg Klint and Stenbjerg. Finally, the main locality of the sciarid *Hyperlasion wasmanni* is Stenbjerg and only a single specimen was caught elsewhere (Hanstholm Reserve-g).

The traps at the five supplementary sites in the grey dunes (Lyngby-g, Nr. Vorupør-g, Graves Bakker-g, Klitmøller-g and Hanstholm Reserve South-g) captured fewer nematocerans than the corresponding traps in the yellow dunes, presumably mainly owing to the fact that the trapping period was different from the activity periods of the predominant species of the grey dunes. Among the supplementary sites in the grey dunes the locality Nr. Vorupør was particularly poor in species (6), but rich in individuals (124), while Graves Bakker, a plantation clearing with stumps of trees, was the poorest in individuals, but among the most species-rich localities (Table 2).

Table 2. Numbers of nematoceran species collected in pitfall traps in dunes, National Park Thy, 2013–2014. For each site the number of pitfalls, their operating period and the number of individuals are shown. Number of species trapped is shown in brackets at each family.

	Yellow dunes (y)								Grey dunes (g)							
	Main study sites			Supplementary study sites					Main study sites			Supplementary study sites				
	20 pitfalls 27 x 2 weeks			10 pitfalls 7 x 2 weeks					20 pitfalls 27 x 2 weeks			10 pitfalls 7 x 2 weeks				
	Agger Tange-y, N=825	Stenbjerg-y, N=870	Hanstholm Res.-y, N=541	Lodbjerg Klint-y, N=84	Lyngby-y, N=202	Bøgsted Rende-y, N=670	Klitmøller-y, N=90	Hanstholm South-y, N=271	Lodbjerg Klint-g, N=902	Stenbjerg-g, N=673	Hanstholm Res.-g, N=476	Lyngby-g, N=103	Nr. Vorupør-g, N=124	Graves Bakker-g, N=38	Klitmøller-g, N=68	Hanstholm South-g, N=60
Anisopodidae [2]			1	1		1					1					
Bibionidae [7]	3	3	5	1	3	1	3	4	4	2	3				1	
Bolitophilidae [1]										1						
Ceratopogonidae [6]		1	3	1					3	3	1	1		2		
Chironomidae [5]	2		1						3	1	3		1	1	1	1
Culicidae [2]			2		1			1								
Dixidae [1]	1															
Keroplatidae [3]	1								1					1		
Limoniidae [7]	3	2	4					1	1			1				1
Mycetophilidae [15]	1	2	2	2		2	5	2	4	1	4			3		1
Psychodidae [4]	2		2		1	1	1	1								
Scatopsidae [10]	2	2	5	2			1	1		3	4					
Sciaridae [38]	7	7	12	3	5	5	4	11	17	20	15	9	5	5	10	5
Tipulidae [7]	2	3	4	1	3		1	3	1	2	3	3		2	1	1
Trichoceridae [4]	4	3	3	2	4	3	3	3	4	4	4				1	2
Sum [112]	28	23	44	13	17	13	18	27	38	37	38	14	6	14	14	11

Differences in the nematoceran fauna of yellow and grey dunes

On the face of it the two types of dune, yellow and grey dune, are very different. Each type is represented by localities with different position in the National Park. For the nematoceran faunas of the six main sites sampled through a full year the quotient of similarity was calculated. The number of species of each site and of shared species in all binary combinations are presented in Fig. 5A. The calculated quotients of similarity in percentages (QS) are shown in Fig. 5B. It is obvious that the highest similarities are found between the sites within grey dunes (QS= 51–56%, mean 53%) and within yellow dunes (QS= 44–54%, mean 50%), whereas the lowest similarities are found when sites in grey dunes and yellow dunes are compared (30–51%, mean 39%). The quotient of similarity between the nematoceran faunas in yellow and grey dune may also be calculated by means of Sørensens index

for the similarity between two groups of populations (Sørensen, 1948). In that case the result is QS= 41%.

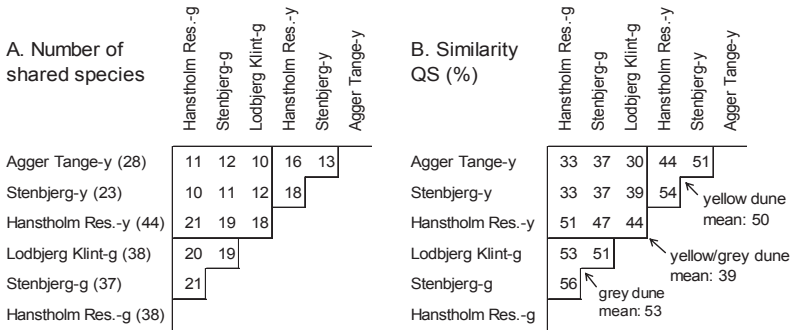

Fig. 5A-B. Nematocerans trapped at the main sites, National Park Thy, 2013–2014. A. Number of species at each site (in parenthesis) and number of shared species of all binary combinations of sites. B. Quotient of similarity (QS, Sörensen) of the same combinations.

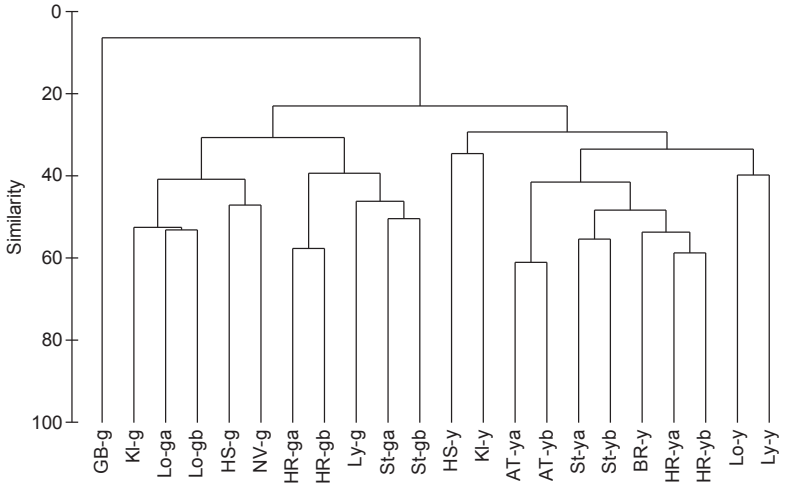

Fig. 6. Cluster Analysis of catches from all study sites. Only males were included. For main localities, traps 1-10 (a) and 11-20 (b) are considered separate sites, thus trapping effort is identical for all sites. For locality abbreviations, see Table 1.

