

Solitary Bees and Bumblebees in a Danish Agricultural Landscape

Friese, Die europäischen Bienen.

Tafel I.



Frühlingsleben auf blühender Weide (Salix) bei Jena (1904). Oben: männliche Blüten (Pollen), unten: weibliche Blüten (Nektar). $\frac{1}{2}$ nat. Gr. (Original).

PhD-Thesis

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Introduction to PhD-study by Isabel Calabuig: Solitary Bees and Bumblebees in a Danish Agricultural Landscape

This PhD-study constitutes a part of the project: "Novel strategies in weed control providing for environment, economy, and landscape resources". The project is a cooperation between four departments of the Danish Institute of Agricultural Sciences (D.I.A.S), the Danish Forest and Landscape Research Institute, and the University of Copenhagen. The project as a whole is part of the research programme: "Land use - farmers as landscape managers (1997-2001)", financed by the Ministries of Environment & Energy and of Food, Agriculture & Fisheries. My supervisor was Associate Professor Mikael Münster-Swendsen, Department of Population Ecology, University of Copenhagen and the PhD-study was carried out at this same department, January 1997 through June 2000.

Twice a year, plans for experiments and analyses and goals achieved were reported to the project leader Svend Christensen (D.I.A.S., Department of Weed Control and Pesticide Ecology), and to the Ministry of Food, Agriculture & Fisheries. Once a year, I presented the plans for field experiments and results of the survey to the other collaborators of the project, and to the farmers involved in the field experiments. Fruitful discussions on general farming practice and management were an important part of the dialogue with the farmers, who have shown great interest in the status of the flora and fauna on their properties.

Teaching biology is an important task during the PhD-study. An autumn semester included teaching in a field course of terrestrial ecology, estimating and discussing the biomass of, and the flux between, the different trophic levels of a forest and a pasture. Spring semesters included teaching population ecology, introducing the application of ecological methods through exercises with model organisms, i.e. life-table analyses, growth-rate estimates, biological control, capture-recapture methods, and functional response in predator-prey systems.

The first step of the PhD-survey consisted in finding suitable areas of arable land that contained a reasonable continuum of different semi-natural habitats and to obtain permissions from the farmers to work on their properties. Secondly, I evaluated different methods to monitor bees along the semi-natural habitats and bee dispersal in crops. I decided on small window-traps in yellow pan-traps and large hanging window-traps. Design of these traps was a challenging but fun task, which included everything from testing different rubber types to hold the window-traps in place, to getting the traps painted yellow by a shipbuilding company.

Learning to design tables and do form- and query-programming in the database programme Access was a prerequisite to handle the data-material collected. Furthermore, all traps and transects had to be mapped with a GPS receiver (Global Positioning System) and in this way, exact locations were mapped and linked to the database material. Changes in the flora and fauna of the area can thus be monitored later on if wanted. I attended a course in ArcView GIS (Geographical Information System) to be able to implement the data and generate maps of the survey-area, but also to be generally up-to-date with the methods which are now the most widely used when species inventories are made. During my PhD-study, I have also attended several conferences and PhD-courses on landscape ecology to present and discuss my results and to be inspired by others working in the same area of interest.

In Denmark, solitary bees have not been studied in detail since the 1920s, and bee taxonomy has changed greatly since Professor Lavritz Jørgensen made his identification key for Danish bee species (Jørgensen 1921). Surveys of the bee fauna in other countries have often included direct observations in transect-walks, sweep-netting, observations on flowers and at soil-nest-sites, and trap-nesting, e.g. (Banaszak 1996; Frankie *et al.* 1998; Steffan-Dewenter & Tscharntke 2000). Examples of the use of yellow pan-traps to evaluate overall fauna of bees are rare, but see O'Toole (1998), and more often, these traps have been used in surveys of species-specific pollinator-plant interactions (Aizen & Feinsinger 1994; Leong & Thorp 1999). It was thus impossible to predict the yield from using window-traps in yellow pan-traps to survey bees for a whole season in a Danish agricultural landscape. Still, the method of yellow pan-traps was preferred because relative abundance, distribution in the landscape, and seasonal activity of species would be obtained in addition to a species inventory. Furthermore, a known benefit from using yellow pan-traps is that common species are trapped, which otherwise are below threshold of perception when netting or observing during transect-walks (Own obs. and Pers.com. C. O'Toole).

The resulting data-material from the survey was overwhelming and the work on species identifications proved to be a very time consuming task since no indications of recommended identification tools for Danish species existed. To provide the prerequisites for this survey, and to make use of the old collections at the Zoological Museum (University of Copenhagen), a revision of the species identification tools for Danish bees, a taxonomic update of the nomenclature, and a preliminary species list of Danish species were therefore initiated and will be completed and published following this PhD-study. Furthermore, the appendixes of this thesis are based on a substantial database, which I have designed for the work on the thesis, but also for future accumulation of information on Danish bee species and their distribution in Denmark.

Specimens of the inquiline genus *Sphecodes* proved difficult to identify, mainly because the morphology, colour, and size of these bees vary considerably within species and even overlap among species. This variability is typical of many inquilines, and part of it stems from the fact that parasite-host species relationships seldom are simple one-to-one relationships (see Appendix 5). Differences in host species size and thus in amount of provision in brood cells are reflected in inquiline morphology and size.

Within host-species, another interesting source of variability may arise from the fact that the inquiline female apparently is unable to detect whether she oviposits in a host brood cell meant for female or male offspring. In many species of *Andrena* and *Lasioglossum*, males are smaller than females, and brood cells meant for male eggs often contain less pollen than female brood cells. Size of inquiline offspring may thus be determined by the different combinations of male or female eggs deposited in host male or female brood cells, e.g. smaller than average females produced in brood cells provisioned for male host offspring. Lack of distinct morphological characters to separate species is a problem with many species of *Sphecodes*, and often, exact identification of females ultimately depends on knowledge of host-species for a given specimen. Males, on the other hand, are relatively easy to identify based on characteristic genitalial morphology. Unfortunately, in many (older) museum collections, pinning of bees has not included exposure of their genitalia. Direct comparisons

of specimens to voucher material are necessary and I therefore made the species identifications of *Sphcodes* (and some problematic specimens of *Lasioglossum*) at the Hope Entomological Collections in Oxford, UK. The Hope museum holds extensive collections of bees curated by Assistant Professor Christopher O'Toole, who kindly assisted and confirmed my species identifications.

In 1996, I worked as an assisting scientist for Associate Professor Mikael Münster-Swendsen. The cooperative research project concerned the behaviour and biology of one species of solitary bee and its nest parasite: "Interaction between the solitary bee *Chelostoma florissomne* and its nest parasite *Sapyga clavicornis* - empty cells reduce the impact of parasites" (Münster-Swendsen & Calabuig 2000). Data analyses, writing, and editing of this paper have been part of the PhD-study. The paper is a more detailed example of foraging, nesting, and offspring protection in a selected solitary bee species.

General introduction to solitary bees and bumblebees

The earliest known fossil bee dates back to the Eocene (Lomholdt 1982), but already in the Cretaceous, a group of wasps belonging to the Super-family Sphecoidea abandoned prey-animals as provision for their offspring and turned to the collection of protein-rich pollen from the early Angiosperms (Michener 1974). Since then, a profound radiation of plant-pollinator mutualisms have occurred, and today, at least 67% of all known flowering plants depend on insects for pollination, others depend on birds and mammals (Kearns & Inouye 1997).

Until the end of the Stone Age, large parts of central Europe were covered with deciduous forest. Wild bee populations were confined to limited areas of open land such as the vast flood plains of river systems, which provided a dynamic and diverse landscape with many different habitat types for bees. In the early agricultural community of Europe, forests were cleared and many new habitats with a rich flora were thereby created, and wild bee populations prospered in the mosaic of uncultured land and small fields (Klemm 1996; Steffan-Dewenter & Tscharntke 1996). Today, the majority of rivers have been contained and farming practice has changed to be dominated by much larger fields with monocultures, and little room for foraging and nesting of bees.

Aculeate Hymenoptera is now probably the most rapidly declining group of insects in Europe (Day 1991; O'Toole 1993), and there is a growing focus on habitat management in order to conserve wild bees and wasps. Thus, a national mapping scheme of bumblebees and their forage plants has been made in Britain (Fussell & Corbet 1992) and the *First European Workshop on Habitat Management for Wild bees and Wasps* was held at Cardiff University in April 1998 (Ed. by: Jones & Munn 1998). Recent species inventories and mapping schemes in neighbouring countries include Germany (Schwenninger 1999; Westrich 1984), The Netherlands (Peeters *et al.* 1999), Sweden (Erlandsson *et al.* 1988; Janzon *et al.* 1991; Norén *et al.* 1998; Svensson *et al.* 1990), and Britain (Kloet & Hincks 1978). In Britain, partial distribution records of bees have been made by Else (1993a and 1993b), and a new key and revised species list is on its way (Else, G.R., *In prep.* – Pers. com C. O'Toole).

In Denmark, wild bee species richness, distribution, and abundance have not been studied in detail for about 75 years (Jørgensen 1921; Lomholdt 1977), and nothing is known about which species are potentially vulnerable or endangered. In the German area Baden-Württemberg, 57% of the listed 429 bee species are endangered or close to extinction (Westrich 1990a), and in Britain, 11.1% of the bee species are considered either vulnerable, endangered or extinct (O'Toole 1994). A rough estimate of solitary bees and bumblebees in Denmark includes approximately 238 species (26 genera) and 29 species respectively (Madsen & Calabuig, *In prep.*). This estimate is presently based only on results from a local survey in an agricultural landscape (I. Calabuig, Manuscript I, *In prep.*), a two year survey on the small Danish Island of Læsø (Münster-Swendsen 2000), a local survey of three different pollination guilds of bees (*Salix*, *Erica* and *Campanula* foragers) (Skov 1999), and the collections of bees held by the Zoological Museum, University of Copenhagen. These inventories have furthermore been supplemented by potential but not recently recorded species, based on checklists from Sweden (Erlandsson *et al.* 1988; Janzon *et al.* 1991; Norén *et al.* 1998; Svensson *et al.* 1990). Thus, a fraction of the estimated species may no longer be present in Denmark, and there is an urgent need for a regional faunistic survey and a review of the status of wild bees in Denmark. Nevertheless, local surveys also serve their right

considering that most decisions in land-management are made on this scale. Farmland is the dominating landscape type in Denmark (65% of the area) (Ed. by: Prip *et al.* 1996), and it is also the landscape type being altered the most by man. Therefore, it seemed reasonable to commence a faunistic survey in an agricultural landscape.

Foraging requirements

Bees are an essential part of the agroecosystem, and they are totally dependent on the availability of nectar and pollen resources. Bees are therefore a relevant group to use when studying links between pollinator and floral diversity. As opposed to honeybees and most bumblebees, many species of solitary bees are mono- or oligolectic (collect pollen from only one family or one or very few species or genera of plants). Through their often highly specialised relationships with the native flora, solitary bees may be used as bio-indicators - a measure of habitat quality - because they pollinate and thereby play a vital role in maintaining the natural vegetation (O'Toole 1994).

Honeybees (*Apis mellifera*) are extensively polylectic and are considered efficient pollinators of most Danish crops. Honeybees and bumblebees (*Bombus spp.*) have long flight seasons with the production of many individuals, and thus depend on a continuous food supply (Holm 1985; Prys-Jones & Corbet 1991), but if necessary, the domesticated honeybees are fed sugar by the beekeeper. Conversely, seasonal shortage of resources may be a limiting factor on bumblebees, which mainly exist as natural, untended populations. In early spring and late summer, bumblebees may encounter a scarcity of pollen and nectar resources. A break in resources for just a few days may be fatal to a colony, since bumblebees only store very little honey (Corbet *et al.* 1994). In Denmark, an increase in risk of shortage has been caused by a decline in both hay meadows and seed production of red and white clover (*Trifolium pratense* and *T. repens*), combined with intensive eliminations of weeds, hedgerows, and other semi-natural habitats during the 1940s through 60s (Hald 1998; Hammer 1950). The hay was used for winter feeding of cattle, and the decline of hay meadows is partly due to a shift in overall Danish farming practice from cattle to dairy production (Hald 1998), a development which has also occurred in other countries (Westrich 1996). The hay meadows provided important and diverse nectar and pollen resources for bumblebees as well as solitary bees, including Red Clover (*T. pratense*) and many perennials such as *Geum rivale* (Skovgaard 1936).

In the agricultural landscape, disused arable land, and areas along hedgerows, dry-stone walls, and small dirt roads are important habitats for perennial herbs, such as *Echium vulgare*, *Pulmonaria officinalis*, *Symphytum officinale*, *Anchusa officinalis*, *Lotus corniculatus*, *Stachys sylvatica* and *Cichorium intybus*. Larger areas being ploughed at least once a year, elimination of hedgerows, and changes in infrastructure have resulted in the loss of areas with bushes, trees, and perennial and biennial herb species (Osborne *et al.* 1991). Compared to the often small and shallow-flowered annual weeds, perennials and biennials are favoured by bumblebees due to their large flowers and generally abundant nectar and pollen production (Corbet *et al.* 1994; Fussell & Corbet 1992), and species with long corollas are especially important to the long-tongued bumblebee species such as *Bombus hortorum* (Prys-Jones & Corbet 1991).

Increased use of herbicides alters the successional availability of flowering plants for bees. Therefore, agricultural management should aim to avoid herbicide treatment of field margins,

hedgerow floors, roadsides and forest edges in the general spraying practice. Destruction of wild flower communities may result in a range of cascade effects. Natural populations of parasitoids of crop-pests may be harmed, since the adult wasps often depend on flowers as a food source, e.g. Ichneumonid wasps exploiting Apiaceae (Proctor *et al.* 1996).

Nesting requirements

In temperate climates, about 70% of the solitary bees are soil-nesters (Westrich 1998), and nest by digging tunnels in the ground. The remaining species are primarily cavity-nesters and build their nests in hollow plant-stems, abandoned insect borings in old wood, etc. For each nest-building species, at least one species is found, which explore the stored provision of their host. Such nest-parasites include inquiline solitary bees and wasps, and the so-called cuckoo bumblebees.

Soils preferred by most soil-nesting species of solitary bees are characterised by being bare or sparsely vegetated, sandy, fine-grained, friable, and dry, with low humus content (Cane 1991; Müller *et al.* 1997; Potts & Willmer 1997; Westrich 1996). Other species are more conservative in their choice of nest substrate, such as *Colletes cunicularius* which is a pioneer species but prefer areas with bare, loose sand, often near streams or in sand dunes. The locations for nesting of solitary bees are chosen to maximise exposure to the sun, for the longest period of time, and the aspect of the surface is therefore most often south-facing and sloping (Potts & Willmer 1997). Areas with sparse vegetation are often preferred to maximise sun-exposure and to avoid that plant roots grow into broodcells. Nesting areas have to be well drained to avoid fungus infestations of stored provision and offspring. Brood cells of most soil-nesting species are lined with a secretion from the Dufours gland, for protection of provision and for maintenance of cell structure. In some families, the Dufours gland secretion is waxy and impregnates the soil (e.g. Andrenidae, Halictidae), whereas in the genus *Colletes* the secretion hardens and forms a transparent membrane lining the brood cell (O'Toole & Raw 1999).

Danish cavity-nesting species primarily nest in abandoned insect borings in dead wood, and in old *Rubus fruticosus*, *R. idaeus* and *Rosa* stems (e.g. *Hylaeus*), and other marrow-containing species such as *Cirsium spp.* and *Arctium spp.* (e.g. *Osmia claviventris*). Small species such as *Chelostoma florissomne* nest in the straws of *Phragmites* stands along streams and lakes, and may be found nesting in large aggregations in thatched roofs (Münster-Swendsen & Calabuig 2000). Several opportunist species, such as *Anthidium manicatum* and *Osmia rufa*, use all kinds of holes and crevices of varying shape and size for nesting, such as between stones and in old half-timber and mortar walls. Other cavity-nesting species are extreme specialists, nesting exclusively in abandoned snail-shells (*Osmia aurulenta*) or in insect-galls (*Hylaeus pectoralis*) (Westrich 1990b). Most Danish cavity-nesting species belong to the family Megachilidae which mainly line their brood cells with gathered material like leaf or petals, and the leaf discs are either used whole to make small containers for the provision (e.g. *Megachile spp.*) or the plant material is masticated to a mouldable substance for cell lining and closure (e.g. *Osmia spp.*).

The solitary bees often need two or three different habitats within a limited geographical range to complete their adult activities and to persist through several generations in a given location:

One habitat for foraging, another for nesting and sometimes a third for collecting building material for their nests (Westrich 1996). Nesting and foraging habitats for bees are distributed discontinuously or patchily in the agricultural landscape. Thus, they depend on restricted areas for foraging and nesting, and are therefore sensitive to agricultural management - especially management of pastures and of the patchwork of semi-natural habitats such as hedgerows. Therefore, solitary bees may also be used to measure the degree of fragmentation of the semi-natural habitats. If one habitat is lost due to events such as elimination of marginal areas of a field, one or more species of bees may no longer be able to inhabit the area, which next may have implications for the flora.

Introduction to survey

A population of the solitary bee *Chelostoma florissomne* and its nest parasite *Sapyga clavicornis* was studied June-August 1996. A large aggregation of *C. florissomne* nested in the thatched roofs of two large buildings at Kristiansminde field station near Sorø in south Zealand, Denmark. A survey of solitary bees and bumblebees was made April through November 1997 and May 1998. The area of study was north of Ringsted, northeast Zealand, Denmark. The study area is an agricultural landscape dominated by conventional farming practice, but with smaller fields than average on Zealand and a higher abundance of hedgerows and other semi-natural habitats. The landscape is dominated by fields, hedgerows, dry-stone walls and small forests on calcareous soils with natural springs and streams.

The aim of this PhD-study was to clarify several aspects of the ecology and biology of solitary bees and bumblebees occurring in the fragmented semi-natural habitats of a Danish agricultural landscape:

- **Interaction between a solitary bee and its nest parasite - behavioural adaptations to reduce parasitism**
- **Seasonal activity and succession of bee species**
- **Species richness and relative abundance**
- **Estimation of the actual number of species occurring in the agricultural landscape**
- **Foraging- and nesting conditions in hedgerows, dry-stone walls, forest edges, field- borders and other linear and areal habitats**
- **Dispersal patterns in a winter oilseed rape field, importance of bees in pollination and potential competition from honeybees**
- **Maintenance and founding of bee habitats for foraging and nesting**

In the survey of 1996, nesting behaviour of *C. florissomne* and interactions with its nest parasite *S. clavicornis* were studied through continual observations of individuals and dissections of bee nests. In the 1997 survey of bees in an agricultural landscape, three transects were selected, each two kilometres long, along varying types of semi-natural habitats. Small window-traps standing in yellow pan-traps with liquid was used to attract and trap the bees. The traps were placed along the habitats with a constant distance of 100 metres, coming to a total of 64 traps. Traps were normally emptied once a week. Trap yields were rinsed and stored in 70% ethanol. The material was sorted and all bee specimens counted and identified to species. Colourimetric properties of the yellow pan-traps were measured, and the traps' efficiency of attracting bees was evaluated.

In spring, summer and late summer, I evaluated the floral composition along the habitats. All flowering herbs were recorded using the semi-quantitative coverage and abundance index (*Total Estimate Scale*) of Braun-Blanquet. The Braun-Blanquet index values were converted to coverage frequencies, so that total flowering plant coverage within a sample could be calculated. A standardised characterisation of the transects was made in cooperation with the Danish Institute of Agricultural Sciences. All transects were divided according to type of habitat (hedgerow, dry-stone wall, forest edge etc.). Further subdivision was applied when necessary. Eight habitat types were represented along the six kilometres of transects, some types had to be subdivided according to type of surrounding area or heterogeneity of the

habitat itself. Within each habitat type and for each trap, several biotic and abiotic parameters were recorded, e.g. species and coverage of bushes and trees, geographical orientation of the habitat, and soil-cover and width of the habitat. All recorded plant species were indexed according to their biological value as nectar and pollen resource for honeybees and bumblebees. When appropriate, cover frequencies of herbs, bushes and trees were weighed by multiplication by the index-values.

Through linear regression and multiple linear regression models, it was thus possible to make analyses of foraging conditions for solitary bees and bumblebees by comparing abundance and species richness of females with plant coverage and species richness. Nesting conditions were investigated by using abundances of *Andrena* males and *Nomada* individuals, counted collectively, as the dependent variable in a Generalised Linear Model (GLM) and with selected habitat parameters as independent variables. In addition, I estimated true species richness and made an evaluation of the sampling methods applied in the survey by means of the free-ware application *EstimateS 5*.

Dispersal patterns of solitary bees, bumblebees and honeybees were studied in a blooming winter oilseed rape field, situated about 200 metres away from the area where bee species richness and abundance were surveyed intensively the preceding year. 24 window-traps were placed in pairs from the edge of the field along a tractor track running perpendicular to the field edge and bees were sampled for a month through the period of blooming of the crop.

Summary of survey results

The study of the behavioural adaptations in a solitary bee species to reduce parasitism by a parasitic wasp revealed that host protection of offspring include 1) discovery and removal of parasite eggs deposited prior to the construction of a cell closure, 2) minimisation of the time when fully provisioned cells may be parasitised successfully, and 3) the construction of empty cells in front of brood cells. These means of protection significantly reduced the success of the parasite and more than 77% of the wasp offspring died at an early stage due to intraspecific interference competition within brood cells and as result of the wasps' oviposition into empty cells.

Estimation of Western Europe number of bee species varies between 2000 and 4500 (Williams 1995) but there are substantial indications of a decline in bee species in Europe and other regions. In Denmark, wild bee species richness, distribution, and abundance have not been studied in detail for about 75 years, and nothing is known about which species are potentially vulnerable or endangered. A rough estimate of solitary bees and bumblebees includes approximately 238 species (26 genera) and 29 species respectively. In a survey of six kilometres of semi-natural habitats in a Danish conventionally managed agricultural landscape, 72 solitary bee species and 19 species of bumblebees were recorded, several of which are considered vulnerable or endangered in neighbouring countries. A new group of non-parametric species richness estimators supplied by the free-ware programme *EstimateS 5* was used to estimate true species richness in the area of study and an additional 23 potential species was depicted from abundance and distribution of the 91 recorded species. The non-parametric species richness estimators are concluded to be promising tools for estimations of true species richness of bees.

The plant community of the studied area is typical of nutrient-rich soils of a conventional farmland, with annuals and species that benefit from fertilisers dominating the flora. The flora community of mellitophilous plant species found may sustain polylectic bee species as well as oligolectics, but unpredictability of the flora, due to land management, is sub-optimal for the persistence of oligolectics. The majority of the solitary non-inquiline bee species recorded (59 species) thus proved to be polylectic, but four oligolectic species foraging on *Salix* and six oligolectics of other plant families were found. Abundance of solitary bees and bumblebees were correlated with mellitophilous plant coverage in south-facing areas, whereas no correlation was found for honeybees. Furthermore, abundance of honeybees was not correlated with abundance of other bees, and resource competition between honeybees and wild bees is apparently rather limited in areas where honeybees form a natural part of the pollinator-community. Bee species richness could not be explained by plant species richness or coverage in a multiple regression.

Soil-nesting species were abundant and represented by many species. Habitat parameters in a generalised linear model were able to predict abundance of males and inquilines, a measure of nest abundances in the habitats. Hence, soil-cover and sun-exposure are important factors for selection of nesting-sites and areal habitats are preferred for foraging as well as nesting, whereas linear habitats are considered more important for foraging than for nesting. Habitat indexation, and abundance and distribution of males and inquilines are a crude measure on which to base analyses of nesting conditions, but it may be constructive for a local survey on the landscape element level. Several cavity-nesting species were recorded, but abundance was

very low, and inclusion of farm gardens and buildings would probably have revealed more species. Although the semi-natural habitats thus seem to be sub-optimal nesting habitats for cavity-nesters, these habitats may play an important role acting as corridors for species dispersal between core-habitats.

The area of study was chosen for its relatively small field sizes and high concentration of semi-natural habitats such as hedgerows, dry-stone walls, ditches, streams, and forest edges. Total number of recorded bee species in traps varied between 5 and 51. Single traps standing in optimal and undisturbed habitats such as a small pasture sampled up to 40 non-Apidae and 11 Apidae species in a season, whereas a north-faced trap along a herbicide treated hedgerow sampled zero non-Apidae species and only five *Bombus* species. Therefore, the study area has proved satisfactory in representing a landscape mosaic, which includes the major range of elements in a typical Danish agricultural landscape, and with varying habitat quality on a sub-local scale. Window-traps in yellow pan-traps, indexation of habitats, and the method of Braun-Blanquet for descriptions of the flora, have proved suitable in investigations of the pollinator fauna, species activity patterns, and in analyses of the nesting and foraging conditions in a local area. Window-traps in yellow pan-traps are furthermore recommended as the initial method for general surveys of bee faunas and bee species richness.

There is no doubt that elimination of border-habitats and the application of various methods to intensify farming practice have caused much damage on both flora and fauna of the agricultural landscape. In agricultural areas where all semi-natural habitats have been removed, and where no core habitats such as pastures or forests exist in the vicinity, the bee fauna will most certainly be poor. Conservation of bees in agricultural semi-natural habitats must include restrictions in the use of herbicides and insecticides, re-establishments of border-habitats, and an increase in set-aside areas and time invested in research on landscape management beneficial to wild bee populations. But the main goal in conserving bees is to pinpoint the locations of core-populations, and of habitat hotspots, and to conserve such areas as a whole, the semi-natural habitats surrounded by arable land thus acting as corridors between core-habitats for bees.

Dispersal distributions of solitary bees and bumblebees were studied in a winter oilseed rape field. 19 species of solitary bees were recorded in window-traps placed along a line transect perpendicular to the field edge. All but four species were polylectic, including Brassicaceae as host-plant family. Solitary bee activity was clearly highest within 30 metres from the field edge and the decline in solitary bee individuals versus distance from field edge significantly fitted a steep two-parameter exponential decay function. Solitary bees forage on oilseed rape but foraging range is limited, and apparently, they do not play any noteworthy role in the pollination of winter oilseed rape. The traps yielded ten species of bumblebees, and a significant linear correlation was found between numbers of individuals and distance from the field edge. This result is attributed to bumblebee foraging behaviour. Bumblebees were abundant in all surveyed parts of the field and presumably are background pollinators of oilseed rape in Denmark. Honeybees are managed pollinators of oilseed rape, and were abundant in a preceding study of the area. For unknown reasons, honeybees were caught in extremely low numbers in this rape field study, and the most likely explanation is a decline in honeybee populations.

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PAPER I – M. Münster-Swendsen and I. Calabuig 2000:

**Interaction between the solitary bee *Chelostoma florissomne*
and its nest parasite *Sapyga clavicornis* – empty cells
reduce the impact of parasites**

Ecological Entomology 25, 63-70

Interaction between the solitary bee *Chelostoma florissomne* and its nest parasite *Sapyga clavicornis*—empty cells reduce the impact of parasites

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Abstract. 1. Nesting behaviour and interactions between the bee *Chelostoma florissomne* (L.) (Megachilidae) and its nest parasite *Sapyga clavicornis* (L.) (Sapygidae) were studied through continual observations of individuals and dissections of bee nests. Protection of bee offspring is based on (1) the bee's discovery and removal of parasite eggs deposited prior to the construction of a cell closure, (2) minimising the time when fully provisioned cells might be parasitised successfully, and (3) the construction of empty cells in front of brood cells.

2. An empty cell was found in front of 64.4% of all brood cells and, if the outermost brood cell in a nest was excluded, in front of 74.3% of inner brood cells. A vestibule closure is most often constructed in front of the outermost brood cell.

3. Following oviposition, the bee made only five flights, which together lasted 6–13 min, to construct a cell closure. A cell closure does not prevent the nest parasite from oviposition inside the brood cell, however, and parasite eggs deposited through the cell closure are not detected and removed by the bee. Only an additional cell closure, i.e. the formation of an empty cell, may protect a brood cell when the bee is not in the nest. The nest parasite often oviposited through the additional cell closure but its offspring were then trapped in the empty cell and starved to death.

4. Only 5.4% of the inner brood cells that were protected by an empty cell were parasitised, compared with 28.9% of those without an anterior, empty cell; 27.4% of the empty cells contained dead parasite offspring (eggs and larvae). Thus, the empty cells provided significant protection and, combined with additional means of protection of brood cells, led to a low degree of parasitism. More than 77% of the wasp offspring died at an early stage due to intraspecific interference competition within brood cells and as result of the wasps' oviposition into empty cells.

Key words. *Chelostoma*, empty cells, interaction, mortality, nest architecture, nest parasite, protection, *Sapyga*, solitary bee.

Introduction

Nest construction of solitary bees, and in particular of those that nest in hollow stems or holes in wood, has been studied in many European species (Malyshev, 1935; Westrich, 1989; O'Toole & Raw, 1991). Members of the genera *Osmia* and *Megachile* are used widely for pollination of crops (Parker *et al.*, 1987; Torchio, 1990; Free, 1993), however the breeding

success of these bees is often reduced notably due to parasitoids and nest parasites (Danks, 1971; Torchio, 1972, 1990; Wcislo, 1996).

In bees, various means have evolved to protect the offspring against nest parasites. These include aggressive behaviour and/or traits in nest construction that hinder oviposition or offspring survival of nest parasites. In this context, it has been discussed whether the formation of empty cells, i.e. brood cells lacking provisions and offspring, has no specific purpose or whether they are constructed to protect brood cells, i.e. to serve as a barrier or to mislead the parasite (Krombein, 1967; Sakagami & Laroca, 1971; Tepedino *et al.*, 1979; Wcislo *et al.*, 1993).

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All species within the genus *Sapyga* are known to be nest parasites of solitary bees, in particular of the megachilid genera *Osmia*, *Megachile*, and *Chelostoma*, and may induce high host mortality. For example, the nest parasite *Sapyga pumila* Cresson induces up to 77% mortality of *Megachile rotundata* (F.) and is regarded as a serious pest (Torchio, 1972). *Sapyga clavicornis* (L.) is known to be associated commonly with *Chelostoma florissomne* (L.) (van Lith, 1957; Westrich, 1989), and larval development of the two species has been described by van Lith (1957). *Chelostoma florissomne* is commonly found in thatched roofs in Denmark, where it forms dense colonies.

The study of *C. florissomne* and *S. clavicornis* reported here aimed to describe adaptations that reduce the effect of parasite attacks and to determine the level of efficiency of the host precautions, with special emphasis on the effect of empty cells.

Materials and methods

Time and location

This study was conducted in June–August 1996, at Kristiansminde field station near Sorø in South Zealand, Denmark (55°25'N, 11°35'E). The field station is situated in a glade and has two large buildings with thatched roofs that house the wasp genera *Trypoxylon*, *Psenulus*, *Passaloecus*, and *Symmorphus*, and the bee genera *Osmia*, *Megachile*, and *Chelostoma*. The dominant species was *C. florissomne*, with several hundred provisioning females at the peak of seasonal activity. Observations of behaviour and removal of nests for dissection took place on the western side of a building, where the density of *C. florissomne* nests reached about 200 within a section of 1 m of eave (about 22 cm thick). Dissections of nests belonging to all the above genera showed that *S. clavicornis* bred only in nests of *C. florissomne*.

Nest observations

To facilitate observations of behaviour of individual bees and wasps and to study several bees on sequential days, 12 aluminium trap-nest boxes were attached to the lower edges of the eaves in April 1996. The boxes were open at front and rear (front 7 cm high and 20 cm wide, depth 20 cm), and each was filled with approximately 320 reeds (*Phragmitis*), 10–20 cm long and with inner diameters of 3–6 mm [widths preferred by *C. florissomne* (van Lith, 1957)]. In all reeds, a node formed a

natural rear end of the potential nest. The females of *S. clavicornis* paid frequent visits to the boxes, investigating and entering bee nests. Time and temperature under the eave were recorded throughout, and dictaphones were used to record observations of bee and wasp activities. One or more individual nests were studied throughout several days (≈ 12 h a day), adding up to 34 nest-days in all.

In six nests in the eave, a long, narrow window was cut in the reed and covered with translucent plastic. The result of each visit of a bee (building of closures, oviposition, etc.) could thus be observed as the reed was removed, inspected and repositioned.

Nest dissections

Immediately after the completion of a nest closure in a box trap-nest, the reed was removed and dissected. The behaviour of the females in these nests and visits of nest parasites had been monitored over the preceding days, rendering it possible to relate observed activities with resulting nest structure, number of provisioned cells, and parasitism. Nests in the eaves with freshly made nest closures were removed and dissected so that all living or dead offspring of *S. clavicornis* could be detected with certainty. A total of 130 nests was dissected.

Results

Nest architecture

The nest of *C. florissomne* consists of a row of cells constructed inside a reed (Fig. 1). The inner half of each brood cell is filled with a mixture of pollen and nectar, onto which an egg is fastened, but empty cells without provisions or eggs are often found. All cells are sealed with a thin, soft closure; a thick, hard closure is built between the outermost cell and the end of the reed, creating an empty space (inner vestibule) between this closure and the row of cells. Finally, a thick nest closure is built at the end of the reed, creating an outer vestibule.

