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Vertical distribution of insect populations in the free air space of beech woodland

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Please note / *Bemærk:*

All figure texts are printed in the correct sequence, but due to an unfortunate oversight, the diagrams (figures) for Figs 1 and 2 have been interchanged.

Samtlige figurtekster er trykt i korrekt rækkefølge, men på grund af en beklagelig uagtsomhed er diagrammerne til Figs 1 og 2 blevet byttet om.

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Vertical distribution of insect populations in the free air space of beech woodland

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The vertical distribution of nocturnal aerial insect populations - especially Diptera Nematocera - in a high-boled beech stand was recorded by means of light traps placed at four levels from the forest floor to the top canopy. The insects were mainly trapped near the forest floor and to some extent in the beech canopy; the number recorded in the trunk space and above the top canopy was distinctly lower. In Tipulinae and Mycetophilidae, the vertical distribution declined with increasing height irrespective of season and weather; 80-85% of all specimens were recorded at ground level. In Limoniinae, Cecidomyiidae, Psychodidae and Sciaridae the vertical distribution pattern changed repeatedly during the season, being unimodal with a peak near the forest floor or bimodal with another one in the beech canopy. During autumn litter fall, changes in the wind profile of the site seem decisive of the vertical distribution of Trichoceridae. Presumably the distribution of insect populations in the free air space is mainly explained by the combined effect of site topography and orientation, forest stand architecture and wind conditions. Insect distribution patterns are discussed in relation to the wind profile of the beech stand and especially that of the open trunk space region.

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Introduction

Stratification of plant and animal communities is a basic structural element of forest ecosystems. In temperate woodland, distinct vertical distribution patterns of arthropod communities occur, and also in populations of insects recorded in the free air space of forests, stratification has been observed, for instance in Tipulidae, Culicidae and Ceratopogonidae (Service 1971a, 1971b, 1973). Based on data from light traps placed at various levels from the forest floor to the top canopy, Schmidt Nielsen (1976, 1977) studied the height of flight of Neuroptera and Lepidoptera in a Danish beech stand and demonstrated distinct distribution patterns. In these light traps a large number of other insects was trapped, and in this paper the distribution of aerial insect populations in the main strata of the beech forest ecosystem is analysed. The main stress is laid on Diptera Nematocera.

Site description

The investigations were done in the mixed, coastal forest of Hestehaven (176 ha) near Rønde, 25 km NNE of Århus, Denmark. The research site (3 ha) was a strip of pure beech (*Fagus silvatica* L.), width about 100 m, orientation NW-SE, situated in an area gently sloping from NW to SE; on the south the site was bounded by regeneration of *Abies grandis* Lindl., on the northwest, the north and the east by high-boled beech, 85-90 years old; glades occurred E and W-SW of the site. Three vegetation strata were present in the site, viz. 1) a high-boled beech overstory, age 90-100 years, density

191 trees per ha, average height about 30 m, average crown depth and width 14.3 m and 9.4 m, respectively, 2) a beech understory, density 174 trees per ha, average height about 9 m, and 3) a field layer composed of herbs and natural reproduction of ash (*Fraxinus excelsior* L.), maximum height about 0.5 m. The site was described by Nielsen (1977).

Methods

Four identical light traps consisting of two metal-cones, viz. a funnel and a roof, separated by a 3.5 cm wide gap were applied. The light sources were Philips HPL 125 W bulbs placed on a level with the narrow gaps, through which the light was emitted. The traps were automatically switched on simultaneously at dusk and off at dawn. The funnels were placed in buckets containing sponges moistened with 1.1.2.2.-tetrachlorethane as a killing agent; the trap was described by Schmidt Nielsen (1976, 1977). Trap No. 1 was placed on the ground, gap just above the herb-layer at 0.6 m, Nos. 2-4 were placed in a 30 m high steel tower at 10 m (upper stem layer), 21 m (mid canopy), and 30 m (just above top canopy), respectively. Apart from some breaks, the traps were run every night from mid May to late November, 1972; during summer the traps were tended daily, during spring and autumn at least once a week. In 1973 the traps were run temporarily. Since for instance at least one million Diptera Nematocera were trapped, the sorting programme had to be strongly reduced. In this study, data from 45 nights representing the whole period from mid May to late November were utilized.