A total of 81 species represented by males in the seven trapping periods were common to main and supplementary sites. Cluster analysis (Fig. 6) shows that the nematoceran fauna of Graves Bakker (the “inland” grey dune site surrounded by plantation) is distinct compared to all other (both yellow

and grey dune) sites. Further, it shows a clear separation of yellow and remaining (coast-near) grey dune sites. It is also noticed that the a and b subsites at all six main localities are more similar to each other than to any of the other sites. The distinctness of the fauna is also revealed by the DCA (Fig. 7). Yellow and grey dunes sites are completely separate, and the Graves Bakker site is removed considerably from all other sites. Though some overlap exists in species composition between the yellow and grey dunes habitats, their communities can be considered distinct.

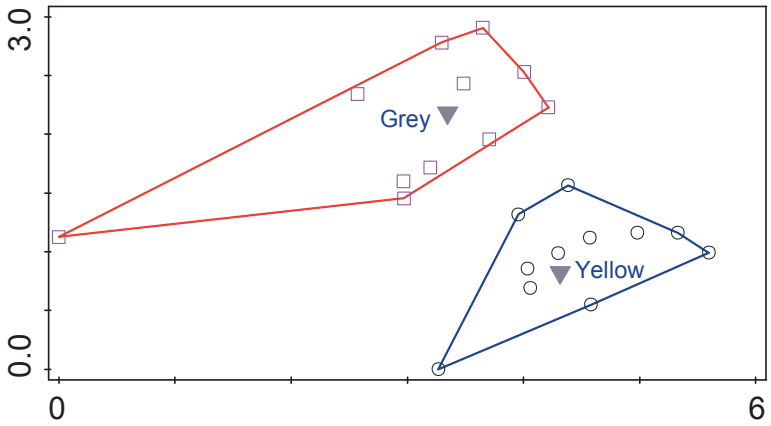

Fig. 7. Detrended Correspondence Analysis (DCA) of catches from all study sites. Only males were included. The grey dune locality to the far left is Graves Bakker.

Phenology

In the yellow dunes, 2013-2014 the epigaeic activity of nematocerans proceeded in two waves (Fig. 8): in early summer (May–June) and in late summer (August–September). The activity was low between the two waves as well as from autumn to the middle of the following spring. The activity peak in early summer was dominated by the sciarid *Bradysia angustoocularis*. In 2013 the activity of this species started in late April when the mean temperature passed 5–6°C (Vestervig, DMI). The following year the activity started two weeks earlier at a mean temperature of 6–7°C. Two bibionid species contributed to the activity wave in spring viz. *Bibio johannis* in May and *Dilophus febrilis* in May–June. The sciarid *B. normalis* was abundant in May–June, but only at Agger Tange.

The distinct activity peak in early summer was succeeded by a period of very low nematoceran activity (July–August). Only the scatopsid *Reichertella geniculata* was frequently trapped. However, a new activity wave began in

the latter half of August, when the tipulid *Tipula paludosa*, the bibionid *Dilophus febrilis*, and the sciarid *Bradysia angustoocularis* were recorded. The activity wave in late summer–autumn declined in early October and was succeeded by a long activity period of the trichocerids *Trichocera regelationis* and *T. saltator* during the winter until the first half of April. A third species, *T. hiemalis* first appeared in early December. Unidentified female nematocerans (93% of them sciarids) follow the activity patterns presented above. The activity of female chironomids (6%) mainly took place in April–May.

In the grey dunes, 2013–2014 the activity of epigaeic nematocerans also peaked in early and late summer, however less pronounced than in the yellow dunes (Fig. 9). The spring wave of activity began in mid April with the sciarid *Bradysia* sp. *a*, which was active on the soil surface through 6 months. Other sciarids active in early summer are *Corynoptera praeforcipata* for a short period, and *C. subparvula* throughout the summer. Also the tipulid *Nephrotoma submaculosa* participated in the spring wave. The activity of the three last mentioned species started in mid May.

The summer activity was low in the grey dunes, but higher than in the yellow dunes. The sciarids *Bradysia* sp. *a, Corynoptera subparvula* and *Hyperlasion wasmanni* in particular were active. The last one, however, at one locality only. The late summer wave started in August by the sciarids *Bradysia flavipila* and *Corynoptera globiformis*. *Bradysia* sp. *a* and *C. subparvula* were still active.

From October and throughout the winter the activity of *Trichocera regelationis* and *T. saltator* was high in all the localities in the grey dunes. Further, the main activity of the chironomid *Bryophaenocladius flexidens* was observed in October–November. It was recorded from all localities in grey dune, but was predominant in one site, viz. Lodbjerg Klint-g. Also in the grey dunes unidentified females followed the general activity pattern. Females of Chironomidae (14%), were active in two periods, viz. late May and late October (presumably mainly *B. flexidens*).