The 130 dissected nests contained a total of 502 cells, comprising 305 cells containing pollen-nectar (average cell length: 12.8 mm \pm 0.1 SE) and 197 empty cells between brood cells (average cell length: 9.1 mm \pm 0.2 SE). The innermost cell was never empty. In total, 64.6% of the brood cells had an empty cell in front of them. Distinguishing between the

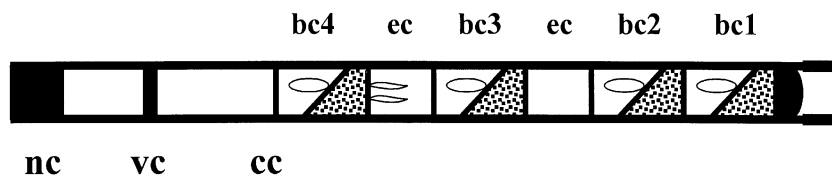


Fig. 1. Outline of nest of *Chelostoma florissomne* having four brood cells with provision and bee egg (bc1–bc4) and two empty cells (ec). Two parasite eggs are indicated in the outermost empty cell. Outermost cell closure (cc). The vestibule closure (vc) bounds an inner vestibule and the nest closure (nc) an outer vestibule.

outermost brood cell and the rest of the brood cells in each nest showed that 42.3% of the outermost brood cells ($n=130$) had an anterior, empty cell, whereas 74.3% of the rest of the brood cells ($n=175$) had an anterior, empty cell ($\chi^2=30.64$, $P<0.001$).

Daily activity

Spring and early summer 1996 were relatively cold, and all adults of *C. florissomne* and *S. clavicornis* emerged within a few days in early June. The overall activity decreased markedly in

late July and early August, and no adults were found after 16 August.

On 25 June, the activity and behaviour of four female bees nesting in a trap-nest box and of all visiting *S. clavicornis* females were recorded throughout the day (Fig. 2). Because the morning was cloudy and cold (13.5 °C at 09.50 hours), the activity of the bees did not begin until 10.00 hours. The four nests received 59 visits by female wasps, of which 26 visits included backward enterings, indicating that oviposition may have taken place. Thus, all the nests were located by the wasps, but although the four nests were entered backwards by the wasps four, seven, seven, and eight times, respectively,

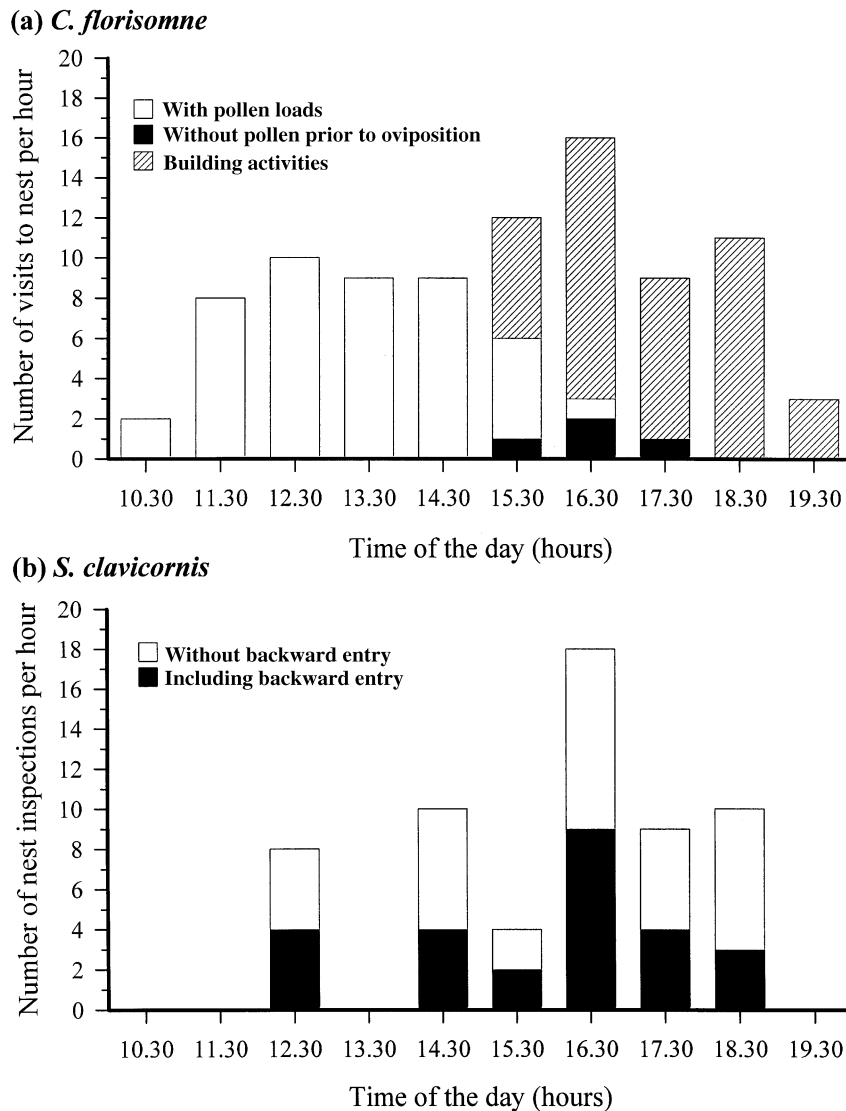


Fig. 2. Activity pattern of four provisioning bees and of *Sapyga clavicornis* females visiting the four nests on 25 June 1996. (a) Number of visits to the nests per hour, divided into visits with pollen loads, visits without pollen prior to oviposition, and visits associated with building activities. (b) Number of visits by female wasps per hour, divided into inspections without backward entry and inspections including backward entry into the nests.

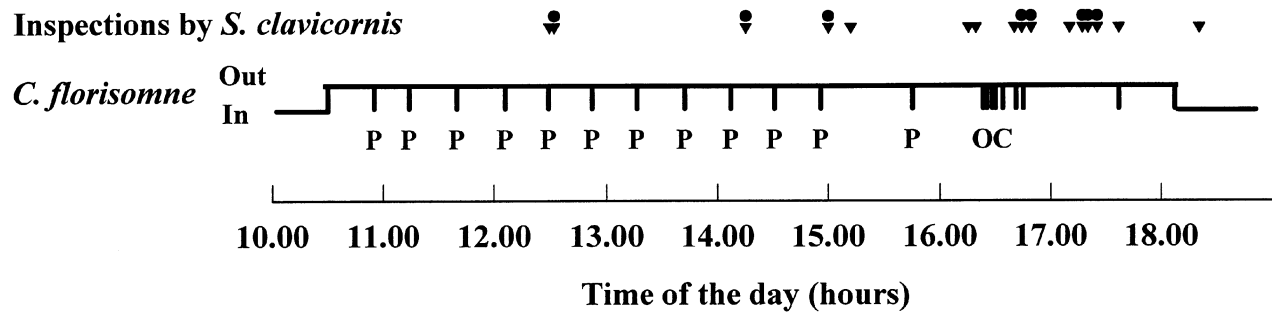


Fig. 3. Flight schedule of individual bees on a day with provision and oviposition. Inspections of the nest by *Sapyga clavicornis* excluding (▼) and including (●) backward entry are shown. The upper part of the line refers to periods when the bee was absent; the lower part refers to periods when the bee was present at or in the nest. *P* indicates the bee's returns with a pollen load, *O* indicates its oviposition, and *C* its cell closure construction.

dissections after completion of nest closures revealed no eggs or larvae of *S. clavicornis*.

The patterns (Fig. 2) demonstrate that the frequency of visits of *S. clavicornis* corresponds with the period of bee oviposition and construction of cell closures.

Provision flights and oviposition in *C. florissomme*

Chelostoma florissomme collects pollen only from *Ranunculus* spp. (Westrich, 1989; analyses of pollen masses). Only *Ranunculus acris* and *R. repens* were found in the area, scattered along ditches in the surrounding forest. This may have had an impact on the duration of each provision flight.

The total time spent on provisioning one cell was 5–6 h (range: 4 h 52 min to 6 h 20 min) and included 12–14 flights, i.e. 11–13 flights where the bees returned with a pollen load, plus one last flight, where the bees returned with little or no pollen (presumably a nectar trip). A pollen trip lasted about 20 min (mean = 21.2 min, SD = 4.9, $n = 61$) and the last flight about 30 min (mean = 32.2 min, SD = 2.9, $n = 6$).

The female enters the nest head first when returning from a flight to add nectar to the provision, after which she backs out, turns round, and enters backwards to unload pollen. Time spent inside the nest after entering forwards was ≈ 50 s (mean = 51.7 s, SD = 31.5, $n = 32$). After the last flight, this stay was longer (mean = 122 s, SD = 45, $n = 7$), as the provision was presumably prepared for subsequent oviposition. The period inside the nest after entering backwards, i.e. delivery of the pollen load, lasted 2 min (mean = 120.0 s, SD = 27.5, $n = 29$), except after the last flight, when the stay during oviposition was shorter (about 1 min). The total time spent on each visit to the nest was ≈ 3 min (mean = 178.2 s, SD = 43.8, $n = 47$). As a result, the nest was left without surveillance for about 4.5 h during the provision cycle (5–6 h). Considerable time was therefore available for the parasites' admittance to a nest during the provision cycle.

The exact time of oviposition was easily detected, as the female carried no pollen when returning from the last provision flight, and as this was followed by a number of excursions with quite short intervals and including only

forward enterings into the nest. These excursions proved to be connected with the construction of a cell closure. The provision cycle of a bee is shown in Fig. 3.

Construction of cell closures

The cell closure of *C. florissomme* consists of a brownish, amorphous material (saliva, nectar, and loam) in which small grains of quartz are embedded. It was made immediately after oviposition and five flights usually sufficed to complete it. The total construction lasted between 10 and 19 min, and the intervals between the first three excursions were short (≈ 30 s construction and 30 s absence), followed by longer intervals between the succeeding flights, when stays both inside the nest and away from it increased progressively. The crucial time, when the egg and provision were left without surveillance during cell closure construction varied between 6 and 13 min, covering five short flight periods interrupted by the bee's arrival at the nest.

The construction of the cell closure was followed by an excursion of highly variable duration (9–45 min), leaving free access for a nest parasite to the thin and soft cell closure. Whenever an extra, empty cell was constructed, this excursion was followed by another five flights, during which another cell closure was constructed.

Construction of vestibule and nest closure

A vestibule closure was constructed prior to nest closure. Both closures were made of clay (3–4 mm thick) in which small stones (mainly quartz particles, but much larger than those found in the cell closures) were embedded. In some of the nests, where an anterior, empty cell (short and with thin and soft closure) followed the last brood cell, no vestibule closure was found.

All activities were recorded during the full construction of one vestibule closure. Completion took 3 h 44 min and included 33 trips. The first flights were made with very short intervals; during the first five excursions, the nest was left

without surveillance for only 3 min 22 s in all, during which time the outermost brood cell was unprotected.

Nest closure construction took 2–5 h and included 23–39 flights. It usually took between 40 and 140 min, including seven to nine flights, to create the first, intact clay membrane.

Host-related behaviour in *Sapyga clavicornis*

Females of *S. clavicornis* deposit their eggs in provisioned bee cells and are capable of penetrating a recent cell wall with the pointed tip of the abdomen to oviposit inside a finished cell (van Lith, 1957). Thus, eggs attached to the inner surface of the cell closure were often found. According to van Lith (1957) and authors' observations, egg incubation time is 2–3 days, whereas that of the bee is \approx 5 days. When superparasitism occurs, only one *S. clavicornis* larva survives the interference competition as conspecific eggs or larvae in the cell are killed. The surviving larva then pierces the bee egg and sucks it dry; this takes 4–5 days, after which it feeds on the pollen and nectar provision (van Lith, 1957; M. Münster-Swendsen & I. Calabuig, pers. obs.).

Details of the behaviour of *S. clavicornis* were observed repeatedly at the nest boxes throughout the season. Female wasps were seldom seen before 12.00 hours, although the bees had usually been active provisioning their cells for some hours (Figs 2 and 3). In the afternoon, wasps patrolled along the eaves and nest boxes, inspecting and entering nests. *Chelostoma florissomne* was never observed to approach and chase away a nest parasite directly, but high activity and frequent appearances of bees due to high nest aggregations inevitably led to frequent disturbances of parasites.

When a female wasp landed on the surface of a nest box, it started to search, tapping the reed ends with its antennae, and when in contact with an open nest, the wasp turned around and wagged its abdomen over the entrance, possibly adding a chemical marker to the nest (Westrich, 1989).

Wasps often settled and hid between reeds, and crouched close to the surface as a bee arrived. When the bee left the nest, the wasp moved quickly to the nest and entered it. Bees that arrived at a nest never showed any reaction to the presence of an immobile, crouching wasp.

The inspection of a nest by *S. clavicornis* led to either waggings and continued search or to entering the nest. A nest was first entered forwards; after 2–15 s, the wasp backed out and either wagged over the nest entrance and continued searching, or turned around and entered the nest backwards. After entering backwards, the stay inside a nest lasted between 4 s and 1 min (mean = 16.3 s, SD = 13.5, $n = 30$). Entering backwards indicated that oviposition may have taken place, however no eggs were found in nests where this behaviour had taken place during the bees' provision flights. Thus, either no egg had been deposited or the egg was subsequently removed by the bee. The observed nests were inspected numerous times, by several wasps during a day. The wagging behaviour never prevented competing, congeneric wasps from entering the nest, but may have led to an easy recognition of suitable nests during succeeding searches.

Parasitism

Parasitism of *C. florissomne* related to nest and cell features is shown in Table 1. Of the 305 brood cells examined, 9.5% were parasitised by *S. clavicornis*, whereas 27.4% of the 197 empty cells contained one or more dead *S. clavicornis* larvae ($\chi^2 = 26.52$, $P < 0.001$). Parasitism in 185 brood cells with an anterior, empty cell and 120 brood cells without an anterior, empty cell was 4.32 and 17.5%, respectively. The presence of an empty cell in front of a brood cell therefore reduced the degree of parasitism in *C. florissomne* significantly ($\chi^2 = 13.19$, $P < 0.001$).

The outermost brood cell is usually protected by a vestibule closure, but was protected by an anterior, empty cell (i.e. a short cell with the characteristic, thin and soft cell closure) in 42.3% of the nests, whereas such an anterior, empty cell was found in 74.3% of the rest of the brood cells ($n = 175$) ($\chi^2 = 30.64$, $P < 0.001$). Exclusion of the outermost brood cells in the analysis, due to their different protection features, revealed a large difference in degree of parasitism between brood cells with and without anterior, empty cells: 5.4% ($n = 130$) and 28.9% ($n = 45$), respectively ($\chi^2 = 16.00$, $P < 0.001$).

The degree of parasitism was lower in those outermost brood cells that were not protected by an anterior, empty cell compared with other brood cells also lacking an anterior, empty cell (10.7 and 28.9%, respectively, $\chi^2 = 5.27$, $P < 0.01$). This may be due to vestibule closures, constructed soon after the completion of the last brood cell in a nest.

The presence of an empty cell in front of a brood cell played a major role in determining the degree of parasitism in brood cells. When the female wasp deposited its egg through a newly finished cell closure, it was apparently unable to determine whether the cell behind the cell closure was a brood cell or an empty cell. Wasp larvae in empty cells were always found to have died in their first instar.

A total of 110 eggs and larvae of *S. clavicornis* was found, 81 of these (73.6%) in 54 empty cells, i.e. on average 1.5 larvae per attacked empty cell (range: one to six larvae). A considerable proportion of offspring was therefore lost due to inexpedient egg deposition. Furthermore, an unknown number of eggs may have been removed from brood cells by the bee during the course of provisioning.

Discussion

Temporal aspects

The daily activity pattern showed that *S. clavicornis* was well adapted to its host. It investigated and entered nests throughout the afternoon as the time of individual bee oviposition varied greatly within the colony and could take place at any time in the afternoon.

Brood cells were left unprotected by the bee at various times during the provisioning and building sequences: (1) Provisioning included 12–14 pollen trips, each about 20 min long, plus one last nectar trip of about 30 min prior to

Table 1. Percentage of *Sapyga clavicornis* attacks related to the cell features in *Chelostoma florissomme*.

Cell features	Percentage of attacks	<i>n</i>
Empty cells, total	27.4 ^a	197
Brood cells, total	9.5	305
Brood cells with anterior empty cell	4.3	185
Brood cells without anterior empty cell	17.5	120
Brood cells with anterior empty cell, excluding outermost brood cell	5.4	130
Brood cells without anterior empty cell, excluding outermost brood cell	28.9	45
Outermost brood cell with anterior empty cell	1.8	55
Outermost brood cell without anterior empty cell	10.7	75

^aAt least one *S. clavicornis* larva found in the empty cell.

oviposition. During these trips, parasites have access to the brood cell, but parasite eggs are easily found and destroyed by the provisioning bee (Westrich, 1989; M. Münster-Swendsen & I. Calabuig, pers. obs.). (2) Immediately after having deposited its egg, the bee began constructing a cell closure. This took 10–19 min and was finished after five short flights during which the cell was left by the bee for 6–13 min in all. (3) After finishing the cell closure, the bee made an excursion (possibly for nectar) that lasted 9–45 min. During this period, it was possible for the nest parasite to oviposit through the cell closure into the brood cell. After this excursion, the bee would either make another excursion or initiate construction of another cell (or vestibule) closure. (4) The activity pattern during formation of an additional cell closure, i.e. an empty cell, was observed only a few times and only after 18.00 hours. It took five flights of 2.5–17 min to finish the additional cell closure. It is not known how much construction and thus how many flights would suffice to prevent the parasite from ovipositing through the brood cell's closure, however the time spent during the first flights and the excursions mentioned above must be regarded as the most crucial period. It may be expected that the time spent on formation of an additional cell closure during mid-afternoon would have been shorter than that observed in the evenings. (5) It took almost 4 h to construct a vestibule closure protecting the outermost brood cell. The building included more than 30 flights, but the first five flights were short, leaving the nest without surveillance for 3 min 22 s in all (only one observation). After these five flights, an intact clay membrane was constructed and the outermost brood cell was thereby protected as by an empty cell.

The construction of an anterior, empty cell is apparently highly effective in limiting parasitism. For the wasp, safe deposition of eggs is restricted to a fairly narrow time window, i.e. from the time when the brood cell closure has been finished until the additional cell closure is made. It seems logical to assume that the greatest efficiency of an anterior, empty cell is obtained if the second cell closure is constructed immediately after the completion of a brood cell.

Efficiency of precautions of C. florissomme

Female *C. florissomme* employ at least three different behavioural means to limit parasitism: aggregation in colonies, removal of parasite eggs, and construction of empty cells; bees might also simply prevent foreign intrusion from inside their nests. Although *S. clavicornis* was not chased away actively, bees arriving and departing at the eaves seemed to have a density-dependent, disturbing effect on its activities. On the other hand, high densities of bee nests might also attract the parasite.

During the provision period, a parasite visit with a backward entry into the nest was commonly followed by the bee's vigorous cleaning of the nest, removal of parasite eggs and even part of the stored pollen. Similar behaviour in *C. florissomme* is described by Westrich (1989). These observations and the dissections of nests that had been observed during construction showed that the bee must be quite efficient in detecting and removing parasite eggs. The frequency of this behaviour and the level of mortality caused to *S. clavicornis* offspring were not studied.

The most distinctive defence shown by *C. florissomme* was the construction of empty cells in front of brood cells. An estimate of the efficiency of this behavioural precaution may be based on the expected degree of parasitism had empty cells not been constructed. If all the nonparasitised brood cells with parasitised anterior, empty cells (51 cells) were added to the number of parasitised brood cells (29 cells), the overall degree of parasitism would have been 26.2%. Thus, the construction of empty cells reduced parasitism from a potential of 26.2% to 9.51% ($\chi^2 = 27.93$, $P < 0.001$). Parker (1988), who studied nesting biology of two American *Chelostoma* species, apparently found no empty cells, but also found no nest parasites.

Earlier suggestions as to the cause and function of empty cells include aberrant behaviour in old age (Malyshev, 1935), exhaustion of egg supply (Linsley, 1958), and protection against parasitism (Wcislo *et al.*, 1993). Nests containing empty cells have been observed in species of soil-nesting

(Wcislo *et al.*, 1993), mud-nesting (Tepedino *et al.*, 1979), and hollow-stem-nesting (Sakagami & Laroca, 1971) bees. Tepedino *et al.* (1979) discussed the protection hypothesis in mud-nesting aculeates on a theoretical basis, but the protective effect against parasitism has not been demonstrated empirically (Wcislo & Cane, 1996).

The study reported here shows a significant protective effect of empty cells. The empty cells seemed to deceive the *S. clavicornis* and function as parasite traps. A similar deception effect of the tumulus in a soil-nesting bee *Panurgus banksianus* Kirby, which excavates a secondary, tumulus-free nest entrance, was observed by Münster-Swendsen (1970). More-or-less hidden nest entrances and closing of a nest with a sand plug during flight excursions to protect offspring are found commonly in soil-nesting bees (Malyshev, 1935).

Mortality

Mortality in *C. florissomne* caused by *S. clavicornis* equals the percentage of successfully parasitised brood cells, which in the present study was 9.5%. Van Lith (1957) found 17% and Maréchal (1933) 3.7% parasitism in *C. florissomne*. For *Sapyga* species attacking species of *Megachile* and *Osmia* with few or no empty cells, 45 and 77% parasitism (Torchio, 1972), 22 and 29% (Torchio, 1990), and 12% parasitism (Medler, 1967) have been observed.

The mortality of eggs and first-instar larvae in *S. clavicornis* is due to (1) interference competition (following superparasitism), (2) starvation of larvae trapped in empty cells, and (3) the bee's removal and destruction of parasite eggs deposited during the provision phase. The level of mortality due to removal and destruction of eggs is unknown, but the frequent backward entry of the female wasps during the provision phase and subsequent removal of stored pollen by the bee indicated that this mortality may have been high. Mortality due to competition and starvation was estimated on the basis of results showing that, in parasitised empty cells, the average number of offspring per cell was 1.50, and all died. Assuming a similar distribution of offspring per parasitised brood cell gives an average of 1.0 survivors and 0.5 dead offspring per cell. By multiplying these figures by the observed frequencies of empty cells and brood cells (0.392 and 0.608), and by their respective frequencies of parasitism (0.274 and 0.095), it was estimated that 76.6% of the eggs and young larvae of *S. clavicornis* died. In addition, an unknown proportion of eggs was killed by the bee. In comparison, Torchio (1972) observed offspring mortality in *S. pumila* due to competition of 76% and 78.5%.

The frequent inspection, marking, and entering of several nests during a day, combined with the high mortality of eggs and first-instar larvae in *S. clavicornis*, suggest an opportunistic strategy; many eggs are deposited, but the majority are lost because only a small proportion is deposited within the narrow window of host vulnerability. Although the bee and its parasite are of similar size, the parasite egg is only half the length and much slimmer than that of the bee (van Lith, 1957). Wcislo

and Cane (1996) also found that parasitic bees produce many, small eggs and invest little in parental care.

It is possible that to avoid the high mortality of eggs and larvae, every female *S. clavicornis* would have to concentrate on only one bee nest at a time, as the precise time of oviposition on a given day varies greatly among the individual bees in a colony. This strategy would result in a maximum of only one offspring produced per day, however, so the opportunistic strategy may provide a higher fitness despite the energy spent on a high number of offspring of which the majority may die at an early stage. Depending on the density of nests in a colony, a mixture of the two strategies could be beneficial, however the opportunistic strategy will generate the highest reproductive efficiency at high host densities.

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MANUSCRIPT I - I. Calabuig:

Assessment of the foraging- and nesting conditions for solitary bees and bumblebees, and their distribution in a Danish agricultural landscape

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Abstract

In a survey April through November 1997, a total of 72 solitary bee species and 19 bumblebee species were recorded in the semi-natural habitats of a Danish conventional agricultural landscape. The majority of the solitary non-inquiline bee species (59) were polylectic, but four oligoleges of Salix and six oligoleges of other plant families were recorded. The plant community of the studied area is typical of nutrient-rich soils of a conventional farmland, with annuals and vigorous species that benefit from fertilisers dominating the flora. Abundant and widespread mellitophilous plant species were all ones that may sustain a species rich but polylectically dominated bee fauna. Abundance of solitary bees and bumblebees were correlated with mellitophilous plant coverage in south-facing areas, whereas no correlation was found for honeybees. Furthermore, abundance of honeybees was not correlated with abundance of other bees. Bee species richness could not be explained by plant species richness or coverage in a multiple regression. Habitat parameters in a generalised linear model were able to predict abundance of males and inquilines, a measure of nest abundances in the habitats.

Introduction

Bee-pollinated crops account for about 30% of the food produced for humans, and the value of this pollination service exceeds the value of produced honey by at least a factor 50 (Corbet *et al.* 1991). Furthermore, thousands of wild plants depend on pollination for seed set and thus persistence in their habitat. The agricultural landscape claims the largest proportion of the total area of Denmark (65%) (Ed. by: Prip *et al.* 1996), and it is also the landscape type being altered the most by man. Pollinators constitute an important part of the fauna in this landscape but apart from the honeybees, nothing is known in Denmark about the current status of an ecologically important group of the pollinators - namely the so-called wild bees.

Apart from nesting places, the most important feature of a landscape that can sustain a diverse bee fauna is a continuous succession of flowering plants, representing a wide range of plant families. Especially Apiaceae, Asteraceae, Fabaceae, Lamiaceae, Ranunculaceae, and Rosaceae are preferred by many Danish polylectic and oligolectic bee species. The continuous succession of plants is important to the social species, which are mainly active April through September in Denmark. Social bees, and solitary bees with long flight-seasons (e.g. *Lasioglossum calceatum* and *L. leucopus*), are most often polylectic and therefore not dependent on the flowering period of only a limited range of plants.

Oligolectic species such as *Salix oligoleges* (e.g. *Andrena clarcella*, *A. praecox*, and *A. vaga*) have to be closely synchronized in emergence with the flowering of their host plants, and are more vulnerable than polyleges to changes in the flora community of the landscape.

The breeding habitats for bees in the Danish agricultural landscape are primarily hedgerows, forest edges, dry-stone walls, and field edges. Generally, soil-nesting species' nests are placed in south-faced, warm, and sun-exposed sites, with loosely packed, dry, sandy soil and patchy or no vegetation (Cane 1991; Müller *et al.* 1997; Potts & Willmer 1997; Westrich 1996). Other species are more conservative in their choice of nest substrate, e.g. *Colletes cunicularius*, which is a pioneer species that prefer areas with bare, loose sand, often near streams or in sand dunes. Breeding sites available to cavity-nesting species are primarily insect borings in dead wood, and in old *Rubus* stems and *Phragmites* stands along streams. Generalist species, such as *Anthidium manicatum* and *Osmia rufa*, nest in all kinds of holes and crevices, between stones and in old half-timber and mortar walls. Other cavity-nesting species are extreme specialists that nest exclusively in places such as abandoned snail-shells (*Osmia aurulenta*) or insect-galls (*Hylaeus pectoralis*).

Unless only a limited area is intensively studied, nests of solitary bees are difficult to locate in the field (own observations; Pers. com. C. O'Toole). Therefore, in this local study the nesting conditions are evaluated on the basis of distribution patterns of males and nest parasites. Broadly stated, in species of solitarily nesting females, the males flock around attractive foraging plants that the females visit, or the males patrol territories or leks. In gregariously nesting females, the males' mating behaviour involves staying close to the nests for female encounters (Cameron *et al.* 1996; O'Toole & Raw 1999). Nest parasites (inquilines) keep close to the nests for quick and undetected entrance when a host female leaves a nest (Münster-Swendsen & Calabuig 2000). Large trap yields of inquilines and males of a gregariously nesting species may therefore indicate presence of a nesting site in vicinity of a given trap. The recording of species richness and distribution of inquiline bees may also be used to indicate other properties of nest building species populations: 1) If no parasites are present, the bee population may not be stable and / or is newly founded. Conversely, presence of parasites may indicate that host populations have been persistent through a sufficient period for parasite detection and invasion to occur. 2) Presence of parasites may indicate host species yet to be recorded in a survey (O'Toole & Ismay 1995). 3) Parasite / host ratio, termed *Cleptoparasitic Load* (Archer 1995), may be used as a measure of habitat quality and of species diversity (I. Calabuig, Manuscript III, *In prep.*)

This study aims to assess whether solitary bees and bumblebees occur as persistent populations in the small semi-natural habitats of a Danish agricultural landscape. Though only one year of intensive data collection was carried out, and populations of bees are known to fluctuate markedly from year to year (Frankie *et al.* 1998), the confirmation of expected seasonal activity patterns of genera, and of presence and activity of inquiline species, are both strong indicators of persistent populations. The purpose of this study was furthermore to monitor on a local scale, the potential foraging- and nesting conditions for solitary bees and bumblebees, and possible competition from honeybees. Since arable land claims so large a fraction of the area of Denmark (65%), a survey of bees in an agricultural landscape also gives an indication of the general status of solitary bees in Denmark.

The main questions I address in order to review the foraging- and nesting conditions are the following: 1) Do solitary bees and bumblebees occur as abundant and persistent populations in a Danish conventional farmland? 2) What characterises the flora community of the semi-natural habitats, and what foraging potential for bees does it provide? 3) Can local coverage and species richness of mellitophilous plants explain species richness and abundance of solitary bees and bumblebees? 4) Which abiotic habitat parameters are significant in predictions of male and parasite abundances of solitary bees, using a generalised linear model?

Materials and methods

Survey area

A survey of solitary bees and bumblebees was made April through November 1997. During December through March 1997, there was no bee activity. The area of study was north of Ringsted, northeast Zealand, Denmark (55°30-32'N, 11°45-47'E; UTM coordinates, Datum ED50, 10 km quadrates: 32UPG75). In 1997, average temperature during the main activity season of bees (April through August) was 13.4°C (4.7% above long-term mean), duration of sunshine was 1316 hours (20.0% above long-term mean), rainfall was 217 mm (12.5% below long-term mean) and mean wind-speed was 4.0 m/sec. Wind conditions are listed in Appendix 1; all data from the Danish Meteorological Institute.

The study area is an agricultural landscape dominated by conventional farming practice, but with smaller fields than average on Zealand and a higher abundance of hedgerows and other semi-natural habitats. The landscape is dominated by fields, hedgerows, dry-stone walls and small forests on calcareous soils with natural springs and streams.

I selected three routes (transects), each two kilometres long, along hedgerows, and other semi-natural habitats. All transects and traps were mapped using a GPS-receiver (Global Positioning System) for implementation in ArView GIS (Geographical Information System). Transects 1, 2 & 3 are shown in Fig. 1. The three transects traversed fields with (in order of declining abundance) winter wheat, winter- and spring barley, peas, beets, and grass mixed with red clover. Another important crop in the area was winter oilseed rape. Transect 2 was laid out in an area used for water-supply, and consequently, there has been no application of herbicides, pesticides, or fertilizers and no outlet of waste-water in the area. Transect 2 is dominated by streams and areas where ground water seeps to the surface, surrounded by pasture and small hills with bushes and trees.

