

## Oligolectic bee species in Northern Europe (Hymenoptera, Apoidea)

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Evolution of flower specialization in bees, the concepts of poly-, oligo- and monolecty are reviewed. About 60 species recorded in the area of Finland and Sweden are regarded as oligolectic. The proportions of oligolectes among all pollen-collecting bee species are about 30 percent in a large area of central and Northern Europe. The proportion is about 15 percent in the northern boreal area of Finland and Sweden, where the percentage of polylectic bumblebees is much greater than in more southern areas. Of the solitary bee species recorded in Finland and Sweden, 25 are regarded as narrow oligolectes, of which 6 species collect pollen from *Campanula* and 5 from *Salix*. Eusocial *Bombus consobrinus* is regarded as a facultative narrow oligolecte of *Aconitum septentrionale* and, apparently, this bee species is the only oligolecte in northern Europe, whose distribution completely covers that of the pollen plant. The distribution limits of some narrow oligolectes (e.g. *Eucera longicornis* and *Andrena hattorfiana*) approximately follow certain frequencies of their principal pollen plants (*Lathyrus pratensis* and *Knautia*, respectively). Of the oligolectic bee species in Finland, 32 occur on the lists of threatened species of England, southwestern Germany or Poland. Records of *E. longicornis* and *A. hattorfiana* from various periods are given as examples of the decline of oligolectic bees in Finland during recent decades.

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### 1. Introduction

Bees (Apoidea) evolved from carnivorous sphecoid wasps. The family Sphecidae (in the traditional concept) is possibly a paraphyletic group and the bees are best regarded as a specialized subgroup of the holophyletic superfamily Sphecoidea (Lomholdt 1982) (nomenclaturally the correct name is Apoidea). Evolution from predatory wasps to pollen-eating bees occurred during the Cretaceous, simultaneously with, or after, the ap-

pearance of entomophilous flowers of the Angiospermae (Michener 1979). Eusocial bees likely evolved after the Cretaceous, and a stingless honeybee (*Trigona*, Meliponinae), originally reported from Cretaceous New Jersey amber (Michener & Grimaldi 1988ab), is possibly of more recent age (Rasnitsyn & Michener 1991). Bees collect food from flowers both for adults and larvae and are the most important group of insect pollinators. They have also been a meaningful factor in the success of the angiosperms, which again has made

possible the evolution of new terrestrial fauna, especially mammals, ever since the Cretaceous. The number of known bee species is 25 000–30 000, and they have been placed in over 4 000 genera (Gauld & Bolton 1988). About 230 species from Finland (Vikberg 1986) and 278 species from Sweden (Erlandsson *et al.* 1988, Svensson *et al.* 1990, Janzon *et al.* 1991) have been recorded.

Some conspicuous characteristics of flowers, especially zygomorphy (bilateral symmetry), have possibly evolved as adaptations to pollination by bees (Proctor & Yeo 1979). It has, however, been suggested that bee pollination has not played an important role in plant evolution in general (Linsley *et al.* 1973, Michener 1979, Westrich 1990). Pollination systems are actually often fairly generalized and only few examples of coevolution occur that have produced new specialized plant and bee species. Similarly, a basic model, in which the optimal diversity of pollinating animals is considered, does not suggest long-term specialization of a plant on one pollinator (Waser *et al.* 1996). Specialization of pollen collecting by a bee to one or more closely related plant species is essentially an ethological character that does not necessarily require any visible morphological qualifications, compared with other related bee species. A specialized bee species may be dependent on a single family, genus or even species of plant, but the plants are usually also pollinated by other bees or insects. The distribution of a plant species is thus often larger than that of its specialized pollinator.

