Hymenoptera flying over a boreal forest landscape

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Hymenoptera were collected in suction traps mounted on a TV-tower in an area of mixed coniferous woodland in western Sweden. Over 32 000 individuals were collected in four traps mounted at 2, 9, 43 and 93 m above ground during the summer of 1980. Over 95% of the individuals belonged to Parasitica and only 4.2 and 0.2 % to Aculeata and Symphyta respectively. The height distribution of flying Hymenoptera as a whole is intermediate compared with other insect groups such as aphids, with high densities at high altitudes, and Lepidoptera which tend to fly closer to the ground. However, our study showed large differences between major groups of Hymenoptera. All Symphyta were confined to the lowest traps as were most Aculeata signifying a low tendency to high altitude migratory flight. The ants were an exception among the Aculeata with high numbers in the upper traps, indicative of long downwind flights high in the air. A large percentage (over 40%) of the flying population of Parasitica were found above the forest canopy indicating that many Parasitica regularly engage in long-distance flights high in the air.

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The Hymenoptera is a large insect order with many ecologically important species (Gauld & Bolton 1988). With regard to the number of species and individuals the order is dominated by the Parasitica, the vast majority of which are parasitoids on other insects. Surprisingly few studies have been concerned with the dispersal habits of Hymenoptera and especially so of the Parasitica. For example, are the flights of Hymenoptera mainly confined to the vegetation layers – the flight boundary layer – or do they regularly engage in wind-dispersed flights high above the forest canopy? Many species are small day fliers which make them likely candidates for high altitude flights.

Johnson (1969), in summarizing earlier studies of insect flight and migration, concluded that little was known about migration in the Hymenoptera. Various flight trapping studies, notably by Glick (1939), showed that ”many species of parasitic Hymenoptera are found high in the air, some with well-defined vertical gradients of density that suggest large-scale aerial mixing”. It was also found that Hymenoptera was among the 3-4 largest insect groups at high altitudes (together with Diptera, Coleoptera and Homoptera). Other observations of Hymenoptera flights, for example on various Aculeata, were indicative of movements mainly within the flight boundary layer.

Dispersal studies of Hymenoptera since Johnson´s book are few (e.g. Chapman *et al*. 2004) and mainly confined to specific groups of larger insects such as the Aculeata. For example, ants often have fairly steep density – height profiles suggestive of long-distance down-wind transport (Duelli *et al*. 1989). Various radar techniques have been employed to study insect move-

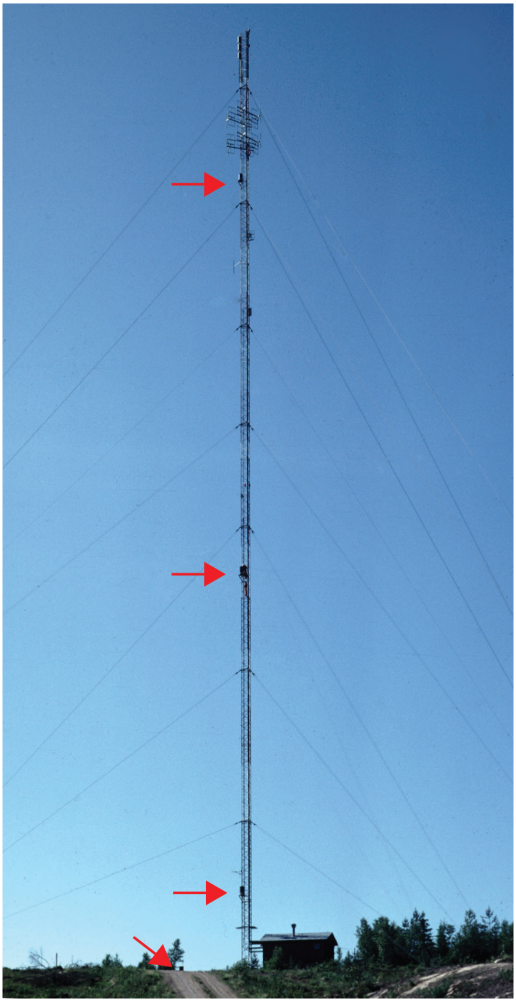

Figure 1. The TV-tower at Ennarbolshammaren. The location of the four suction traps at 2, 9, 43 and 93 m above ground are indicated by the red arrows.