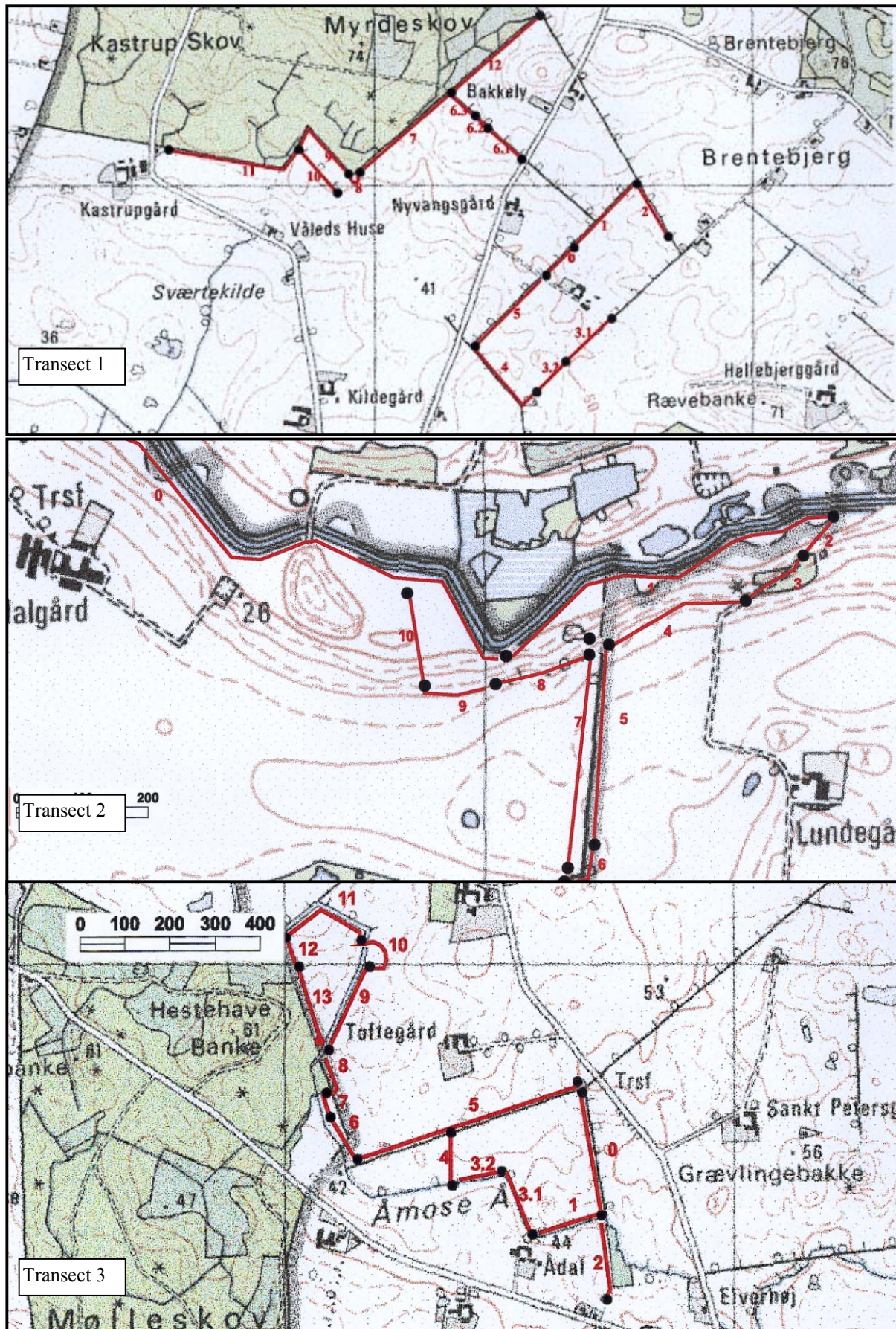


Fig. 1 Area of survey: Transect 1, 2 and 3 (habitat numbers and transect routes are marked in red).

Faunistic survey

Small window-traps (cross of ricacryl sheets, 30 x 30 cm and 22 x 30 cm) standing in yellow pan-traps (Fig. 2) placed on the ground were used to attract and thereby trap the bees. The pan-traps consisted of a rectangular plastic pan with slightly sloping sides (35 x 27 x 6 cm). The traps were coloured yellow with Hempel Poly Best (2 component enamel, no. 20250), which is a sunlight and water resistant paint. Each pan-trap was filled with approximately 3.5 litres of a 1% solution of Rodalon (Bie & Berntsen) in water. Rodalon has a faintly sweet smell that might add to attract the bees. It preserves the insects and lowers surface tension, causing the insects to sink and not escaping from the water surface.

Colourimetric properties of the yellow pan-traps were measured using a Monolithic Miniature Spectrometer (10 nm resolution (Rayleigh-criterion), model MMS1, Zeiss), with a reflection measuring head (model OMK 500-H, Zeiss) in ultra-violet and visible light (wavelengths 319-950 nm). Measuring field: 20 mm, light source type: D65, illumination angle: 0° and detection: diffuse at 45°. Standard: pure white Russian opal tile. The spectral reflectance curves of an unused trap and a trap used for the whole sampling season are shown in Fig. 3, both traps containing water. According to Daumer (1958), the reflectance spectrum of the traps represent the UV group (300-390 nm) and the yellow group (500-650 nm) of colours perceived by bees. Exposure to sunlight for eight months during the survey does not seem to have altered the colour of the traps. (Analyses made by Broch & Michelsen, Denmark).



Fig. 2 Window-trap in yellow pan-trap.

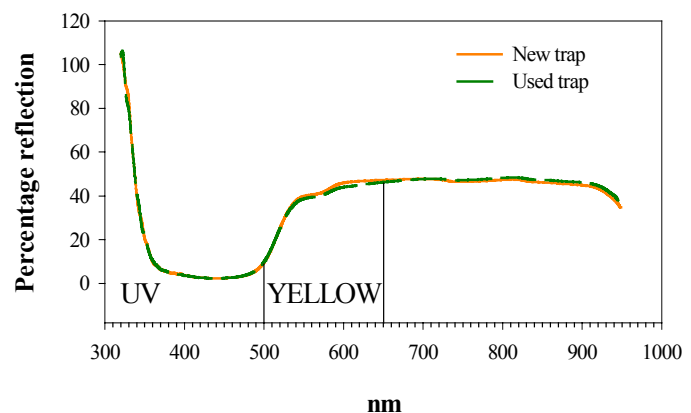


Fig. 3 Trap colour reflection of light (traps with water).

The traps were placed along the habitats with a constant distance of 100 metres, coming to a total of: 21, 21 and 22 traps along transects 1, 2 and 3 respectively (64 traps in all). As the vegetation on the neighbouring fields grew higher and threatened to obscure the traps, I removed the vegetation in a radius of one metre around the traps to keep the exposure of the traps relatively constant. Traps of transects 1 and 2 were emptied 20 times, April 30 through November 4, 1997. Transect 3 traps were emptied 17 times, May 27 through November 4, 1997. Traps were normally emptied once a week. In the warmest periods, traps were emptied with intervals a little less than a week to avoid desiccation of the traps and decomposition of

trapped insects. In cold and rainy periods, the traps were left unattended for up to 13 days at a time. The trap yields were rinsed and stored in 70% ethanol.

The material was sorted and all bee specimens counted and identified to species. Voucher specimens are deposited in Department of Population Ecology, University of Copenhagen, Denmark. All non-bee insects and other arthropods were not examined further. They belonged primarily to Arachnida, Diptera, Coleoptera, Thysanoptera, Homoptera, and Hemiptera.

Species identifications were made according to Alford (1975), Amiet (1996), Dathe (1980), Prys-Jones & Corbet (1991), Scheuchl (1995), Scheuchl (1996), Schmid-Egger & Scheuchl (1997), and George R. Else (*In prep.*, drafts for *Andrena*, *Halictus*, *Lasioglossum*, *Sphecodes*, *Nomada*, *Colletes*, and *Hylaeus*). Additional literature was consulted and included Celary (1999), Ebmer (1987), Jørgensen (1921), Perkins (1922), Sustera (1959), and Warncke (1992). Nomenclature was updated using Madsen & Calabuig (*In prep.*), Schwarz *et al.* (1996), and Westrich (1990b). Parasite-host relationships for the genera *Sphecodes* and *Nomada* were listed according to Scheuchl (1995) and Westrich (1990a) and was supplemented by Jørgensen (1921) and Lomholdt (1977). Parasite-host relationships for the (sub)genus *Psithyrus* were listed according to Amiet (1996), Hagen (1994), Jørgensen (1921), Løken (1984), Prys-Jones & Corbet (1991), and Westrich (1990b).

Flora survey

In spring, summer, and late summer, I evaluated the floral composition along the habitats. All flowering herbs were recorded using the semi-quantitative coverage and abundance index (*Total Estimate Scale*) of Braun-Blanquet (Braun-Blanquet 1983; Mueller-Dombois & Ellenberg 1974; Smith 1996). It should be noted that the modified version of the *Total Estimate Scale* was used, as described by Smith (1996), which is fine-scaled in the lower sections of the intervals of coverage, and this was considered more suitable for the type of flowering plant community found in the present survey.

In the *Total Estimate Scale* (Table 1) index, a given plant species is assigned to 1 of 8 classes according to its abundance, density, and coverage of the area. The *Total Estimate Scale* is recommended when surveying larger areas (>1-2 m²) and/or many species (Braun-Blanquet 1983).

Table 1 *Total Estimate Scale*, abundance plus coverage (modified from Smith (1996)).

r	Solitary, one observation, coverage very small
+	Individuals of a species sparsely present in the stand; coverage very small
1	Individuals plentiful, but coverage small
2	Individuals very numerous if small; if large, covering at most 5% of area
3	Individuals few or many, collectively covering 6-25% of the area
4	Individuals few or many, collectively covering 26-50% of the area
5	Plants cover 51-75% of the area
6	Plants cover 76-100% of the area

The index method of Braun-Blanquet was applied along the transects for every 100 metre stretches (relevés), with each pan-trap being the mid point of a relevé. The data were recorded during a slow walk along the habitat, first listing all flowering species of plants, then assigning the index values of the *Total Estimate Scale* for each species occurring. In addition, coverage of butterbur (*Petasites hybridus*), Bedstraw (*Galium aparine*), grass and non-flowering herbs (combined), and bare soil was estimated. Data was checked for accuracy

during a third walk through the relevé, before continuing to the next. A presence/absence index was calculated, listing in how many of the relevés each species was present.

Processing of Braun-Blanquet values for statistical analysis

The index of Braun-Blanquet was recorded for each species of plants, but in order to correlate overall occurrence of flowering plants to relative bee abundance, it was necessary to pool plant species. For this purpose, the Braun-Blanquet index values were converted to coverage frequencies, which may be summed within a sample. In addition, all recorded plant species were indexed according to their biological value as nectar and pollen resource for honeybees and bumblebees. First, the primary species list was compared to the checklist of plants visited by solitary and social bees as indicated by Westrich (1990a). All remaining flowering species with no nectar or pollen value at all for bees, e.g. wind-pollinated species (11 in this survey according to Proctor *et al.* (1996)), were eliminated from further analyses, and the resulting list of mellitophilous species is to be found in Appendix 3. I then evaluated several different bee plant calendars (Christensen 1984; Hagen 1994; Hodges 1952; Howes 1979), but to ensure constancy in these relative measures, the nectar and pollen values indicated in Christensen (1984) were primarily used for further calculations. Since flowering periods vary between regions, this plant calendar was also chosen due to its Danish origin. The plant calendars rank species pollen- and nectar content with 0, 1, 2 or 3 which corresponds to "no, little, some, plenty" respectively. These values for nectar and pollen were combined into one index value for each plant species. When appropriate, coverage of herbs, bushes and trees were weighed by multiplication by the index values.

Habitat types and abiotic survey

A standardised characterisation of the transects was made in cooperation with the Danish Institute of Agricultural Sciences. All transects were divided according to type of habitat (hedgerow, dry-stone wall, forest edge etc.). Further subdivision was applied when necessary, e.g. a distinct change in vegetation density of a hedgerow. Eight habitat types were represented along the six kilometres of transects (Table 2), some types had to be subdivided according to type of surrounding area or heterogeneity of the habitat itself.

Table 2 Habitat types along transects 1-3.

Hedgerow	All traversed fields with annual crops a) Type Hedgerow: Trap standing next to woody vegetation b) Type Hedge-hole: Trap standing in an open area of hedgerow
Forest edge	All were flanked by fields with annual crops
Pond edge	An areal habitat in connection with forest edge and flanked by cereal crops
Bog edge	An areal, damp habitat with bushes and trees, flanked by cereal crops
Stream	a) Flanked by uncultured pastures on either side and with no or very few bushes and trees growing along the sides b) Traversed fields with annual crops and with no or very few bushes and trees growing along the sides c) Traversed fields with annual crops and with high density of trees and bushes growing along the sides
Pasture	Transect traversed set-aside pasture
Road side	a) Flanked by dense bushes and trees on one side and field with cereal crop on the other side b) Flanked by dry, sloping set-aside pasture on one side and field with cereal crop on the other side
Field strip	Cereal crops on both sides of elevated strip of soil with vegetation

Within each habitat type and for each trap, the following parameters were recorded (Table 3):

Table 3 Habitat characteristics. Parameters in brackets or with no abbreviation indicated were not implemented in the Generalized Linear Model (see below). (All lengths and widths in metres, all cover values in frequencies).

Abbrev.	
TNO	Transect number
HTYP	Habitat type
O	Geographical orientation (and full length) - E.g.: A trap placed on the southern side of a hedgerow running west to east was thus defined as having a south-facing aspect
HERB	Absence / presence of traces on the vegetation from herbicide use
PET	Absence / presence of extensive <i>Petasites hybridus</i> (Butterbur) cover
	Species of bushes and trees
WC	Total woody cover (and coverage for each species - measured by the Braun-Blanquet Index)
BW	Width of the habitat
WW	Width of woody cover if present
SW	Width of uncultured strip of soil along the side of the linear or areal habitat proper
SLOPE	Uncultured strip of soil distinctively sloping, relative to surrounding area
SSC	Soil, (grass and herb) cover of uncultured strip
BSC	Soil, (grass and herb) cover of base of habitat
HSC	Soil, (grass and herb) cover of base of any holes present in hedgerows
ST	Amount of larger stones and gravel in the habitat, classes: 1= none, 2= few, 3= some 4= plenty
LEV	Levelling of habitat base (e.g. hedgerow floor) above surrounding area, classes: 1= 0-0.25, 2= 0.25-0.50, 3= 0.5-1 and 4= >1 metre above level of surrounding area
	Height of dry-stone wall if present
	Vegetation cover of dry-stone wall if present

Data Analyses

All quantitative data were tested for normality using a Kolmogorov-Smirnov test (with Lilliefors' correction). Some parameters needed a $\ln(x+1)$ transformation to meet criteria for normality and homoscedasticity. Cover frequencies with extensive spanning in data values were ArcSin-Squareroot transformed prior to analysis (Sokal & Rohlf 1995). Spreadsheets and statistical packages used: Excel 2000, Sigma Stat ver. 2.03, Sigmaplot ver. 5.01, SAS for Windows ver. 6.12 (SAS Institute Inc.). Nesting conditions were analysed using a generalised linear model (SAS: PROC GLM) with Sum of Squares: Type 3 and all pairwise comparisons of class variables (MEANS X/TUKEY CLM CLDIFF). Further explanations of data analyses are given in the results section.

Results

Species richness and composition

The bees have all been identified to species, rendering a total of 72 species of solitary bees (13 genera), 13 species of bumblebees (*Bombus spp.*), 6 species of parasitic bumblebees (*Psithyrus spp.*) and the honeybee (*Apis mellifera*); see Table 4 and species inventory in Appendix 2. Note that two species of *Andrena* could not be separated with certainty. Therefore, the number of species in further analyses is 91 (see Appendix 2).

Table 4 Number of individuals collected.

	Males	Females	Workers	Total
<i>Apis mellifera</i>	-	-	2181	2181
<i>Bombus spp.</i>	442	690	1671	2803
<i>Psithyrus spp.</i>	252	328	-	580
Non-Apidae bees	2743	5396	-	8139
Total	3437	6414	3852	13703

The total of 91 bee species comprised 13703 individuals and a species abundance distribution is shown in Fig. 4. About 20% of the species were represented by only one individual and 32% by two to 15 individuals. Only two species (*Andrena helvola* and *Lasioglossum leucopus*) occurred in numbers higher than 1000, followed by the honeybee, which was the most abundant species recorded in the survey (2181 workers).

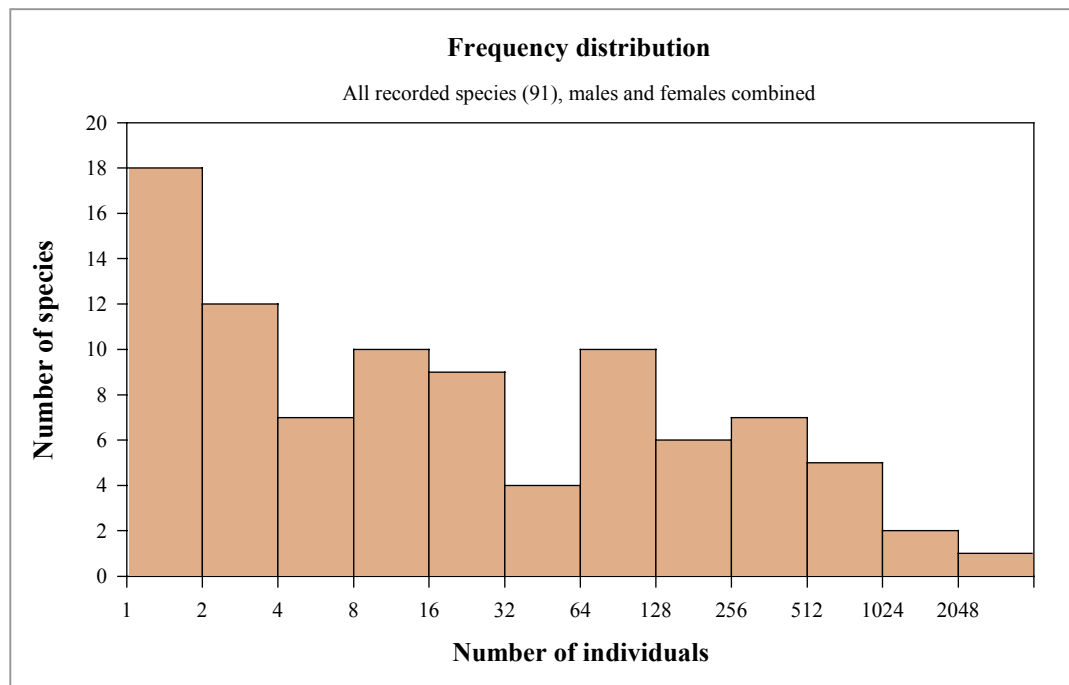


Fig. 4 Species frequency distribution. Log₂ octaves are used as the intervals of abundance categories, axis labels showing the lower boundary of a class. For clarity, species represented by only one individual are plotted separately (i.e. 2⁰).

The species most commonly found in the study area are listed in Table 5 and Table 6. The honeybee (*Apis mellifera*) and all the recorded bumblebees (*Bombus sp.*) (Table 5) are polylectic, i.e. collect pollen from a wide range of plant families and/or genera.

Table 5 Abundant social bees, all transects combined.

Species	Number of individuals			
	Males	Females	Workers	Total
<i>Apis mellifera</i>	0	0	2181	2181
<i>Bombus hortorum</i>	78	86	159	323
<i>Bombus lapidarius</i>	43	56	218	317
<i>Bombus lucorum</i>	109	126	407	642
<i>Bombus pascuorum</i>	89	154	587	830
<i>Bombus terrestris</i>	65	182	91	338

Of the abundant solitary species (Table 6), only *Andrena praecox* is oligolectic, i.e. restricted in pollen collection to only a few species or a single genus or family of host plants. *A. praecox* is strictly oligolectic on willow (*Salix spp.*). The rest of the most common solitary species recorded are all polylectic or inquiline, i.e. members of the genus *Nomada* are all parasites of other solitary bees, mainly on representatives of the genus *Andrena* (see also Appendix 4 and Appendix 5). Catch numbers do not express real densities in the landscape, but may be used as relative measures of species abundances.

Table 6 Abundant solitary bees, all transects combined.

Species	Number of individuals			Pollen source
	Males	Females	Total	
<i>Andrena bicolor</i>	12	233	245	Polylectic
<i>Andrena haemorrhoa</i>	347	172	519	Polylectic
<i>Andrena helvola</i>	1051	192	1243	Polylectic
<i>Andrena minutula</i>	126	267	393	Polylectic
<i>Andrena praecox</i>	30	215	245	Oligolectic
<i>Andrena scotica</i>	93	135	228	Polylectic
<i>Halictus tumulorum</i>	24	505	529	Polylectic
<i>Lasioglossum calceatum</i>	10	269	279	Polylectic
<i>Lasioglossum leucopus</i>	169	1822	1991	(Polylectic)
<i>Lasioglossum quadrinotatum</i>	25	383	408	(Polylectic)
<i>Nomada marshamella</i>	141	200	341	None (inquiline)
<i>Nomada panzeri</i>	465	192	657	None (inquiline)

Phenology and seasonality

Data from Transect 1 (Fig. 5 and Fig. 6) are used to illustrate the pattern of seasonality and activity of the bees. Abundance is shown as frequencies within genus to allow for comparative measures in seasonal activity among genera. In early spring the females and males of *Andrena* and *Nomada* appeared (Fig. 5a and Fig. 6a). The majority of males were active during a period of about three weeks (Fig. 6a), with a maximum of individuals recorded in the traps on April 30, whereas most of the females were recorded during two months, peaking around May 29.

The seasonal pattern of the parasites (*Nomada*) was completely synchronised with that of their hosts (*Andrena*).

The other major group of bees, *Halictus* and *Lasioglossum*, also appeared in early spring (Fig. 5b). Some species of these two genera appeared later in the season, others produced offspring, that emerged late in the season to mate and over-winter. All together, a second peak of individuals was recorded August 8 through September 29. During this second peak of female individuals, the males of *Halictus* and *Lasioglossum* also hatched (Fig. 6a). Females of *Sphcodes* were completely synchronised with their host genera *Halictus* and *Lasioglossum* (Fig. 5b). Males of *Sphcodes* were too scarcely represented in the traps to illustrate any seasonal pattern (5, 13, and 10 individuals in transects 1, 2, 3 respectively) but all were caught July 30 through September 22, which corresponds with the second peak of females.

The queens of *Bombus spp.* emerged from their hibernation in early spring (Fig. 6b). The queens forage for a short period and seek out a suitable nesting place. After the production of the first workers, the queens stay under ground and are no longer caught in the traps. The first workers were recorded in the traps around June 9 (Fig. 6b). Later in the season, (June through July in 1997, Fig. 6a-b), the males and new queens were caught, as they hatch and take off from the nests to mate in the end of the season. The males die and the new queens burrow into the soil for over-wintering.

Unlike solitary bee inquilines, which parasitise one brood cell at a time and therefore are active outside nests all through the main period of host activity, *Psithyrus* females carry out a one-time invasion of *Bombus* nests. The *Psithyrus* females emerged from hibernation a little later than their *Bombus* hosts (Fig. 6b), and they were primarily caught in spring and early summer, as they search for established host nests. For the remainder of the season, *Psithyrus* females stay under ground, tended by *Bombus* workers, producing only reproductive offspring. Thus, the constant but very low fraction of *Psithyrus* females that were caught all through the summer and autumn presumably were new females that mate, and which otherwise are seen foraging rather listlessly until time comes to burrow into the soil for over-wintering. *Psithyrus* males were primarily trapped June 25 through August 25 (Fig. 6a). The honeybees appeared rather late in the traps (Fig. 6b) and the majority of individuals were caught between September 1 and October 9.

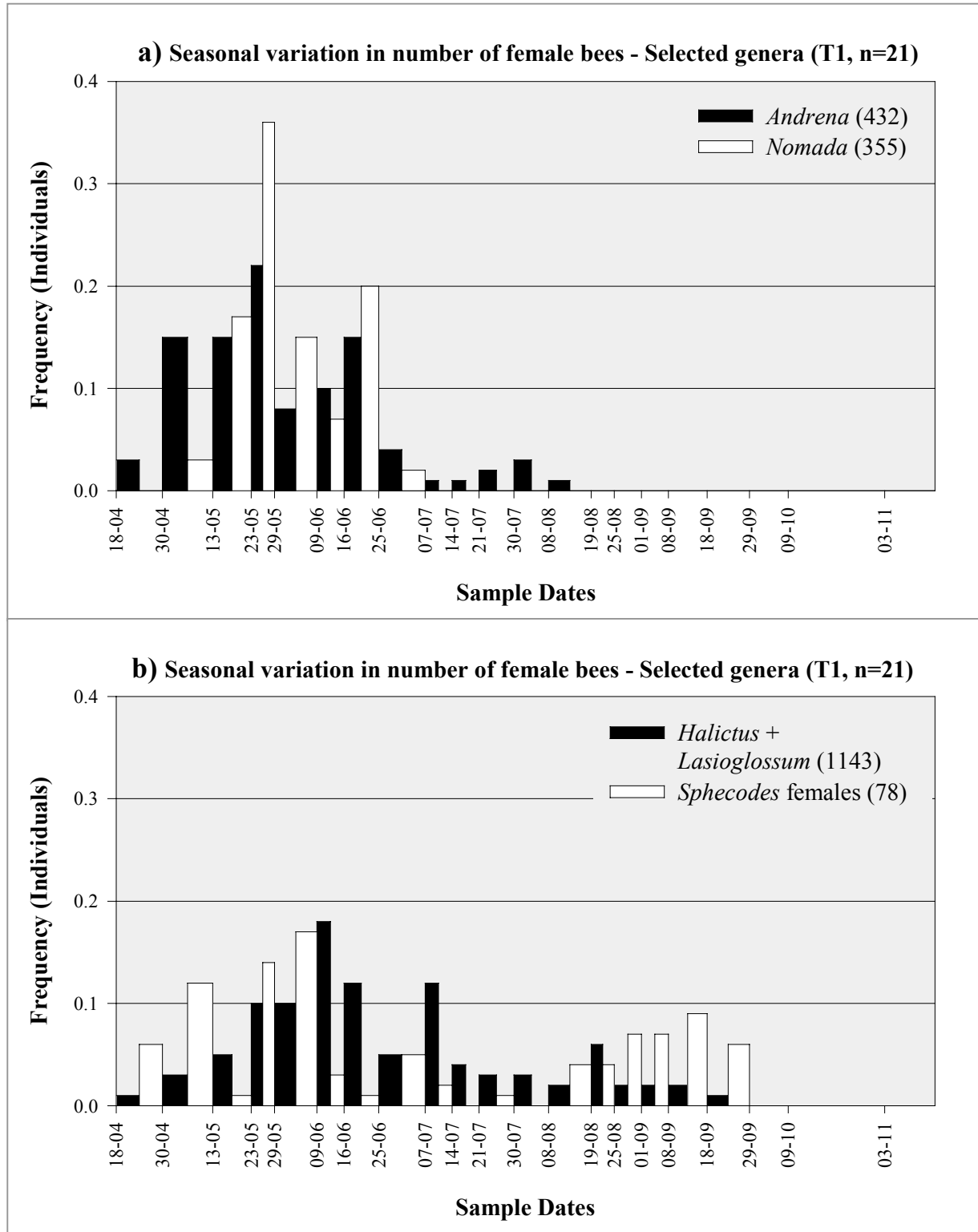


Fig. 5 a)-b) Seasonal variation in number of female bees - selected genera. Data are expressed as frequencies of relative catch per day. On each sample date, all 21 traps were emptied and the data are pooled for each date. Width of bars indicates number of days between sample dates. Legend numbers in brackets indicate number of individuals caught in all during the season. (Transect 1, n=21 traps per date).

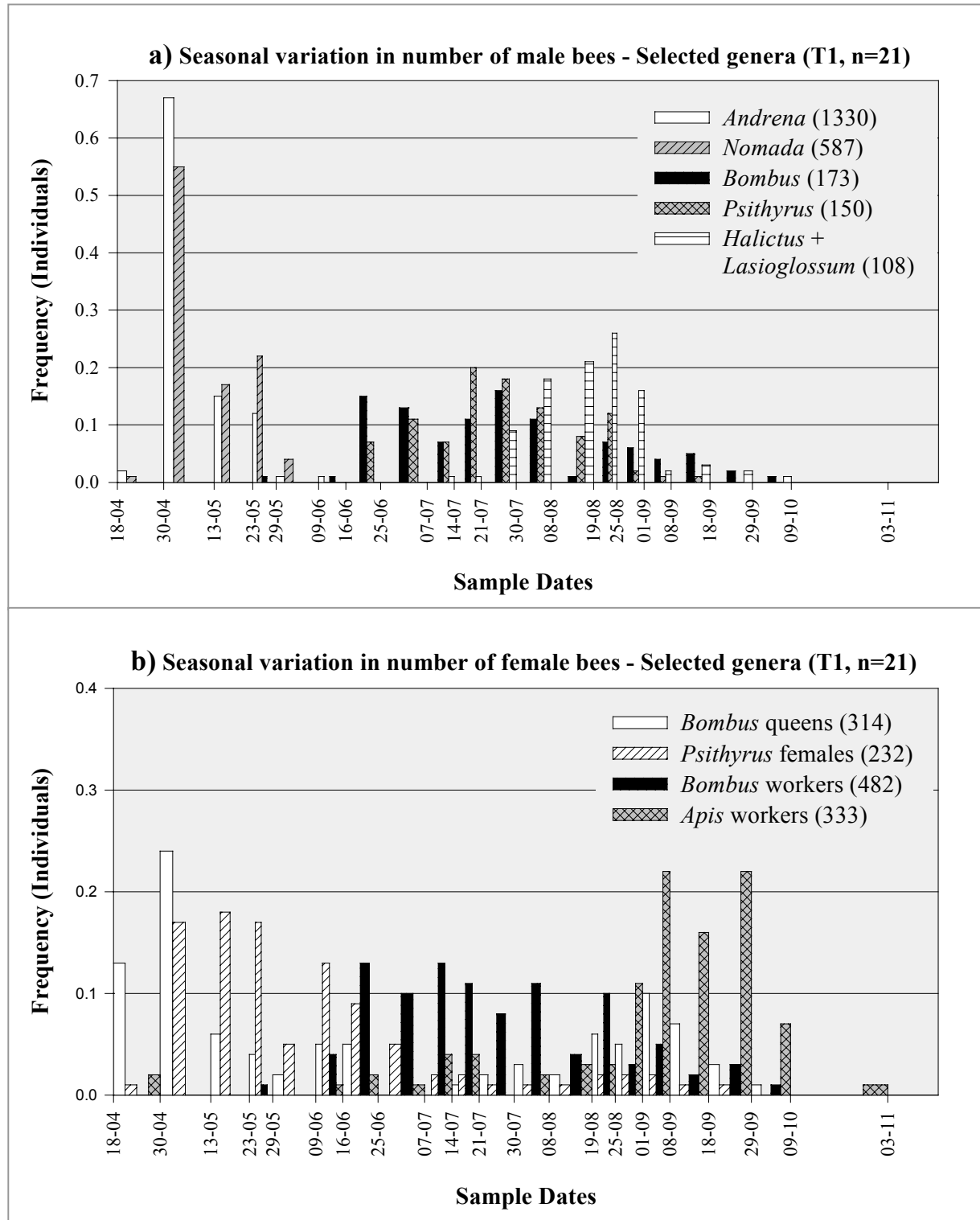


Fig. 6 **a)** Seasonal variation in number of male bees - selected genera. **b)** Seasonal variation in number of Apidae females (queens and workers). See explanatory caption in Fig. 5.

Plant community and forage value of the semi-natural habitats

A total of 126 mellitophilous plant species in 29 families were recorded in the 64 relevés (i.e. 100 metre stretches with each pan-trap as midpoint). Asteraceae was clearly the most species rich family in this survey (Fig. 7) and four of the species were present in almost half of all relevés (Appendix 3). Asteraceae, Lamiaceae, Apiaceae, and Scrophulariaceae were the most widespread plant families in the area, each recorded in about 40 to 45 of the relevés (Fig. 7). About half of the families were patchily distributed and only recorded in ten or less relevés.

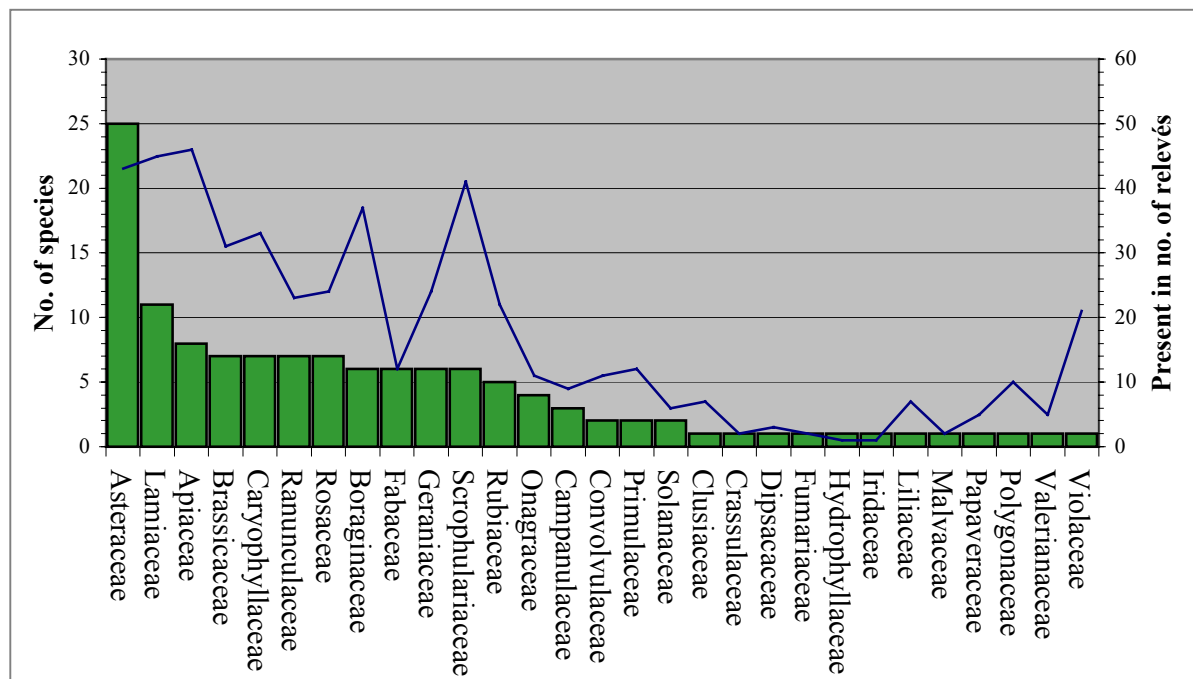


Fig. 7 Number of plant species recorded per plant family (bar-chart, left Y-axis), and plant family represented in number of relevés (line-chart, right Y-axis). Transects 1-3, number of relevés = 64.