In August, 1972, two suction traps (9 inches, Johnson-Taylor, Burkard Manufacturing Comp.) were run temporarily; one trap was placed at ground level, another about 30 m above the forest floor. The catch was divided into hourly samples.

In 1972 air temperature (9 m, 21 m and 40 m; May-December) and wind speed (3 m, 10 m, 22 m and 40 m; from September onwards) were recorded in the beech stand by means of a datalogger (I. Aanderaa, Bergen). Further, in 1974 wind speed and air temperature were measured at several levels in Hestehaven (Rasmussen et al. 1982).

Results

Fauna recorded

About 250,000 insects caught in light traps in the Hestehave beech stand were treated (Table 1); Diptera (47%), Hemiptera (33%) and Lepidoptera (16%) contributed about 96% of the insects recorded.

Among Diptera the suborder Nematocera (N = about 115,000; Table 2) was the predominant taxon (97%). On an annual basis Ceratopogonidae >38%, Trichoceridae >18%, Sciaridae >13% and Cecidomyiidae (c. 8%) contributed about 77% of all Nematocera (cf. Table 2). However, due to the phenology of the taxa, their contribution to the fauna of Nematocera recorded changed seasonally. For instance, Trichoceridae were only recorded in September-November, and during this period the relative abundance of the winter gnats increased from about 12% to 97% of all Nematocera.

The species composition and phenology of Ceratopogonidae are presented elsewhere (S. Achim Nielsen, in prep.). Among the Trichoceridae *Trichocera saltator* Harris (N = about 16,000) was predominant winter gnat, and further *T. regelationis* (L.), *T. hiemalis* (D.G.) and *T. parva* Mg. occurred. All Psychodidae (N = about 8,500) belonged to the genus *Psychoda* Latr.; *Ps. severini parthenogenetica* Tonn., *Ps. phalaenoides* Tonn., *Ps. trinodulosa* Tonn. and *Ps. albipennis* Zett. were abundant, but generally the psychodids were badly preserved which constituted a serious obstacle to specific identification. Sciaridae, Cecidomyiidae and other Nematocera were only dealt with at family or subfamily level.

Among Hemiptera *Fagocyba cruenta* (H.-S.) (Auchenorrhyncha) made up 95%; about

	1	2	3	4	Total	
Hemiptera	57,326	9,607	15,412	1,251	83,596	(32.9)
	(68.6)	(11.5)	(18.4)	(1.5)	(100.0)	
Neuroptera	158	131	1,196	86	1,571	(0.6)
	(10.1)	(8.3)	(76.1)	(5.5)	(100.0)	
Trichoptera	756	90	354	129	1,329	(0.5)
	(56.9)	(6.8)	(26.6)	(9.7)	(100.0)	
Lepidoptera	27,280	3,491	9,117	1,492	41,380	(16.3)
	(65,9)	(8.4)	(22.0)	(3.6)	(99.9)	
Coleoptera	3,254	487	492	802	5,035	(2.0)
	(64.6)	(9.7)	(9.8)	(15.9)	(100.0)	
Hymenoptera	2,082	248	529	172	3,031	(1.2)
	(68.7)	(8.2)	(17.5)	(5.7)	(100.1)	
Diptera	63,989	15,075	34,091	5,307	118,462	(46.6)
	(54.0)	(12.7)	(28.8)	(4.5)	(100.0)	
Total	154,845	29,129	61,191	9,239	254,404	(100.1)
	(60.9)	(11,4)	(24.1)	(3.6)	(100.0)	

Table 1. Insects trapped in four light traps in a beech stand. 1: just above the herb layer (at 0.6 m); 2: in upper stem layer (at 10 m); 3: in mid canopy (at 21 m); 4: just above top canopy (at 30 m). Percentages in brackets.