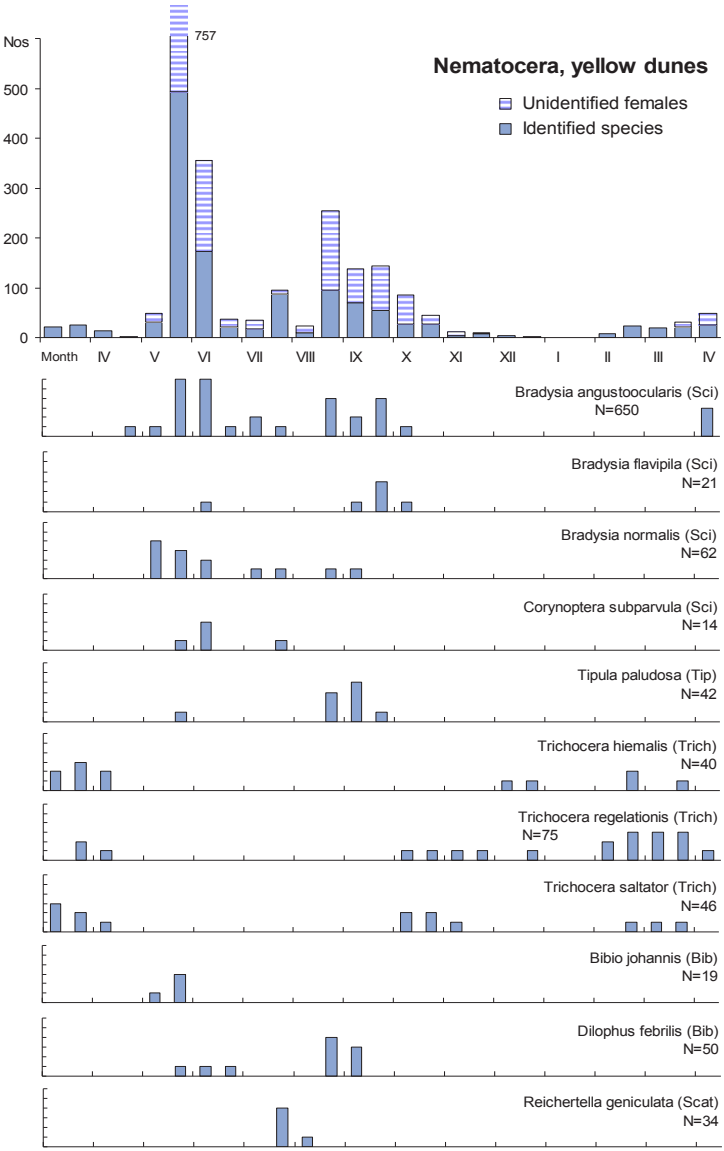

Fig. 8. Seasonal activity of epigaeic nematocerans in yellow dunes of National Park Thy. Main study sites, March 2013–April 2014. Above, the total activity of all species and unidentified females. Below, phenology of the most abundant species, numbers on a progressive scale with 6 steps: 1-5, 6-10, 11-20, 21-40, 41-80 and >80 individuals.

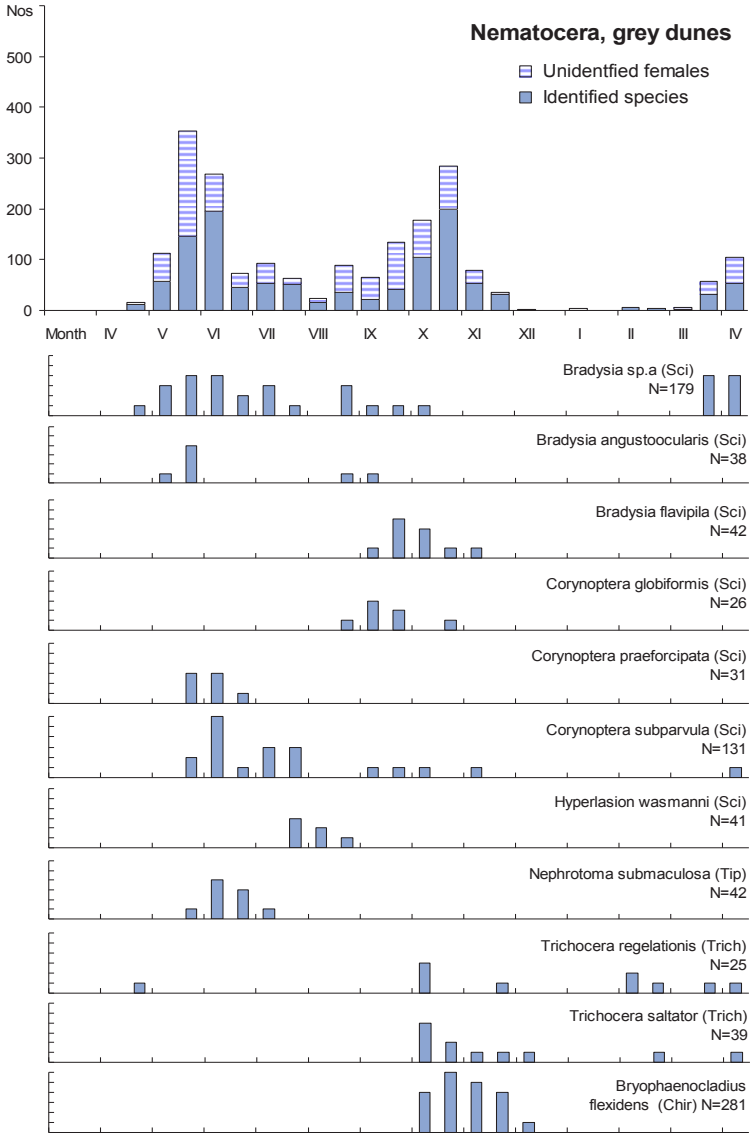

Fig. 9. Seasonal activity of epigaeic nematocerans in grey dunes of National Park Thy. Main study sites, March 2013–April 2014. Above, the total activity of all species and unidentified females. Below, phenology of the most abundant species, numbers on a progressive scale with 6 steps: 1-5, 6-10, 11-20, 21-40, 41-80 and >80 individuals.

Discussion

Previously, some nematoceran species have been collected in dunes now included in National Park Thy (Ardö, 1952; Pedersen, 1965), e.g. the bibionids *Dilophus febrilis*, *D. femoratus* and *Bibio nigriventris* Hal., and the tipulid *Nephrotoma submaculosa*. During the investigations 2013–2014, 112 species of Diptera Nematocera were collected in pitfall traps in yellow and grey dunes indicating that at the moment of catching the specimens trapped have been active on the soil surface (epigaeic), e.g. in connection with hatching and emergence, oviposition or mating. A closer examination (see next section) confirms that the nematocerous flies of dunes to a great extent are associated with the soil and litter layer. Exactly half of all species in the catch are singletons or doubletons suggesting that the species in question are either less active, are associated with widely scattered habitats, represent stray insects from other habitats, or they are truly rare species of the habitat. On the other hand, a number of species are abundant (>20 individuals) which may indicate that they are frequently active on the surface of the sand and indigenous to the dunes. Finally, a few species (7) are very abundant (>100 individuals). The preferred habitats of these species are most certainly present in the dunes, or the species are very active, e.g. forming swarms. The most abundant species of Nematocera (N>20) in yellow and grey dune are presented in Table 3, representing 89% and 83% of the catch in the two types of dune, respectively.

Table 3. The most abundant species of Diptera Nematocera (N>20) in yellow and grey dunes of National Park Thy, 2013-2014, ranked according to relative abundances.