In Table 7 are listed the number of non-Apidae bee species that utilise the recorded plant families. Asteraceae, Rosaceae, Ranunculaceae, and Brassicaceae were the families that the largest number of bee species includes in their foraging repertoire, e.g. 68% of the recorded non-Apidae non-inquiline (NANI) bee species forage on Asteraceae (Table 7, Appendix 4), though only *Colletes daviesanus* is strictly oligolectic on this plant family. The four most abundant plant families were also ones that were utilised by at least 20% of the bee species. Eight of the plant families (i.e. 27.6%) are not listed as host for any of the recorded solitary species.

Nine species of *Salix* were recorded (mostly as single individuals) in 13 relevés along the linear habitats, and Salicaceae is included at the end of Table 7 to indicate that 41.5% of the bee species utilise this family, and of these species, *Andrena clarcella*, *A. praecox*, *A. vaga* and *Colletes cunicularius* are strictly oligolectic on *Salix*. Six other oligolectic or limited polylectic species were recorded (Appendix 4) and they forage on Fabaceae, Lamiaceae, Scrophulariaceae, Campanulaceae, Ranunculaceae, and Asteraceae.

Table 7 Recorded plant families and number of recorded solitary bee species foraging on these families (data extracted from Appendix 4). Number of bee species also given as percentage of recorded non-inquiline solitary species, for which lecti is known (53 species in all).

Plant family	No. of bee species	%	Plant family	No. of bee species	%
Asteraceae	36	67.92	Dipsacaceae	4	7.55
Rosaceae	34	64.15	Geraniaceae	4	7.55
Ranunculaceae	27	50.94	Papaveraceae	4	7.55
Brassicaceae	25	47.17	Onagraceae	2	3.77
Apiaceae	17	32.08	Primulaceae	2	3.77
Campanulaceae	16	30.19	Polygonaceae	1	1.89
Scrophulariaceae	16	30.19	Fumariaceae	0	0.00
Fabaceae	14	26.42	Hydrophylaceae	0	0.00
Caryophyllaceae	13	24.53	Iridaceae	0	0.00
Lamiaceae	11	20.75	Malvaceae	0	0.00
Boraginaceae	8	15.09	Rubiaceae	0	0.00
Liliaceae	7	13.21	Solanaceae	0	0.00
Clusiaceae	6	11.32	Valerianaceae	0	0.00
Convolvulaceae	6	11.32	Violaceae	0	0.00
Crassulaceae	6	11.32	Salicaceae (Salix)	22	41.5

General foraging conditions and geographical orientation of traps

Non-inquiline species of bees in transects 1 and 3 were divided into four different groups that were analysed separately: 1) Non-Apidae, non-inquiline (NANI) females, 2) *Apis* workers, 3) *Bombus* workers, and 4) *Bombus* queens. For each of the bee groups, the data were grouped according to each trap's geographical position relative to linear or areal habitat (see category *O* in Table 3). A Two-Way ANOVA including interactions on all four bee groups and the four aspect groups of traps (data $\ln(x+1)$ transformed) showed that mean number of individuals differed between aspect groups ($P < 0.001$), and the distribution patterns of the four groups of bees differed from each other ($P < 0.001$).

Within bee groups, NANI females were most abundant in south-facing traps ($P < 0.05$), and sparse in north and east-facing traps (Fig. 8). West-facing traps contained an intermediate number of individuals (not significantly different from east). Trap yields of *Apis* workers varied greatly and no significant differences were found between aspect groups. *Bombus* workers were more frequently trapped in south-, east- and west-facing traps compared to the north-facing, but only the difference between south and north was significant ($P = 0.039$). *Bombus* queens were more abundant in south-facing than in north- and west-facing traps ($P < 0.001$ for both).

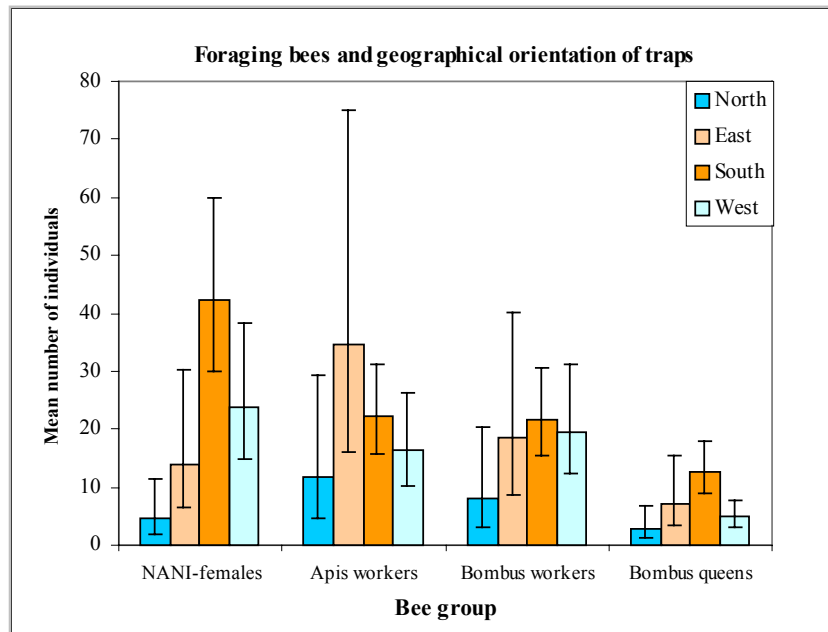


Fig. 8 Bees grouped in 1) *non-Apidae*, *non-inquiline* female bees (NANI females), 2) *Apis* workers, 3) *Bombus* workers, and 4) *Bombus* queens. All individuals within a group summed for each trap. Traps grouped according to aspect. Geometric mean and SE, based on ln-transformed data, calculated for each of the *bee x aspect* groups. (Two Way-ANOVA and all pairwise multiple comparison (Student-Newman-Keuls)). (East: $n=6$, North: $n=5$, South: $n=20$, West: $n=12$).

For each aspect group, I made linear regressions on coverage of mellitophilous herbs versus number of NANI females, *Apis* workers, *Bombus* workers and queens. For NANI females, no significant correlation was found regarding east- and west-facing traps. Percentage plant cover along north-facing traps was positively correlated with female number, but generally, plant coverage and number of females were extremely low along north- and east-facing traps, and these relevés were not analysed further. A distinct positive correlation between coverage and NANI females resulted when analysing south-facing aspects (Fig. 9a, $n=20$, $r=0.592$, $P=0.006$).

Abundance of *Apis* workers was not correlated with late season flowering plant coverage (corresponding to the main period of honeybee catches in the traps). Additional weighing of coverage according to nectar and pollen values of the plant species (Christensen 1984; Howes 1979) did not alter the result (Fig. 9b).

Bombus workers and queens were analysed separately according to their differences in overall activity period (see Fig. 6b). Abundance of over-wintered queens was compared with plant coverage recorded early in the season, and new queens with late-season coverage, whereas workers were compared with overall plant coverage of the season (average of early and late summer recordings). Neither queens nor workers showed a correlation with percentage plant cover in north- west- or east-facing areas.

In south-facing areas, abundance of over-wintered *Bombus* queens was positively correlated with percentage plant cover early in the year ($n=20$, $r=0.548$, $P=0.012$). This relationship was even more pronounced after weighing of coverage according to nectar and pollen values of the plant species (Christensen 1984; Hagen 1994; Howes 1979) (Fig. 9c, $n=20$, $r=0.686$, $P<0.001$). Abundance of *Bombus* workers was also significantly correlated with flowering herb cover of south-facing areas (Fig. 9d, $n=20$, $r=0.487$, $P=0.029$), but the correlation was not improved by weighing the coverage by nectar and pollen values of the plant species.

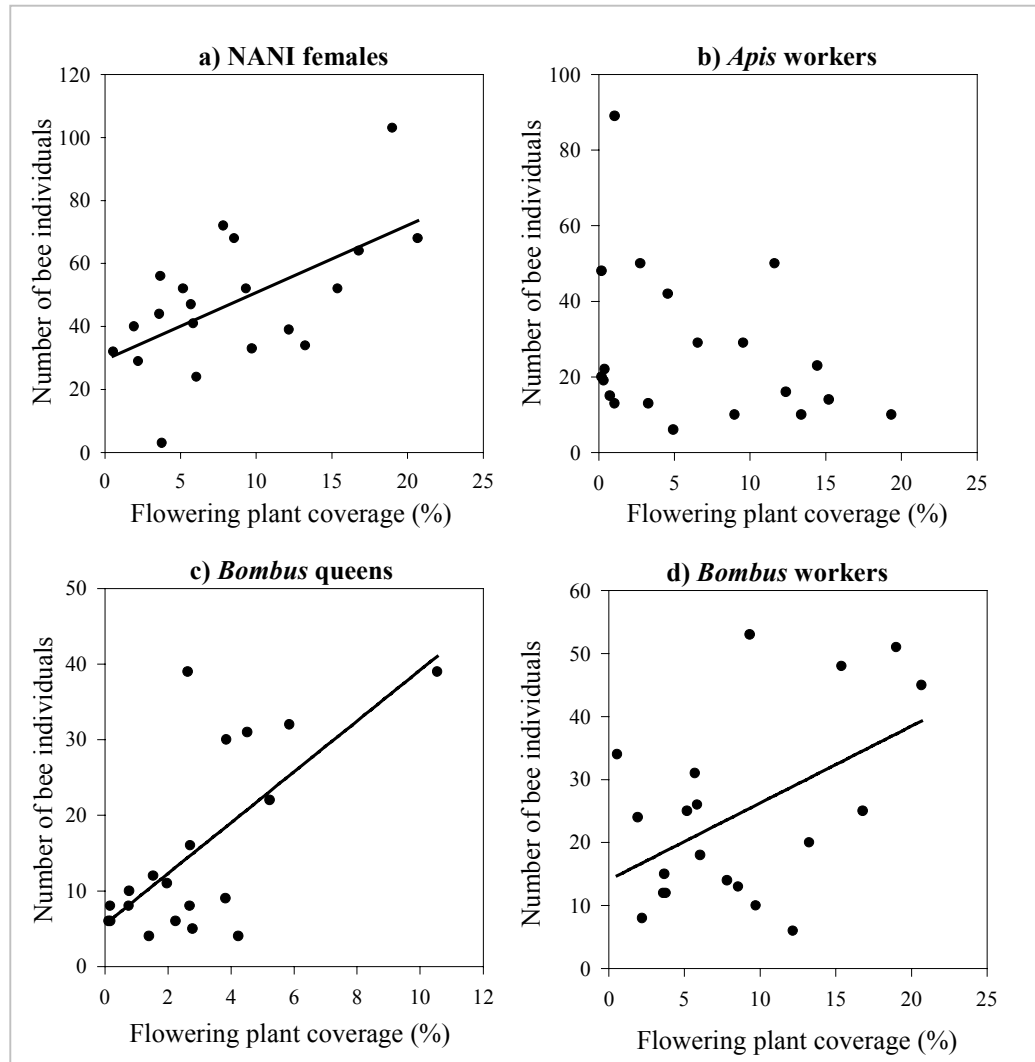


Fig. 9 a)-d) Relationship between mellitophilous plant coverage (%) and number of bee individuals in south-facing areas. **a)** Non-Apidae non-inquiline (NANI) females and average plant cover ($n=20$, $y=29.390+2.136x$, $F=9.700$, $r=0.592$, $P=0.006$). **b)** *Apis mellifera* workers and late season weighed plant cover (not significant, $n=20$, $r=0.297$, $P=0.203$). **c)** *Bombus* queens and weighed early season plant cover ($n=20$, $y=5.561+3.364x$, $F=16.034$, $r=0.686$, $P<0.001$). **d)** *Bombus* workers and average plant cover ($n=20$, $y=14.068+1.221x$, $F=5.592$, $r=0.487$, $P=0.029$).

No correlation was found between number of *Apis* individuals present in traps versus number of NANI females, *Bombus* queens or workers.

Shrub/tree coverage, weighed according to the value of each species as pollen and nectar source (Christensen 1984; Howes 1979), was not correlated with number of NANI females, *Apis mellifera* workers, *Bombus* workers or queens.

Herb coverage and richness were entered in a backwards stepwise regression with number of solitary bee species as the dependent variable. Number of NANI-species was also analysed separately. Early summer coverage, late summer coverage, as well as overall coverage were tested together with herb species richness in different model expressions, but bee species richness could not be predicted by any of the selected parameters.

Nesting conditions and parasite-host distributions

Species richness was high (23.7% of the 59 solitary, non-inquiline bee species), but abundance of individuals of cavity-nesting species was so low in this survey (79 individuals in all), that no analyses or general conclusions may be drawn on the nesting conditions for this group of bees. The few but consistent observations are discussed qualitatively in I. Calabuig (Manuscript III, *In prep.*). The following results and analyses thus refer to soil-nesting species only.

All inquiline species recorded belonged to the genera *Nomada* and *Sphecodes*, and their host species primarily belong to the genera *Andrena* and *Lasioglossum*+*Halictus*, which were the most abundant and species rich genera in this survey (22 and 20+2 species respectively). No inquiline species were found without corresponding recordings of potential host species (Appendix 5), and inquiline species richness did not exceed host richness in the samples (Fig. 10a-b).

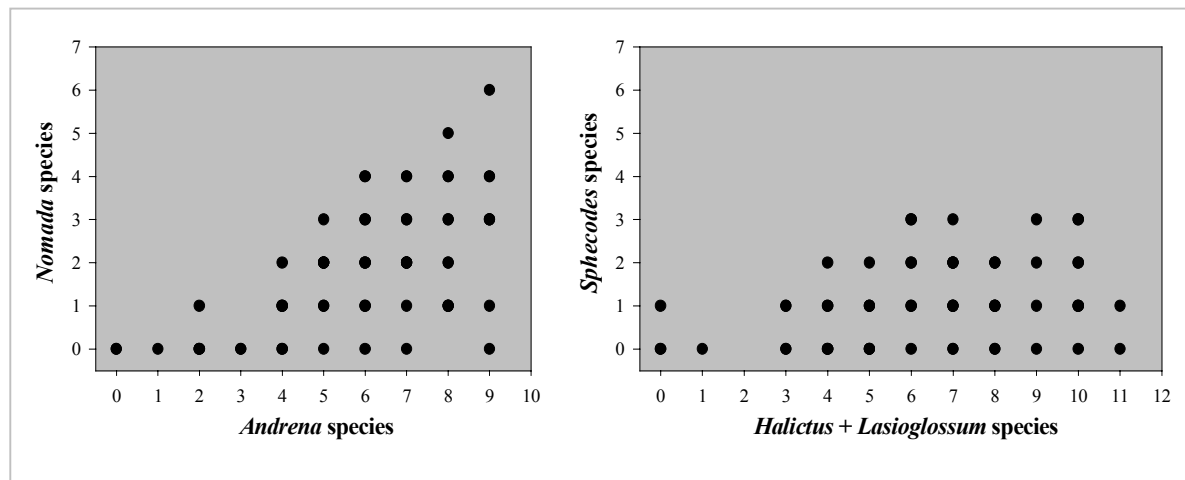


Fig. 10 a)-b) Species numbers of parasites versus hosts in transects 1-3 (n=64). a) *Nomada* versus *Andrena*. b) *Sphecodes* versus *Halictus*+*Lasioglossum*.

A linear regression of *Nomada* males and females versus *Andrena* males showed a distinct, positive correlation (Fig. 11a, $n=64$, $r=0.856$, $P<0.001$), which indicates a similar distribution of the two genera in the traps. Number of *Sphecodes* individuals was positively correlated with number of *Halictus* and *Lasioglossum* males combined (Fig. 11b, $n=64$, $r=0.533$, $P<0.001$).

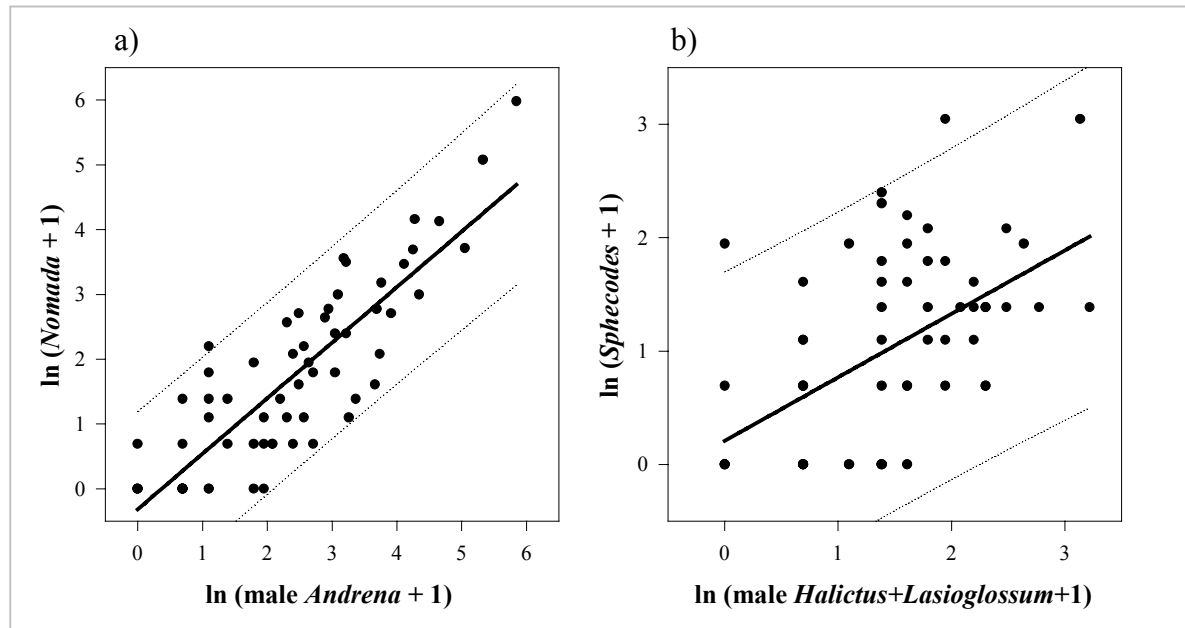


Fig. 11 **a)-b)** Number of inquiline males and females versus host male individuals. **a)** All *Nomada* males and females versus *Andrena* males ($n=64$, $y=-0.317 + 0.857x$, $F=169.268$, $r=0.856$, $P<0.001$). **b)** All *Sphcodes* males and females versus *Halictus* + *Lasioglossum* males ($n=64$, $y=0.209 + 0.559x$, $F=24.666$, $r=0.533$, $P<0.001$).

For several reasons, the inquiline-host complex of *Nomada* - *Andrena* was considered more appropriate for analysis of nesting conditions than the *Sphcodes* - *Lasioglossum*+*Halictus* complex: 1) Although species richness of *Andrena* and of *Lasioglossum*+*Halictus* were equally high, species richness of corresponding inquiline genera in total (Appendix 2) and in single traps (Fig. 10) was more than twice as high in *Nomada* compared to *Sphcodes*. 2) The species richness distribution was more clear-cut in Fig. 10a) than in b). 3) A much stronger correlation and predictive value was found in Fig. 11a) compared to b). 4) *Nomada* individuals and *Andrena* males were much more abundant and widespread (1116 and 1721 individuals respectively) compared to the 188 *Sphcodes* individuals and the 296 *Lasioglossum*+*Halictus* males recorded. 5) Only three species (plus one unidentified species) of *Andrena* were recorded without any corresponding inquiline bee species, and potential Danish inquiline species are known (Appendix 5). The apparently un-parasitised *Andrena* species were all rare, only represented by four males and eight females in all. Inquiline species of both of the recorded *Halictus* species were found, but nine species (plus three unidentified species) of *Lasioglossum* were recorded without any potential inquiline bee species in the area (Appendix 5). In all, the inquiline-host complex was therefore considered more completely revealed for *Andrena* than for *Lasioglossum* + *Halictus*.

Abundances of *Andrena* males and *Nomada* individuals were thus counted collectively as the dependent variable in a Generalised Linear Model (GLM) with selected habitat parameters as independent variables, listed in Table 8. The abundance and distribution of bees were strongly correlated with site (transect, a describing variable); but since the purpose of the model was to assess general nesting conditions in different habitat types, using predictor variables, the random effect of transect number was removed from succeeding analyses. The variables listed in Table 8 were removed backwards stepwise until only significant predictive variables entered the model. The non-significant (NS) variables are listed in Table 8 in order of elimination from the model.

Table 8 Independent quantitative and qualitative variables implemented in a GLM (for further details see Table 3).

Abbrev.	Parameter	F =	P =	
TNO	Transect number	6.24	0.0054	
HERB	Herbicide	0.00	NS	
WW	Wood cover width	0.02	NS	
SLOPE	Presence / absence of strip slope	0.05	NS	
ST	Stone abundance	0.38	NS	
SSC	Strip soil-cover	0.01	NS	
SW	Strip width	0.49	NS	
PET	<i>Petasites hybridus</i> dominating	0.63	NS	
WC	Woody cover	0.93	NS	
HSC	Hole soil-cover	1.24	NS	
LEV	Levelling of habitat	1.52	NS	
Final model parameters:		F =	P =	d.f.
O	Geographical orientation	4.32	0.0090	3
HTYP	Habitat type	9.11	0.0001	11
BW	Habitat-base width	9.05	0.0042	1
BSC	Habitat-base soil-cover	13.07	0.0007	1

Generalised Linear Model (GLM):
 Corrected total *d.f.* = 63, (model: 16 *d.f.*, error 47 *d.f.*)
n=64, *F*=14.33, *r*² = 0.83, *P*<0.001.

When significant differences and estimated means from the model are extracted from Table 9, abundance of males and parasites are ranked within pairs of habitats as follows in Table 10. Estimated mean abundances (Table 9) indicated by the model are biased, and are only to be interpreted in a relative manner, comparing habitat types.

Table 9 All pairwise comparisons (Tukey) of habitat types, regarding number of *Andrena* males and *Nomada* individuals summed. Comparisons significant at the *P*<0.05 level are indicated by ***.

Estim. Mean	S.E		Hr		Hh		Fe		Pe		Be		Sa		Sb		Sc		P		Ra		Rb		Fs
2.272	0.859	Hedgerow	Hr	-	Hh																				
2.323	0.896	Hedgehole	Hh		-	Fe																			
21.803	5.708	Forest edge	Fe	***		-	Pe																		
22.637	5.742	Pond edge	Pe				-	Be																	
19.844	5.800	Bog edge	Be				***																		
3.248	0.489	Stream a	Sa				***																		
3.441	0.651	Stream b	Sb	***	***	***	***																		
4.749	0.898	Stream c	Sc																						
21.765	5.731	Pasture	P							***	***	***													
20.213	5.732	Road side a	Ra																						
18.673	5.698	Road side b	Rb				***														***				
3.837	0.765	Field strip	Fs				***																		

Table 10 Significant differences in estimated means of male and inquiline abundances in different habitat types.

Forest edge > Hedgerow	Forest edge > Bog edge
Forest edge > Road side b	Forest edge > Stream a
Forest edge > Stream b	Forest edge > Field strip
Pasture > Bog edge	Pasture > Stream a
Pasture > Stream b	Pasture > Road side b
Stream b < Pond edge	Stream b < Stream c
Stream b < Field strip	Stream b > Hedgehole
Stream b > Hedgerow	Stream b > Stream a

Excluding the “East versus West” comparison, all pairwise comparisons of aspect of traps (Tukey) were significant at the $P < 0.05$ level. Abundance of males and parasites ranked in order of declining estimated mean abundance as follows: $S > E > W > N$. Male and parasite abundance was positively correlated with soil-cover and width of habitat (see Table 8).

Discussion

Species richness and composition

A species abundance distribution of all bees sampled is presented in Fig. 4 (page 24). The distribution is skewed with many species being rare, and few very abundant. The pan-traps assumedly catch bees according to species abundance as well as activity level. There might be a slight difference among species in the ratio between these two components, but the traps are still considered well suited to compare relative abundances among species.

Yellow traps have been found generally attractive to polylectic bees (Leong & Thorp 1999). The reflectance spectrum of the pan-traps used in this survey represent the ultra-violet group (300-390 nm) and the yellow group (500-650 nm) of colours perceived by bees (Proctor *et al.* 1996), and a reflectance of virtually zero in the complementary spectrum to bee yellow, i.e. 390-410 nm (see Fig. 3, page 20). A low affinity to the traps by certain oligolectic species, due to the yellow colour, cannot be ruled out (Kirk 1984; Leong & Thorp 1999). Nevertheless, the high reflection of UV light is also generally attractive, and with the yellow reflection pattern, it may even produce a mix that appear bee-purple to the bees (Daumer 1958).

Support for the assumption that the pan-trap yields are not biased due to the yellow colour also comes from recordings of males and inquilines. Males have been observed to be less selective in their flower preferences than females (own obs.). Inquilines are expected to utilise any given nectar resource and recordings of inquiline species may indicate presence of host species not detected in the traps (O'Toole & Ismay 1995). If for example *Andrena hattorfiana* is abundant in an area, but not attracted to the yellow traps due to its preference for the purple-coloured herb species *Knautia*, at least some males of *A. hattorfiana* and individuals of *Nomada armata* would be caught in the traps. Since no males or inquilines of oligolectic species were recorded without the respective females or host species, there is thus no indications of such sampling bias. Therefore, when excluding factors from inadequate sampling effort (only one sampling season), a rather precise illustration of the actual bee fauna in the studied area has been achieved (I. Calabuig, Manuscript III, *In prep.*).

The high exposure time of the traps compared to any effort of active sampling by sweep-netting also adds to the benefits of using window-traps in yellow pan-traps. Using the same pan-traps as designed for this survey, 104 species of solitary and social bees were recorded through only one season of sampling on the Danish island Læsø (1998-99) (Münster-Swendsen 2000). Prior to the trap sampling on Læsø, only 58 species had been recorded through several decades of selective sweep-netting.

Phenology and seasonality

Many species of solitary bees have only a limited period of activity - one or two months - during the year, which often corresponds with the flowering of their host plants. In Denmark, the majority of solitary species peak in spring, corresponding with a general flowering peak of Danish bushes, trees and herbs. In other European countries, bees in the agricultural landscape have been studied rather extensively, e.g. Ed. by: Matheson (1994), Ed. by: Matheson *et al.*

(1996), Steffan-Dewenter & Tschardtke (1995), Steffan-Dewenter & Tschardtke (1996). In Denmark, nothing is known about the status of solitary bee populations, and of the impact of the changes in farming practice and agricultural management. The data from Transect 1 (Fig. 5 and Fig. 6, pages 27 and 28) demonstrate the expected patterns of seasonality in population activities for the bee genera *Halictus*, *Lasioglossum*, *Sphecodes*, *Andrena*, *Nomada*, *Bombus* and *Psithyrus* (Ebmer 1969; Ebmer 1971; Jørgensen 1921; Peeters *et al.* 1999; Schmid-Egger & Scheuchl 1997; Westrich 1990b). The presence of inquiline species for most of the corresponding host species of *Andrena* and *Lasioglossum* (Appendix 5), the distribution of inquilines and hosts in the traps (Fig. 10, page 33), and the seasonal patterns of activity for the different genera, add to the conclusion that stable and abundant populations of bees exist in the agricultural landscape.

Plant community and forage value of the semi-natural habitats

The studied plant community is typical of nutrient-rich soils of conventional farmland, with species that benefit from fertilisers dominating the flora (Appendix 3). Of these, *Anthriscus sylvestris* was the most widespread of all species recorded in the relevés (43 recordings out of 64 relevés), and it is a vigorously growing species that may oust other herbs, but it is also an important nectar and pollen source for many smaller species of *Andrena* (Westrich 1990a). Species of Apiaceae are rather uniform in flower-morphology with readily accessible nectar (Proctor *et al.* 1996) and generally, bees foraging on members of this family do not have special species preferences. Apiaceae was the most widespread plant family (46 relevés, and generally high relative coverage) and it is included as host family for 10 of the recorded species of *Andrena*. Conversely, this plant family is not preferred by the recorded species of *Lasioglossum*, other than *L. calceatum*. The flowering period of the eight recorded species of Apiaceae (Appendix 3), which are all common in Denmark, provide a succession of potential host plants from May to September. Such a lasting resource may be of special importance to species with long adult activity periods such as *L. calceatum*, which was recorded in the traps May through September.

Apart from Apiaceae, the other dominating plant families, Lamiaceae, Asteraceae, and Scrophulariaceae, are also readily visited by a wide spectrum of bee species (Proctor *et al.* 1996; Westrich 1990a) (see Fig. 7 page 29, Table 7 page 30, and Appendix 4). Species of Lamiaceae were recorded in 45 of the relevés, and *Lamium purpureum* was the dominating species (38 relevés) followed by *Galeopsis tetrahit* and *Lamium album*. Generally, these species were seen growing gregariously, and all recorded species of Lamiaceae are rather good foraging plants for bees. Species with large flowers and long corollas, such as *G. tetrahit* and *L. album*, are frequently visited by long-tongued bumblebees and are preferred by *Bombus pascuorum* (Prys-Jones & Corbet 1991). Scrophulariaceae is a family typical of the agricultural border-habitats and of gardens, and it was represented by six species recorded in 41 of the relevés (Fig. 7, page 29). In Westrich (1990b), 30% (mainly *Andrena spp.*) of the recorded bee species are listed as pollen-collectors of Scrophulariaceae, though the major importance and value of this family probably is to be found in the abundant nectar production.

Asteraceae (43 relevés) was the most species rich family (25 species), and was mainly represented by *Lapsana communis* (34 relevés), *Taraxacum Sect. Ruderalia* (31 relevés), *Cirsium arvense* (28 relevés), and *Carduus crispus* (24 relevés). Whereas species of *Taraxacum* are visited by a wide variety of bees all through the spring and summer, *Lapsana*

is not listed by Westrich (1990a). Proctor *et al.* (1996) mention it as utilised by hoverflies, and Howes (1979) indicates some nectar and pollen value to honeybees. Own observations of bees on *Lapsana* have included small species of *Lasioglossum* and male *Sphecodes*. In Westrich (1990a), *Carduus spp.* have mainly been observed to be visited by species of *Osmia* whereas *Cirsium spp.* are used by a high number of species of many genera, e.g. *Osmia*, *Megachile*, *Halictus*, *Lasioglossum*, and *Andrena*. Both of these Thistle genera are among the most important forage plants for all groups of bumblebees observed in Fussell & Corbet (1992). 68% of the recorded NANI species (Table 7, page 30) and all bumblebee species visit Asteraceae, and the numerous species recorded supply a continuous bloom, ranging from *Petasites hybridus* in the early spring to the late August and September blooming of *Lapsana*, *Cirsium*, and *Carduus spp.*. All together, Asteraceae is considered the most important plant family for bee forage in the surveyed area.

Although eight of the plant families (i.e. 27.6%) are not listed as host for any of the recorded solitary species (Table 7, page 30), all of the recorded plant species, or at least genera, are listed as mellitophilous according to Westrich (1990a), Proctor *et al.* (1996) or Howes (1979). Apart from Rubiaceae and Violaceae, the other six families were very rare in the area. Rubiaceae (22 relevés) is probably of lesser value, but to some degree it is visited by bees (Batra 1984). The only recorded species of Violaceae was *Viola arvensis* (23 relevés), and Westrich (1990a) indicates a limited importance to bees, though observations are scarce. The majority of the recorded herbs offer some amount of nectar, of which many bee species presumably are less host-specific (Pekkarinen 1997). Members of the eight families not listed as forage for the recorded bee species may therefore still contribute to the overall foraging conditions discussed below.

The abundant plant families recorded along the border-habitats are all listed as host families for many polylectic as well as oligolectic bee species (Pekkarinen 1997; Westrich 1990a). Hence, among the 22 recorded species of *Andrena*, 81% include at least one of the families Apiaceae, Asteraceae, or Scrophulariaceae in their forage plant repertoire. Though all recorded species of *Lasioglossum* are polylectic or extensively polylectic (Appendix 4), only Asteraceae was normally preferred among the abundant plant families mentioned.

The surveyed area does not include farm-gardens, set-aside fields or meadows, and the flora of the border-habitats may vary from year to year, depending on soil treatment of the field-borders and of herbicide use. Annuals are bound to dominate in such a landscape, and abundant bee species will mainly be polyleges that are not solely dependent on a limited range of plants. This proved to be the general picture of the recorded bee fauna, including the relatively high number of bumblebee species. One exception was the four solitary bee species that are oligoleges of *Salix*, which accordingly is a stable and predictable nectar- and pollen resource of the hedgerows.