Tabel 1. Insekter indsamlet i fire lysfælder i en bøgebevoksning. 1: lige over urtevegetationen (højde 0,6 m); 2: øvre del af stammerummet (højde 10 m); 3: midt i kronelaget (højde 21 m); 4: lige over trætoppene (højde 30 m). Procenter i parentes.

75% of all *F. cruenta* were trapped in October. The species composition and phenology of Lepidoptera of the site were treated by Schmidt Nielsen (1976).

Diurnal periodicity of flight of Diptera

Light trap catches reflect actual flight activity of night-flying and crepuscular insects as well as activity of day-flyers activated by the artificial light. In suction trap catches in Hestehaven, 1972, Sciaridae (N = about 1,100), Ceratopogonidae (N = about 1,000), Cecidomyiidae (N = about 2,000) and Mycetophilidae (N = about 175) were obtained at all hours, but about 50% of the Sciaridae and 70-80% of the latter three taxa were caught between 1700 and 0600 hours. Limoniinae (N = about 200), Tipulinae (N = about 100), and Psychodidae (*Psychoda* sp.) (N = about 1,200) were generally active between 1800 and 0600 hours, mainly being crepuscular or night-flyers. Based on the suction trap catches from Hestehaven and records of diurnal flight periodicity of insects presented by Lewis and Taylor (1965) and Service (1971a), at least Tipulidae, Mycetophilidae, Ceratopogonidae, Cecidomyiidae, Psychodidae (*Psychoda* sp.) and Culicidae were considered primarily night-flyers or crepuscular. Apparently, some taxa, e.g. Sciaridae, were at least to some extent night-flyers. Light trap catches of pronounced day-flyers were neglected.

	1	2	3	4	Total	
Trichoceridae	11,653	2,168	6,835	301	20,957	(18.2)
	(55.6)	(10.3)	(32.6)	(1.4)	(99.9)	
Tipulidae						
Tipulinae	418	30	44	29	521	(0.5)
	(80.2)	(5.8)	(8.4)	(5.6)	(100.0)	
Limoniinae	4,226	690	1,645	238	6,799	(5.9)
	(62.2)	(10.1)	(24.2)	(3.5)	(100.0)	
Psychodidae	6,295	396	1,756	126	8,573	(7.5)
	(73.4)	(4.6)	(20.5)	(1.5)	(100.0)	
Culicidae	3,278	352	693	100	4,423	(3.9)
	(74.1)	(8.0)	(15.7)	(2.3)	(100.1)	
Ceratopogonidae	16,290	7,965	17,165	2,516	43,936	(38.3)
	(37.1)	(18.1)	(39.1)	(5.7)	(100.0)	
Chironomidae	1,067	334	677	505	2,583	(2.2)
	(41.3)	(12.9)	(26.2)	(19.6)	(100.0)	
Simuliidae	1	–	1	–	2	(–)
	(–)	(–)	(–)	(–)	(–)	
Anisopodidae	28	81	258	110	477	(0.4)
	(5.9)	(17.0)	(54.1)	(23.1)	(100.1)	
Bibionidae	128	23	–	32	183	(0.2)
	(–)	(–)	(–)	(–)	(–)	
Mycetophilidae	1,928	192	138	32	2,290	(2.0)
	(84.2)	(8.4)	(6.0)	(1.4)	(100.0)	
Sciaridae	9,971	1,540	2,610	976	15,097	(13.1)
	(66.1)	(10.2)	(17.3)	(6.5)	(100.1)	
Cecidomyiidae	7,225	435	1,307	56	9,023	(7.9)
	(80.1)	(4.8)	(14.5)	(0.6)	(100.0)	
Total	62,508	14,206	33,129	5,021	114,864	(100.1)
	(54.4)	(12.4)	(28.8)	(4.4)	(100.0)	

Table 2. Diptera Nematocera trapped in four light traps in a beech stand. 1: just above the herb layer (at 0.6 m); 2: in upper stem layer (at 10 m); 3: in mid canopy (at 21 m); 4: just above top canopy (at 30 m). Percentages in brackets.