TV-tornet på Ennarbolshammaren vid Klarälvsdalen i mellersta Värmland. De röda pilarna visar placeringen av de fyra sugfällorna på 2, 9, 43 respektive 93 meters höjd ovan marken.

ments (Chapman *et al*. 2011), but with regard to the Hymenoptera they have mainly been used to study low altitude foraging flights in bees and bumblebees (Chapman *et al*. 2011). Most Hymenoptera are too small to be detected with conventional entomological radars (Chapman *et al*. 2011), and it is only recently that radars have become available that can track small insects (Wood *et al*. 2009). Nevertheless, identification of small insects is not feasible with radars. They have to be collected to be identified (unless the aeroplankton is totally dominated by one species or group). Accordingly, knowledge of Hymenoptera flight altitudes mostly stem from trap collections. In a recent aerial net trapping study in England it was found that Hymenoptera was the third most abundant order at 200 m above ground. It was dominated by small-sized members of the superfamilies Ichneumonoidea and Chalcidoidea (Chapman *et al*. 2004).

Little is known about Hymenoptera flight habits in the northern boreal forest region, as to what are the dominating groups of Hymenoptera in the air and how they are distributed altitudinally and seasonally. Here we describe the vertical distribution of major Hymenoptera groups from suction trap catches on a TV tower in a boreal forest area of western Sweden. Although this material was collected more than three decades ago it is still a fairly unique sample from this region. Our study demonstrates that the airborne wasp fauna is totally dominated by the parasitic wasps, many of which undoubtedly travel far with the wind high above the forest canopy.

Material and Methods

The insects were collected during the summer of 1980 in the province of Värmland in western Sweden (60º 18´ N, 13º22´E). Four suction traps were mounted on a TV tower on a low flat-topped hill, Ennarbolshammaren, next to the Klarälven river valley (Fig. 1, cf Svensson & Solbreck 2008). The tower is situated in a large forested area dominated by Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). The immediate area around the tower had been clear-cut a few years before the present study.

The suction traps were of the enclosed cone type (Johnson & Taylor 1955, Taylor 1955). They had a 50 cm diameter axial fan providing an airflow of 6000 m^3 per hour. The metal mesh of the cone net had 0.4 x 0.4 mm openings. The traps were mounted with their openings 2, 9, 43 and 93 m above ground (Fig. 1). The traps were operated from 14th of May to 15th of September,

Table 1. Numbers and height distribution of Hymenoptera taxa in the suction traps.
Antal och höjdfördelning av olika Hymenoptera taxa i sugfällorna.