## 2. Oligo- and polylecty

A bee collects either pollen or nectar, or both, from the same flower, and bee species are usually more specialized for pollen than nectar collecting. Robertson (1925) introduced the terms *oligolecty* and *polylecty* to describe the degree of specialization in pollen collecting of a bee species. Oligolectic bee species collect pollen from a small number of species of a single genus or family of plants. The term *monolecty* has been used to describe a condition of extreme oligolecty when a bee collects pollen from a single species or a small number of very closely related species of plants (Faegri & Van der Pijl 1979). However, the term *narrow*

*oligolecty* is more recommendable than *monolecty*, which actually refers to specialization on one single plant species (see also Westrich 1990: 289). The terms *oligo-* and *polytropy* (Loew 1884) have been defined to mean the number of all flower species visited (Käpylä 1978: 57, Proctor & Yeo 1979: 372), while *oligo-* and *polyphily* deal with the degree of specialization of a plant species for its pollinators (Faegri & Van der Pijl 1979). Oligo- or polylecty should not be confused with the terms *flower fidelity* or *flower constancy*, which mean the temporary behaviour of an individual bee during foraging trips. However, Faegri & Van der Pijl (1979) defined *constancy* as a general term, describing all the relationships mentioned above. The difference between oligo- and polylectic species is not stable and there exist many intermediate species and also areal differences in the specialization of the same species.

## 3. Areal richness of oligolectic bees

Eusocial bee species are almost without exception polylectic, since the flowering season of a single pollen plant species or genus usually covers only a small part of the season of the colony. Eusocial polylectic Meliponinae, Apinae and even Halictinae are the most remarkable bees in the tropics (Michener 1979). The proportion of oligolectic bees is greatest in xeric semidesert, scrubland and dry steppe biomes. Moldenke (1976) noted that about 60% of the (pollen-collecting) bee species were oligolectic in the desert areas and about 50% in the Mediterranean climate areas of California. Species richness is also greatest in these biomes, and about 1 500 species have been recorded from the Californian area (Moldenke 1979) and over 1 000 species from Spain (Ceballos 1956). In these kinds of areas of a slight precipitation, flowering is concentrated in the short moist period during spring and the large number of oligolectes is an obvious result of resource competition (Michener 1954).

The proportion of oligolectic bees is about 30% in the former West Germany (Westrich 1990) as well as in Lithuania (Monsevičius 1995) and the same proportion (30%) also appears to be fairly evenly distributed among various vegetational areas of Northern Europe (Fig. 1). In the northern

boreal areas of Fennoscandia, the proportion of oligoleges is < 20%, and the number of solitary bee species is very low compared with polylectic bumblebees (Elfving 1972, Pekkarinen & Teräs 1993). In the northernmost Fennoscandian fjeld area (shaded in Fig. 1), however, 24 pollen-collecting solitary bee species have been recorded, of which four are oligolectic: *Andrena clarkella* and *A. ruficrus* (both on *Salix*), *A. lapponica* (on *Ericaceae*) and *Megachile lapponica* (on *Chamaenerion*; Niemelä 1936). On the other hand, the local abundance of oligolectic bees may be remarkably lower compared with polylectic bees; e.g., about 40% of bee species in the steppe area of the lower Don in Russia are oligolectic, but their proportion is estimated to be below 10% of all individual bees (Pesenko 1995). According to Pesenko, very few vernal oligoleges occur in the temperate areas; however, he excluded all *Salix* oligoleges that form a remarkable portion of vernal bee fauna in temperate and boreal areas.

#### 4. Oligolectic bees in Finland and Sweden

The numbers of oligolectic bee species in various genera are given in Table 1. It is worth noting that no oligoleges occur in Northern Europe in the large and closely related genera *Lasioglossum* and *Halictus*. The present records of pollen and nectar plants with oligoleges in Finland (Table 2) are based mainly on Elfving (1968), whose main source was the magnificent unpublished M.Sc.-thesis of the late Paavo Niemelä (over 13 000 observations) (Niemelä 1934; see also Valle 1951). Some older works from Finland (Westerlund 1893, Poppius 1903, Silén 1906ab, 1909) have also been consulted. The records after a slash in Table 2 indicate mainly nectar plants on which a bee species was observed. The figures imply that many oligolectic species are, however, fairly polytropic and this concerns especially the male specimens, which collect nectar only.