Tabel 2. Diptera Nematocera indsamlet i fire lysfælder i en bøgebevoksning. 1: lige over urtevegetationen (højde 0,6 m); 2: øvre del af stammerummet (højde 10 m); 3: midt i kronelaget (højde 21 m); 4: lige over trætoppene (højde 30 m). Procenter i parentes.

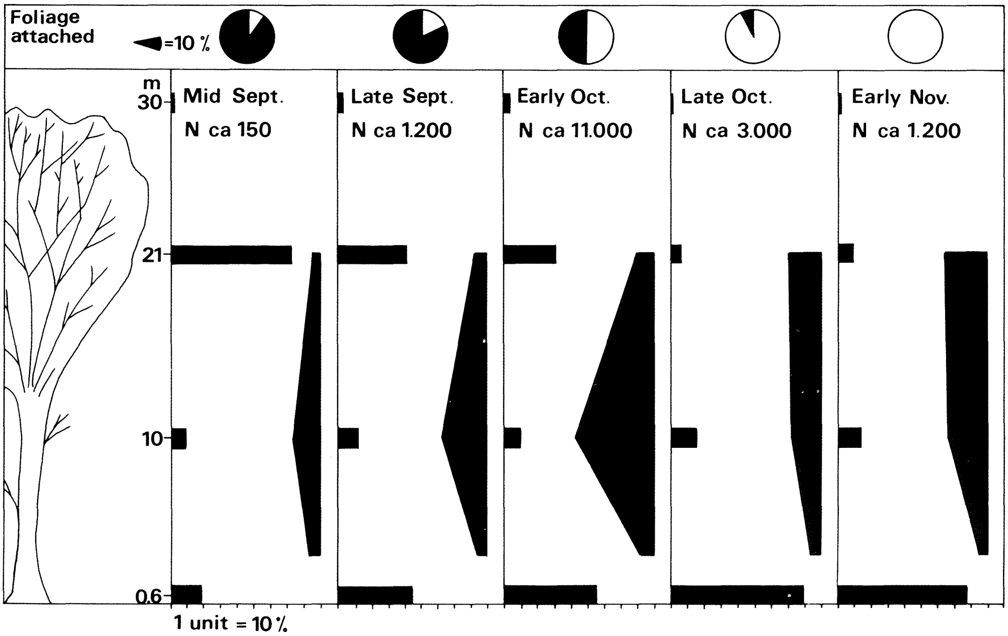

Fig. 1. Relative abundance of Diptera Nematocera in four strata of a beech stand recorded by means of light traps, 1972 (May-October): Tipulinae, N = 521; Mycetophilidae, N = 2,302; Limoniinae, N = 6,799; Psychodidae, N = 8,575.

Fig. 1. Den relative hyppighed af Diptera Nematocera registreret ved hjælp af lysfælder i fire højder i en bøgebevoksning 1972 (maj-oktober): Tipulinae, N = 521; Mycetophilidae, N = 2.302; Limoniinae, N = 6.799; Psychodidae, N = 8.575.

Vertical distribution patterns of insects

About 61% of all insects were trapped just above the herb layer and c. 24% in the mid canopy (Table 1). This trend is repeated in the catch of Hemiptera, Trichoptera, Lepidoptera, Hymenoptera and Diptera (Table 1); the vertical distribution pattern of Lepidoptera in the beech stand was treated by Schmidt Nielsen (1976). About 75% of all Neuroptera were trapped in the mid canopy and only 6-10% in each of the other three layers (Table 1); for details, see Schmidt Nielsen (1977). Finally, nearly 65% of Coleoptera were recorded near the forest floor, but only about 10% in the mid canopy (Table 1). In most beetles, e.g. the Scarabaeidae *Aphodius rufipes* (L.), *Serica brunnea* (L.) and *Melolontha melolontha* L., the relative abundance declined with increasing height.