Group/Grupp	Number at different heights/ Antal på olika höjder 2 m	9 m	43 m	93 m	Total	Percent of all Hymen. Procent av alla steklar	Percent high*) Procent på hög höjd *)	b **)	R^2	Median flight date***) Median för flygdatum***)
Andrenidae	38	2	0	0	40	0.12	0.00			30 Jul
Apidae	11	2	0	0	13	0.04	0.00			05 Aug
Megachilidae	28	0	0	0	28	0.09	0.00			12 Jun
Sphecidae	94	6	0	0	100	0.31	0.00			12 Jun
Bethylidae	13	0	0	0	13	0.04	0.00			05 Aug
Chrysididae	7	0	0	0	7	0,02	0.00			12 Jun
Dryinidae	8	0	0	0	8	0.02	0.00			09 Jul
Formicidae	733	312	20	8	1073	3.31	2.61	-1.239	95.8	05 Aug
Sapygidae	9	1	0	0	10	0.03	0.00			23 May
Tiphiidae	27	0	0	0	27	0.08	0.00			23 Jun
Vespidae	32	2	0	0	34	0.10	0.00			14 Jul
Aculeata	**1000**	**325**	**20**	**8**	**1353**	**4.17**	**2.07**	**-1.352**	**97.7**	
Ceraphronidae	2008	200	38	20	2266	6.98	2.56	-1.198	98.6	24 Jul
Megaspilidae	184	18	2	4	208	0.64	2.88	-1.102	82.2	24 Jul
Chalcidoidea	12401	2867	486	202	15956	49.17	4.31	-1.077	99.6	24 Jul
Cynipoidea	1196	54	19	2	1271	3.92	1.65	-1.518	95.0	5 Aug
Evaniidae	1	0	0	0	1	0.00	0.00			14 Jul
Gasteruptiidae	9	0	0	0	9	0.03	0.00			12 Jun
Braconidae	2160	288	89	32	2569	7.92	4.71	-1.055	98.6	24 Jul
Ichneumonidae	1275	171	44	28	1518	4.68	4.74	-0.994	97.8	14 Jul
Platygastridae	3156	345	59	18	3578	11.03	2.15	-1.316	99.7	12 Jun
Scelionidae	2232	218	46	21	2517	7.76	2.66	-1.198	98.7	24 Jul
Diapriidae	759	127	40	12	938	2.89	5.54	-1.028	98.6	24 Jul
Proctotrupidae	186	7	2	2	197	0.61	2.03	-1.178	88.1	05 Aug
Parasitica	**25567**	**4295**	**825**	**341**	**31028**	**95.62**	**3.76**	**-1.115**	**99.9**	
Siricidae	62	1	0	0	63	0.19	0.00			23 May
Argidae	1	0	0	0	1	0.00	0.00			14 Jul
Tenthredinidae	4	1	0	0	5	0.02	0.00			05 Aug
Symphyta	**67**	**2**	**0**	**0**	**69**	**0.21**	**0.00**	**-2.334**		
Total	**26634**	**4622**	**845**	**349**	**32450**	**100.00**	**3.68**	**-1.124**	**100.0**	

*) Percentage of insects in the group collected at 43 + 93 m./ Procent av insekterna som fångades på 43 + 93 m höjd.
**) Slope of linear regression of log no vs log height./ Lutning för regressionslinjen av log antal mot log höjd.
***) Expressed as collecting date./ Uttryckt som insamlingsdatum.

and the collecting bottles were emptied every 10-12 days.

All insects were stored in 70-80% ethanol. The Hymenoptera material was sorted to super-family/family level during 2012 by E.W. (Table 1). The material was also sorted according to the dates of trap emptying and the four different height categories. The classification of Douwes *et al*. (1997) was used. The material is deposited at The Swedish Museum of Natural History.

Before analysis both insect abundances and heights were log-transformed. There are two reasons for this. First a linear log density - log height distribution has often been found for the vertical distribution of insects in the air (Johnson 1957). Second, temporal insect data tend to have a log-normal distribution.

A linear model was constructed with abundance as response variable and height, date and date x altitude interaction as explanatory variables. We first analysed whether there were any differences in height distribution between the different sampling periods. Since there was no significant interaction between the date and