Westrich (1990) classified all 5 oligoleges of *Campanula* (in Table 2) as narrow, and the results of Käpylä (1978) confirm this with respect to the two *Chelostoma* species. In Europe, 4 species of *Chelostoma* have been reported to be oligoleges of *Campanula* and their males to be visitors of the orchid *Cephalanthera rubra*, which mim-

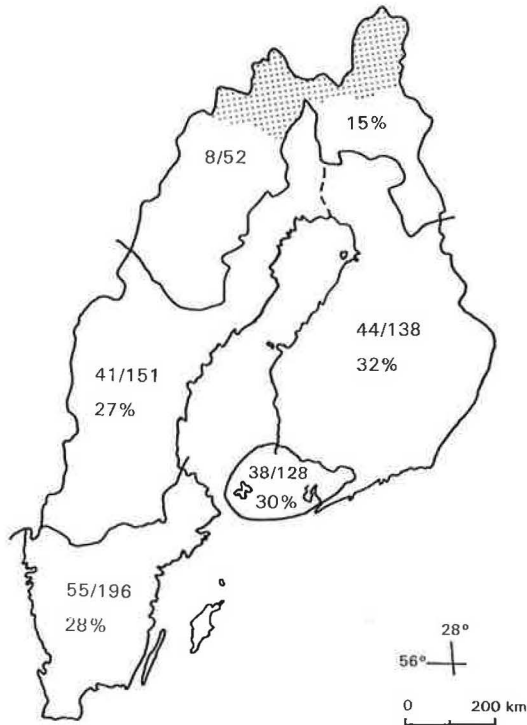


Fig. 1. Numbers of oligolectic and all pollen-collecting bee species and percentages of oligoleges occurring in Finland and Sweden (nest parasites excluded). The records of bees are mainly according to Elfving (1968), Erlandsson *et al.* (1988), Svensson *et al.* (1990) and Janzon *et al.* (1991), and classification as oligo- or polyleges mainly according to Westrich (1990). Areas delimited on the bases of biogeographic provinces roughly correspond to temperate and hemiboreal, and southern, middle and northern boreal vegetation areas in Fennoscandia (Ahti *et al.* 1968, Abrahamsen *et al.* 1982). The shaded area is the northernmost fjeld area of Fennoscandia.

ics the flowers of *Campanula* (Nilsson 1983, Nazarov & Ivanov 1990). Both *Macropis* species in Finland are narrow oligoleges that collect not only pollen, but also lipids containing oil from *Lysimachia* (Vogel 1986). *Lysimachia* species do not produce nectar, while *Macropis* species collect nectar from many other flowers (see also Pekkarinen *et al.* 1998). *Andrena tarsata* is a narrow oligolege of *Potentilla* (Westrich 1990; see also Janzon 1983: 172, 176). *A. hattorfiana* occurs in Finland as a narrow oligolege of *Knautia* (Valkeila 1953) as possibly does also *A. marginata* (Westrich 1990). *A. lathyri* and *Eucera longicornis* are

in Finland narrow oligoleges of *Lathyrus* and *Colletes daviesanus*, a narrow oligolege of *Tanacetum* (Niemelä 1934, 1949). According to Westrich (1990), all oligoleges of *Salix* recorded in Finland are narrow, with the exception of *A. clarkella*, but Niemelä (1934) (see also Gebhardt & Röhr 1987) regarded also this species as a narrow oligo-

Table 1. Numbers of oligo- (Ol) and polylectic (Po) bee species in Finland and Sweden in various genera. The figures in parentheses indicate the numbers of narrow oligoleges. The records and classification are according to Vikberg (1986) (completed with some later records), Erlandsson *et al.* (1988), Svensson *et al.* (1990) and Janzon *et al.* (1991). Classification as oligo- and polyleges mainly according to Westrich (1990).