Yellow dunes (y)	Nos	Relative abundance	Grey dunes (g)	Nos	Relative abundance
Bradysia angustoocularis	1078	0.5185	*Bryophaenocladius flexidens*	342	0.2558
Trichocera regelationis	101	0.0486	*Bradysia sp. a*	191	0.1429
Corynoptera subparvula	87	0.0418	*Corynoptera subparvula*	148	0.1107
Bradysia flavipila	75	0.0361	*Nephrotoma submaculosa*	82	0.0613
Bradysia normalis	64	0.0308	*Bradysia flavipila*	55	0.0411
Dilophus febrilis	62	0.0298	*Trichocera saltator*	42	0.0314
Reichertella geniculata	61	0.0293	*Hyperlasion wasmanni*	41	0.0307
Trichocera saltator	60	0.0289	*Bradysia angustoocularis*	39	0.0292
Bradysia sp. a	53	0.0255	*Corynoptera praeforcipata*	34	0.0254
Tipula paludosa	51	0.0245	*Bibio johannis*	34	0.0254
Trichocera hiemalis	42	0.0202	*Corynoptera globiformis*	30	0.0224
Bibio johannis	42	0.0202	*Trichocera regelationis*	27	0.0202
Philosepedon humeralis	29	0.0139	*Ctenosciara hyalipennis*	22	0.0165
Mycetophila fungorum	25	0.0120	*Bibio varipes*	21	0.0157
Corynoptera sp a	23	0.0111	Sum	1108	0.8287
Sum	1853	0.8912			

The frequency distribution of nematoceran species is similar in the yellow and grey dunes (Fig. 4), but in spite of a considerable overlap of species the species compositions are distinct (Fig. 6–7). This is no wonder considering the differences in vegetation coverage and diversity between the two habitat types. A strong local element is also evident. Thus, the catch of the a and b trap series (traps 1–10 and 11–20, respectively) of the main sites were always more similar to each other than to the catch of any other site (Fig. 6). This was expected for the catches at the grey dune sites but not for those of the yellow dune sites, where the subsites a and b were chosen as having scattered and dense vegetation, respectively. The result indicates that geographic position (i.e. some local factor) is a stronger determinant of faunistic (nematoceran) composition than vegetation density.

Microhabitat association and trophic relation

Based on information in the literature on larval microhabitats and feeding biology the species recorded are grouped according to microhabitat association and trophic relation (Appendix). Out of 75 and 77 species caught in yellow and grey dunes the larvae of 51 (68%) and 56 (73%), respectively, are associated with soil, litter layer, or other sorts of plant debris. This for instance applies to the abundant families, Sciaridae, Tipulidae, Trichoceridae and Bibionidae. Another group of nematocerans present in the dunes develop in the fruiting bodies of macrofungi or in dead, decomposing wood; this refers especially to mycetophilids s.l. (Bolitophilidae, Keroplatidae and Mycetophilidae). In the yellow dunes at least 12 species (16%) are associated with macrofungi or dead wood, in grey dune 15 species (19%). Finally, 13 species (17%) in yellow dunes and 7 species (9%) in grey dunes are associated with aquatic or semi-aquatic habitats, e.g. some Limoniidae, Dixidae, Culicidae, Chironomidae, Ceratopogonidae and Psychodidae. They may have come from the shallow oligotrophic lakes found near some of the sites. The importance of these wetland habitats varies between the localities.

A trophic classification of the dune fauna agrees with the microhabitat associations presented above: both in yellow and grey dunes the fauna of Nematocera is dominated by phytosaprophages mainly feeding on dead plant material in the soil or litter layer, including fungal material and humus. In yellow dunes the phytosaprophages make up 66% of all nematoceran species, in grey dunes 71%. They are primarily represented by species of Sciaridae, Tipulidae, Trichoceridae and Bibionidae. In some tipulids e.g. *Tipula paludosa*, sciarids e.g. *Corynoptera subparvula*, and in the bibionids *Bibio johannis* and *Dilophus febrilis* the larvae may also attack roots and stems of living plants (partly phytophages). Another trophic group

established in the dunes is the macromycetophages, the larvae of which usually feed on the fruiting bodies of macrofungi. In yellow and grey dunes this trophic group – all belonging to Mycetophilidae s.l. – contributed about 13% of the species. Finally, the larvae of some nematocerans are microsaprophages feeding on fragments of fungal hyphae and microscopic algae as well as amorphous humus, etc. This especially applies to larvae of Ceratopogonidae and Chironomidae making up 15% and 13% of all species caught in yellow and grey dunes, respectively.

Comments on some nematoceran species from sand dunes

Sciaridae

In most terrestrial habitats sciarids are among the most species-rich families of Diptera Nematocera (Heller, 1996). Adults are readily trapped in pitfall traps since they are frequently running on the soil surface where copulation and oviposition take place. From the sand dunes in National Park Thy 38 species of sciarids were recorded; 19 are new to the Danish fauna (Appendix). Only 3 publications mention the sciarid fauna of habitats in Denmark, viz. arable land (Nielsen & Nielsen, 2004, N=8807), beech forest (Nielsen & Nielsen, 2007, N=7150) and a former heath area (Nielsen & Nielsen, 2006, N=56). In the first two investigations emergence traps were applied. The sciarid fauna of the sand dunes has 10 species in common with that of the beech forest, but only 5 in common with arable land. The similarities (Sørensen, 1948) are rather low, viz. 27% with beech forest, 21% with arable land.

Bradysia angustoocularis is the most abundant nematoceran species in the dunes of National Park Thy. A total of 1078 males and probably a similar number of females were trapped at the localities in yellow dunes, but also a smaller number in some grey dune localities (Table 3). The larval habitat is still unknown, but the large number caught in the yellow dunes may indicate a closer association with this particular habitat or presence of adaptations that are profitable at the exposed sites. Adults are active on the dune surface from late April to mid October (Fig. 8). Possibly two generations are present. *B. angustoocularis* was originally described on a few specimens found in mountains in Kyrgystan (Mohrig et al., 1989). Later 46 individuals have been recorded from arable fields on sandy soils and gardens in Northern Germany (Heller, 1996, 2014), a few from mountains in Ober Bayern (Rudzinski, 2006), and a few from gardens in Britain (Menzel et al., 2006). The identity of two Danish specimens is confirmed by means of barcoding (GBOL, 2016).

"*Bradysia* sp. *a*", which is new to science, is the most abundant sciarid in the grey dunes (Table 3). Barcoding confirms that the species is identical with specimens collected at a sandy locality in Southern Germany, but undescribed (GBOL, Heller, pers. comm.). A total of 191 males were caught in the grey dune localities, in particular at Lodbjerg Klint and Stenbjerg, and 53 males in the yellow dunes. The period of adult activity is rather long, viz. April to October (Fig. 9). A break in activity in early August may be due to high precipitation (DMI).

Bradysia flavipila is also abundant and widespread in the dune landscape. Tuomikoski (1960) reported this species from farmyards in Finland. In Britain, it was found in coastal localities and open mountainous habitats. According to Seeber et al. (2012) it is common in high alpine localities, and Heller (2014) caught large numbers in malaise-traps placed in gardens in Northern Germany. In Thy, the species was trapped in almost all localities in both types of dune. The adult activity is highest in September–October, but a few were also trapped in June (Fig. 8–9).