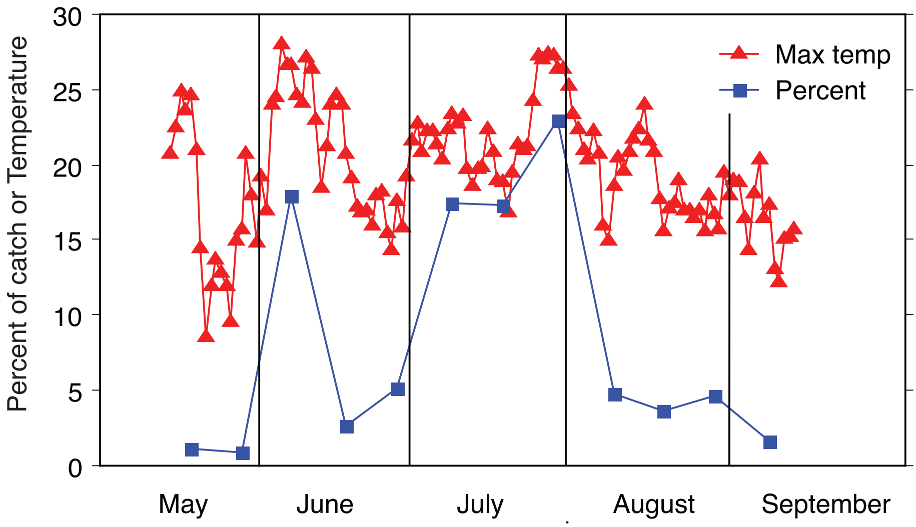

Figure 2. The seasonal distribution of all Hymenoptera caught in the suction traps during the summer of 1980 and the daily maximum air temperature.

Den säsongsmässiga fördel-ningen av alla steklar fångade i sugfällorna samt den dagliga maxtemperaturen.

height distribution for either the total material ($F_{11,24}$ = 1.780, NS) or for the separate families/superfamilies (Appendix 1) we pooled the data for all periods in the analysis of height distribution.

Results

Over 32 000 Hymenoptera individuals were collected in the four suction traps during the summer of 1980, the vast majority (95.62 %) consisting of Parasitica (Table 1). Aculeata comprised 4.17 % and Symphyta only 0.21%. The five largest families/superfamilies were Chalcidoidea (49.17 % of all Hymenoptera), Platygastridae (11.03%), Braconidae (7.92%), Scelionidae (7.76%) and Ceraphronidae (6.98%). Among the Aculeata ants (Formicidae) dominated the catch (Table 1).

Hymenoptera were caught during all collecting periods, but with considerably lower numbers during the months May and September. A dip was also noted during late June, coinciding with a period of cool weather (Fig. 2). There were considerable differences between different groups of wasps (Table 1, Fig. 3). For example, Platygastridae and several Aculeata groups were early fliers, whereas Cynipoidea, Proctotrupidae and Formicidae had late flight peaks.

The Parasitica were so dominating that the height distribution of all Hymenoptera was identical with that of the Parasitica (Fig. 4). Aculeata, with the exception of Formicidae, flew proportionally lower than the Parasitica, whereas Symphyta seemed to be most confined to low altitudes (Fig. 4, Table 1). As a comparison the height profile of all Hymenoptera collected from airplanes by Glick (1939) in southern USA are shown.

The height profiles of most Parasitica groups are fairly similar (Fig. 5, Table 1). However, the Cynipoidea seem to fly closer to the ground than most other groups.

Compared with other orders/groups the Hymenoptera seem to have intermediately steep height-density profiles. In Fig. 6, comparisons are made between four groups for the trapping period 2-12[th] of June. The Hymenoptera profile is very similar to that of beetles but considerably shallower than that of the extreme high altitude migrants such as aphids. The profile of Hymenoptera is, however, considerably steeper than that of the Lepidoptera, a group dominated by low altitude flights.