In Tipulinae and Mycetophilidae 80-85% of all specimens were trapped in the lower light trap, viz. just above the herb layer, and only 6-8% in the trunk space and the mid canopy (Table 2); irrespective of date and weather the majority of these insects was always trapped near the forest floor, the relative abundance declining with increasing height (unimodal distribution, Fig. 1). In Ceratopogonidae, however, the annual catches near the forest floor and in the beech canopy were nearly equal; thus, the vertical distribution pattern was bimodal (Table 2). Details on the distribution of Ceratopogonidae in the beech stand are presented elsewhere (S. Achim Nielsen, in prep.). Anisopodidae were mainly trapped in the canopy (Table 2).

Limoniinae, Psychodidae, Sciaridae and Cecidomyiidae were mainly trapped near the forest floor (62-80%); 5-10% and 15-24% were recorded in the trunk space and the mid canopy, respectively (Table 2). On an annual basis the vertical distribution pattern of these gnats was apparently slightly bimodal; however, during the summer the distribution changed repeatedly. In Limoniinae the relative abundance declined with increasing height in May-July, whereas a bimodal distribution pattern was observed in August, September and October (Fig. 1). However, this bimodal distribution is due to a strong peak in the mid canopy in only 7 nights; when these nights were neglected, the relative abundance of Limoniinae in the latter three months also declined with increasing height and annually more than 70% of all Limoniinae were trapped just above the herb layer. In Psychodidae (Fig. 1), Sciaridae and Cecidomyiidae the vertical distribution was still more variable, frequently changing from unimodal to bimodal distribution - even from one night to the next. This means that in some nights the majority of the gnats was trapped near the forest floor, whereas in other nights the catches in the latter layer and in the canopy were nearly equal.

Seasonal changes in vertical distribution

Schmidt Nielsen (1976) suggested that during the period of autumn leaf fall the relative abundance of Lepidoptera in the canopy layer of the beech stand declined, but since very few specimens were collected during late autumn, this assumption could not be substantiated. During the autumn a large number of Trichoceridae were recorded in the beech stand; Fig. 2 presents changes in vertical distribution of the predominant species *T. saltator* (N = about 16,000) from mid September to late November, wind profiles based on wind speed records in the stand, and phenology of autumn beech litter fall (cf. Nielsen 1977). In mid September a distinct peak of *T. saltator* occurred in the canopy, in late September to mid October the distribution was bimodal, but in late October, when nearly all beech leaves were shed and the relative wind speed in the canopy increased, the relative abundance of the trichocerids declined with increasing height. In October the same distribution pattern was observed in the mosquito *Culex pipiens pipiens* (L.) (♂♂).

From mid April to early May, 1973, viz. before beech leafing, all Trichoceridae and >95% of all Nematocera were trapped just above the forest floor. In late May only about 50% of Nematocera were recorded in this stratum, and the relative abundance of the taxon in the beech canopy increased correspondingly. From mid May to late May a comparable change in vertical distribution pattern was observed in Lepidoptera of the site (Schmidt Nielsen 1976).

Discussion and conclusion

In studies on the height of flight of individual insect species, light traps often give misleading results (cf. Southwood 1966, Johnson 1969, Service 1976). In the present study no detailed analysis of the »preferred« height of flight of insect species was made. Instead the light traps were used for a simultaneous trapping of insects present in the main strata of the beech stand and for the record of changes in relative abundance of the same taxa in the same site. For these purposes light traps may be rather useful (cf. Service, op. cit.) and presumably the abundance of nocturnal and crepuscular insects in the four strata considered is reasonably outlined. In some insect taxa the distribu-