Apart from the *Salix*-oligoleges and *Colletes daviesanus* (Asteraceae), the remaining six oligolectic, or limited polylectic, species were very rare (10 or less individuals, (Appendix 4), though their forage plants, Fabaceae, Lamiaceae, Scrophulariaceae, Campanulaceae, and Ranunculaceae, were all reasonably well represented in the area. The scarcity of oligoleges may thus be due to special nesting requirements not present in the area (e.g. *Chelostoma florissomne*, (Münster-Swendsen & Calabuig 2000)), but unpredictability of the flora-composition in border-habitats, compared to permanent or long term set-aside areas, is also a limiting factor on the persistence of oligoleges.

Only a small fraction of the recorded plant species along the border-habitats was observed to grow in the crop area. Though no attempt was made to quantify this, the general picture seemed comparable to the findings described in Marshall (1989), with a limited number of annuals such as *Veronica spp.*, *Viola spp.*, and *Stellaria spp.* growing in the crop area as well. Marshall (1989) concluded that most weeds do not originate from the border-habitats, though some serious pests such as *Bromus sterilis*, *Elytrigia repens* and *Galium aparine* unfortunately do. These results are likely to be confirmed in Denmark also, by an ongoing project at the Danish Institute of Agricultural Sciences that includes similar experiments. If conclusions similar to Marshall's (1989) are reached, they must be communicated to the public, and by doing so, it may add to change the general perception of weeds spreading from border-habitats. This change in knowledge may hopefully be reflected in legislation concerning restrictions on herbicide treatment of field boundaries and may add to a general acceptance by farmers of such legislation. On the long term, diversity and abundance of bees will undoubtedly benefit from a more diverse flora in the border-habitats, and especially bumblebees may thrive if more perennials are re-established in the landscape (Fussell & Corbet 1992).

General foraging conditions and geographical orientation of the traps

Generally, solitary bees prefer sun-exposed sites and thus nest in south-facing spots and forage in east- and south-facing areas with shelter. North-facing areas receive the least amount of sunlight and furthermore, in this survey there was no notable flowering plant coverage in the north- and east-facing areas. Although flowering plant coverage was relatively high in west-facing areas, a combination of sub-optimal factors such as shade and wind blurs the expected correspondence between bee abundance and flowering plant coverage. West-faced areas are poorly sheltered, as west-winds dominate in Denmark (Appendix 1). Also, west-facing areas only receive sunlight in the afternoon, whereas probably most Danish solitary bees prefer to forage from morning to early afternoon, allocating afternoon activities primarily to nest building (Cameron *et al.* 1996; Münster-Swendsen 1968; Münster-Swendsen & Calabuig 2000). Therefore, relationships between coverage and species richness of mellitophilous plants versus number of bee individuals and species are most clearly revealed under optimal foraging conditions, i.e. for south-facing areas. The solitary bees recorded in this survey appear to prefer south-facing areas to the east-, west-, and north-facing (Fig. 8, page 31), whereas the preferences seen in the social bees are less distinct.

Bumblebees are able to forage early in the morning and into the night due to their self-heating abilities, but they also forage all through the day (Corbet *et al.* 1994; Prys-Jones & Corbet 1991). Honeybees and solitary bees are not able to forage under as adverse weather conditions, nor as early and late in the day, as bumblebees. These differences in foraging behaviour and physiology may explain the differences in the aspect distribution patterns between the solitary bees, bumblebees and honeybees, especially the lack of preference seen in *Bombus* workers (Fig. 8, page 31). The early and late season foraging distribution pattern of *Bombus* queens is expected to be influenced by the search for nesting or hibernation places. However, nesting and hibernation habitat preferences for bumblebees have not been investigated in this survey, whereas other extensive studies exist, e.g. Prys-Jones & Corbet (1991), Skovgaard (1936), Svensson *et al.* (2000).

The late appearance of honeybees in the yellow pan-traps (Fig. 6b, page 28) may be explained by their foraging strategy that involves many individuals working in unison on an abundant nectar and pollen resource. The relatively scattered and limited amount of flowering herbs in the periphery of fields may only become attractive late in the season, when there are no more mass-flowering crops to forage on (Ginsberg 1983). No negative correlation was found between number of honeybee individuals versus *Bombus* queens, workers, or non-inquiline, non-Apidae (NANI) females. Furthermore, no correlation between honeybee abundance and late-season mellitophilous herb coverage was found, as opposed to the positive correlations found regarding non-*Apis* bees. Therefore, there might be a limited degree of resource overlap between honeybees and other bees in the linear semi-natural habitats. Similar findings are reported by Ginsberg (1983) and Steffan-Dewenter & Tschardtke (2000).

This survey supports the conclusions reached by Steffan-Dewenter & Tschardtke (1996) and Steffan-Dewenter & Tschardtke (2000), as it cannot be concluded that honeybees have a negative impact on other groups of bees living in a conventionally managed agricultural landscape. Honeybees and wild bees have co-existed in Denmark for thousands of years and I suggest that before making conclusions about the impact of honeybees on the native fauna, it is important to distinguish between nature types where honeybees have been introduced and others where they are a natural part of the community. In isolated habitat types, on islands, or in habitats that have changed dramatically, the introduction of honeybees or other bee species may surely inflict damage and/or changes on the native flora and bee fauna, especially in areas where only solitary species are the native species (Dafni & Shmida 1996; Frankie *et al.* 1998; Kato *et al.* 1999; Westrich 1990a) .

Species richness of all solitary species, and of NANI-species analysed separately, could not be explained by coverage or species richness of herbs. Apart from the *Salix oligoleges* and *Colletes daviesanus*, all abundant non-inquiline species found in this survey are polylectic (see Table 6 on page 25 and Appendix 4). The lack of correlation indicates the importance for polylectic bees of a sufficient and continuous succession of suitable flowers (Corbet *et al.* 1994), rather than a very diverse flora at the level of plant species. Such a continuous succession may be mediated by diversity of plants at the family level. However, to sustain a diverse bee fauna that includes abundant oligoleges, the diversity, composition, and the predictability of the flora community is undoubtedly crucial. Two other surveys made in agricultural landscapes by Steffan-Dewenter & Tschardtke (1996; 2000) support the conclusion that other factors, such as nesting conditions, are more important than plant coverage and species richness in predictions of bee species richness in communities dominated by polyleges. In a survey on set-aside fields of different age, Steffan-Dewenter & Tschardtke (1996) recorded 129 species, of which 22 were oligoleges (17%). In a study on calcareous grasslands, the same authors (2000) recorded 98 species including 8 oligoleges (8%). Unfortunately, abundance of the bees is not comparable to this survey due to differences in sampling methods and effort, but Steffan-Dewenter & Tschardtke (1996) found a distinct positive correlation between plant and bee species richness, which was not repeated in Steffan-Dewenter & Tschardtke (2000). I interpret these contradicting results to be caused by the distinct difference in oligolectic-polylectic ratio of the observed communities, and find that my survey is comparable to Steffan-Dewenter & Tschardtke (2000).

Hedgerows are the dominating type of habitat flanking the arable land of this survey (38.5% of the total length of transects). Blackthorn (*Prunus spinosa*) is by far the most abundant species in the hedgerows, comprising 41.6% of the uncorrected coverage of bushes and trees and 65.4% of the coverage when weighing all the species according to their nectar and pollen values (Christensen 1984; Howes 1979). Although Blackthorn is a species with abundant nectar and pollen, it is a time limited resource, only flowering for a few weeks in May. Willow (*Salix sp.*) was another important, but local and patchily distributed, spring species of the hedgerows. Willow mainly occurred as single trees here and there (present in 13 relevés), but it undoubtedly attracts bees from quite a large area when in bloom, and 41.5% of the recorded NANI bees utilise this genus (see Appendix 4). The rest of the season, the studied hedgerows in themselves are of no real foraging value to the bees. This may add to explain why no correlation was found between flowering shrub/tree coverage and number of foraging female bees. Nevertheless, Blackthorn and Willow play an important role early in the season, to maintain a continuous succession of forage plants, especially for bumblebees.

Nesting conditions and parasite – host distributions

General soil-nesting conditions were analysed using the following hypothesis: Traps with high yields of males and nest parasites of gregariously nesting species are likely to have been placed in vicinity of a colony or aggregation of nests. Abundance of males and inquilines may thus be compared to habitat characteristics of trap surroundings. A Generalised Linear Model (GLM), with geographical orientation of habitat, habitat type, and width and soil-cover of habitat, was able to predict abundance of *Andrena* males and *Nomada* individuals in the traps ($n=64$, model: 16 *d.f.*, error 47 *d.f.*, $F=14.33$, $r^2 = 0.83$, $P<0.001$, see Table 8, page 35). Several other parameters were tested, but they did not enter the model.

In early spring (generally 2-3 weeks in March or April), *Petasites hybridus* (Butterbur) is an important nectar and pollen source for a variety of nectar- and pollen-eating insects (Christensen 1984; Westrich 1990b). Later in the season, the large leaves shade and inhibit the growth of other plants, creating a dark and humid environment beneath the leaves. Furthermore, *P. hybridus* grows in quite humid soils, often near streams etc. Uncultured strips dominated by butterbur are therefore potentially poor bee nesting habitats. *P. hybridus* coverage was recorded separately to pinpoint such habitats, and a negative correlation with male and inquiline abundance was expected in the model but not found.

Lack of predictive value in the model from herbicide treatment, cover of *Petasites hybridus*, and width and soil-cover of the uncultured strip along the habitat-base indicate that nests in the agricultural landscape are not primarily placed along the field boundary, or that nests are abandoned or unsuccessful (Wuellner 1999). The strip of uncultured soil varies in width from year to year, and often, cutting of field edges disrupt the strip. Species that nest deep in the ground (40-110 cm in *Dieunomia triangulifera*), and complete nest-building activities before or after ploughing, can nest in agricultural fields (Wuellner 1999). Although nest depth varies greatly and is not directly correlated with size of the species (Cane 1991; Malyshev 1935), most species of *Andrena* and *Lasioglossum* nest within depths of 5 - 60 cm (Müller *et al.* 1997; O'Toole & Raw 1999). For the majority of species found in this survey, nest depths are therefore quite possibly within depth of ploughing or soil-cutting of field edges, and nest contents will be destroyed. The uncultured strip between the habitat-base and a field may

therefore be more important as foraging habitat ($P=0.006$ for NANI females, see Fig. 9a, page 32).

Habitat-base width and soil-cover entered the GLM (Table 8, page 35), indicating a positive correlation between available nesting space and abundance of males and inquilines. Soil-cover was the best predictor variable of all tested variables ($F=13.07$, $P=0.0007$) and habitat-base width explained a little less of the variation than habitat type ($F=9.05$, $P=0.0042$ and $F=9.11$, $P=0.0001$ respectively). Contrary to the uncultured strip along the habitat-base, the soils of the habitat-base itself are more or less undisturbed. Normally, no mechanical soil treatments are applied by the farmer, and provided there is not too much shading from bushes and trees nesting conditions should be quite suitable. Soil-cover and herbal vegetation type of the hedgerow-base often change in areas where tree and shrub coverage is interrupted (a hedgehole). Therefore, hedgeholes were recorded as a separate habitat type. No conclusions may be drawn as to why soil-cover of hedgeholes did not enter the model.

Slope of the uncultured soil-strip and levelling of the habitat-base did not enter the model, whereas aspect was an important factor ($F=4.32$, $P=0.0093$ in the GLM, Table 8, page 35). Similar findings are reported for the nesting requirements of *Halictus rubicundus* (Potts & Willmer 1997). Except for east versus west, all pairwise comparisons (TUKEY) of aspect were significant ($P<0.05$), with males and inquilines being more abundant in south- and east-facing traps. This is in concordance with the general observations of nests being placed to optimise exposure to the sun. As expected, there was linear dependency between aspect and habitat type, but unfortunately, a combination of the two parameters did not enter the model, and the bias could not be removed. I consider this bias unavoidable since it was impossible to plan a landscape survey in which all habitat types were found represented in all four geographical aspect groups, and this would probably be necessary for a combination-parameter (aspect*habitat type) to enter the model. To give an example, this means that males and inquilines are not always abundant in south-facing areas, but that abundance also depends on habitat type (see further discussion below).

Contrary to expectations, abundance of stones did not contribute to the model. Stones enhance microclimatic conditions through heating from the sun and may provide cryptic nest entrances, difficult to find for nest parasites (Potts & Willmer 1997). There are probably differences in general and local nesting requirements of females seeking nest-sites, and preferences for slope and for stone abundance in nest-site selection are not revealed in a survey on such a general scale as this. Woody cover and width also failed to enter the model, and again, measures of shade tolerance for nesting are probably only revealed in a direct study of nests and not through measures of general males and inquiline abundance.

All the factors that were quantified and entered in the GLM were chosen for their assumed relevance for bee nesting and foraging, but it is not possible to quantify completely what characterises a given habitat for bees. In addition, the requirements of bees for several different habitat types (i.e. for nesting, foraging, and sometimes collection of building material) introduce other complex factors such as distance between suitable habitats. Random factors and behavioural factors, such as nest-fidelity and potential for dispersal, also add to determine distribution patterns of bees. All the different habitat types surveyed are thus characterised by factors of their own, and they can only be discussed qualitatively, but the habitats also include all the model parameters discussed above, e.g. any given habitat has a geographical orientation in the landscape, and a certain fraction of the habitat-base will be

bare soil. Habitat type proved to be an important predictor of male and inquiline abundance (Table 8, page 35), though a possible outcome of the model could have been that parameters such as soil-cover and aspect were the sole important predictors, regardless of habitat type. As discussed earlier, the estimated mean abundances (Table 9, page 35) indicated by the model are biased, and are only to be interpreted in a relative manner, comparing habitat types.

Abundance of males and inquilines was significantly higher along forest edges and in pastures than along several of the other linear habitats (Table 10, page 36). Though not revealed by the model, observed abundances of males and inquilines along hedgerows were either medium high, or nearly zero, depending on the orientation of the hedgerow, e.g. south- versus north-facing traps, but a combination of habitat type and aspect did not enter the model. Still, along south-faced hedgerows, more males and inquilines were caught than along streams of type a) and b) (see Table 2, page 22), which were both characterised by shallowness, humid surroundings, vast patches of *P. hybridus*, and little or no woody vegetation growing along the sides. Streams of type c) were broad and ran deep, with steep sloping sides and trees and bushes alongside. Abundance of males and inquilines were significantly higher along streams of type c) than along types a) and b). It seems that males and inquilines are more abundant in areal than along linear habitats, and that within linear habitats, broader types with higher structural complexity (i.e. hedgerows and streams of type c) are favoured.

A synopsis of general quality of the habitat types found in the studied agricultural landscape is thus to be made from the analyses of general foraging- and nesting conditions. In the current conventional farming practice, the uncultured strip of soil between the habitat-base and a field is considered an important foraging habitat for polylectic bee species, but is generally unsuitable for nesting of bees. This condition may be changed by a limitation in mechanical soil-treatments of field edges, which will promote nesting conditions in the often sloping and sun-exposed uncultured strips. Furthermore, restrictions in herbicide use may enhance establishment of biennial and perennial herbs and general predictability of flora composition, which in turn will promote living-conditions for oligoleges. Humid environments, such as along streams and bog edges, are more important for foraging than for nesting, and provide an important resource in spring, due to presence of patches with *Petasites hybridus*. Areal habitats such as small forests and pastures are the most important habitats for nesting as well as for foraging, and may act as core-habitats for bee populations to disperse in linear habitats such as hedgerows (I. Calabuig, Manuscript III, *In prep.*).

Conclusion

Resource competition between honeybees and other bees is apparently rather limited in areas where honeybees form a natural part of the pollinator-community. In nature conservation of agricultural semi-natural habitats, it therefore seems much more important to restore and conserve suitable foraging- and nesting conditions for wild bees, than to limit the amount of honeybees in the area. For the major part of the flowering season, honeybees presumably utilise other resources such as flowering crops, rather than the wild flora. Solitary bees and bumblebees are surprisingly abundant and species rich in the studied, conventionally managed farmland. They utilise the wild flora and undoubtedly play an important role as pollinators. The flora community found is suitable for polyleges as well as oligoleges, but unpredictability of the flora, due to land management, is sub-optimal for persistence of oligoleges. Window-traps in yellow pan-traps and the semi-quantitative method of Braun-Blanquet have proved suitable in investigations of the pollinator fauna, species activity patterns, and in analyses of the foraging conditions in a local area. Habitat indexation, and abundance and distribution of males and inquilines are a crude measure on which to base analyses of nesting conditions, but it may be constructive for a local survey on the landscape element level. Hence, soil-cover and sun-exposure are important factors for selection of nesting-sites and areal habitats are preferred for foraging as well as nesting, whereas linear habitats are important for foraging and for dispersal of bees between core areal habitats. This study has proved it possible to make assessments of general nesting and foraging conditions for bees in an agricultural landscape, and I consider the methods employed a potential for management of bee habitats on a landscape scale.

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MANUSCRIPT II - I. Calabuig:

**Dispersal of solitary bees and bumblebees in a winter
oilseed rape field**

MANUSCRIPT II - I. Calabuig: Dispersal of solitary bees and bumblebees in a winter oilseed rape field

Abstract

Dispersal distributions of solitary bees and bumblebees were studied in a winter oilseed rape field. Window-traps were placed in the rape field along a line transect perpendicular to the field edge. 19 species of solitary bees were recorded and all but four species are polylectic, including Brassicaceae as host-plant family. Through non-linear regression, the decline in solitary bee individuals versus distance from field edge significantly fitted a steep two-parameter exponential decay function. Activity of solitary bees was clearly highest within 30 metres from the field edge. Apparently, solitary bees do not play any noteworthy role in the pollination of winter oilseed rape in Denmark. The traps yielded ten species of bumblebees, and a significant linear correlation was found between numbers of individuals and distance from the field edge. This result is attributed to bumblebee foraging behaviour. Bumblebees were abundant and presumably are important background pollinators of oilseed rape. Honeybees are managed pollinators of oilseed rape, and were abundant in a preceding study of the area. For unknown reasons, honeybees were caught in extremely low numbers in this study, and the most likely explanation is a decline in honeybee populations.

Introduction

Bee-pollinated crops account for about 30% of the food produced for humans, and the value of this pollination service exceeds the value of produced honey by at least a factor 50 (Corbet *et al.* 1991). Most European flowering crops that depend on cross-pollination by bees or insects are mainly pollinated by managed honeybees, but some crops are more efficiently pollinated by solitary bees or bumblebees than by honeybees (Corbet *et al.* 1991). Crops belonging to the family Fabaceae, such as Alfalfa (*Medicago sativa*), Field Bean (*Vicia faba*), and Red Clover (*Trifolium pratense*), are largely self-incompatible and characterised by deep corollas, and a flower-morphology that needs the weight of a visiting pollinator to trigger their petals and anthers for successful pollen transfer. Long-tongued species of solitary bees and bumblebees can reach the nectar and in doing so, trip the flowers for pollen-release. Long-tongued bumblebees such as *Bombus hortorum* are especially important to the new triploid strains of Red Clover that have deeper corollas than traditional strains and are completely dependent on cross-pollination for seed-set. Short-tongued species such as honeybees “cheat” and collect nectar from the sides of the flower or through holes made by nectar-robbing species (e.g. *Bombus terrestris*) (Appendix 4). Flowers of Tomato (*Lycopersicon esculentum*) and Peppers (*Capsicum sp.*) have poricidal anthers that need to be vibrated for pollen-release. Contrary to honeybees, bumblebees are capable of such “buzz-pollination” and are successfully managed (often in greenhouses) for this purpose (Williams 1996).

Winter oilseed rape (*Brassica napus*) is self-fertile but incompletely auto-self-pollinated and Williams *et al.* (1987) concluded from an experiment with controlled pollination that the

actual yield in harvesting the crop is enhanced by cross-pollination of flowers by honeybees. Pods were more synchronised and uniform in ripening, which reduce loss of seeds due to shattering of over-ripe pods. Honeybees are also managed in rape fields due to the abundant nectar production of the flowers, and rape-honey constitutes a large part of the honey-production since oilseed rape is among the most abundant crops in Denmark and Europe as a whole. Winter rape is also assumed to be an important nectar and pollen source for many species of insects due to its early blooming period, where other resources may be limited (Roberts 1994). The flowering period of oilseed rape in Denmark is May, which is often dominated by unstable, cold weathers. Though May is early in the year for their annual colonies (Prys-Jones & Corbet 1991), bumblebees may be more reliable pollinators than honeybees, since bumblebees are able to forage under more adverse weather conditions (Corbet *et al.* 1993).

Apart from a few managed species such as *Megachile spp.* and *Osmia spp.* (Corbet *et al.* 1991), the role of solitary bees as pollinators of crops and the importance of crops as forage for solitary bees in Europe is poorly investigated (Torchio 1994), whereas bumblebees are clearly recognised as important pollinators (Williams 1996). The main purpose of this study was to investigate whether solitary bees and bumblebees constitute any significant part of the pollinator-community of winter oilseed rape in Denmark, and to achieve indications of their general foraging range and dispersal patterns. Furthermore, recordings of species richness and abundance could be compared to the results of an intensive survey that was carried out the preceding year in the border-habitats of the area (e.g. hedgerows, field-borders, and forest edges) (I. Calabuig, Manuscripts I & III, *In prep.*).

Materials and methods

In May 1998, a survey of the dispersal of solitary bees, bumblebees and honeybees was made in a blooming winter oilseed rape field (*Brassica napus*, Brassicaceae) in a Danish conventional agricultural landscape. The rape field was situated about 200 metres from an area where bee species richness and abundance were surveyed intensively April through November 1997 (to the north of Ringsted, northeast Zealand, Denmark (55°30-32'N, 11°45-47'E)) (I. Calabuig, Manuscripts I & III, *In prep.*). 24 window-traps were placed in pairs from the edge of the field along a tractor track running perpendicular to the field edge. One trap of a pair was placed about one metre, the other about three metres from the track. The twelve trap pairs were placed at distances of 0, 9, 18, 27, 36, 45, 63, 81, 99, 117, 153, and 189 metres from the field edge, reaching the middle of the field.

Each window-trap consisted of a ricacryl sheet (68.3 x 76.2 cm) suspended between two metal poles (160 cm high) and with a piece of roof gutter (78 cm long, closed in both ends), attached to the lower edge. The gutter was filled with approximately 1 litre of a 1% solution of Rodalon (Bie & Berntsen) in water. Rodalon preserves the insects and lowers surface tension, causing the insects to sink and not escaping from the water surface. The height of the window-traps was adjusted to ensure that the lower edge of a trap was in line with the lower part of the flower heads of the winter oilseed rape. The traps were emptied 8 times during the flowering period: May 6 through 26, 1998. Trap yields were sorted, specimens identified, counted and stored as described in I. Calabuig, Manuscript I, (*In prep.*).

Results

The window-traps yielded 19 species of solitary bees, 10 species of bumblebees (*Bombus*), 4 species of cuckoo bumblebees (*Psithyrus*), and the honeybee *Apis mellifera* (Table 1). Apart from one male *Andrena cineraria*, all species were previously recorded in the area (Appendix 2). The majority of the recorded solitary species are extensively polylectic with Brassicaceae indicated as a host-plant family (Appendix 4). The exceptions are: *Andrena helvola* (polylectic species but Brassicaceae not listed as host-family), *A. praecox* (strictly oligolectic on *Salix sp.*), *Lasioglossum leucopus* (sparse observations, but probably polylectic on Asteraceae and Rosaceae), and *L. minutissimum* (polylectic, utilising Asteraceae and Lamiaceae). *Nomada panzeri* was the only inquiline species recorded (three individuals), and is a nest-parasite of *Andrena varians*, *A. helvola* and *A. fucata* (Appendix 5).

The social bees were a little more abundant than the solitary bees (Table 1). The dominating nest-building species were *Bombus hortorum*, *B. terrestris*, *B. lapidarius*, *B. pascuorum*, and *B. lucorum*, which are all polylectic species (Appendix 4). The majority of recorded cuckoo bumblebees belonged to the species *Psithyrus rupestris* and *P. vestalis*, which each preferably parasitise nests of *B. lapidarius* and *B. terrestris* respectively (second and third most abundant species). A low number of honeybees were recorded in the window-traps, only 13 individuals in all.

Table 1 Window-trap-yields in winter oilseed rape May 1998, and maximum distance from field edge recorded for each solitary species (Max).

Genus	Species	♂	♀	Σ	Max
<i>Andrena</i>	<i>bicolor</i>	0	14	14	153
	<i>carantonica</i>	0	3	3	81
	<i>cineraria</i>	1	0	1	189
	<i>fulva</i>	0	2	2	81
	<i>haemorrhoea</i>	30	74	104	189
	<i>helvola</i>	5	15	20	153
	<i>minutula</i>	0	2	2	9
	<i>nigroaenea</i>	3	46	49	189
	<i>praecox</i>	0	2	2	0
	<i>tibialis</i>	0	1	1	27
	<i>varians</i>	1	1	2	81
<i>Halictus</i>	<i>rubicundus</i>	0	2	2	81
	<i>tumulorum</i>	0	23	23	189
<i>Lasioglossum</i>	<i>calceatum</i>	0	11	11	153
	<i>leucopus</i>	0	9	9	189
	<i>minutissimum</i>	0	3	3	9
	<i>quadrinotatum</i>	0	17	17	189
<i>Nomada</i>	<i>panzeri</i>	2	1	3	0
<i>Osmia</i>	<i>rufa</i>	0	3	3	0
TOTAL		42	229	271	

Genus	Species	♂	♀	♀	Σ
<i>Apis</i>	<i>mellifera</i>	0	0	13	13
<i>Bombus</i>	<i>hortorum</i>	0	37	41	78
	<i>hypnorum</i>	0	0	1	1
	<i>lapidarius</i>	0	28	7	35
	<i>lucorum</i>	0	12	5	17
	<i>muscorum</i>	0	4	0	4
	<i>pascuorum</i>	0	17	1	18
	<i>pratorum</i>	0	0	1	1
	<i>soroensis</i>	0	2	0	2
	<i>sylvarum</i>	0	1	0	1
	<i>terrestris</i>	0	29	9	38
<i>Psithyrus</i>	<i>bohemicus</i>	0	2	0	2
	<i>rupestris</i>	0	64	0	64
	<i>sylvestris</i>	0	1	0	1
	<i>vestalis</i>	0	18	0	18
TOTAL		0	215	78	293

The non-Apidae bees were primarily trapped within 27 metres from the field margin (Fig. 1). Through non-linear regression, the decline in individuals versus distance from field edge significantly fitted a two-parameter exponential decay function of: $f = y(0) + a \cdot \exp(-b \cdot x)$, ($y(0) = 14.7809$, $a = 45.6800$, $b = 0.0730$, and $r^2 = 0.93$, $P < 0.0001$). About five times as many individuals were caught in the traps at the field margin, compared to 200 metres out in the field (Fig. 1).

Number of *Bombus* individuals showed a positive correlation with distance from field edge. The number of individuals is expected to reach an upper level, and the last three traps, placed 117, 153, and 189 metres from the field edge, almost yielded identical numbers of individuals. Linear regression on number of individuals versus traps up to and including 117 metres from the field edge showed a significant positive correlation of: $y = 8.4377 + (0.1205 \cdot \text{distance})$, ($r^2 = 0.6172$, $P < 0.0071$) (Fig. 1).

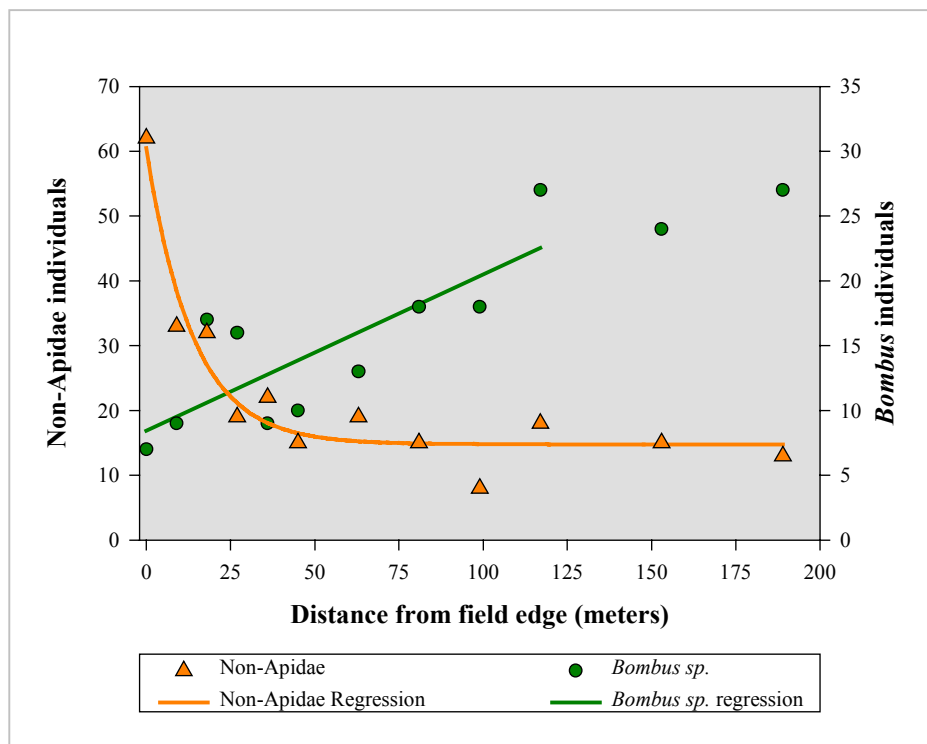


Fig. 1 Total number of individuals caught in window-traps, winter oilseed rape field, near Transect 1 forest edge, May 6 through 26 1998 (n=24).

Discussion

Generally, winter oilseed rape attracts all kinds of insects, especially bumblebees and honeybees, and crop yield is enhanced by their pollination (Corbet *et al.* 1991). Winter oilseed rape is important to bees due to its abundant nectar production and time of blooming in spring and early summer, where other resources may be limited (Roberts 1994). The spring bee-fauna of Denmark is dominated by species of *Andrena* (Jørgensen 1921), and this genus represented 58% of the solitary bee species (19 in all), and 74% of the solitary bee individuals - one species (*A. haemorrhoea*) accounting for 104 of the 271 individuals (Table 1). Compared to the 1997-survey (I. Calabuig, Manuscript I, *In prep.*), only *Andrena cineraria* was a new species to the area (Appendix 2). The observation of only one new species supports the conclusion that a rather precise illustration of the actual bee fauna in the area studied was achieved in the pan-trap survey of 1997 (I. Calabuig, Manuscripts I & III, *In prep.*). Furthermore, all solitary species but for *A. fulva*, *A. tibialis*, *A. varians*, and *Osmia rufa* were among the most abundant species recorded in the survey of 1997 (Appendix 4 and Appendix 5).

All but four species of the recorded solitary bees are listed in Westrich (1990b) as generally polylectic (Appendix 4), with Brassicaceae mentioned as host-plant family, and winter rape may be an important resource for these species in early spring. Many bee species are less conservative in their nectar foraging than in pollen collection (Pekkarinen 1997), and since winter rape produces abundant nectar, it may therefore also be foraged on by bee species that do not prefer Brassicaceae as pollen source (e.g. *Andrena praecox* and *Lasioglossum minutissimum*).

May is early in the season for most bumblebee species, and accordingly, the majority of individuals recorded were queens (Table 1). The only exception was *Bombus hortorum*, which is an early emerging species with a short lifecycle (Prys-Jones & Corbet 1991), and thus was the most abundant bumblebee in the traps, with queens and workers being equally abundant. *B. hortorum* is primary host for the cuckoo bumblebee *Psithyrus barbutellus*, which was not recorded in the traps. Abundance of *B. hortorum* workers (Table 1) indicates that nests of this species were already well established at the time of the survey. If they were present in the area, female *P. barbutellus* may already have invaded nests, and were therefore not recorded during the short time-span of window-trap exposure. On the other hand, only two female *P. barbutellus* were recorded in one whole season in the pan-trap survey of 1997 (Appendix 5), which indicates that this species for unknown reasons may be rare in the area. Since parasites are totally dependent on presence of host-populations, hosts that are very rare and scattered, or only locally abundant in an area, are less likely to be detected and to sustain inquiline populations. The opposite of course goes for abundant, widespread, and stable host-populations, which suffer a greater risk of parasite detection. Hence, excluding the seasonal or unknown factors mentioned above, the recorded species of cuckoo bumblebees are ones that are primary inquilines of the most abundant true bumblebee species (Appendix 5).

Bumblebees have relatively high energy requirements and need to collect considerable amounts of nectar for their own use during foraging trips (Corbet *et al.* 1994). Furthermore, foraging trips may involve nectar collection only or handling of only pollen producing plant species (e.g. *Filipendula sp.* and *Hypericum sp.*) (Prys-Jones & Corbet 1991). Since oilseed

rape produces abundant nectar, it may therefore serve as an extra profitable nectar source or as a nectar supplement for workers returning with pollen-loads only.

The window-traps in this survey were placed in the midpoint and perpendicular to one side of the rape field, which was situated about 100 metres away from a forest edge and a farm. On the other two sides were extensive areas with cereal crops. As it seemed, the nearest potential nesting sites were therefore about 100 metres away from the field edge.