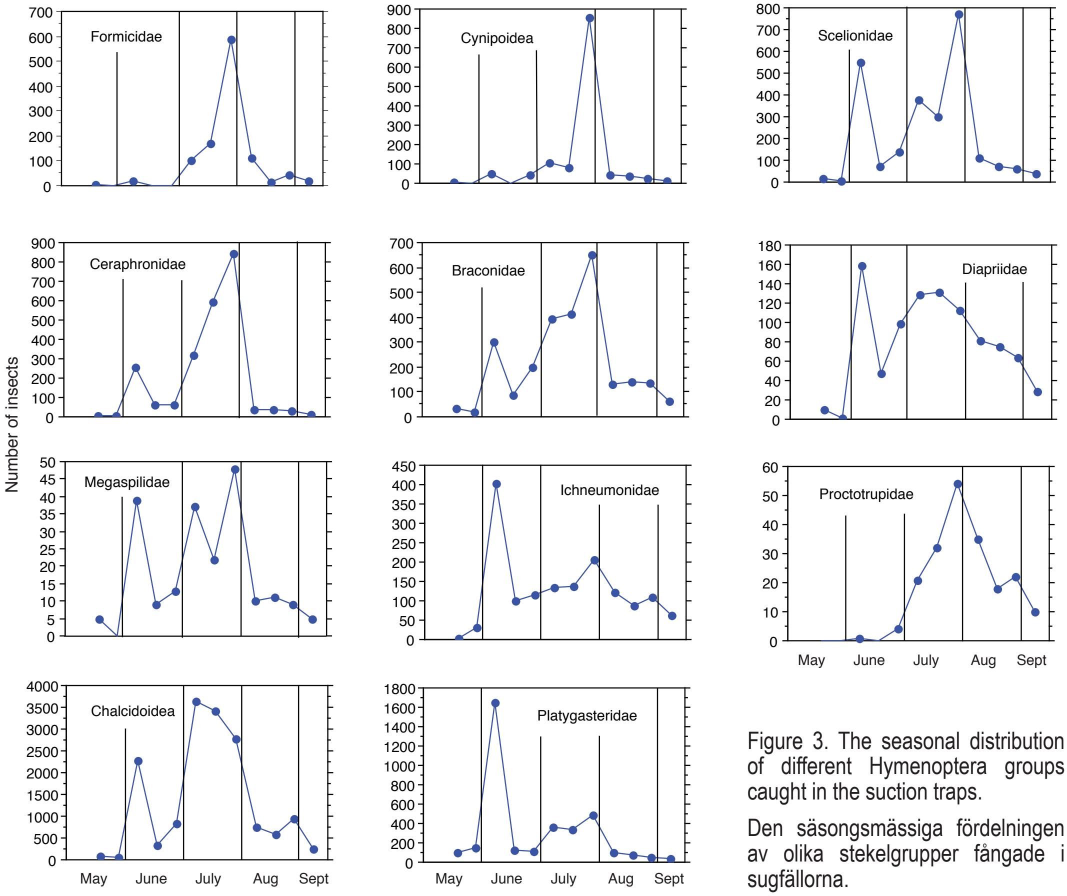

Figure 3. The seasonal distribution of different Hymenoptera groups caught in the suction traps.

Den säsongsmässiga fördelningen av olika stekelgrupper fångade i sugfällorna.

Discussion

Abundance of different Hymenoptera groups

Suction trap catches, compared with most other sampling methods, provide fairly unbiased samples of different insect groups (Johnson 1957). There is a moderately lowered efficiency for larger sized insects (Taylor 1962), and it is also likely that the abundance of the very smallest species has been underestimated by us. Some individuals may have slipped through the 0.4x0.4 mm openings of the mesh and some may have been lost among debris in the sorting process. Keeping these uncertainties in mind we can nevertheless allow ourselves to make broad comparisons of the relative commonness of different groups.

The Hymenoptera in the air are totally dominated by the Parasitica, and among them the Chalcidoidea form the largest group. The Chalcidoidea were almost five times as common as the second most common group Platygastridae. The chalcidoids also dominated in the two highest traps (43 and 93 m) followed by Braconidae, and then of about equal numbers of Platygastridae, Ichneumonidae, Scelionidae, Ceraphronidae and Diapriidae. Chapman *et al* (2004) found that Chalcidoidea and Ichneumonoidea (Braconidae+Ichneumonidae) dominated at 200 m above ground in England. Glick (1939) also found that Chalcidoidea and Ichneumonoidea dominated at 65 m height in southern USA. However, in our study the Chalcidoidea are rela-

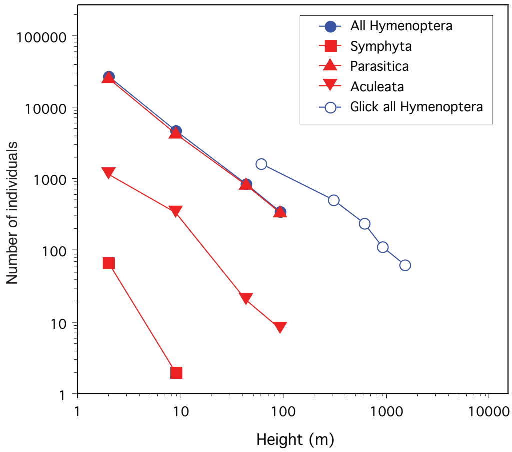

Figure 4. Height distribution of all Hymenoptera and of Symphyta, Parasitica and Aculeata collected in the suction traps. As a comparision is shown the distribution of airplane-netted Hymenoptera from Louisiana, USA (Glick 1939).