Bradysia normalis exhibits a remarkable distribution: 60 males were trapped in a single locality in the yellow dunes, 4 were trapped in other localities, and only one in grey dunes. According to Menzel et al. (2006) males of this species are observed swarming in shelter of dunes, on sand among marram in an exposed situation facing the Atlantic Ocean. Tuomikoski (1960) often found the species at farmyards in Finland. In National Park Thy the main locality is the yellow dunes at Agger Tange, an exposed narrow strip of land between the North Sea at West and a brackish lagoon, Krik Vig at East and without grey dunes nearby (Fig. 2A). The activity is highest from May to mid June, but a few individuals were also trapped in July and August-September (Fig. 8).

Corynoptera subparvula takes third place in the rank of nematocerans in yellow as well as grey dunes (Table 3). It is a ubiquitous species known from woodland, wetland, dry grassland, coastal habitats, gardens etc. (Fritz, 1982; Rudzinsky, 1992; Heller, 2002, 2003, 2014; Menzel et al. 2006). In the national park it is trapped at almost all localities, but is particularly numerous at one site in yellow dunes (Hanstholm Reserve South) and two in grey dunes (Hanstholm Reserve, Stenbjerg). Two separate periods of activity in the grey dunes suggest two annual generations (Fig. 9).

"*Corynoptera* sp. *a*" is probably new to science. In the yellow dunes at Hanstholm Reserve 22 specimens were caught and 5 in the grey dunes 330 m at East (Hanstholm Reserve-g). The species is obviously associated with the *C. parvula*-group (Menzel & Mohrig, 1999), and barcoding seems to

confirm that it is undescribed (GBOL – Heller, pers. comm.). The period of adult activity is short, i.e. from July to mid August.

Corynoptera globiformis and *Ctenosciara hyalipennis* were found in most localities in the grey dunes. Both species are common in various habitats in woodland, wetland and heathland in Europe (Heller, 1996, 2003; Menzel et al., 2006), and both have emerged from leaf litter and dead wood in a Danish beech forest (Nielsen & Nielsen, 2009). *Corynoptera globiformis* is active late in the year (August to October), whereas adults of *Ctenosciara hyalipennis* are active in two periods, viz. March to May and September to October, which may be explained as two generations.

Hyperlasion wasmanni was trapped at a single locality in grey dunes (Stenbjerg). It is reported to be myrmecophilous, and mass occurrences were observed in summer, e.g. July–August in a beech forest in Sweden (Heller et al., 2009). It is found in woodland, heathland and wetland in many parts of Europe. It is notable that females of this species may be identified, and that ♂:♀ ratios are often skewed, e.g. 6:35 in the actual material, 12:460 and 92:2618 in Sweden (Heller et al., 2009), 1:26 in East Anglia (Laurence, 1994), and 2:104 in La Gomera (Menzel et al., 1997). The period of adult activity lasts from mid July to the end of August (Fig. 9).

Mycetophilidae

The larvae of most species live in the fruiting bodies of fungi, under the bark of trees or in dead wood, and usually the pupation takes place in the soil (Søli et al., 2000). In National Park Thy, the family was fairly species-rich, but rather poor in individuals (Fig. 3). Ten out of fifteen species trapped are singletons. *Mycetophaga fungorum* is the predominant mycetophilid species, in particular in the yellow dunes. The species is widespread in Denmark and extremely polyphagous, since the larvae may feed on practically all species of fungi, whether they grow on the ground or on dead wood (Dely-Draskovits, 1974; Chandler, 1978; Hackman & Meinander, 1979; Alexander, 2002). *M. fungorum* is also bred from dead branches (Hövemeyer & Schauermann, 2003). Three species are new to the Danish fauna (Appendix).

Bibionidae

Bibio johannis and *Dilophus febrilis* were the most abundant bibionid species in the sand dunes. *B. johannis* is common in grassland in most parts of Europe (Krivosheina, 1986) and is together with *D. febrilis* the predominant bibionid species in cultivated grassland. At first the larvae feed on dead, decomposed plant material, later on they may attack and damage roots and stems of living plants (D'Arcy-Burt & Blackshaw, 1991; Skartveit, 2004). Both

species are widespread in Denmark and the latter one is previously recorded from a number of localities in the Hanstholm Reserve, e.g. at dunes at Isbjerg (Pedersen, 1965). In the sand dunes in Thy *B. johannis* was recorded in April–May, in Norway it is the earliest flying bibionid (Skartveit, 1995). *D. febrilis* was trapped in May–June and August–September (Fig. 8). The species may be bivoltine or – more likely – two cohorts of the same generation with well defined activity periods occur (Freeman & Lane, 1985; Blackshaw & D'Arcy-Burt, 1992; Skartveit, 2004).

Chironomidae

Bryophaenocladius flexidens was the most abundant nematoceran trapped in the grey dunes (N= 228♂♂) and presumably all *Bryophaenocladius* females (116) belong to this species. The majority (169♂♂, 74%) derive from Lodbjerg Klint-g, the rest mainly from other sites in grey dunes, only two specimens were trapped in yellow dunes (Hanstholm Reserve). All *B. flexidens* were caught 1.10–16.12.2013 (Fig. 9). *B. flexidens* is recorded from e.g. Britain, Denmark, Norway, Sweden, Finland, Poland, Germany and the Netherlands. The larva seems to be associated with semiaquatic habitats and has been collected along small watercourses (Lehmann, 1971; Pillot, 2013). At the main site, Lodbjerg Klint-g, a permanent pond is situated less than 100 m from the row of pitfall traps.

Telmatogeton japonicus is a marine element in the fauna of the sand dunes. From mid October, 2013 to mid April, 2014, 4♂♂ and 3♀♀ were trapped in the pitfalls in yellow dunes at Agger Tange. Larvae and pupae of the species are associated with rock or other hard substrates in salt- or brackish water, for instance moles, breakwaters, offshore windmills and hulls. In August 2015 twelve larvae and six pupae were collected in a dense growth of green algae (*Ulva* (*Enteromorpha*) sp.) on a groyne opposite the dune site (Fig. 10), presumably the adult midges were carried by the wind from the groyne to the yellow dune ridge, a distance of 142 m. The larva of *T. japonicus* lives in the marine zone between tidemarks (Cranston, 1983) protected in a tube consisting of a secretion from the salivary glands and fastened to the substrate (Neumann, 1976). The larvae feed on growth of green algae, diatoms and blue-green bacteria on the substrate. *T. japonicus* is able to fly, but is often seen scurrying away on rocks in the splash zone, seeking a mate or mating (Neumann, 1988; Cranston et. al., 1989). The native area of *T. japonicus* is Japan and possibly Hawaii, but now the species is very widespread occurring in e.g. Northern Europe, North America and the Pacific (Jensen, 2010). Shipping is considered to be the vector (Brodin and Andersson, 2004). In 2003 the alien species was found on Danish wind

farms in the North Sea, and it is now recorded from a number of localities in Denmark, e.g. Blåvandshuk, Skagen, Aarhus and Sjællands Odde.