Trap yields of solitary bees decreased distinctively with distance from field edge (Fig. 1), and followed a steep exponential decay function of $f = 14.7809 + 45.6800 * \exp(-0.0730 * x)$, $r^2 = 0.93$, $P < 0.0001$). From the field edge to a distance of 30 metres, trap yields dropped more than 60%, and 54% of the individuals were caught within the first four trap pairs out of twelve (i.e. at 0, 9, 18, 27 metres). Therefore, solitary bee activity and relative abundance were clearly highest within the first 27 metres of the line transect into the field. Apart from *Andrena cineraria*, all sparsely represented species were trapped within 81 metres from the edge, whereas the more abundant species dispersed to all surveyed parts of the field, though in much lower numbers.

Assuming that the recorded species cannot nest in the field proper, where mechanical soil treatments are applied at least once a year (I. Calabuig, Manuscript I, *In prep.*), the bees must have covered a distance of at least 100 metres to reach the rape field from their nesting areas. Support for this assumption comes from the yield of only three inquiline individuals of *Nomada panzeri* in the traps. The almost complete lack of inquiline solitary bees cannot be ascribed to seasonal activity patterns, since the emergence of parasites is synchronised with that of their hosts (I. Calabuig, Manuscript I, *In prep.*). The reason is more likely to be too great a distance between foraging- and nesting area, since inquilines stay near to nests for quick entrance when host-females leave to forage (Münster-Swendsen & Calabuig 2000).

Though several species of non-inquiline solitary bees have been found able to return from distances up to 400 metres (Wesserling & Tschardtke 1995), smaller species' foraging ranges are probably rather limited if resources are abundant nearby (Käpylä 1978; Westrich 1990a). Furthermore, the resource being so abundant also leaves the question whether it is necessary for the bees to forage further out in the field, if there is no competition. It must be concluded that in this survey, solitary bees do not play any noteworthy role in the pollination of winter oilseed rape.

Bumblebees are fast and efficient pollinators, and when they leave on a forage trip or are returning with a load, they fly high up in the air and are not caught in the window-traps. As suggested by Dramstad (1996), the most energetically efficient way of foraging is to collect pollen and nectar on the way back to the nest. In that way, the heavier the bee gets, the shorter a distance it has to cover before it is back in the colony. This hypothesis is supported by the rape field experiment. The curve in Fig. 1 seems to level off at about 117 metres, but a full evaluation of bumblebee distance distribution has not been shown in this experiment. Still, a clear positive relationship is seen between distance and number of individuals in the first 117 metres of the line transect: On their way home the bumblebees get fully loaded at different distances from the field edge and take off to fly back. Hence, there is a declining probability to catch them in the traps with decreasing distance to the field edge. Bumblebees were abundant in the traps and dispersed at least 200 metres into the fields. On flower-heads with multiple

inferences, bumblebees may be faster workers than honeybees. Thus, bumblebees presumably contribute significantly to the pollination of winter oilseed rape in Denmark.

In the yellow pan-trap survey of 1997, honeybees were more abundant than *Bombus* workers (2181 and 1671 workers respectively) (I. Calabuig, Manuscript I, *In prep.*). However, since honeybees in 1997 were trapped primarily from September 1 and on, it was concluded that other and more abundant resources than wild, flowering herbs of border-habitats were utilised when possible. Therefore, it is surprising that in this rape-field experiment of 1998, the honeybees were much less abundant than the bumblebees, and that only 13 individuals were found in all. This suggests that in 1998 there might have been even more attractive nectar resources than the rape field examined, or that the honeybee populations in the area have declined from 1997 to 1998. Unfortunately, the latter suggestion is highly likely since honeybee populations in recent years have declined dramatically in Denmark, partly due to diseases (e.g. *Varroa* mites) and partly due to a decline in number of beekeepers.

Conclusion

Winter oilseed rape is likely to be an important pollen source to solitary bees that utilise species of Brassicaceae. Furthermore, other bee species may benefit from the abundant nectar, especially in spring where other resources may be limited. Solitary bees were abundant within 30 metres from the field edge but decreased distinctively with distance out in the field. They utilise oilseed rape, but their foraging range is limited, and they apparently do not play any role in overall cross-pollination of this crop when fields are situated too far away from nesting areas. Bumblebees were trapped in all surveyed parts of the field, but in decreasing numbers the nearer to the field edge. This result is attributed to their foraging behaviour. Bumblebees were abundant and presumably contribute to the pollination of oilseed rape in Denmark. Honeybees are wellknown and managed pollinators of oilseed rape, and were abundant in the pan-traps of a preceding survey. For unknown reasons, honeybees were caught in extremely low numbers in this study, and the most likely explanation for this result is a decline in honeybee populations in the area.

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MANUSCRIPT III - I. Calabuig:

Estimating species richness and status of solitary bees and bumblebees in agricultural semi-natural habitats

MANUSCRIPT III - I. Calabuig: Estimating species richness and status of solitary bees and bumblebees in agricultural semi-natural habitats

Abstract

Estimation of Western Europe number of bee species varies between 2000 and 4500 (Williams 1995) but there are substantial indications of a decline in bee species in Europe and other regions. In Denmark, wild bee species richness, distribution, and abundance have not been studied in detail for about 75 years, and nothing is known about which species are potentially vulnerable or endangered. A rough estimate of solitary bees and bumblebees includes approximately 238 species (26 genera) and 29 species respectively. In a pan-trap survey of six kilometres of semi-natural habitats in a Danish agricultural landscape, 72 solitary bee species and 19 species of bumblebees were recorded, several of which are considered vulnerable or endangered in neighbouring countries. Nesting conditions for rare cavity-nesting species and the possible role of the semi-natural habitats as corridors for species dispersal are discussed. A new group of non-parametric species richness estimators, supplied by the free-ware programme EstimateS 5 (Colwell 1997), was used to estimate true species richness in the area of study and an additional 23 potential species was depicted from abundance and distribution of the 91 recorded species. Efficiency of window-traps in yellow pan-traps for bee fauna surveys is evaluated and is found to be an efficient method for investigations of species richness and relative abundance of bees.

Introduction

One of the major environmental issues today is biodiversity, and the enormous problem of species loss due to human activities was addressed at the *U.N. Conference on the Environment and Development* in Rio, 1992, where the *Convention on Biological Diversity* was signed by 155 countries. Since then, more than 120 countries, including Denmark, have ratified the convention and must fulfil *Article 6* and *Agenda 21* of the convention, which state that countries shall prepare national strategies for the protection and sustainable exploitation of biodiversity, and must make *country studies* of biodiversity, as the point of departure on which to base national strategies. A report on the Danish fulfilment of a national strategy was issued from the *Ministry of Environment and Energy* and the *Danish Forest and Nature Agency* in 1996 (Ed. by: Prip *et al.* 1996). The report outlines the present status of the Danish nature types, and the flora and fauna, including action-plans for future work. Denmark is the European country in which arable land claims the greatest proportion of the total area (65%), and the agricultural landscape includes many small but important habitat types, such as bogs, humid permanent grassland, and uncultured grassland, which are included in the *Nature Protection Act*. Other small habitat types such as hedgerows, field-borders, shrub and small plantations are not protected (Ed. by: Prip *et al.* 1996). Hymenoptera is not included in the protection plans mentioned in the report, though some of their important habitats such as heath and moors are (Ed. by: Prip *et al.* 1996). No Hymenopteran species are listed in the *Danish Red Data Book* (Ed. by: Stoltze & Pihl 1998), simply because little is known about this important group of insects, especially the species-rich Aculeate Hymenoptera. Recently, the European Union has decided to sponsor a four-year project called *Fauna Europaea*, with

the goal of making a complete species inventory of the terrestrial and limnic fauna. The collection of data will be coordinated by the Zoological Museum, University of Copenhagen. Aculeate Hymenoptera is thus one of the groups particularly in need of a faunistic revision, and hopefully, more light will be shed on which species may be in need of protection.

Faunistic surveys of invertebrates in Denmark have recently included beetles (Hansen 1996), and butterflies (Stoltze 1996), the latter in a large-scale national mapping scheme survey running 1989 through 1994, employing hundreds of amateur recorders. Several beetle and butterfly species are listed in the Danish *Red Data Book*, and are under Danish nature protection law (Ed. by: Prip *et al.* 1996; Ed. by: Stoltze & Pihl 1998). Distribution of bees have not been surveyed in Denmark, but recent species inventories and mapping schemes in neighbouring countries include Germany (Schwenninger 1999; Westrich 1984), The Netherlands (Peeters *et al.* 1999), Sweden (Erlandsson *et al.* 1988; Janzon *et al.* 1991; Norén *et al.* 1998; Svensson *et al.* 1990), and Britain (Kloet & Hincks 1978). In Britain, partial distribution records of bees have been made by Else (1993a and 1993b), and a new key and revised species list is on its way (Else, G.R., *In prep.* - Pers. com. C. O'Toole).

There are substantial indications of a decline in Aculeate Hymenoptera populations in Europe and other regions (Day 1991; O'Toole 1993), and there is a growing focus on habitat management in order to conserve wild bees and wasps. Thus, a national mapping scheme of bumblebees and their forage plants has been made in Britain (Fussell & Corbet 1992) and the *First European Workshop on Habitat Management for Wild bees and Wasps* was held at Cardiff University in April 1998 (Ed. by: Jones & Munn 1998). In the German area Baden-Württemberg, 57% of the listed 429 bee species are endangered or close to extinction (Westrich 1990a), and in Britain, 11.1% of the bee species are either vulnerable, endangered or extinct (O'Toole 1994). In Denmark, wild bee species richness, distribution, and abundance have not been studied in detail for about 75 years (Jørgensen 1921; Lomholdt 1977), and nothing is known about which species are potentially vulnerable or endangered. A rough estimate of solitary bees and bumblebees includes approximately 238 species (26 genera) and 29 species respectively in Denmark (Madsen & Calabuig, *In prep.*). This estimate is presently based only on results from a local survey in an agricultural landscape (I. Calabuig, Manuscript I, *In prep.*) (see Appendix 2), a two year survey on the small Danish Island of Læsø (Münster-Swendsen 2000), a local survey of three different pollination guilds of bees (*Salix*, *Erica* and *Campanula* foragers) (Skov 1999), and the collections of bees held by the Zoological Museum, University of Copenhagen. These inventories have furthermore been supplemented by potential but not recently recorded species, based on checklists from Sweden (Erlandsson *et al.* 1988; Janzon *et al.* 1991; Norén *et al.* 1998; Svensson *et al.* 1990) and the Swedish *ArtDatabanken* on the Internet: <http://www-umea.slu.se/MiljoData/webrod/RodSvar.cfm>. Thus, a fraction of the estimated species may no longer be present in Denmark, and there is an urgent need for a regional faunistic survey and a review of the status of wild bees in Denmark. However, local surveys also serve their right considering that most decisions in land-management are made on this scale. Farmland is the dominating landscape type in Denmark (65% of the area) (Ed. by: Prip *et al.* 1996), and the one being altered the most by man. Therefore, it seemed reasonable to commence a faunistic survey in an agricultural landscape.

This study is based on trappings of bees on a local scale, along six kilometres of semi-natural habitats in a typical Danish conventional farmland, situated in northeast Zealand, Denmark. The main issues addressed in this paper are: **1)** Potential species richness of the bee fauna of a Danish farmland. **2)** Judgement of the sampling effort needed in future investigations of the

bee fauna. **3)** Evaluation of the species recorded in a typical agricultural landscape. **4)** Role of the farmland as stepping stone between core habitats for rare bee species, requiring certain habitat types not found in the farmland.

Surveys to make species inventories are almost never exhaustive, and final species richness estimation, and evaluation of the sampling effort and -methods used, can be achieved through several different approaches. Among others, the classical methods of richness estimation include 1) extrapolation of species-accumulation curves using asymptotic or non-asymptotic functions, and 2) estimation of richness by integration, after fitting of a parametric distribution model to patterns of relative abundance. A widely used parametric distribution model is the lognormal, and patterns of relative abundance are normally expressed as frequency distributions of species abundances (Magurran 1988).

A new group of non-parametric richness estimators have been developed and basically, they all use the number of rare species in samples, and the change of these in cumulative sub-sampling from the dataset, to estimate true species richness in assemblages. In the abundance-based estimators, the cumulative curves are based on models employing species represented by only one (singletons) or two (doubletons) individuals. In the incidence-based estimators, the backbone of the models are species occurring in only one (uniques) or two (duplicates) samples relative to frequent species in the sub-samples. For further theoretical background and application, see the extensive evaluations by Chazdon *et al.* (1998), Colwell & Coddington (1994), and Walther & Morand (1998).

Since the methods of non-parametric species richness estimators is a relatively new field, and since no conclusive recommendations for use have been reached (Colwell 1997; Walther & Morand 1998), I find it informative to evaluate and present all the estimators supplied by the free-ware programme *EstimateS 5* by Colwell (1997). Therefore, analyses of the bee species richness from relative abundance data included: 1) A species-accumulation curve (*sensu* Chazdon *et al.* (1998)), 2) The Coleman random placement curve (Coleman 1981; Coleman *et al.* 1982), 3) One parametric and seven non-parametric species richness estimators.

Materials and methods

Data collection

A survey of solitary bees and bumblebees was made April through November 1997 in a Danish conventional agricultural landscape, situated north of Ringsted, northeast Zealand, Denmark (55°30-32'N, 11°45-47'E). 64 small window-traps standing in yellow pan-traps were placed on the ground in distances of 100 metres along six kilometres of hedgerows, and other semi-natural habitats (three transects, each of about two km). The traps were emptied approximately once a week. Study area and methods for sampling of bees are described in detail in I. Calabuig, Manuscript I (*In prep.*).

Evaluation of data collection and estimation of species richness

Optimally, estimation of species richness from samples should be made in a homogeneous landscape, with the purpose of avoiding total sampling of the area. In reality, a homogeneous

landscape is most often a fine-grained mosaic of habitats. The survey area comprises a mosaic of linear and areal semi-natural habitats in a matrix of agricultural fields. These semi-natural habitats vary in their quality as bee habitats and thus in the number of species and individuals sampled. The order in which samples are added to a species-accumulation curve determines the shape of the curve. Different orders of the same sampling material result in variable curves due to heterogeneity of the samples (Chazdon *et al.* 1998; Colwell & Coddington 1994). Therefore, the species-accumulation curves and the richness estimates presented here are based on a number of randomisations of the order in which the samples are added to the curves.

Species and abundance data were analysed using the free-ware application *EstimateS 5* (Colwell 1997) and were based on 100 randomisations (default: 50 randomisations). Upper abundance limit for rare or infrequent species was set to 10 individuals (default). Samples were added to the analysis in random order and without replacement to generate a mean species-accumulation curve (*sensu* Chazdon *et al.* (1998)).

To assess whether the samples are sufficiently homogeneous to be used for richness estimation, the observed mean species-accumulation curve (S_{obs}) is compared to a Coleman random placement curve (Coleman 1981; Coleman *et al.* 1982). In the Coleman curve, cumulative richness is estimated by randomly taking sub-samples from the pooled dataset, and by pooling the dataset, the effect of contagiously distributed species is removed. If the mean species-accumulation curve lies distinctly below the Coleman curve, the samples are too heterogeneous for richness estimation (Colwell 1997).

Apart from a mean species-accumulation curve and the Coleman random placement curve, *EstimateS 5* (Colwell 1997) generate richness estimate curves based on 1) a parametric estimator that uses asymptotic extrapolation (Michaelis-Menten), and 2) seven different non-parametric species richness estimators, presented below. Two types of the two-parameter hyperbolic function of Michaelis-Menten with Raijmakers maximum likelihood modifications (Raijmakers 1987) are computed, but only the type *MMMeans* is presented here. *MMMeans* is generated by the programme once, after calculation of a mean species-accumulation curve.

The seven non-parametric species richness estimators are:

- **Chao₁** (Abundance-based estimator of species richness) (Chao 1984)
- **Chao₂** (Incidence-based estimator of species richness) (Chao 1987)
- **Jack₁** (First order Jack-Knife procedures) (Burnham & Overton 1978; Burnham & Overton 1979; Heltshe & Forrester 1983; Smith & Belle 1984)
- **Jack₂** (Second order Jack-Knife procedures) (Burnham & Overton 1978; Burnham & Overton 1979; Palmer 1991; Smith & Belle 1984)
- **ACE** (Abundance-based coverage estimator of species richness). May also be used for computation of complementarity (e.g. jaccard index) (Chao *et al.* 1993; Chazdon *et al.* 1998)
- **ICE** (Incidence-based coverage estimator of species richness) (Chazdon *et al.* 1998; Lee & Chao 1994)
- **Bootstrap** (Smith & Belle 1984)

Spreadsheets and statistical packages used: Excel 2000, Sigma Stat ver. 2.03, Sigmaplot ver.5.01. Further explanations of data analyses are to be found in the results section.

Results

Estimation of true species richness and evaluation of sampling effort

In this survey, 72 species of non-Apidae bees (13 genera) and 20 species belonging to Apidae were recorded in 64 yellow pan-traps exposed for one season April through November 1997 (Table 1, Appendix 2). These findings represent 30.3% of the solitary bee species and 66.7% of the social bee species (*Bombus*, *Psithyrus* and *Apis*) occurring in Denmark (estimated 238 species in 26 genera, and 30 species respectively, (Madsen & Calabuig, *In prep.*). A relative abundance distribution of the recorded species is presented in Fig. 1. For 19.8% of the species, only one individual was recorded, and 29 species (31.9%) were recorded in numbers between 2 and 15.

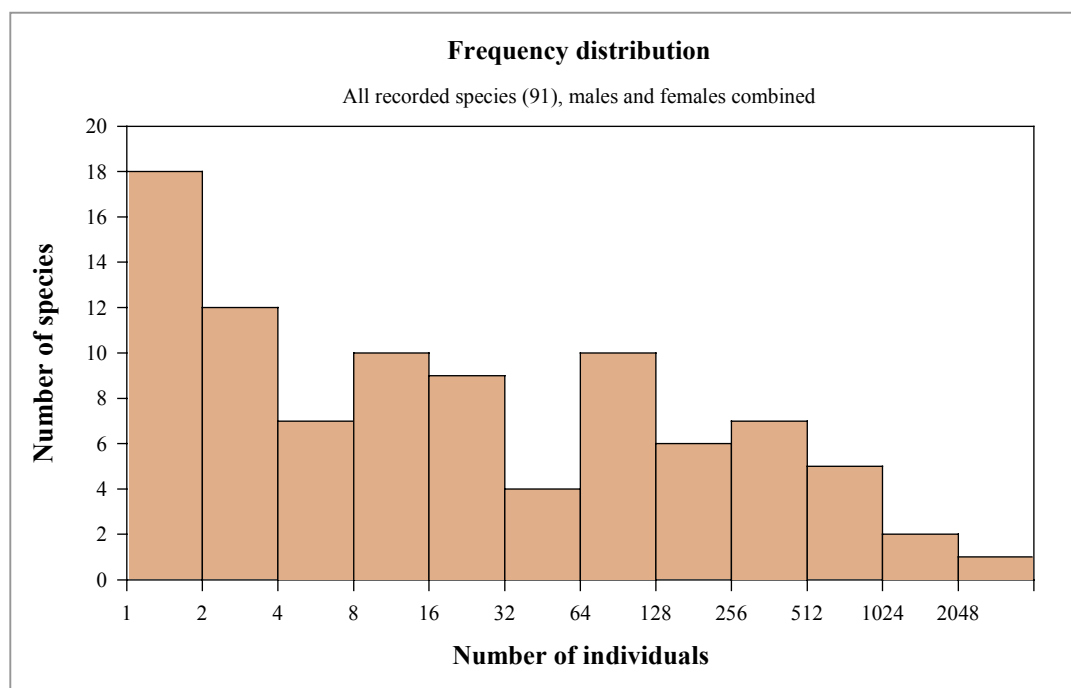


Fig. 1 Species frequency distribution. Log₂ octaves are used as the intervals of abundance categories, axis labels showing the lower boundary of a class. For clarity, species represented by only one individual (singletons) are plotted separately (i.e. 2⁰). Note that only 91 species are counted in the graph since two species were counted collectively (see Appendix 2).

100 randomisations were used to obtain a smooth mean species-accumulation curve (Fig. 2) (Chazdon *et al.* 1998) and rendered slightly more smooth and stable curves than the programme default of 50 randomisations (Colwell 1997). Curves resulting from randomisations up to 1000 times (200, 500, and 1000) were almost identical and did not alter the result. The species-accumulation curve (S_{obs}) was almost indistinguishable from the Coleman randomisation curve (Coleman 1981; Coleman *et al.* 1982) (Fig. 2), and no marked difference from the unmodified species-accumulation curve was found when using the shuffle option of the programme (all individuals within species shuffled between samples). These two results indicated sufficient homogeneity of the samples for species richness estimation (Colwell & Coddington 1994; Colwell 1997). However, the species-accumulation curve and the Coleman curve failed to reach stable values, and were still increasing at the final sub-sampling efforts (Fig. 2).

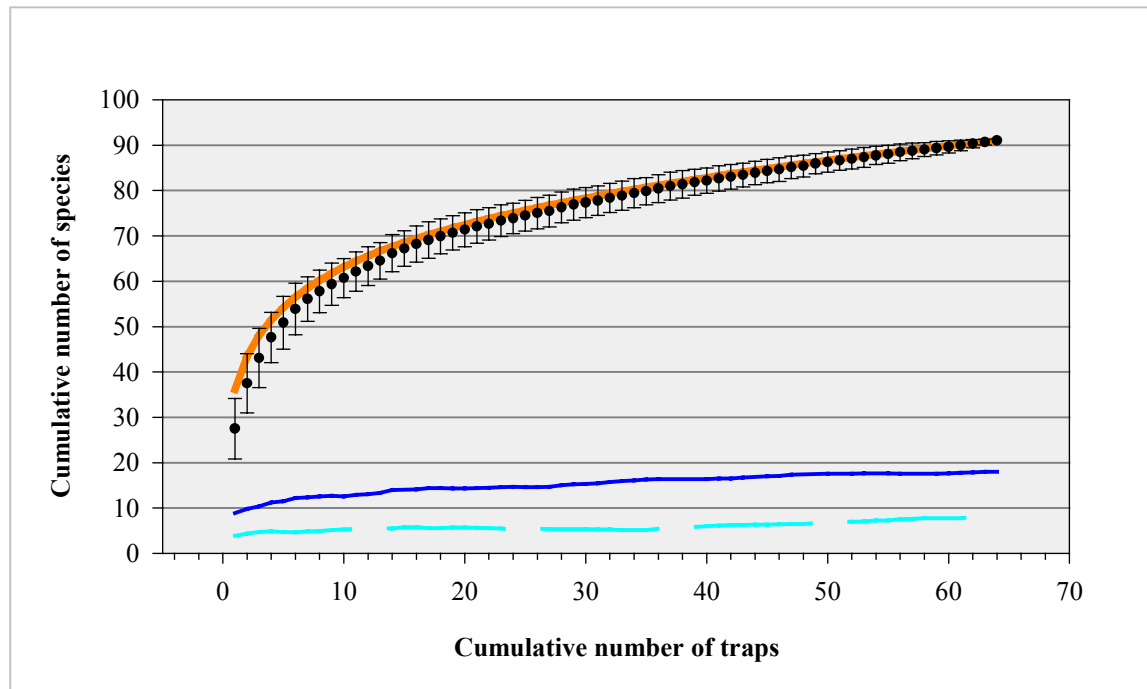


Fig. 2 Mean species-accumulation curve (S_{obs} , black dots) and standard deviation. Coleman randomisation curve (orange line). Lower thin lines indicate singletons (dark blue, solid line) and doubletons (light blue, stippled line).

The level of singletons (no. of species represented by only one individual) and doubletons (no. of species represented by two individuals) showed a rather constant but slow climb (Fig. 2). The Jackknife ($Jack_1$ & $Jack_2$), ACE, and ICE estimators continued to rise, though with decreasing slopes (Fig. 3a)-b) and e)-f)). The bootstrap estimator mirrored the accumulation curve, though on a slightly higher level (Fig. 3c). The mean Michaelis-Menten curve followed that of the species-accumulation curve, but levelled off a little faster, terminating on a slightly lower level than the accumulation curve (Fig. 3d).

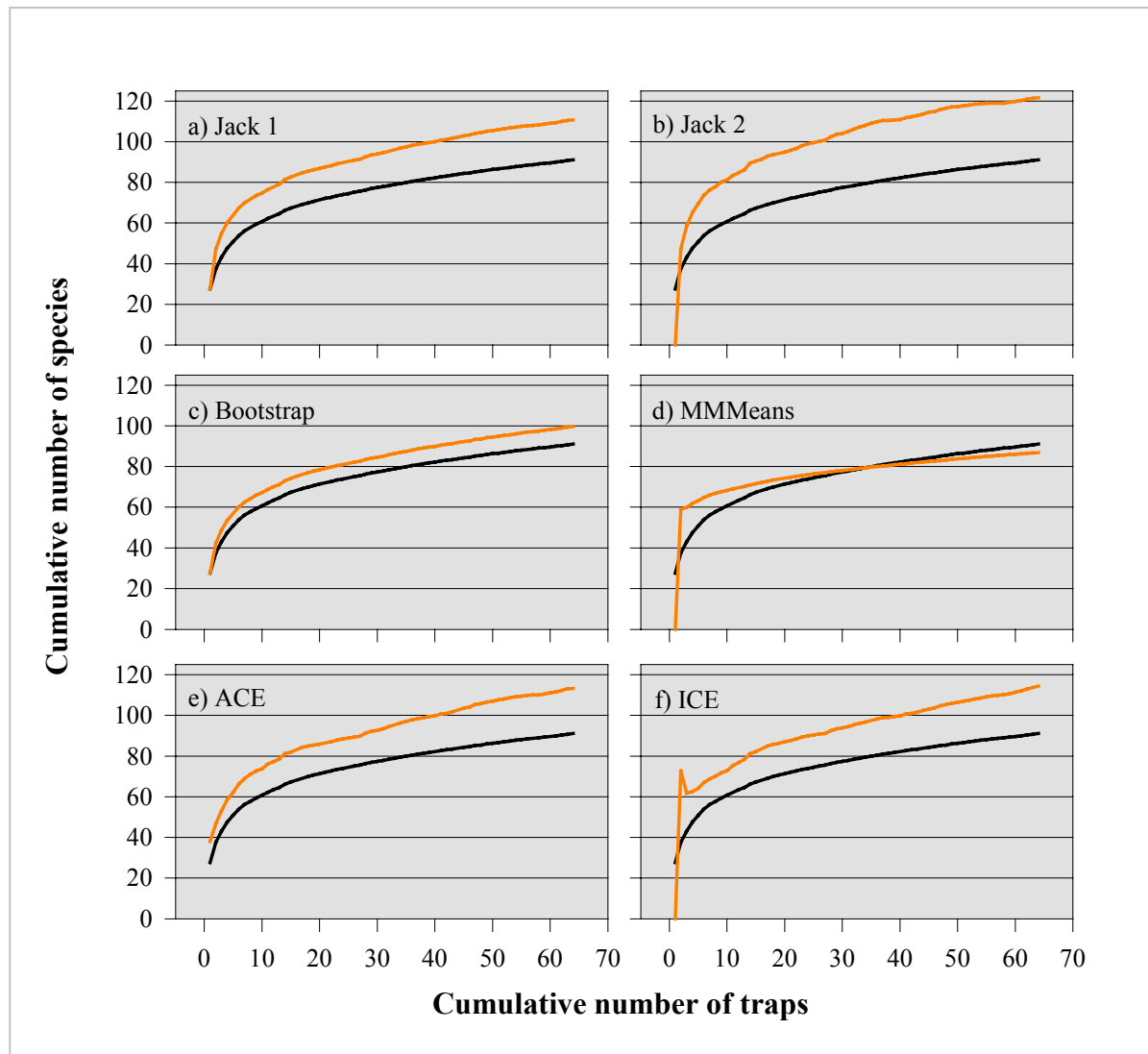


Fig. 3 **a-f**): Species-accumulation curve (S_{obs} , lower black lines) and species richness estimators (upper orange lines). Cumulative number of species (S_{obs}) in increasing number of traps sub-sampled randomly (randomisation 100 times without replacement).

Only the Chao₁ and Chao₂ estimators reached a stable equilibrium (Fig. 4) after sub-sampling of about half the maximum sampling effort of 64 traps. The Chao₁ (Fig. 4a) estimator reached an equilibrium at 34 traps sub-sampled, ranging between an estimate of 110 and 114 species. The Chao₂ curve (Fig. 4b) levelled off at 35 sub-samples with an estimate ranging between 114 and 117 species.

Gleason (1922) proposed the non-asymptotic log-linear model for the species-accumulation curve, and performance was evaluated by Palmer (1990). The model assumes a linear relationship between number of observed species ($S(n) = S_{obs}$) and the logarithm to area sampled or number of samples (n). Colwell & Coddington (1994) emphasise that such non-asymptotic models are suitable for prediction of increase in species richness with increase in sampling effort. Regression of S_{obs} on the logarithm to number of traps (n), showed an almost perfect correlation of $S_{obs} = 35.347(\log(n)) + 25.84$, $r^2 = 0.9979$. Solving the equation for $S_{obs} = 114$, rendered a forecast of 312 samples needed to obtain the Chao₁ and Chao₂ estimates of a true richness of 114 species. On the same terms, doubling the sampling effort from 64 to 128 traps would have revealed 9 more species.

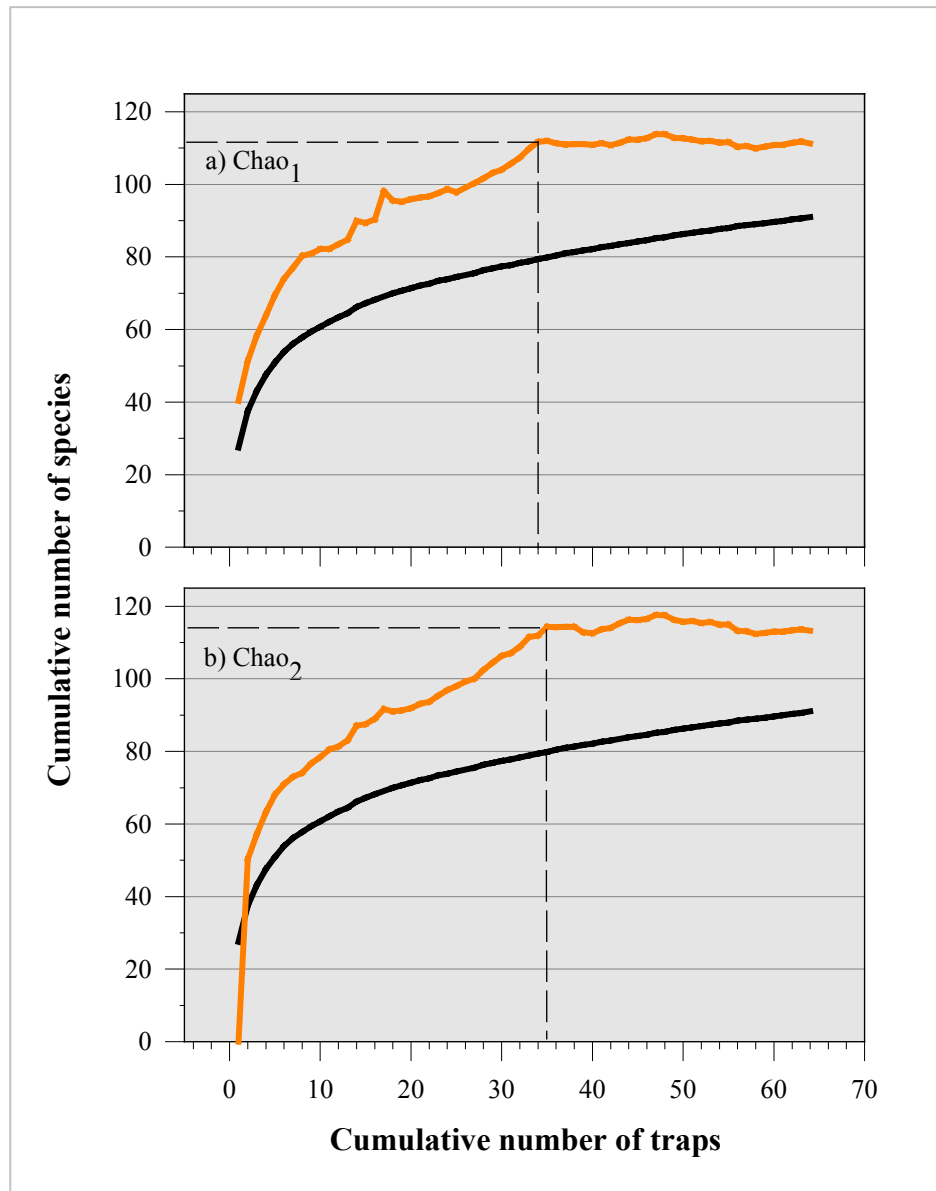


Fig. 4 **a)-b)**: Species-accumulation curve and species richness estimators. Cumulative number of observed species (S_{obs}) in increasing number of traps sub-sampled randomly (randomisation 100 times without replacement). **a)** and **b)**: S_{obs} = Lower, black lines). **a)** Chao₁ = Abundance-based species richness estimator (Upper, orange line) **b)** Chao₂ = Incidence-based species richness estimator (Upper, orange line).