Höjdfördelning av alla Hymenoptera, Symphyta, Parasitica och Aculeata i sugfällorna. Som jämförelse visas höjdfördelningen av steklar håvade från flygplan i Louisiana, USA av Glick (1939).

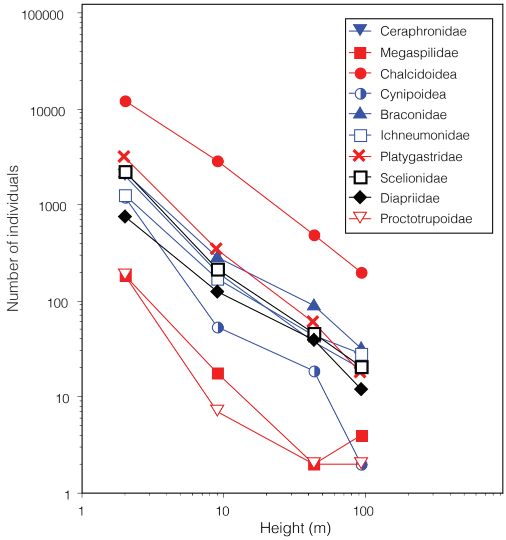

Figure 5. Height distribution of superfamilies and families of Parasitica caught in the suction traps.

Höjdfördelning av olika överfamiljer och familjer av parasitsteklar fångade i sugfällorna.

tively more abundant than in the two mentioned studies. It is evident that species-rich groups and small bodied species are generally represented by more individuals. The Tenthridinidae are obviously very poor fliers; only 5 individuals (and none above 9 m) were caught of this relatively species-rich group.

Seasonal patterns

The total catches of Hymenoptera show two peaks during the summer. It is likely that the double peak pattern is the result of the specific weather conditions during the year of study. The peak in June coincides with an unusually warm period preceded and followed by cool periods inhibiting flights (Fig. 2). Among the Aculeata there is considerable variation in median flight time. Some groups like Megachilidae, Sphecidae and Sapygidae have early flight peaks, whereas for example, Apidae and Formicidae have late peaks. Among the Parasitica there is less variation, with most groups peaking in July.

Height distribution

Insect flights can be classified into two types; migratory and ”trivial” flights (Hansson *et al*. 1992). Migratory flights are those that take the insect on a longer journey to new areas. During a phase in the life cycle the insect is physiologically and behaviourally committed to flight, in order to leave its old habitat in search for a new one where it can reproduce (or sometimes hibernate). Trivial flights (often synonymous with foraging flights) are the daily flights in search of, for example, food and mates. In some insect groups, for example in many Aculeata, flight is the normal way of moving around during daily foraging activities, but they rarely engage in migratory flights that take them permanently to a new habitat. This is reflected in the height distribution of the Aculeata. With the exception of ants, no individual among the Aculeata was caught above 9 m. It is also noteworthy that most of the Aculeata are large insects with powerful flight which can easily move in their own preferred directions of flight if they fly within the flight boundary layer.

Ants are a special case. After a very brief flight period the males die and females bite off their wings. Ants are abundant high in the air, and it is evident that many individuals engage in high altitude flights (Duelli *et al*. 1989). With the aid of wind transport they can move far from their place of origin and colonize new habitats.

Studies of parasitic wasp movements have largely been centred on short range movements and on the orientation mechanisms employed during host and resource discovery (e.g. Rohani & Miramontes 1995, French & Travis 2001). As this and other studies show, many parasitoids undertake long migratory flights. They obviously fly upwards to gain height with the aim of moving far on winds. Insects or inert particles like seeds ascending with the aid of aerial currents high above the tree canopy will easily be transported tens of kilometers (Solbreck 1980; Forsse & Solbreck 1985; Solbreck & Andersson 1987).