*Fig. 2. Årstidsmæssige ændringer i vertikalfordeling (vandrette, sorte bjælker) af vintermyggen*Trichocera saltator *Harris (N = ca. 16.000) registreret ved hjælp af lysfælder i fire højder i en bøgebevoksning fra midten af september til først i november 1972. De lodrette, sorte figurer angiver vindprofilen i bevoksningen, nemlig den gennemsnitlige vindhastighed midt i kronelaget samt i stammerummet udtrykt i procent af vindhastigheden over trækronerne i 40 mś højde. Bladmængden, der på et givet tidspunkt er tilbage i trækronerne (»foliage attached«), er angivet.*

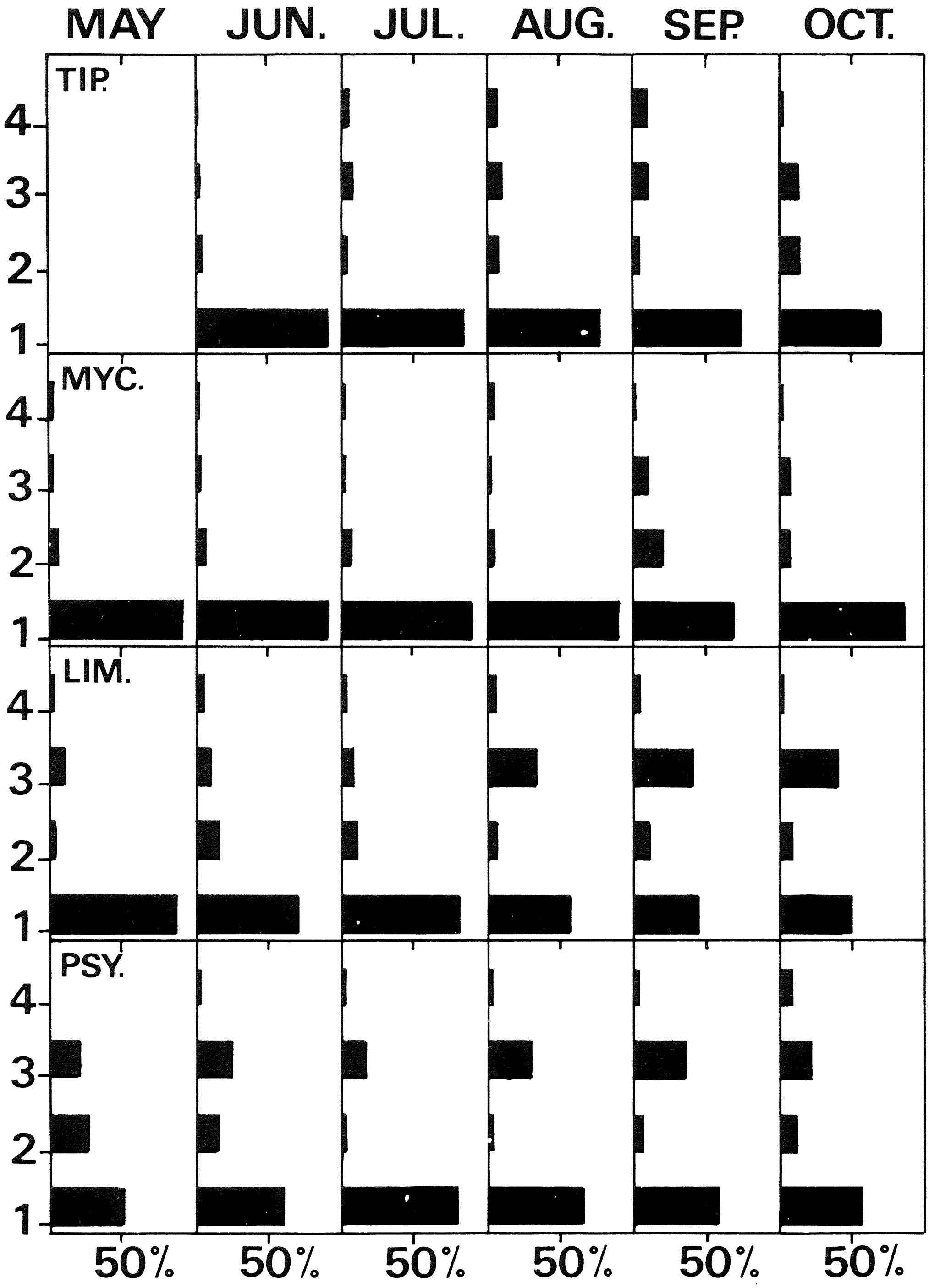

Fig. 2. Seasonal changes in vertical distribution pattern (horizontal bars) of *Trichocera saltator* Harris (N = about 16,000) recorded by means of light traps in a beech stand from mid September to early November, 1972. Vertical black figures indicate the wind profile of the site, viz. average wind speed in mid canopy and trunk space in percentages of wind speed above top canopy (40 m). The amount of attached foliage in the canopy is presented.

tion pattern demonstrated by means of light traps was substantiated by data from sticky traps (Nielsen & Nielsen, 1986).

In the free air space of the beech stand the nocturnal and crepuscular insects were mainly trapped near the forest floor and to some extent in the beech canopy, whereas the number of insects recorded in the trunk space and above the top canopy was distinctly lower (Table 1 & 2). Presumably these results reflect that the aerial activity of these insects is actually concentrated in the former two layers.

During the night >60% of the insects were trapped just above the forest floor. The bulk of Diptera Nematocera was also recorded in this layer; this may reflect the close association of these generally weak-flying insects with the forest floor, representing the main larval habitat. The majority of the Diptera Nematocera recorded