In October-November 2015 fifteen (9♂♂, 6♀♀) *Limnophyes minimus* hatched from 3 out of 20 soil samples taken in the grey dune at Lodbjerg

Fig. 10. Green algae, *Ulva (Enteromorpha)* sp. on rocks of groyne at Agger Tange. Breeding habitat of the alien chironomid *Telmatogeton japonicus*. Photo Lise Brunberg Nielsen.

Klint, close to the location of the pitfall traps 2013-2014. In late November 2013 1♀ *Limnophyes* sp. (probably *L. minimus*) has been collected in a pitfall trap in grey dunes at Lodbjerg Klint. The larva may live in water, but more often in humid or wet soil (Pillot, 2005). According to Delettre (1986) larvae of *L. minimus* are abundant in heathland soil during the winter, the adults hatching in spring. On the whole, a summer generation of larvae often dies due to drought and only a minority survives and hatches in the autumn (Delettre, 2000).

Tipulidae

Nephrotoma submaculosa and *T. paludosa* were predominant species contributing 45% and 30%, respectively, of all tipulids. *N. submaculosa* is characteristic of sandy habitats and is often recorded from dunes (Theowald,

1967; Oosterbrook, 1978; Noll, 1985; Hofsvang, 1986). The larva is found under moss or short grass and at grass roots in sandy soil. *N. submaculosa* and *T. paludosa* are widespread in Denmark and are previously recorded from the Hanstholm Reserve (Pedersen, 1965). In the present study *N. submaculosa* was primarily trapped in grey dunes in May–June while *T. paludosa* was recorded in yellow dunes in mid August–early October (Fig. 8–9). A strongly skewed sex ratio (3.5% males, 96.5% females) suggests that the species is mainly trapped in connection with oviposition.

Trichoceridae

Trichocera regelationis, *T. saltator*, *T. hiemalis* and *T. major* were all widespread in the sand dunes of the National Park. *T. regelationis* and *T. saltator* are predominant. *T. major* was caught only in October–December, the other species in September–December and February–April (Fig. 8–9). Similar activity patterns are previously observed in e.g. Sweden, Denmark and Lithuania (Dahl, 1966; Nielsen, 1970; Podenas, 1995). *T. hiemalis* is bivoltine (Dahl, 1966). In the catch of *T. regelationis*, *T. saltator* and *T. major* females were strongly in excess of males.

Psychodidae

The most abundant species, *Philosepedon humeralis* was only recorded from yellow dunes 15.7–17.10.2013. Since only females were trapped, the catch may reflect oviposition activity. The female, which lacks an ovipositor, is larviparous and deposits newly hatched 1st instar larvae in dead snails, in which the larval development and the pupation are completed (e.g. Spärck, 1929; Vaillant, 1960-61; Beaver, 1972, 1977). *P. humeralis* is mostly bred from *Cepaea hortensis*, *C. nemoralis* and *Ariante arbustorum* and is widespread in Denmark. It is recorded from dunes in the British Isles (Beaver, 1977).

Scatopsidae

Reichertella geniculata was mainly found in yellow dunes in the latter half of July (Fig. 8). It is widespread in Denmark and is often observed on flowering creeping thistle (*Cirsium arvense*) or aggregating in the vegetation (Freeman, 1985), now and then forming aggregations of up to 25,000 individuals (Nielsen, 2009). *R. geniculata* has been reared from the soil in cereal fields in Denmark (Nielsen et al., 1996) and is recorded from coastal localities in Norway and Sweden (Ardö, 1957; Andersson, 1982).

Three species of *Colobostema* were recorded. All of them are new to the Danish fauna. A number of *Colobostema*-species are considered to be

myrmecophilous. Presumably, the larvae are scavengers and feed on dead organic matter in the ants' nests (Haenni, 1997). *C. nigripenne*: (1♂, 1♀ trapped in grey dune, Stenbjerg 16.5.-30.5.2013 and 1♂ in grey dune, Hanstholm Reserve 16.5.-30.5.2013) the species is widely distributed in Europe. In the British Isles the larvae live as scavengers in nests of the ants *Lasius fuliginosus* and *Formica rufa* (O'Toole, 1978), and in Sweden adults have been swept near *Formica*-anthills (Andersson, 1982). *C. infumatum*: (1 ♀ trapped in grey dune, Hanstholm Reserve, 16.5.-30.5.2013). It is a North- and Central European species, possibly myrmecophilous (Haenni & Greve, 1995). In the southern part of its distribution the species is restricted to peat-bogs and heathland (Haenni & Greve, 1995). *C. obscuritarse*: (4♂♂ trapped in grey dunes, Hanstholm Reserve, 16.5.-30.5.2013; 1♂ in grey dune, Stenbjerg, 16.5.-30.5.2013; 1♂ grey dune, Stenbjerg, 2.5.-16.5.2013; 1♂ yellow dune, Lodbjerg Klint, 16.5.-30.5.2013; 1♂ yellow dune, Lodbjerg Klint, 17.5.-31.5.2013). The species is known from the Alps in Austria and Switzerland, the Sumara-mountains in the Czech Republic, the Vosges mountains and the Pyrenees in France, and from a mountainous locality in Southern Norway, seemingly indicating a mountainous distribution pattern (Haenni, 2013). However a recent record of the species from Finland (Haenni, pers. comm.) and the records from Thy, Denmark tell against this assumption.

Swammerdamella acuta is new to the Danish fauna (1♀ yellow dune Hanstholm Reserve, 17.8.-1.9.2013; 1♀ yellow dune, Lodbjerg Klint, 31.5.-15.6.2013). The species is recorded from several European countries, e.g. Britain, Norway, Finland, Sweden, Poland, Germany and the Netherlands (Fauna Europaea, 2013). In Sweden *S. acuta* has been collected in late May (Andersson, 1982) and in France in September–October in a peat bog (Brunhes & Haenni, 1982).