From the equation describing the height distribution of all Parasitica, log(no of insects) = 4.7252-1.1147 * log(height) one can calculate what percentage of the flying population that is above the forest canopy. Assuming a canopy roof at 30 m and extrapolating the height distribution equation to an assumed flight roof at 600 m (a conservative value) (cf Ottersten 1970, Wood *et al*. 2009), 41.4% of the insects are flying above the forest canopy (lowering the flight roof to 400 m lowers this value to 40.0%). This means that a very large percentage of the individuals are engaged in flight at altitudes where they can be transported far by winds.

The density-height profiles of our study are calculated averages for several days. Instant measures of such profiles usually reveal a more complicated vertical (and horizontal) density structure (Chapman *et al*. 2011). Nevertheless, density height profiles for longer periods of time are good indicators of the propensity of a certain group or species to engage in high altitude flight. Thus well-studied insects like aphids, which we know are adapted for wind transport high in the air (Reynolds & Reynolds 2009), also have very steep profiles in temporally extended samples (Fig. 6). It is also noteworthy that the density height profile of Hymenoptera from a different continent and climatic region is so similar (Glick 1939) (Fig. 4) to ours.

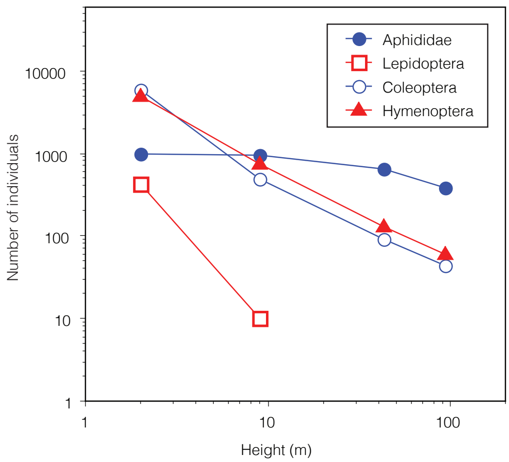

Figure 6. A comparison of the height distribution of four insect groups collected during the period 2-12 June 1980.

Jämförelse av höjdfördelningen för fyra insektsgrupper under fångstperioden 2-12 juni 1980.

Migration is an adaptation to habitats, which are ephemeral with regard to resources, enemy pressure or physical conditions. Unfortunately, the ecology of the Parasitica is poorly known, making it difficult determine the character of their habitats and resources. Thus we do not attempt to explain the moderate differences found in the height distribution of different Parasitica groups.

The order Hymenoptera is, compared with other insect groups, an average with regard to high altitude flight. It is not as extreme as the aphids nor as confined to low altitudes as most Lepidoptera (Fig. 6). Nevertheless, with regard to the Parasitica, there are numerous species and individuals migrating high in the air. They will undoubtedly be transported tens of kilometres in their search for new habitats. Studies of parasitoid movements are not uncommon, but they have mostly been confined to short-range movements and orientation during host finding (e.g. Powell & Poppy 2001, Wajnberg *et al*. 2008). However, it is evident that movements occur on all spatial scales (Cronin & Reeve 2005). As suggested by the present study and also shown by Hastings (2000), movements on a scale that is measured in tens or hundreds of kilometres also have to be considered for these insects.

Acknowledgements
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Svensk sammanfattning

Steklarna är en mycket artrik och ekonomiskt viktig insektsordning. Gruppen rymmer bland annat många viktiga pollinatörer och naturliga fiender till skadeinsekter. Lite är känt om steklarnas spridningsvanor, särskilt vad gäller den mycket stora gruppen parasitsteklar. Man kan fråga sig om steklarna främst flyger marknära inom de,t tunna luftlager som begränsas av vegetationen, eller om de regelbundet beger sig upp i lufthavet där de kan transporteras långt av vindarna. Många arter är små och dagaktiva, vilket antyder att vindtransport kan vara viktigt.