in the free air space hatches from the soil and litter layer. In 1968-1972 the annual hatching of soil Diptera in the site was 750-2500 individuals per m^2 (Nielsen, in prep.). A conspicuous vertical exchange between the populations of soil Diptera emerging from the forest floor and the populations of weak-flying, nocturnal and crepuscular insects circulating in the free air space of the beech stand occurs. In Lepidoptera and Neuroptera larval feeding biology seemed to affect the vertical distribution of the adults (Schmidt Nielsen 1976, 1977).

Tipulinae and Mycetophilidae were mainly recorded just above the herb layer; the distribution pattern of Tipulinae in Hestehaven corresponded with that recorded in a mixed deciduous forest in England (Service 1973). During the leaf-bearing period of the beech the vertical distribution pattern of Ceratopogonidae, Limoniinae, Cecidomyiidae, Sciaridae and Psychodidae changed repeatedly. Presumably species of the latter four taxa are primarily active near the forest floor; however, they are often abundant in the mid canopy, too. This variation is explained by the interaction of several biotic and abiotic factors affecting the aerial activities of the gnats. No doubt differences in general biology, phenology, swarming, etc. of individual species should be considered. Apart from female ceratopogonids the influence of adult feeding activity (cf. Altmüller 1979) on the vertical distribution of the above-mentioned gnats seems negligible. However, swarming activity has been observed in most of the families (cf. McAlpine & Munroe 1968) and no doubt the actual vertical distribution pattern recorded depends chiefly on flight ability, swarming behaviour and the effect of abiotic factors on take-off and appetitive flight of Nematocera. For instance, several authors have drawn the attention to the restraining effect of wind on insect swarming and dispersal by flight.