Species composition

Since nothing is known of the present status of Apoidea in Denmark, all evaluation and discussion of common and rare species has to be based on literature from neighbouring countries. The recorded bee species belong to the genera listed in Table 1. The estimated number of Danish species within genera are according to (Madsen & Calabuig, *In prep.*), and the total species inventory, and an indication of genera not represented in this survey are to be found in Appendix 2. Abundance data for all species are listed in Appendix 4 and Appendix 5.

Table 1 Species and individual numbers in genera (Megachilid genera in bold).

Genera	Number of species			No. of individuals	Nesting of recorded spp.
	Recorded	Estimated in Denmark	Percentage		
<i>Colletes</i>	2	7	28.6	32	Soil & self-made cavity
<i>Hylaeus</i>	4	18	22.2	20	Cavity
<i>Andrena</i>	22	57	38.6	3040	Soil
<i>Halictus</i>	2	8	25.0	627	Soil
<i>Lasioglossum</i>	20	32	62.5	3088	Soil
<i>Sphecodes</i>	4	13	30.8	188	- (hosts in soil)
<i>Chelostoma</i>	2	3	66.7	11	Cavity
<i>Osmia</i> (incl. <i>Hoplitis</i>)	3	15	20.0	5	Soil
<i>Megachile</i>	2	11	18.2	2	Cavity
<i>Anthidium</i>	1	3	33.3	7	Cavity
<i>Nomada</i>	9	31	29.0	1116	- (hosts in soil)
<i>Anthophora</i>	1	6	16.7	3	Cavity
<i>Bombus</i> (excl. <i>Psithyrus</i>)	13	21	61.9	2803	Under or above ground
Subgenus <i>Psithyrus</i>	6	8	75.0	580	- (Hosts under or above ground)
<i>Apis</i>	1	1	100.0	2181	- (managed hives)

The abundant bumblebee species in this survey (Appendix 4), are the same as the ones now common in Britain, Germany, and the Netherlands (Kwak *et al.* 1996; Prys-Jones & Corbet 1991; Westrich 1990a). In addition, three species considered most vulnerable: *Bombus muscorum*, *B. ruderarius*, *B. soroeensis*, and two species presumed extinct: *B. subterraneus* and *B. sylvarum* were recorded, though in low numbers.

Four of the recorded species are new to the Danish fauna: *Andrena subopaca*, *Lasioglossum lativentre*, *L. rufitarse*, and *L. semilucens*, though all are reported as occurring in Sweden (Svensson *et al.* 1990). One species of *Andrena* and three species of *Lasioglossum* remain unidentified, and they do not conform to any Danish species by their morphology, and may thus be new species to the Danish fauna.

According to the *Red Data Book of bees* in O'Toole (1998), only *Andrena vaga* is considered endangered, but *A. varians*, *Lasioglossum parvulum* and *L. smeathmanellum* are listed in the Swedish *Red Data Book* on the Internet (Swedish Red Data Book 2000) as extinct in southern Sweden. According to Westrich (1990a), 11 more of the recorded species are listed as threatened (Table 2). No attempt was made to calculate the *Archer National Quality Score* (Archer 1995), since far too little is known about the overall status and distribution of bee species in Denmark.

Table 2 Recorded *Red Data Book* species.

		Reference			Category
		Westrich 1990a	Swedish Red Data Book	O'Toole 1998	
<i>Andrena</i>	<i>barbilabris</i>	X			Endangered
	<i>cineraria</i>	X			Endangered
	<i>clarcella</i>	X			Endangered
	<i>praecox</i>	X			Endangered
	<i>vaga</i>			X	Endangered
	<i>varians</i>		X		Extinct
	<i>wilkella</i>	X			Endangered
<i>Anthophora</i>	<i>furcata</i>	X			Endangered
<i>Colletes</i>	<i>cunicularius</i>	X			Endangered
<i>Nomada</i>	<i>leucophthalma</i>	X			Endangered
<i>Osmia</i>	<i>pilicornis</i>	X			Vulnerable
<i>Lasioglossum</i>	<i>lativentre</i>	X			Strongly endangered
<i>Lasioglossum</i>	<i>parvulum</i>	X	X		Extinct / Endangered
<i>Lasioglossum</i>	<i>quadrinotatum</i>	X			Vulnerable
<i>Lasioglossum</i>	<i>smeathmanellum</i>		X		Extinct

Six species of *Andrena*, two *Nomada* species, *Halictus tumulorum*, and three *Lasioglossum* species were very abundant in this survey, each represented by more than 200 individuals in the traps (Appendix 4 and Appendix 5). *Lasioglossum leucopus* is a gregariously nesting species, and was far the most abundant and widespread bee species (169 males and 1822 females out of 8139 solitary bee individuals). The primary inquiline bee species of *L. leucopus* is most likely *Sphecodes geofrellus*, which was the second most abundant species within that genus. *S. geofrellus* parasitises small species of *Lasioglossum*: *L. leucopus*, *L. morio* (very similar to *L. leucopus*) and *L. nitidiusculum* (not found in this survey).

Inquilines and "Cleptoparasitic load"

Recordings of inquiline species may be used as a measure of habitat quality since lack of inquilines may indicate that host populations are either newly founded, or not persistent or abundant, in the landscape. Furthermore, recordings of inquilines may indicate presence of host species yet to be discovered in an area (O'Toole & Ismay 1995), but in this survey, no inquiline species were recorded without at least one host species also occurring in the traps (Appendix 5), (I. Calabuig, Manuscript I, *In prep.*).

Only three species (plus one unidentified species) of *Andrena* were recorded without any corresponding, inquiline bee species, though potential Danish species are known (Appendix 5). These *Andrena* species were all rare, only represented by four males and eight females in all.

Inquiline species of both of the *Halictus* species were recorded. Nine species (plus three unidentified species) of *Lasioglossum* were recorded without any potential inquiline bee species in the area (Appendix 5). Six of the identified species were rare, 4 males and 35 females in all, and no inquilines are indicated with certainty in Westrich (1990b). Three species were more abundant: *Lasioglossum fulvicorne* (95 females), *L. minutissimum* (54 females), and *L. semilucens* (62 females), but only zero, three and seven males, respectively, were recorded. Of these, Danish inquiline species are confirmed only for *L. fulvicorne*.

Only inquilines of *Andrena*, *Lasioglossum*, and *Halictus* were found in this survey, none were found for the remaining host genera listed in Table 1. No attempt was made to monitor non-bee inquilines such as the members of Mutillidae, Chrysididae, and inquiline wasp species (e.g. *Sapyga clavicornis* (Münster-Swendsen & Calabuig 2000)) However, *Cleptoparasitic Load* as suggested by Archer (1995), thus involving bee-inquilines only, is indicated in Table 3.

Table 3 Frequency of inquiline species (Only the identified species and species with known Danish inquilines are included).

Host group	No. of hosts (H)	No. of inquilines (I)	<i>Cleptoparasitic load</i> (100 * I/(H+I))
<i>Andrena</i>	22	11	33.33
<i>Lasioglossum</i> + <i>Halictus</i>	12	4	25.00
<i>Soil-nesters</i>	35	14	28.57
<i>Cavity-nesters</i>	14	0	0
<i>All solitary species</i>	49	13	20.96

Frequency of cavity-nesters

By comparing number of species with individuals in Table 1, it becomes clear that the cavity-nesting family Megachilidae and the genus *Hylaeus* are reasonably well represented by species in this survey, but that abundances of individuals within species are extremely low.

All Danish species of *Andrena*, *Lasioglossum*, and *Halictus* nest in the soil (Table 1). *Nomada* and *Sphecodes* are primarily inquilines of *Andrena* and *Lasioglossum* /*Halictus* respectively. *Colletes cunicularius* nest in sand, and *C. daviesanus* nest in self-made cavities of soft clay-, mortar-, or sandstone-walls of buildings. The 14 cavity-nesting species (Table 4) thus comprised 23.7% of the solitary, non-inquiline bees (59 species) and 19.4% of the total number of solitary bees (72 species). The value of 23.7% corresponds to the index of *Archer Aerial Nester Frequency* (Archer 1995), which in this survey hence are within the same range as the findings in the *Chafford Hundred Survey* (22.3%) by O'Toole & Ismay (1995), reviewed by O'Toole (1998). In all, the cavity-nesters were represented by 79 individuals (1 species, *C. daviesanus*, accounting for 31 individuals), which is only 0.97% of the total recorded number of solitary bee individuals (8139, non-Apidae). No representatives of their inquiline genera were found (i.e. *Coelioxys*, *Stelis*, *Epeolus spp.*).

Table 4 All recordings and abundance of bee species nesting in cavities (selected nesting habits according to Westrich (1990b)).

	♂	♀	Nesting habitat
<i>Colletes daviesanus</i>	10	21	Self-made cavities in soft clay-, mortar-, or sandstone walls.
<i>Hylaeus brevicornis</i>	3	4	Old <i>Rubus fruticosus</i> & <i>R. idaeus</i> stems, beetle borings in old wood.
<i>Hylaeus communis</i>	0	2	Opportunist, e.g. old <i>Rubus</i> and <i>Rosa</i> stems, insect borings in old wood, crevices in buildings.
<i>Hylaeus confuses</i>	2	7	Old insect borings in wood, old <i>Rubus fruticosus</i> stems, and oak galls made by <i>Andricus kollari</i> .
<i>Hylaeus hyalinatus</i>	0	2	Opportunist, e.g. old <i>Rubus</i> and <i>Rosa</i> stems, crevices in buildings, and old Megachilidae nests.
<i>Anthidium manicatum</i>	4	3	Opportunist, all kinds of pre-existing holes and crevices.
<i>Chelostoma campanularum</i>	1	0	Tubular cavities, diam.≈ 2-2.5 mm, e.g. insect borings in wood, (<i>Phragmites</i>) straws of thatched roofs.
<i>Chelostoma florissomme</i>	7	3	Tubular cavities, diam.≈ 3.5 mm, e.g. insect borings in wood, (<i>Phragmites</i>) straws of thatched roofs.
<i>Megachile lapponica</i>	1	0	Pre-existing holes, e.g. insect borings in old wood.
<i>Megachile willughbiella</i>	0	1	Self-made or pre-existing cavities in old, rotten wood.
<i>Osmia claviventris</i>	0	1	Stems of marrow-containing plant species, e.g. <i>R. fruticosus</i> , <i>Cirsium sp.</i> , <i>Arctium sp.</i>
<i>Osmia pilicornis</i>	0	3	Probably different sorts of pre-existing cavities.
<i>Osmia rufa</i>	1	0	Opportunist, pre-existing cavities of varying shape and size.
<i>Anthophora furcata</i>	1	2	Self-made, branching, cavities in old, rotten wood.
TOTAL	30	49	

Discussion

Estimation of species richness and sample effort

The Jackknife estimators 1&2, the Abundance-based coverage estimator (ACE), and the Incidence-based coverage estimator (ICE) did not perform well on this data material (Fig. 3), and they will not be discussed further. ACE and ICE may be used to calculate indices of complementarity (or similarity) of species assemblages, e.g. when comparing different landscape or habitat types. Since ACE and ICE did not reach stable values in this survey, no attempt was made to analyse differences in species composition between habitat types.

Chao₁ and Chao₂ reached stable values after a little more than half of the maximum sub-sample effort (34-35 traps, Fig. 4). They estimated potential true species richness in the surveyed agricultural landscape to be about 114 species. Chao (1984) indicates that the estimators are lower bounds, but that they are known to perform well on datasets like this, where a preponderance of rare species is found (Fig. 1). Despite the fact that only the Chao₁ and Chao₂ estimators performed convincingly, the other estimators are still promising tools for assessment of the bee fauna on a local scale, and for comparing the bee fauna of different regions.

The log-linear model performed a little better than the log-log model, and similar findings are indicated by Palmer (1990). The log-linear model was therefore chosen to predict the number of traps needed to obtain the estimated 114 species depicted from the Chao₁ and Chao₂

richness estimators. The forecast of 312 traps needed is of course only a rough estimate, but still useful for overall evaluation or planning of a survey (Colwell & Coddington 1994). Doubling the sampling effort from 64 to 128 traps apparently could have revealed about nine more species. However, extensive labour of handling samples, and potential exhaustion of the bee populations already recorded, are both serious drawbacks of intensive pan-trapping in order to obtain a few more species. Window-traps in yellow pan-traps have proved to be an efficient and reliable sampling-method (I. Calabuig, Manuscript I, *In prep.*). Once a preliminary knowledge of the fauna and relative abundances thus has been achieved by intensive pan-trapping, recommended methods for monitoring changes in the fauna will be fewer pan-traps exposed in chosen seasonal intervals (e.g. every fifth season) combined with sweep-netting, observations on flowers and at soil-nest-sites, and trap-nesting, (e.g. see Frankie *et al.* (1998) and Steffan-Dewenter & Tschardt (2000)).

Species composition

From Fig. 1, Appendix 4, and Appendix 5 it is seen that as many as 29 species (31.5% of the total species number) were represented by five or less individuals. Some species must be considered accidental visitors within transects, maybe nesting in areas far away from the traps. Other species probably are rare and scattered, but persistent. Similar findings of small, isolated populations are reported by O'Toole (1994).

Bombus muscorum, *B. ruderarius*, and *B. soroensis* are considered most vulnerable in other countries (Kwak *et al.* 1996; Prys-Jones & Corbet 1991; Westrich 1990a) but in Denmark they are not rare and seem to thrive, *B. muscorum* mainly in Jutland and the other two species mainly on Zealand. Still, they are not as common as e.g. *B. pascuorum*, *B. lucorum*, *B. lapidarius*, and *B. terrestris*, and they probably never were. *B. subterraneus* and *B. sylvarum*, which were also recorded in this survey, have never been common in Denmark, and species that are naturally uncommon or only very locally abundant will of course be the ones most vulnerable to changes in the landscape. Especially the decline in *Trifolium* seed production, and the decline in areas of hay-meadows, which provide both nesting and foraging for bumblebees, have had detrimental effects on populations.

15 solitary bee species that are considered vulnerable or endangered in other countries were recorded in this survey (Table 2). Several of these species are polylectic but have special nesting requirements such as for loose sand (*Andrena barbilabris*) or for short grass on sandy soils (*A. vaga*). Some species are naturally rare and were already noted as such by Lavritz Jørgensen (1921) (e.g. *A. cineraria*, *A. vaga*). Others species are common but vulnerable due to their special foraging requirements, e.g. for Fabaceae (*A. wilkella*), and for *Salix* (*A. praecox*, and *A. clarcella*). Potential decline in *A. clarcella* populations will affect its nest inquiline *Nomada leucophthalma*, which therefore is considered vulnerable also. *Lasioglossum lativentre* is new to Denmark but may have been overlooked in older collections of bees since it is closely related and very similar to *L. quadrinotatum*. Both species nest solitarily, but no special nesting or foraging requirements are otherwise known. Still, only one male *L. lativentre* was recorded whereas *L. quadrinotatum* was the second most abundant *Lasioglossum* species (Appendix 4).

Anthophora furcata is most certainly endangered in Denmark since it has special foraging requirements for *Lamiaceae* (Appendix 4) and special nesting requirements for old wood (Table 4). The making of brood cells in rotten wood is slow work, and reproductive output per nesting female is low. Furthermore, old rotten wood is a scattered resource since forestry has been intensified and few undisturbed forests exist in Denmark. Another endangered species that depend on undisturbed forests (mainly clearings) may thus be *Osmia pilicornis*, which also primarily nest in insect borings in old wood.

Colletes cunicularius is strictly oligolectic on *Salix*, which was quite abundant in some restricted areas along the surveyed semi-natural habitats. *C. cunicularius* is a pioneer species that rapidly invades areas with bare, loose sand, often near streams or in sand dunes, and it is often found in large aggregations (Westrich 1990b). The species is also known to cover substantial distances between nesting- and foraging areas. Still, only a single male individual was recorded, and no suitable nesting sites were observed in the area. This observation may be an example of proper foraging conditions but lack of nesting habitats within reasonable distance. In many cases, distance between habitats may be a problem for bee species persistence in the scattered semi-natural habitats of the agricultural landscape (Westrich 1996). Abundant bee species in the agricultural landscape are thus most likely to be opportunist soil- or cavity-nesters that are polylectic in their pollen requirements. Being a generalist leaves more opportunities for nesting sites in the semi-natural habitats and makes one less vulnerable to changes in the flora community (I. Calabuig, Manuscript I, *In prep.*). Hence, species like *Andrena bicolor*, *A. minutula*, *Halictus tumulorum*, *Lasioglossum calceatum*, and *L. leucopus* are abundant, and their nesting- and foraging conditions in the agricultural landscape are discussed in I. Calabuig (Manuscript I, *In prep.*).

Inquilines and “Cleptoparasitic Load”

Recordings of species richness and distribution of inquiline bees may be compared to the distribution of host species in two ways: 1) If no parasites are present, the bee population may not be stable, and / or is newly founded, or population density is too low for parasite detection. Conversely, the presence of parasites may indicate that host populations have been persistent through a sufficient period for parasite detection and invasion to occur. 2) Presence of parasites may indicate host species yet to be recorded in a survey (O'Toole & Ismay 1995).

The inquiline-host complex of *Nomada* and *Andrena* is considered more or less revealed in this study, since no inquilines were found without at least one of the known host species, and only three very rare *Andrena* species out of 21 identified species were recorded without hosts (Appendix 5). This leads to the conclusion that the majority of *Andrena* species have been recorded in this study, and that the species nest and forage in the agricultural landscape (I. Calabuig, Manuscript I, *In prep.*).

Halictus tumulorum was abundant in the survey (Appendix 4), and its inquiline species *Sphcodes ephippius* was the most abundant *Sphcodes* species (Appendix 5). Contrary to the other recorded species of this genus, *S. ephippius* also parasitises species of *Andrena*, and distinct groups of morphotypes varying in colour and size were found. This variation in inquiline morphology is presumably a result of the range in host species size and thus in amount of provision in brood cells.

The inquiline-host complex of *Sphecodes* and *Lasioglossum* species is more complicated to evaluate. No inquilines of *Lasioglossum* were recorded without potential host species (Appendix 5), and therefore it seems that the majority of *Lasioglossum* species occurring in the area have been recorded in the traps. Nine species (plus three unidentified species) of *Lasioglossum* were recorded without any potential inquiline bee species in the area (Appendix 5). Six of the identified species were rare, but no indications of whether they are persistent and nest in the area are to be found, since no inquilines of these species are confirmed with certainty (Westrich 1990b). The remaining three *Lasioglossum* species were more abundant: *L. fulvicorne* (95 females, 0 males), *L. minutissimum* (54 females, 3 males), and *L. semilucens* (62 females, 7 males), but Danish inquiline species are confirmed only for *L. fulvicorne*, i.e. *Sphecodes ferruginatus*. The low number of males recorded in the traps indicates that these three species do not nest along the transects, but this may not apply to *L. fulvicorne*. *L. fulvicorne* is known to nest gregariously in many soil- and habitat types, and it is polylectic, including *Asteraceae*, which was abundant along the transects (I. Calabuig, Manuscript I, *In prep.*).

Epeolus variegatus (Apidae) was not found although 10 males and 21 females of its host-species *Colletes daviesanus* were recorded. *C. daviesanus* is strictly oligolectic on *Asteraceae*. Consistently, only two or three individuals of *C. daviesanus* were recorded at a time, in 21 different traps of all three transects. These scattered recordings suggest that *C. daviesanus* does not nest in the semi-natural habitats. The species is known to nest in large aggregations in self-made cavities in soft clay- mortar- or sandstone-walls of older buildings, where it may cause severe damage (Westrich 1990b). Thus, this species and its inquiline species presumably would have been found in greater numbers, had old farm-buildings been included in the survey.

As discussed below, abundances of all cavity-nesters (Table 4) were low and accordingly, no representatives of their inquiline genera were found (i.e. *Coelioxys*, *Stelis*, *Epeolus spp.*).

Cleptoparasitic Load (CL) is normally calculated for the bee community as a whole (Archer 1995), but in this survey there was such a distinct difference in abundance and distribution between soil- and cavity-nesters, that it seemed more correct to calculate CL for separate groups of bees (Table 3). Though at first glance the semi-natural habitats may seem unsuitable for persistence of cavity-nester (CL=0), the role of these habitats is probably important (see detailed discussion in the next paragraph). Many soil-nesting species are abundant and persistent in the semi-natural habitats, and the foraging- and nesting conditions for these species are treated in I. Calabuig, Manuscript I (*In prep.*). Support for the conclusion that the semi-natural habitats supply both foraging- and nesting areas for populations of *Andrena* and *Lasioglossum* is reflected in the relatively high *Cleptoparasitic Load* (CL=28.57).

Frequency of cavity-nesters

Although the *Aerial Nester Frequency* (Archer 1995) of 23.7% is within close range of the findings in the *Chafford Hundred* area in Essex (O'Toole 1998), I find that the low abundance of cavity-nesters in this survey makes the over-all result unsuitable for comparative measures of habitat quality for persistent populations. The high number of cavity-nesting species but low number of individuals is rather to be interpreted as an indication of semi-natural habitats

functioning as corridors between optimal core-habitats. In these habitat-corridors, small numbers of individuals nest and may slowly disperse between core-habitats. Indications for this conclusion come from the lack of inquiline species of cavity-nesters in this study, and from the constancy in yields of cavity-nesters from certain traps. Hence, the majority of cavity-nesters have all been found in relatively few traps, of which most were placed along undisturbed habitats such as old, dense hedgerows and near or along forest edges. For example, all three instances of *Chelostoma florissomne* recordings were in the same trap on three different dates, June 20, 27 and July 23, which coincides well with the activity period of *C. florissomne* observed during the survey of 1996 (Münster-Swendsen & Calabuig 2000). The trap was placed some 150 metres from a forest, and the surrounding habitat was relatively humid and undisturbed, with abundant, old, dead wood, and dry plant stems. From the same trap plus the two neighbouring traps came one out of seven recordings of *Anthidium manicatum*, three out of seven recordings of *Hylaeus confusus*, both recordings of *Megachile spp.*, the single recording of *Osmia claviventris*, and one out of three *O. pilicornis* individuals (see Table 4). In addition, several recordings of cavity-nesting wasps (*Trypoxylon*, *Pemphredon* etc.) were made in these traps. Though recordings and individual numbers are scarce, this constancy in trappings indicates that several of the species are probably not just accidental guests within the transects.

Soil-nesting species with shallow nest depths cannot nest in unstable habitats such as the field proper, where mechanical soil treatments are applied at least once a year (I. Calabuig, Manuscript I, *In prep.*). But cavity-nesters may be considered even more vulnerable than soil-nesters since they require habitats that have been left undisturbed for a long period of time, and which contain nesting substrates such as dead shrub material or old wood with abandoned insect borings. Furthermore, cavity-nesters generally have lower population densities, their nesting places being a more scattered resource in the agricultural landscape than suitable soils. Exceptions are species that establish in anthropogenic surroundings, such as thatched roofs (Münster-Swendsen & Calabuig 2000) or old half-timbering and mortar walls (*Colletes daviesanus*). Cavity-nesters are probably not abundant in the Danish, rather open, agricultural landscapes, but trap-nesting in combination with pan-traps may reveal even more species, and bee-boards placed by the farmer may enhance nesting conditions for this group of bees (Tscharrntke *et al.* 1998). Several of the cavity-nesting species are important pollinators of orchard trees and some flowering crops (e.g. Alfalfa), and opportunist species such as *Osmia rufa* and *Megachile centuncularis* were expected in this survey but not found, presumably due to insufficient nesting conditions.

Still, in this survey it seems that when the right conditions are present, many species of cavity-nesters are found, though in low numbers. Therefore, I consider these rare habitats to function as important corridors between more optimal core-habitats, and these corridors may be substantially improved if bee-boards are installed on poles or in woody vegetation along the semi-natural habitats (Frankie *et al.* 1998; Tscharrntke *et al.* 1998). More cavity-nesting species with higher abundances would probably be recorded if farm-gardens, thatched roofs, houses, and barns were included in a survey similar to this.

Conclusion

There are substantial indications of a decline in wild bee populations in Europe and other regions (Day 1991; O'Toole 1993). Considering the general worry in Denmark of the conventional farmland developing into an agricultural desert, the number of bee species recorded in this study (92) is therefore quite surprising, and an uplifting result. Window-traps in yellow pan-traps is recommended as the initial method for surveys of bee faunas and non-parametric estimators are promising tools for estimations of true species richness of bees.

There is no doubt that elimination of border-habitats and the application of various methods to intensify farming practice have caused much damage to the flora as well as the fauna of the agricultural landscape. The high number of species recorded in this survey is therefore not a message to *rest on one's laurels* but rather an encouragement to *keep up the good work* on minimising the use of herbicides and insecticides, re-establishing border-habitats, and to increase set-aside areas and time invested in research on beneficial landscape management. In agricultural areas where all semi-natural habitats have been removed, and where no core habitats such as pastures or forests exist in the vicinity, the bee fauna will most certainly be poor. In my opinion, the main goal in conserving bees in agricultural habitats is not single-species-conservation. Rather the goal should be to pinpoint the locations of core-populations, and of habitat hotspots, and to conserve such areas as a whole.

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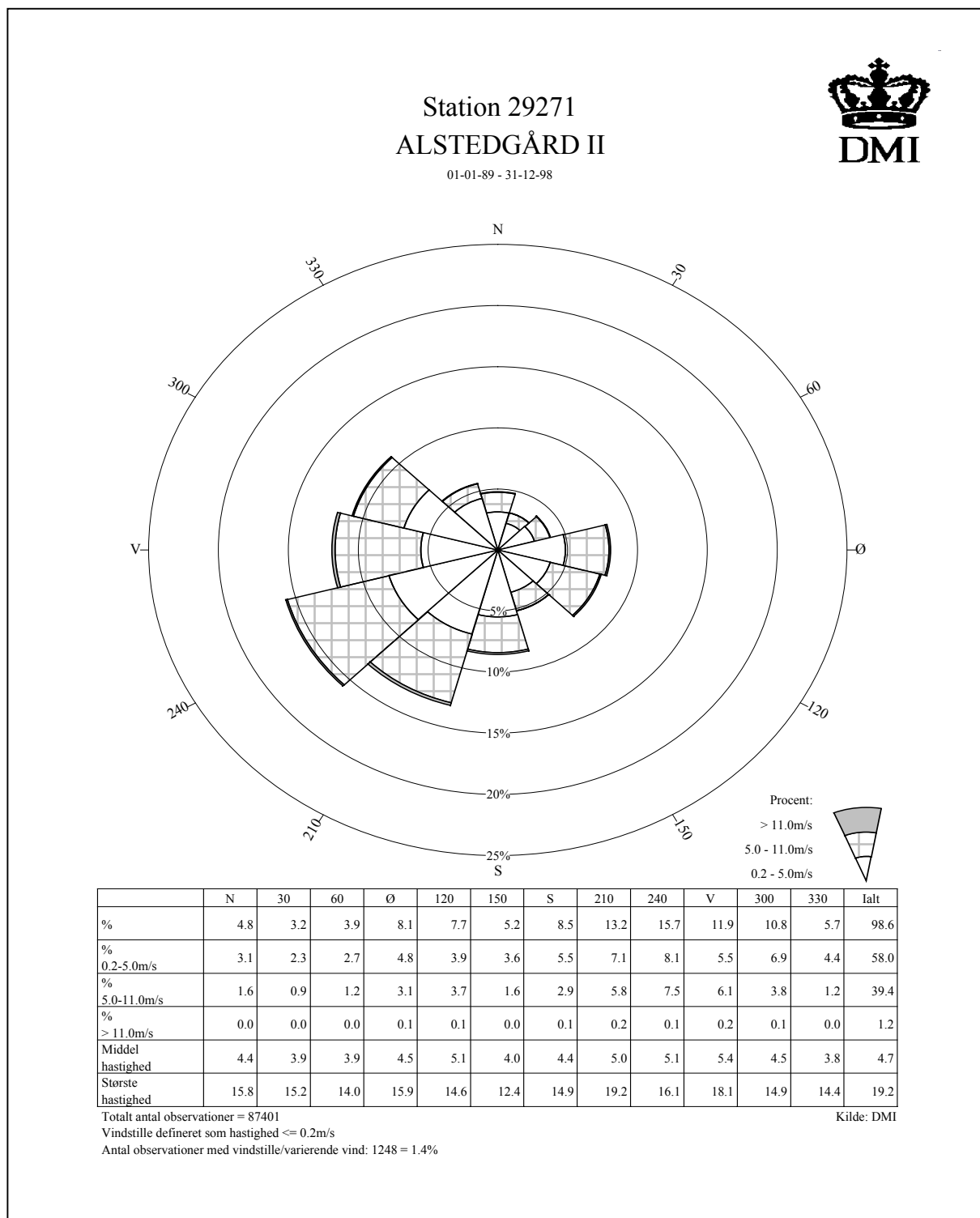
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APPENDIX

Appendix 1 Wind conditions



Wind properties, April through August 1997

Month	Mean wind m/s	Direction of wind, % abundance								
		Calm	N	NE	E	SE	S	SW	W	NW
April	5.4	0	24	6	2	4	6	12	32	14
May	4.5	0	16	10	16	7	16	11	17	7
June	3.9	<	6	5	16	20	15	8	24	6
July	3.3	0	18	12	10	9	13	8	17	12
August	2.8	<	8	6	9	17	33	8	13	4

Appendix 2 Species inventory of yellow pan-trap survey 1997

This species list is arranged according to the latest suggestions to a system of bee taxonomy by (Schwarz *et al.* 1996) pp. 190-197, in collaboration with Professor Michener (Kansas). However, for practical reasons and due to differences in biology, Non-Apidae bees mentioned in the manuscripts I, II, III (I. Calabuig, *In prep.*) refer to all species excluding *Bombus sp.*, *Psithyrus sp.* and *Apis mellifera*. Recordings of *Bombus magnus* may have been *Bombus terrestris*. *B. magnus* (if a true species) is primarily known from moorland habitats (Prys-Jones & Corbet 1991). For comparative measures, all genera occurring in Denmark are indicated, though not all are represented in this survey.

For data analyses, the effective number of species is 91: The species *Andrena minutula* and *A. minutuloides* are very similar, with a range of morphological characters that vary and sometimes overlap. For proper identification, the individuals should all have been dried and pinned, a task too time-consuming for a data material as large as this. With the specimens being wet, only the extreme morphotypes could be identified with certainty. Therefore, in I. Calabuig, Manuscript I, (*In prep.*) all individuals of these two species were counted collectively.

*Unidentified to species level at present, but clearly distinct from all other identified or unidentified species.

** Parasitic species belonging to the sub-genus *Psithyrus*

*** One male recorded in window-trap, rape field experiment 1998 (I. Calabuig, Manuscript II, *In prep.*: *Dispersal of solitary bees and bumblebees in a winter oilseed rape field*).