Vi samlade in steklar med hjälp av stora sugfällor monterade 2, 9, 43 och 93 meter över marken på en TV-mast vid Klarälvsdalen. Över 32000 stekelindivider infångades under sommaren av vilka mer än 95% var parasitsteklar (Parasitica) medan gaddsteklar (Aculeata) och växtsteklar (Symphyta) utgjorde 4,2 resp. 0,2%. Steklarna har jämfört med andra insektsgrupper en mellanställning vad gäller höjdfördelningen. De är inte lika extrema höghöjdsflygare som bladlössen men inte heller så markbundna som fjärilarna. Det var stora skillnader mellan olika stekelgrupper. Samtliga växtsteklar, liksom de flesta gaddsteklar fångades enbart på låg höjd vilket antyder att de huvudsakligen flyger nedan trädtoppshöjd. Bland gaddsteklarna utgjorde myrorna ett undantag med många individer i de högsta fällorna, vilket antyder att de regelbundet transporteras långa sträckor med vindarna. Beräkningar av höjdfördelningen visar att mer än 40% av de flygande parasitsteklarna befann sig ovanför trädtoppshöjd. Tidigare studier av parasisteklars spridning har mestadels begränsats till kortdistansspridning och orientering vid värdlokaliseringen. Men spridningen sker uppenbarligen på alla rumsskalor. Vår studie antyder att de ofta kan spridas många mil.

Appendix 1. Results of ANOVA of log abundance vs log altitude and date for groups with total samples exceeding 100.

Resultat av ANOVA för log abundans mot log höjd och datum för stekelgrupper med minst 100 individer totalt

Family	Dependant variable	Result
Braconidae	Altitude x date	$F_{11,18} = 0.169$, NS
	Date	$F_{11,18} = 18.970$, $p < 0.05$
	Altitude	$F_{1,18} = 352.223$, $p < 0.05$
Ichneumonidae	Altitude x date	$F_{11,19} = 0.948$, NS
	Date	$F_{11,19} = 4.124$, $p < 0.05$
	Altitude	$F_{1,19} = 232.940$, $p < 0.05$
Ceraphronidae	Altitude x date	$F_{10.12} = 0.576$, NS
	Date	$F_{11,12} = 4.392$, $p < 0.05$
	Altitude	$F_{1,12} = 26.643$, $p < 0.05$
Chalcidoidea	Altitude x date	$F_{11,20} = 1{,}948$, NS
	Date	$F_{11,20} = 71{,}086$, $p < 0.05$
	Altitude	$F_{1,20} = 861{,}757$, $p < 0.05$
Cynipoidea	Altitude x date	$F_{9.9} = 1{,}488$, NS
	Date	$F_{9.9} = 2.256$, NS
	Altitude	$F_{1,9} = 81{,}458$, $p < 0.05$
Diapriidae	Altitude x date	$F_{9.15} = 0.860$, NS
	Date	$F_{11,15} = 9.667$, $p <0.05$
	Altitude	$F_{1,15} = 183.919$, $p < 0.05$
Formicidae	Altitude x date	$F_{8.9} = 2.814$, NS
	Date	$F_{9,9} = 7.542$, $p < 0.05$
	Altitude	$F_{1,9} = 53.121$, $p < 0.05$
Platygastridae	Altitude x date	$F_{11,15} = 1.290$, NS
	Date	$F_{11,15} = 20.944$, $p < 0.05$
	Altitude	$F_{1,15} = 491{,}999$, $p < 0.05$
Proctotrupidae	Altitude x date	$F_{4.1} = 60.242$, NS
	Date	$F_{8.1} = 106.961$, NS
	Altitude	$F_{1,1} = 1121.802$, $p < 0.05$
Megaspilidae	Altitude x date	$F_{5.6} = 0.334$, NS
	Date	$F_{10.6} = 0.611$, NS
	Altitude	$F_{1,6} = 38.725$, $p < 0.05$
Scelionidae	Altitude x date	$F_{11,15} = 0.280$, NS
	Date	$F_{11,15} = 5.200$, $p < 0.05$
	Altitude	$F_{1,15} = 66.718$, $p < 0.05$