Final remarks

The coastal sand dunes of National Park Thy are habitats of several species of Diptera Nematocera, however, they do not constitute a specific dune fauna, as all species are previously listed from other types of habitats. For instance about a third of the species are also recorded from woodland, a fifth from meadow, while another fifth are ubiquists. A dozen of species are previously recorded from dunes or heathland, but are not specific for these habitats. The results reflect a considerable diversity of habitats within the dune landscape, at least in grey dunes, where nematocerans associated with various habitats may find suitable conditions.

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Appendix 1. List of nematoceran species trapped in pitfalls in dunes, National Park Thy, 2013-2014. + New to the Danish fauna (ref: Fauna Europaea version 2.6, 2013). Reference refers to [Ref.no.] in list of references.

Oversigt over myggearter fanget i faldfælder i klitter, National Park Thy, 2013-2014. +Ny for den danske fauna (iflg. Fauna Europaea version 2.6, 2013). Reference henviser til [Ref.nr.]i litteraturlisten.

Abbreviations, habitats *(Forkortelser, habitater)*: a=aquatic *(akvatisk)*, asb=aquatic salt/brackish *(salt-/brakvand)*, b=burrows of small mammals or birds' nests *(gange og boer af småpattedyr eller fuglereder)*, d=dung *(gødning)*, dr=drains *(afløb)*, f=soil-inhabiting fungi *(svampe på jorden)*, fw=wood-inhabiting fungi *(svampe på ved)*, m=dead snails *(døde skalbærende snegle)*, mo=moss *(mos)*, mu=mud *(mudder)*, my=ants' nests *(myreboer)*, pd=plant debris *(døde plantedele)*, r=living roots *(levende rødder)*, s=soil *(jordbund)*, sa=semi-aquatic *(semiakvatisk)*, sm=wet soil *(våd jord)*, w=dead wood *(dødt ved)*.

Abbreviations, trofic group *(Forkortelser, trofisk gruppe)*: mamy=macromycetophage *(lever i storsvampe)*, mi=microsaprophage *(æder bakterier, mikroskopiske alger og findelt organisk materiale)*, ph=phytophage *(planteæder)*, phs=phytosaprofage *(æder døde plantedele)*, z=zoophage *(rovdyr)*, zs=zoosaprofage *(æder døde dyr)*.

	Nos				
	Yellow dune	Grey dune	Micro-habitat	Trofic-group	Reference
Anisopodidae					
Sylvicola cinctus (Fabricius, 1787)	3		s,d,w,f	phs	34,49
Sylvicola punctatus (Fabricius, 1787)		1	s, d	phs	34,49
Bibionidae					
Bibio ferruginatus (Linnaeus, 1767)	5		s?	phs	
Bibio johannis (Linnaeus, 1767)	42	34	s	phs	13,57
Bibio lanigerus Meigen, 1818	1	14	s?	phs	58
Bibio longipes Loew, 1864	9		s?	phs	
Bibio varipes Meigen, 1830	4	21	s	phs	57
Dilophus febrilis (Linnaeus, 1758)	62	8	s	phs	58
Dilophus femoratus Meigen, 1804	6		s	phs	58
Bolitophilidae					
Bolitophila hybrida (Meigen, 1804)		1	f,w	mamy	9,31,68,70
Ceratopogonidae					
Culicoides grisescens Edwards, 1939	5	1	s,mo	mi	42
Culicoides impunctatus Goetghebuer, 1920	4	3	s,mo	mi	42
Culicoides lupicaris Downes & Kettle, 1952		1	mu	mi	19
Forcipomyia costata (Zetterstedt, 1838)		8	w (pd)	mi	25,55
+ *Forcipomyia hygrophila* Kieffer, 1925	1	4	w (pd)	mi	25
Forcipomyia palustris (Meigen, 1804)		1	w (pd)	mi	25
Chironomidae					
Bryophaenocladius flexidens (Brundin, 1947)	2	342	sa/a	mi	51
Bryophaenocladius tuberculatus (Edwards, 1929)		1	sa,s	mi	
Chironomus plumosus (Linnaeus, 1758)	16	3	a	mi	52
Limnophyes minimus (Meigen, 1818)		1	sa,s	mi,ph?	10,14,15,50
Telmatogeton japonicus Tokunaga,1933	7		asb	ph,mi	7,10,11,33