No effect of air temperature on the vertical distribution could be demonstrated. In the summer of 1972, wind speed and direction in the beech stand were not measured; however, unquestionably the combined effect of site topography and orientation, forest stand architecture and wind conditions on insect flight activity is a key factor in the vertical distribution pattern of Nematocera recorded in the free air space. In several forest stands the wind profile occasionally shows a variable bulge within the trunk space region (Kiese 1971, Oliver 1975). In summer the wind speed of the lower trunk space (3 m) in Hestehaven can be about 70% greater than in the canopy, presumably due to a blow-through phenomenon (Rasmussen et al. 1982). The conspicuous vertical difference in wind speed observed in the site is due to the very open stem layer and the short distance to open land; the wind profile varies according to wind direction (Rasmussen et al., op. cit.). Under these circumstances two boundary layers (cf. Taylor 1958) may appear in the beech stand, viz. one near the forest floor and another in the beech canopy, separated by the stem layer in which a higher wind speed prevails. During night a relatively low insect activity was recorded in the stem layer of the site (see also Schmidt Nielsen 1976, 1977). Generally the beech forest Nematocera are poor flyers and no doubt the flight of these insects is hampered by the higher wind speed in the open trunk space. Consequently, the flight activity is primarily confined to the boundary layer just above the herb layer or to the latter stratum and the beech canopy.

Presumably, the continual variation in vertical distribution observed in some insect taxa is also mainly explained by changes in the state of wind in the trunk space.

During the period of autumn litter fall and beech leafing in spring, distinct seasonal changes in the vertical distribution of aerial insect populations occurred. In Trichoceridae the change recorded during autumn seemed correlated with the amount of attached beech leaves in the canopy and displacements in the wind profile of the site. The swarming of trichocerids is hampered by wind (Dahl 1965). In August the wind speed in the beech canopy (height 22 m) corresponded to about 30% of that recorded in the lower trunk space (height 3 m), while in the upper trunk space it was 75-80%; after leaf fall the wind profile was reversed and the wind speed in the canopy was either equal to or greater than that of the stem layer (Rasmussen et al. 1982). During the winter the wind speed in a German beech forest also decreased with depth of penetration (Kiese 1971). Presumably the autumnal change in vertical distribution observed in *Culex p. pipiens* (♂♂) is also explained by the interaction of leaf fall and wind speed. The change in vertical distribution of Diptera Nematocera and Lepidoptera in May may reflect the effect of beech leafing on the wind profile of the forest.

Sammendrag

Vertikalfordeling af flyvende insekter i en bøgeskov

Den vertikale fordeling af flyvende, nataktive insekter i en højstammet bøgeskov blev undersøgt ved hjælp af fire lysfælder placeret på skovbunden, i det åbne stammerum (10 m), i bøgekronerne (21 m), samt over trætoppene (30 m). Undersøgelsen baseredes på ca. 250.000 insekter, hvoraf Diptera udgjorde >45%. Hos nogle insekter var det vertikale fordelingsmønster altid det samme uanset årstid og vejrforhold. Hos svampemyg (Mycetophilidae), stankelben (Tipulinae), samt visse biller, f. eks. gødningsbillen *Aphodius rufipes*, natoldenborren *Serica brunnea* og den almindelige oldenborre *Melolontha melolontha*, aftog den relative hyppighed med højden; i disse tilfælde indsamledes 75-90% af individerne nær skovbunden. Derimod blev vinduesmyg (Anisopodidae) især fanget i kronelaget. Om efteråret ændrede bøgeskovens vindprofil og det vertikale fordelingsmønster af vintermyg (Trichoceridae) sig i takt med efterårsløvfaldet. Hos småstankelben (Limoniinae), galmyg (Cecidomyiidae), sommerfuglemyg (Psychodidae) og sørgemyg (Sciaridae) ændrede det vertikale fordelingsmønster sig gentagne gange sæsonen igennem, idet disse insekter visse døgn havde et maksimum nær skovbunden, andre døgn yderligere et maksimum i bøgekronerne. Generelt registreredes de fleste af de undersøgte nat- og tusmørkeaktive insekter nær skovbunden, men også luftrummet mellem bøgekronerne syntes at spille en betydelig rolle som aktivitetsområde. Derimod var fangsten i det åbne stammerum væsentlig lavere og over trætoppene særdeles lav. Den kombinerede virkning af vindhastighed og -retning, lokalitetens topografi og orientering, samt vegetationens højde og struktur på de undersøgte insekters aktivitet og fordelingsmønster i bøgebevoksningen fremhæves.

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