APOIDEA

Colletidae

Colletinae

Colletes Latreille, 1802

cunicularius (Linnaeus, 1761)

daviesanus Smith, 1846

Hylaeinae

Hylaeus Fabricius, 1793

brevicornis Nylander, 1852

communis Nylander, 1852

confusus Nylander, 1852

hyalinatus Smith, 1842

Andrenidae**Andreninae***Andrena* Fabricius, 1775*barbilabris* (Kirby, 1802)*bicolor* Fabricius, 1775*carantonica* Pérez, 1902 = *scotica* Perkins, 1919*chrysoceles* (Kirby, 1802)*cineraria* (Linnaeus, 1758)****clarkella* (Kirby, 1802)*flavipes* Panzer, 1799*fucata* Smith, 1847*fulva* (Müller, 1766)*haemorrhoea* (Fabricius, 1781)*helvola* (Linnaeus, 1758)*labiata* Fabricius, 1781*minutula* (Kirby, 1802)*minutuloides* Perkins, 1914*nigroaenea* (Kirby, 1802)*praecox* (Scopoli, 1763)*subopaca* Nylander, 1848*tibialis* (Kirby, 1802)*trimmerana* (Kirby, 1802)*vaga* Panzer, 1799*varians* (Kirby, 1802)*wilkella* (Kirby, 1802)*Andrena* sp. 2 ***Panurginae**

Panurgini

Panurgus Panzer, 1806

Halictidae**Rophitinae**

Rophites Spinola, 1808
Dufourea Lepeletier, 1841

Halictinae

Halictini

Halictus Latreille, 1804

rubicundus (Christ, 1791)

tumulorum (Linnaeus, 1758)

Lasioglossum Curtis, 1833

albipes (Fabricius, 1781)

calceatum (Scopoli, 1763)

fratellum (Pérez, 1903)

fulvicorne (Kirby, 1802)

lativentre (Schenck, 1853)

leucopus (Kirby, 1802)

leucozonium (Schrank, 1781)

minutissimum (Kirby, 1802)

morio (Fabricius, 1793)

parvulum (Schenck, 1853)

punctatissimum (Schenck, 1853)

quadrinotatum (Kirby, 1802)

rufitarse (Zetterstedt, 1838)

semilucens (Alfken, 1914)

sexmaculatum (Schenck, 1853)

smeathmanellum (Kirby, 1802)

villosulum (Kirby, 1802)

Lasioglossum sp. 3 *

Lasioglossum sp. 4 *

Lasioglossum sp. 5 *

Sphecodes Latreille, 1804

crassus Thomson, 1870

ephippius (Linnaeus, 1767)

geoffrellus (Kirby, 1802)

monilicornis (Kirby, 1802)

Melittidae**Dasypodinae**

Dasyпода Latreille, 1802

Melittinae

Melitta Kirby, 1802

Macropis Panzer, 1809

Megachilidae**Megachilinae**

Osmiini

Heriades Spinola, 1808

Hoplitis Klug, 1807

claviventris Thomson, 1872

Chelostoma Latreille, 1809

campanularum (Kirby, 1802)

florisomne (Linnaeus, 1758)

Osmia Panzer, 1806

pilicornis Smith, 1846

rufa (Linnaeus, 1758)

Anthidiini

Trachusa Panzer, 1804

Stelis Panzer, 1806

Anthidium Fabricius, 1804

manicatum (Linnaeus, 1758)

Megachilini

Megachile Latreille, 1802

lapponica Thomson, 1872

willughbiella (Kirby, 1802)

Coelioxys Latreille, 1809

Apidae**Nomadinae**

Nomadini

Nomada Scopoli, 1770*fabriciana* (Linnaeus, 1767)*ferruginata* (Linnaeus, 1767)*flavoguttata* (Kirby, 1802)*fulvicornis* Fabricius, 1793*leucophthalma* (Kirby, 1802)*marshamella* (Kirby, 1802)*panzeri* Lepeletier, 1841*ruficornis* (Linnaeus, 1758) = *bifida* Thomson, 1872*succincta* Panzer, 1798

Biastrini

Biastris Panzer, 1806

Epeolini

Epeolus Latreille, 1802**Apinae**

Eucerini

Eucera Scopoli, 1770

Anthophorini

Anthophora Latreille, 1803*furcata* (Panzer, 1798)

Melectini

Melecta Latreille, 1802

Bombini

Bombus Latreille, 1802*barbutellus* (Kirby, 1802) ***bohemicus* (Seidl, 1837) ***hortorum* (Linnaeus, 1761)*hypnorum* (Linnaeus, 1758)*lapidarius* (Linnaeus, 1758)*lucorum* (Linnaeus, 1761)*magnus* Vogt, 1911*muscorum* (Linnaeus, 1758)*norvegicus* Sparre Shneider, 1918 ***pascuorum* (Scopoli, 1763)

Bombus Latreille, 1802*pratorum* (Linnaeus, 1761)*runderarius* (Müller, 1776)*rupestris* (Fabricius, 1793) ***soroensis* (Fabricius, 1776)*subterraneus* (Linnaeus, 1758)*sylvarum* (Linnaeus, 1761)*sylvestris* (Lepelletier, 1832) ***terrestris* (Linnaeus, 1758)*vestalis* (Geoffroy, 1785) **

Apini

Apis Linnaeus, 1758*mellifera* Linnaeus, 1758

Appendix 3 List of recorded mellitophilous plant species

126 mellitophilous plant species in 29 families (64 Relevés were surveyed)

*Species present in
number of relevés*

Apiaceae

<i>Aegopodium</i>	<i>podagraria</i>	8
<i>Aethusa</i>	<i>cynapinum</i>	16
<i>Anthriscus</i>	<i>sylvestris</i>	43
<i>Chaerophyllum</i>	<i>temulum</i>	10
<i>Heracleum</i>	<i>pubescens</i>	2
<i>Heracleum</i>	<i>sphondylium</i>	9
<i>Sium</i>	<i>latifolium</i>	3
<i>Torilis</i>	<i>japonica</i>	2

Asteraceae

<i>Achillea</i>	<i>millefolium ssp. millefolium</i>	7
<i>Achillea</i>	<i>ptarmica</i>	1
<i>Arctium</i>	<i>lappa</i>	5
<i>Arctium</i>	<i>minus</i>	1
<i>Bellis</i>	<i>perennis</i>	2
<i>Carduus</i>	<i>crispus</i>	24
<i>Centaurea</i>	<i>scabiosa</i>	2
<i>Chamomilla</i>	<i>recutita</i>	4
<i>Chamomilla</i>	<i>suaveolens</i>	12
<i>Chrysanthemum</i>	<i>segetum</i>	4
<i>Cichorium</i>	<i>intybus</i>	1
<i>Cirsium</i>	<i>acaule</i>	1
<i>Cirsium</i>	<i>arvense</i>	28
<i>Cirsium</i>	<i>oleraceum</i>	6
<i>Cirsium</i>	<i>palustre</i>	6
<i>Cirsium</i>	<i>vulgare</i>	11
<i>Eupatorium</i>	<i>cannabinum</i>	2
<i>Lactuca</i>	<i>serriola</i>	1

			<i>Species present in number of relevés</i>
Asteraceae			
	<i>Lapsana</i>	<i>communis</i>	34
	<i>Leucanthemum</i>	<i>vulgare</i>	4
	<i>Matricaria</i>	<i>perforata</i>	16
	<i>Petasites</i>	<i>hybridus</i>	16
	<i>Senecio</i>	<i>vulgaris</i>	2
	<i>Sonchus</i>	<i>arvensis ssp. arvensis</i>	8
	<i>Taraxacum</i>	<i>Sect. Ruderalia</i>	31
Boraginaceae			
	<i>Anchusa</i>	<i>officinalis</i>	3
	<i>Echium</i>	<i>vulgare</i>	3
	<i>Myosotis</i>	<i>arvensis</i>	33
	<i>Myosotis</i>	<i>scorpioides</i>	2
	<i>Myosotis</i>	<i>sp.</i>	2
	<i>Myosotis</i>	<i>sylvatica</i>	5
Brassicaceae			
	<i>Alliaria</i>	<i>petiolata</i>	7
	<i>Barbarea</i>	<i>vulgaris ssp. arcuata</i>	2
	<i>Brassica</i>	<i>napus</i>	1
	<i>Capsella</i>	<i>bursa-pastoris</i>	15
	<i>Cardamine</i>	<i>pratense ssp. pratense</i>	1
	<i>Sinapis</i>	<i>arvensis</i>	12
	<i>Thlaspi</i>	<i>arvense</i>	5
Campanulaceae			
	<i>Campanula</i>	<i>rapunculoides</i>	3
	<i>Campanula</i>	<i>rotundifolia ssp. rotundifolia</i>	2
	<i>Campanula</i>	<i>trachelium</i>	7
Caryophyllaceae			
	<i>Cerastium</i>	<i>arvense</i>	1
	<i>Cerastium</i>	<i>fontanum ssp. vulgare var. vulgare</i>	4
	<i>Moehringia</i>	<i>trinervia</i>	2
	<i>Silene</i>	<i>dioica</i>	5

			<i>Species present in number of relevés</i>
Caryophyllaceae			
	<i>Stellaria</i>	<i>graminea</i>	5
	<i>Stellaria</i>	<i>holostea</i>	31
	<i>Stellaria</i>	<i>media</i>	16
Clusiaceae			
	<i>Hypericum</i>	<i>perforatum</i>	6
Convolvulaceae			
	<i>Calystegia</i>	<i>sepium ssp. sepium</i>	1
	<i>Convolvulus</i>	<i>arvensis</i>	14
Crassulaceae			
	<i>Sedum</i>	<i>telephium ssp. telephium</i>	4
Dipsacaceae			
	<i>Knautia</i>	<i>arvensis</i>	3
Fabaceae			
	<i>Lathyrus</i>	<i>pratensis</i>	1
	<i>Medicago</i>	<i>lupulina</i>	1
	<i>Ononis</i>	<i>repens</i>	1
	<i>Trifolium</i>	<i>pratense</i>	3
	<i>Trifolium</i>	<i>repens</i>	5
	<i>Vicia</i>	<i>cracca</i>	5
Fumariaceae			
	<i>Corydalis</i>	<i>cava</i>	2
Geraniaceae			
	<i>Geranium</i>	<i>columbinum</i>	4
	<i>Geranium</i>	<i>dissectum</i>	2
	<i>Geranium</i>	<i>molle</i>	4
	<i>Geranium</i>	<i>pusillum</i>	6
	<i>Geranium</i>	<i>pyrenaicum</i>	9
	<i>Geranium</i>	<i>robertianum var. robertianum</i>	9

			<i>Species present in number of relevés</i>
<hr/>			
Hydrophyllaceae	<i>Phacelia</i>	<i>tanacetifolia</i>	1
<hr/>			
Iridaceae	<i>Iris</i>	<i>pseudacorus</i>	1
<hr/>			
Lamiaceae	<i>Galeopsis</i>	<i>speciosa</i>	5
	<i>Galeopsis</i>	<i>tetrahit</i>	20
	<i>Glechoma</i>	<i>hederacea</i>	6
	<i>Lamium</i>	<i>album</i>	12
	<i>Lamium</i>	<i>purpureum</i>	38
	<i>Mentha</i>	<i>aquatica</i> var. <i>aquatica</i>	3
	<i>Mentha</i>	<i>aquatica</i> x <i>arvensis</i>	3
	<i>Prunella</i>	<i>vulgaris</i>	1
	<i>Satureja</i>	<i>vulgare</i>	1
	<i>Stachys</i>	<i>palustris</i>	6
	<i>Stachys</i>	<i>sylvatica</i>	6
<hr/>			
Liliaceae	<i>Gagea</i>	<i>lutea</i>	7
<hr/>			
Malvaceae	<i>Malva</i>	<i>sylvestris</i> ssp. <i>sylvestris</i>	2
<hr/>			
Onagraceae	<i>Circaea</i>	<i>lutetiana</i>	1
	<i>Epilobium</i>	<i>angustifolium</i>	5
	<i>Epilobium</i>	<i>hirsutum</i>	7
	<i>Epilobium</i>	<i>montanum</i>	2
<hr/>			
Papaveraceae	<i>Papaver</i>	<i>rhoeas</i>	6
<hr/>			
Polygonaceae	<i>Persicaria</i>	<i>maculosa</i>	9

		<i>Species present in number of relevés</i>
Primulaceae		
<i>Anagallis</i>	<i>arvensis ssp. arvensis</i>	10
<i>Lysimachia</i>	<i>nummularia</i>	1
Ranunculaceae		
<i>Anemone</i>	<i>nemorosa</i>	10
<i>Anemone</i>	<i>ranunculoides</i>	5
<i>Caltha</i>	<i>palustris ssp. palustris</i>	2
<i>Ranunculus</i>	<i>acris ssp. acris</i>	5
<i>Ranunculus</i>	<i>ficaria ssp. bulbifera</i>	20
<i>Ranunculus</i>	<i>repens</i>	1
<i>Ranunculus</i>	<i>sp.</i>	6
Rosaceae		
<i>Agrimonia</i>	<i>eupatoria</i>	1
<i>Filipendula</i>	<i>ulmaria</i>	3
<i>Geum</i>	<i>rivale</i>	2
<i>Geum</i>	<i>urbanum</i>	21
<i>Potentilla</i>	<i>anserina ssp. anserina</i>	2
<i>Potentilla</i>	<i>reptans</i>	2
<i>Rubus</i>	<i>fruticosus</i>	1
Rubiaceae		
<i>Galium</i>	<i>aparine</i>	10
<i>Galium</i>	<i>mollugo</i>	3
<i>Galium</i>	<i>odoratum</i>	4
<i>Galium</i>	<i>verum</i>	11
<i>Sherardia</i>	<i>arvensis</i>	2
Scrophulariaceae		
<i>Scrophularia</i>	<i>nodosa</i>	1
<i>Veronica</i>	<i>arvensis</i>	2
<i>Veronica</i>	<i>beccabunga</i>	1
<i>Veronica</i>	<i>chamaedrys</i>	27
<i>Veronica</i>	<i>hederifolia ssp. hederifolia</i>	1
<i>Veronica</i>	<i>persica</i>	27

			<i>Species present in number of relevés</i>
<hr/>			
Solanaceae			
	<i>Solanum</i>	<i>dulcamara var. dulcamara</i>	2
	<i>Solanum</i>	<i>nigrum ssp. nigrum</i>	3
<hr/>			
Valerianaceae			
	<i>Valeriana</i>	<i>sambucifolia ssp. sambucifolia</i>	5
<hr/>			
Violaceae			
	<i>Viola</i>	<i>arvensis</i>	23

Appendix 4 Bee abundance, lecti and host-plant families

Abundance of bees recorded in pan-trap survey 1997 (I. Calabuig, Manuscript I, *In prep.*).

Indications of lecti and number of plant families according to Westrich (1990b), but only Danish plant families listed in detail. *One male recorded in window-trap, rape field experiment 1998 (I. Calabuig, Manuscript II, *In prep.*: *Dispersal of solitary bees and bumblebees in a winter oilseed rape field*)

		Males	Females	Lecti	No. of plant families
<i>Andrena</i>	<i>barbilabris</i>	0	1	Polylectic	13
Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Campanulaceae, Cornaceae, Fagaceae, Oleaceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>bicolor</i>	12	233	Extensively polylectic	14
Asteraceae, Boraginaceae, Brassicaceae, Campanulaceae, Caryophyllaceae, Convolvulaceae, Geraniaceae, Liliaceae, Primulaceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>carantonica</i>	93	135	Extensively polylectic	10
Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Cornaceae, Fagaceae, Ranunculaceae, Rosaceae, Salicaceae					
<i>Andrena</i>	<i>chrysoceles</i>	8	14	Polylectic	10
Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Cornaceae, Ranunculaceae, Rosaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>cineraria*</i>	1	0	Polylectic	6
Apiaceae, Asteraceae, Brassicaceae, Ranunculaceae, Rosaceae, Salicaceae					
<i>Andrena</i>	<i>clarkella</i>	7	34	Oligolectic <i>Salix</i>	1 Salicaceae
<i>Andrena</i>	<i>flavipes</i>	1	1	Extensively polylectic	17
Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Campanulaceae, Caryophyllaceae, Clusiaceae, Convolvulaceae, Fabaceae, Fagaceae, Lamiaceae, Papaveraceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>fucata</i>	0	1	Polylectic	6
Apiaceae, Brassicaceae, Ranunculaceae, Rosaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>fulva</i>	5	6	Extensively polylectic	10
Aceraceae, Brassicaceae, Caprifoliaceae, Fagaceae, Grossulariaceae, Ranunculaceae, Rosaceae, Salicaceae.					

		Males	Females	Lecti	No. of plant families
<i>Andrena</i>	<i>haemorrhoa</i>	347	172	Extensively polylectic	15
Aceraceae, Apiaceae, Asteraceae, Betulaceae, Brassicaceae, Caryophyllaceae, Cornaceae, Fagaceae, Grossulariaceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>helvola</i>	1051	192	Polylectic	5
Asteraceae, Grossulariaceae, Liliaceae, Rhamnaceae, Rosaceae.					
<i>Andrena</i>	<i>labiata</i>	2	1	Polylectic	7
Asteraceae, Brassicaceae, Caryophyllaceae, Lamiaceae, Ranunculaceae, Rosaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>minutula</i> *	126	267	Extensively polylectic	11
Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Crassulaceae, Lamiaceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae.					
*including individuals of <i>A. minutuloides</i>					
<i>Andrena</i>	<i>minutuloides</i> *	-	-	Polylectic	7
Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Rosaceae, Salicaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>nigroaenea</i>	30	28	Extensively polylectic	12
Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Ericaceae, Fabaceae, Ranunculaceae, Rosaceae, Salicaceae.					
<i>Andrena</i>	<i>praecox</i>	30	215	Oligolectic <i>Salix</i>	1 Salicaceae
<i>Andrena</i>	<i>subopaca</i>	1	0	Polylectic	4
Caryophyllaceae, Liliaceae, Rosaceae, Scrophulariaceae.					
<i>Andrena</i>	<i>tibialis</i>	1	4	Polylectic	5
Aceraceae, Asteraceae, Brassicaceae, Rosaceae, Salicaceae.					
<i>Andrena</i>	<i>trimmerana</i>	1	1	Extensively polylectic	10
Aceraceae, Apiaceae, Asteraceae, Brassicaceae, Cornaceae, Fagaceae, Ranunculaceae, Rosaceae, Salicaceae.					
<i>Andrena</i>	<i>vaga</i>	0	6	Oligolectic <i>Salix</i>	1 Salicaceae
<i>Andrena</i>	<i>varians</i>	1	4	Extensively polylectic	12
Aceraceae, Apiaceae, Asteraceae, Betulaceae, Brassicaceae, Caryophyllaceae, Grossulariaceae, Ranunculaceae, Rosaceae, Salicaceae.					

		Males	Females	Lecti	No. of plant families
<i>Andrena</i>	<i>wilkella</i>	3	5	Oligolectic <i>Onobrychis, Vicia, Trifolium.</i>	1 Fabaceae
<i>Anthidium</i>	<i>manicatum</i>	4	3	Limited polylectic	3 Fabaceae, Lamiaceae, Scrophulariaceae.
<i>Anthophora</i>	<i>furcata</i>	1	2	Oligolectic	1 Lamiaceae
<i>Chelostoma</i>	<i>campanularum</i>	1	0	Oligolectic <i>Campanula</i>	1 Campanulaceae
<i>Chelostoma</i>	<i>florisomne</i>	7	3	Oligolectic <i>Ranunculus</i>	1 Ranunculaceae
<i>Colletes</i>	<i>cunicularius</i>	1	0	Oligolectic <i>Salix</i>	1 Salicaceae
<i>Colletes</i>	<i>daviesanus</i>	10	21	Oligolectic	1 Asteraceae
<i>Halictus</i>	<i>rubicundus</i>	48	50	Polylectic	9 Asteraceae, Brassicaceae, Campanulaceae, Dipsacaceae, Fabaceae, Geraniaceae, Ranunculaceae, Rosaceae, Salicaceae.
<i>Halictus</i>	<i>tumulorum</i>	24	505	Extensively polylectic	14 Asteraceae, Brassicaceae, Campanulaceae, Caryophyllaceae, Clusiaceae, Convolvulaceae, Fabaceae, Lythraceae, Papaveraceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae.
<i>Hylaeus</i>	<i>brevicornis</i>	3	4	Polylectic	6 Apiaceae, Campanulaceae, Crassulaceae, Fabaceae, Polygonaceae, Rosaceae.
<i>Hylaeus</i>	<i>communis</i>	0	2	Extensively polylectic	10 Apiaceae, Asteraceae, Boraginaceae, Brassicaceae, Campanulaceae, Crassulaceae, Lamiaceae, Liliaceae, Lythraceae.
<i>Hylaeus</i>	<i>confusus</i>	2	7	Polylectic	5 Asteraceae, Campanulaceae, Fabaceae, Rosaceae.
<i>Hylaeus</i>	<i>hyalinatus</i>	0	2	Polylectic	7 Apiaceae, Asteraceae, Brassicaceae, Campanulaceae, Crassulaceae, Rosaceae.

	Males	Females	Lecti	No. of plant families
<i>Lasioglossum albipes</i> Apiaceae, Asteraceae, Campanulaceae, Caryophyllaceae, Dipsacaceae, Ranunculaceae, Rosaceae.	0	1	Polylectic	8
<i>Lasioglossum calceatum</i> Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Clusiaceae, Dipsacaceae, Ericaceae, Geraniaceae, Lamiaceae, Liliaceae, Primulaceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae.	10	269	Extensively polylectic	15
<i>Lasioglossum fratellum</i> Ericaceae	0	4	Probably polylectic	1
<i>Lasioglossum fulvicorne</i> Asteraceae, Brassicaceae, Ericaceae, Rosaceae, Salicaceae.	0	95	Polylectic	5
<i>Lasioglossum lativentre</i> Asteraceae, Fabaceae, Ranunculaceae.	1	0	Polylectic	4
<i>Lasioglossum leucopus</i> Asteraceae, Rosaceae.	169	1822	Probably polylectic	2
<i>Lasioglossum leucozonium</i> Asteraceae, Campanulaceae, Clusiaceae, Convolvulaceae, Dipsacaceae, Geraniaceae, Ranunculaceae, Rosaceae.	0	17	Extensively polylectic	10
<i>Lasioglossum minutissimum</i> Asteraceae, Lamiaceae.	3	54	Polylectic	2
<i>Lasioglossum morio</i> Asteraceae, Boraginaceae, Brassicaceae, Campanulaceae, Caryophyllaceae, Clusiaceae, Convolvulaceae, Lythraceae, Ranunculaceae, Rosaceae.	1	16	Polylectic	9
<i>Lasioglossum parvulum</i> Asteraceae, Campanulaceae, Ranunculaceae, Salicaceae.	1	15	Polylectic	4
<i>Lasioglossum punctatissimum</i> Asteraceae, Ericaceae, Fabaceae, Liliaceae, Ranunculaceae, Rosaceae, Scrophulariaceae.	0	90	Polylectic	7
<i>Lasioglossum quadrinotatum</i> Asteraceae, Brassicaceae.	25	383	Probably polylectic	2

		Males	Females	Lecti	No. of plant families
<i>Lasioglossum</i>	<i>rufitarse</i>	1	14	Polylectic	4
Asteraceae, Ericaceae, Ranunculaceae, Rosaceae.					
<i>Lasioglossum</i>	<i>smeathmanellum</i>	1	0	Extensively polylectic	12
Apiaceae, Asteraceae, Boraginaceae, Brassicaceae, Campanulaceae, Lamiaceae, Liliaceae, Papaveraceae, Ranunculaceae, Rosaceae, Scrophulariaceae.					
<i>Lasioglossum</i>	<i>villosulum</i>	4	18	Polylectic	5
Asteraceae, Boraginaceae, Convolvulaceae, Ranunculaceae, Scrophulariaceae.					
<i>Megachile</i>	<i>lapponica</i>	1	0	Oligolectic <i>Epibolium</i>	1 Onagraceae
<i>Megachile</i>	<i>willughbiella</i>	0	1	Polylectic	5
Asteraceae, Campanulaceae, Crassulaceae, Fabaceae, Onagraceae.					
<i>Osmia (Hoplitis)</i>	<i>claviventris</i>	0	1	Polylectic	6
Asteraceae, Boraginaceae, Clusiaceae, Crassulaceae, Fabaceae, Rosaceae.					
<i>Osmia</i>	<i>pilicornis</i>	0	3	Polylectic	4
Boraginaceae, Fabaceae, Lamiaceae, Rosaceae.					
<i>Osmia</i>	<i>rufa</i>	1	0	Extensively polylectic	18
Aceraceae, Betulaceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Fabaceae, Fagaceae, Lamiaceae, Papaveraceae, Ranunculaceae, Rosaceae, Salicaceae.					
<i>Andrena</i>	<i>sp.2</i>	1	0	-	-
<i>Lasioglossum</i>	<i>sp.3</i>	0	1	-	-
<i>Lasioglossum</i>	<i>sp.4</i>	0	1	-	-
<i>Lasioglossum</i>	<i>sp.5</i>	1	0	-	-
<i>Lasioglossum</i>	<i>semilucens</i>	7	62	unknown, probably polylectic	-
<i>Lasioglossum</i>	<i>sexmaculatum</i>	0	2	unknown, probably polylectic	-

		Males	Females	Workers	Lecti		Tongue + head length category	Active nectar-robbers or re-users
<i>Apis</i>	<i>mellifera</i>	0	0	2181	Polylectic		<i>Very short</i>	Re-users
<i>Bombus</i>	<i>hortorum</i>	78	86	159	Polylectic		<i>Very long</i>	
	<i>hypnorum</i>	14	21	30	Polylectic		<i>Medium</i>	Re-users
	<i>lapidarius</i>	43	56	218	Polylectic		<i>Short</i>	Re-users
	<i>lucorum</i>	109	126	407	Polylectic		<i>Very short</i>	Active
	<i>magnus</i>	0	3	0	Polylectic		<i>Very short</i>	Active
	<i>muscorum</i>	3	7	13	Polylectic		<i>Medium</i>	
	<i>pascuorum</i>	89	154	587	Polylectic		<i>Long</i>	Re-users
	<i>pratorum</i>	28	18	100	Polylectic		<i>Medium</i>	
	<i>runderarius</i>	9	31	48	Polylectic		<i>Medium</i>	
	<i>soroensis</i>	0	1	12	Polylectic		<i>Short</i>	Re-users
	<i>subterraneus</i>	0	0	1	Polylectic		<i>Long</i>	
	<i>sylvarum</i>	4	5	5	Polylectic		<i>Long</i>	
<i>terrestris</i>	65	182	91	Polylectic		<i>Very short</i>	Active	

Appendix 5 Inquiline bee abundance and host relationships

Only the inquiline species recorded in pan-trap survey of 1997 are listed, including abundance. Host relationships according to Westrich (1990a) and suppl. by Jørgensen (1921) and Lomholdt (1977). Potential Danish host species indicated, including species recorded in pan-trap survey of 1997 (I. Calabuig, Manuscript I, *In prep.*)

Inquiline species	Males	Females	Notes	Host species	Pan-traps
<i>Nomada fabriciana</i>	6	3	Primary host	<i>Andrena bicolor</i>	Yes
				<i>Andrena chrysoseces</i>	Yes
				<i>Andrena nigroaenea</i>	Yes
<i>Nomada ferruginata</i>	29	37		<i>Andrena praecox</i>	Yes
				<i>Colletes cunicularius</i>	Yes
				<i>Andrena humilis</i>	
				<i>Andrena labialis</i>	
<i>Nomada flavoguttata</i>	11	8		<i>Panurgus banksianus</i>	
				<i>Andrena minutula</i>	Yes
				<i>Andrena minutuloides</i>	Yes
				<i>Andrena nana</i>	
<i>Nomada fulvicornis</i>	1	0	Primary host	<i>Andrena subopaca</i>	Yes
				<i>Andrena barbilabris</i>	Yes
				<i>Andrena tibialis</i>	Yes
<i>Nomada leucophthalma</i>	0	2	Primary host	<i>Andrena bimaculata</i>	
				<i>Andrena gravida</i>	
				<i>Andrena labialis</i>	
				<i>Andrena nitida</i>	
				<i>Andrena pilipes</i>	
				<i>Andrena thoracica</i>	
<i>Nomada marshamella</i>	141	200	Primary host	<i>Andrena clarkella</i>	Yes
<i>Nomada panzeri</i>	465	192		<i>Andrena carantonica</i>	Yes
				<i>Andrena fucata</i>	Yes
				<i>Andrena helvola</i>	Yes
				<i>Andrena nigroaenea</i>	Yes
				<i>Andrena trimmerana</i>	Yes
<i>Nomada ruficornis</i>	13	6	Primary host	<i>Andrena varians</i>	Yes
				<i>Andrena wilkella</i>	Yes
				<i>Andrena lapponica</i>	
				<i>Andrena nitida</i>	
				<i>Melitta haemorrhoidalis</i>	
<i>Nomada succincta</i>	2	0		<i>Andrena carantonica</i>	Yes
<i>Nomada succincta</i>	2	0		<i>Andrena nigroaenea</i>	Yes
				<i>Andrena tibialis</i>	Yes
				<i>Andrena cineraria</i>	
				Possibly <i>Andrena curvungula</i>	
				Primary host <i>Andrena nitida</i>	
				<i>Andrena thoracica</i>	

Only the inquiline species recorded in pan-trap survey of 1997 are listed, including abundance Potential Danish host-species indicated, including the species recorded in pan-trap survey of 1997 (I. Calabuig, Manuscript I, *In prep.*) Host species listed according to Scheuchl (1995) and Westrich (1990b) and supplemented by Jørgensen (1921).

Inquiline species		Males	Females	Notes	Host-species		Pan-traps	
<i>Sphecodes</i>	<i>crassus</i>	2	9	Primary host	<i>Lasioglossum</i>	<i>punctatissimum</i>	Yes	
					<i>Lasioglossum</i>	<i>nitidiusculum</i>		
<i>Sphecodes</i>	<i>ephippius</i>	2	79		<i>Andrena</i>	<i>barbilabris</i>	Yes	
					<i>Andrena</i>	<i>bicolor</i>	Yes	
					<i>Halictus</i>	<i>tumulorum</i>	Yes	
					<i>Lasioglossum</i>	<i>leucozonium</i>	Yes	
					<i>Lasioglossum</i>	<i>villosulum</i>	Yes	
					Possibly	<i>Andrena</i>	<i>chrysopyga</i>	
	<i>Andrena</i>	<i>ovatula</i>						
<i>Sphecodes</i>	<i>geoffrellus</i>	23	66		<i>Lasioglossum</i>	<i>leucopus</i>	Yes	
					<i>Lasioglossum</i>	<i>morio</i>	Yes	
					<i>Lasioglossum</i>	<i>nitidiusculum</i>		
<i>Sphecodes</i>	<i>monilicornis</i>	1	6		<i>Halictus</i>	<i>rubicundus</i>	Yes	
					<i>Lasioglossum</i>	<i>albipes</i>	Yes	
					<i>Lasioglossum</i>	<i>calceatum</i>	Yes	
					<i>Lasioglossum</i>	<i>quadrinotatum</i>	Yes	
					Primary host	<i>Lasioglossum</i>	<i>malachurum</i>	
						<i>Lasioglossum</i>	<i>zonulum</i>	

Andrena and *Lasioglossum* host-species with no potential inquilines recorded, or none known

Host species		♂	♀	Notes	Potential Danish host-species, not recorded in pan-traps	
<i>Andrena</i>	<i>flavipes</i>	1	1		<i>Nomada</i>	<i>fucata</i> Panzer 1798
<i>Andrena</i>	<i>labiata</i>	2	1		<i>Nomada</i>	<i>guttulata</i> Schenk 1861
<i>Andrena</i>	<i>vaga</i>	0	6		<i>Nomada</i>	<i>lathburiana</i> (Kirby 1802)
					<i>Sphecodes</i>	<i>gibbus</i> (Linnaeus 1758)
<i>Andrena</i>	<i>sp. 2</i>	1	0	Unidentified	-	-
<i>Lasioglossum</i>	<i>fratellum</i>	0	4	Inquilines unknown		
	<i>fulvicorne</i>	0	95		<i>Sphecodes</i>	<i>ferruginatus</i> Hagens 1882
				Not (yet) recorded in Denmark	<i>Sphecodes</i>	<i>hyalinatus</i> Hagens 1882
	<i>lativentre</i>	1	0	Inquilines unknown		
	<i>minutissimum</i>	3	54	Not (yet) recorded in Denmark	<i>Sphecodes</i>	<i>longulus</i> Hagens 1882
	<i>parvulum</i>	1	15	Probably	<i>Nomada</i>	<i>distinguenda</i> Morawitz 1874
	<i>rufitarse</i>	1	14	Inquilines unknown		
	<i>semilucens</i>	7	62	Inquilines unknown		
	<i>sexmaculatum</i>	0	2	Inquilines unknown		
	<i>smeathmanellum</i>	1	0	Inquilines unknown		
	<i>sp. 3</i>	0	1	Unidentified	-	-
	<i>sp. 4</i>	0	1	Unidentified	-	-
	<i>sp. 5</i>	1	0	Unidentified	-	-

Only the species recorded in pan-trap survey of 1997 are listed (I. Calabuig, Manuscript I, *In prep.*). Other potential Danish host species not indicated. Host species according to Amiet (1996), Hagen (1994), Jørgensen (1921), Løken (1984), Prys-Jones & Corbet (1991), and Westrich (1990b).

Cuckoo species		Males	Females	Notes	Host species		Pan-traps
<i>Psithyrus</i>	<i>barbutellus</i>	0	2	Primary host	<i>Bombus</i>	<i>hortorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>hypnorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>pratorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>runderarius</i>	Yes
<i>Psithyrus</i>	<i>bohemicus</i>	43	133	Primary host	<i>Bombus</i>	<i>lucorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>magnus</i>	Yes
<i>Psithyrus</i>	<i>norvegicus</i>	1	11	Primary host	<i>Bombus</i>	<i>hypnorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>pratorum</i>	Yes
<i>Psithyrus</i>	<i>rupestris</i>	133	92	Primary host	<i>Bombus</i>	<i>lapidarius</i>	Yes
				Secondary host	<i>Bombus</i>	<i>pascuorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>pratorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>sylvarum</i>	Yes
<i>Psithyrus</i>	<i>sylvestris</i>	53	68	Secondary host	<i>Bombus</i>	<i>hortorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>lucorum</i>	Yes
				Primary host	<i>Bombus</i>	<i>pratorum</i>	Yes
				Secondary host	<i>Bombus</i>	<i>runderarius</i>	Yes
				Secondary host	<i>Bombus</i>	<i>soroensis</i>	Yes
				Secondary host	<i>Bombus</i>	<i>terrestris</i>	Yes
<i>Psithyrus</i>	<i>vestalis</i>	22	22	Secondary host	<i>Bombus</i>	<i>lucorum</i>	Yes
				Primary host	<i>Bombus</i>	<i>terrestris</i>	Yes

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