	Nos				
	Yellow dune	Grey dune	Micro-habitat	Trofic-group	Reference
Culicidae					
Culiseta morsitans (Theobald, 1901)	2		a	mi	41
Culex pipiens Linnaeus, 1758	2		a	mi	41
Dixidae					
Dixella autumnalis (Meigen, 1838)	1		sa/a	mi	18
Keroplatidae					
Orfelia nemoralis (Meigen, 1818)		2	s,w,mo	z?	59
Pyratula perpusilla (Edwards, 1913)		1			
Pyratula zonata (Zetterstedt, 1855)	1				
Limoniidae					
Dicranomyia chorea (Meigen, 1818)	2		s,mu	phs	46
Dicranomyia modesta (Meigen, 1818)	4		s	phs	53
Limonia flavipes (Fabricius, 1787)	8	2	s,sa	phs	46,53
Molophilus obscurus (Meigen, 1818)		1	s,sa/a	phs	46
Molophilus ochraceus (Meigen, 1818)	1		s,sa	phs	46
Phylidorea fulvonervosa (Schummel, 1829)	1		s,sa,mu	z	46,53
Symplecta stictica (Meigen, 1818)	1		s,sa/a	phs	67
Mycetophilidae					
Boletina gripha Dziedzicki, 1885)	1	3	f,fw,w	mamy	31,70
Cordyla brevicornis (Staeger, 1840)	1	1	f,w	mamy	21,31,35,68,70
Cordyla fusca (Meigen, 1804)		1	f	mamy	9,21,35,70
Cordyla murina Winnertz, 1863		1	f	mamy	17,21,70
Exechia fusca (Meigen, 1804)	6	3	f,fw,w	mamy	1,21,32,70
+ *Exechia spinigera* Winnertz, 1863	2		f	mamy	9,21
+ *Exechiopsis hammi* (Edwards, 1925)		1		mamy	20
Mycetophila fungorum (De Geer, 1776)	25	6	f,fw,w	mamy	9,20,21,31,70
Mycetophila alea Laffoon, 1965	1		f	mamy	9,17,21
Mycetophila unipunctata Meigen, 1818	1		f?	mamy	
Mycetophila vittipes Zetterstedt, 1852		1	f	mamy	1,9,35
Phronia nigricornis (Zetterstedt, 1852)	1		w	mamy	70
+ *Sceptonia concolor* Winnertz, 1863		1		mamy	
Sciophila lutea Macquart, 1826	1		f,fw	mamy	1,9,30,69,70
Synplasta gracilis Winnertz, 1863	1			mamy	
Psychodidae					
Paramormia ustulata (Walker, 1856)	1		sa/a,mu,pd	mi	66
Philosepedon humeralis (Meigen, 1818)	29		m	zs	4,5,60,63,64
Psychoda albipennis Zetterstedt, 1850	2		sa/a,pd,dr	mi	31,61
Psychoda satchelli Quate, 1955	1		sa/a,dr	mi	61
Scatopsidae					
Coboldia fuscipes (Meigen, 1830)	1		s,fw,pd	phs	2,22,24,26,
+ *Colobostema infumatum* (Haliday, 1833)		1	pd,my?	phs	23
+ *Colobostema nigripenne* (Meigen, 1830)		3	pd,my	phs	23
+ *Colobostema obscuritarse* (Strobl, 1898)	2	6	pd,my	phs	23
Reichertella geniculata (Zetterstedt, 1850)	61	2	s,pd	phs	2,3,22,44
Scatopse notata (Linnaeus, 1758)	5		s,pd	phs	22
+ *Swammerdamella acuta* Cook, 1956	2		s,pd?	phs	8,22
Swammerdamella brevicornis (Meigen, 1830)	1		s,pd?,fw	phs	2,26,44,65
Thripomorpha bifida (Zilahi-Sebess, 1956)		1	s,pd?	phs	
Thripomorpha verralli (Edwards, 1934)	1		s,pd?	phs	2
Sciaridae					
+ *Bradysia angustoocularis* Mohrig & Krivosheina, 1989	1078	39	s	phs	26
+ *Bradysia flavipila* Tuomikoski, 1960	75	55	s	phs	54,56
Bradysia nitidicollis (Meigen, 1818)		1	s,f	phs	20,26,54
Bradysia nocturna Tuomikoski, 1960	3	2	s,w,b	phs	20,26,29,39,45

	Nos				
	Yellow dune	Grey dune	Micro-habitat	Trofic-group	Reference
+ *Bradysia normalis* Frey, 1948	64	1	s,pd	phs	38,56
+ *Bradysia* sp. a (not described)	53	191			
Bradysia tilicola (Loew, 1850)		7	s	phs	54,59
Bradysia trivittata (Staeger, 1840)	1	6	s,b	phs	26,38,54,56
Corynoptera forcipata (Winnertz, 1867)		1	s,w	phs	29,40,45
Corynoptera globiformis (Frey, 1945)	6	34	s,w	phs	26,45
+ *Corynoptera grothae* Mohrig & Menzel, 1990		1		phs	
Corynoptera inundata Fritz,1982		17	s,w	phs	37,38
Corynoptera irmgardis (Lengersdorf, 1930)		1	s	phs	26,45
Corynoptera perpusilla Winnertz,1867	16		s	phs	26,37,45,54
+ *Corynoptera postglobiformis* Mohrig, 1993		1	s	phs	37
+ *Corynoptera praeforcipata* Mohrig & Mamaev, 1987	19	34		phs	
+ *Corynoptera saetistyla* Mohrig & Krivosheina, 1985	1		s	phs	26
+ *Corynoptera setosa* Freeman, 1983		3		phs	
+ *Corynoptera sphenoptera* Tuomikoski, 1960	1	1		phs	
Corynoptera subparvula Tuomikoski, 1960	87	148	s,w,r	phs	36,40,54,56
+ *Corynoptera subtilis* (Lengersdorf, 1929)	1	19	s	phs	45,56
Corynoptera trepida (Winnertz, 1867)	2	7		phs	
+ *Corynoptera* sp a (not described)	23	5		phs	
+ *Corynoptera verrucifera* (Lengersdorf, 1952)		1	b	phs	20, 29
+ *Camptochaeta camptochaeta* (Tuomikoski, 1960)		2	s	phs	26
Cratyna nobilis (Winnertz, 1867)		2	s	phs	26
Cratyna uliginosa (Lengersdorf, 1929)	4	6	s	phs	26
Ctenosciara hyalipennis (Meigen, 1804)		22	s,w,b	phs	20,37,38,39,45
Epidapus atomarius (DeGeer, 1778)		1	s,b	phs	26,29,37,40,45
+ *Hyperlasion wasmanni* Schmitz, 1918		41	s,my	phs	26,27,54
Lycoriella castanescens (Lengersdorf, 1940)	2	2	s,b	phs	26,29,36,38,56
Lycoriella inconspicua Tuomikoski, 1960		1	s,w	phs	38
Peyerimhoffia vagabunda (Winnertz, 1867)	5	17	s,w,d	phs	26,38,40,45
+ *Phytosciara flavipes* Meigen, 1804)	1		s	phs	26
+ *Phytosciara ungulata* (Winnertz, 1867)		2		phs	
Scatopsciara atomaria (Zetterstedt, 1851)	1	1	s,w,b,fw	phs	26,37,38,45,56
+ *Scatopsciara tricuspidata* (Winnertz, 1867)		1		phs	
+ *Trichosia borealis* (Frey, 1942)		1		phs	
Tipulidae					
Nephrotoma flavescens (Linnaeus, 1758)	1	7	s,w	phs	28,46,47,62
Nephrotoma submaculosa Edwards, 1928	3	82	s,mo	phs	28,46,47,62
Nigrotipula nigra (Linnaeus, 1758)	16		s,w	phs	6,28,46,62
Tipula confusa van der Wulp, 1883		5	s,mo	phs	28,46,62
Tipula paludosa Meigen, 1830	51	6	s	phs, ph	6,28,46,62
Tipula scripta Meigen, 1830	1		s,mo,w	phs	1,6,30,46
Tipula varipennis Meigen, 1818	7		s	phs	6,28,46,62
Trichoceridae					
Trichocera hiemalis (De Geer, 1776)	42	13	s,w,f	phs	12,16,21,31,43
Trichocera major Edwards, 1921	17	7	s,w	phs	12,30,31,43,46
Trichocera regelationis (Linnaeus, 1758)	101	27	s,b	phs	9,12,20,46
Trichocera saltator (Harris, 1776)	60	42	s,w,d,b,f	phs	12,20,21,30,43
Total (112 species)	**2078**	**1344**			