	Ol	Po	Total
<b>Colletidae</b>			
<i>Colletes</i>	6 (3)	2	8
<i>Hylaeus</i>	2 (1)	16	18
<b>Andrenidae</b>			
<i>Andrena</i>	22 (7)	34	56
<i>Panurgus</i>	2	—	2
<i>Panurginus</i>	—	1	1
<b>Halictidae</b>			
<i>Dufourea</i>	4 (3)	—	4
<i>Rophites</i>	1	—	1
<i>Halictus</i>	—	8	8
<i>Lasioglossum</i>	—	28	28
<b>Melittidae</b>			
<i>Melitta</i>	4 (2)	—	4
<i>Dasypoda</i>	3	—	3
<i>Macropis</i>	2 (2)	—	2
<b>Megachilidae</b>			
<i>Trachysa</i>	1	—	1
<i>Anthidium</i>	—	3	3
<i>Heriades</i>	1	—	1
<i>Chelostoma</i>	3 (3)	—	3
<i>Osmia</i>	2 (1)	12	14
<i>Hoplitis</i>	2 (1)	3	5
<i>Anthocopa</i>	1	—	1
<i>Chalicodoma</i>	1	—	1
<i>Megachile</i>	3 (1)	11	14
<b>Anthophoridae</b>			
<i>Eucera</i>	1 (1)	—	1
<i>Anthophora</i>	1	4	5
<i>Melecta</i>	—	1	1
<i>Ceratina</i>	—	1	1
<b>Apidae</b>			
<i>Bombus</i>	1 (1)	29	30
<b>Total</b>	<b>63 (26)</b>	<b>153</b>	<b>216</b>

lege of *Salix* in Southern Finland. *Colletes succinctus* and *A. fuscipes* are in Finland narrow oligoleges of *Calluna* (Niemelä 1934; see also Gebhardt & Röhr 1987). *Megachile lapponica* is a narrow oligolege of *Chamaenerion* in Southern Finland (Niemelä 1934, 1936), and *Chelostoma florissomne* a narrow oligolege of *Ranunculus* (Käpylä 1978). *Hylaeus signatus* is a narrow oligolege of *Reseda* (Westrich 1990) and only single records exist of this species from Finland (Elfving 1968) and Sweden (Erlandsson 1984).

The following 3 species recorded from Sweden, but not from Finland, are according to Westrich (1990) narrow oligoleges: *Dufourea minuta* Lepeletier (on *Jasione*), *Melitta tricineta* Kirby (on *Odontites*) and *Hoplitis mitis* Nylander (on *Campanula*; see also Janzon 1983: 173). Furthermore, *Panurgus banksianus* (Kirby) and *P. calcaratus* (Scopoli) have been observed to be narrow oligoleges of *Hypochoeris radicata* on the island of Öland (Tengö *et al.* 1988; see also Nielsen 1934 and Münster-Swendsen 1968). In some other areas, however, these bees have been observed to collect pollen from flowers belonging to several genera and often yellow-coloured Asteraceae (Niemelä 1934, Westrich 1990; see also Table 2).

*Bombus consobrinus* can be regarded in Northern Europe as a facultative narrow oligolege foraging almost exclusively on *Aconitum septentrionale* during its flowering season (June 20 to August 20 in Southern Norway) and on other flowers only during a short time at the beginning and end of the season (Løken 1961, Mjelde 1983). *Aconitum* already attracts *B. consobrinus* queens before flowering in early summer (Mjelde 1983). The dependence of the bee on *Aconitum* is evident and their distributions are almost completely identical in Northern Europe (Løken 1973, Pekkarinen 1979). Furthermore, the bee is a more efficient pollen collector of *Aconitum* than other generalist bumblebee foragers (Thøstesen & Olesen 1996).

## 5. Decline of oligolectic bees in Finland

The ranges of all narrowly oligolectic solitary bees in Finland (with the exception of *A. ruficrus*) extend no further than 66°N. The pollen plants, however, are distributed over the entire country (*Cam-*

Table 2. Oligolectic bee species and records of the families and genera of their main pollen plants in Finland. The figure after a slash (/) indicates the number of other plant genera on which an individual bee has been recorded. Few records are available (< 20 localities) of the species marked with an asterisk (\*). The food plant records are mainly according to Westerlund (1893), Silén (1906ab, 1908), Niemelä (1934), Käpylä (1978) and Elfving (1968), plant nomenclature mainly according to Hämet-Ahti *et al.* (1986), bee nomenclature according to Vikberg (1986) and classification as oligolectes mainly according to Westrich (1990).

Apiaceae

***Andrena nanula*** Nylander

*Aegopodium, Carum, Heracleum, Pimpinella* / 2

Asteraceae and Cichoriaceae

***Colletes daviesanus*** F. Smith

*Achillea, Leucanthemum, Solidago, Tanacetum, Tripleurospermum, Taraxacum* / 4; principally on *Tanacetum vulgare* (Niemelä 1934)

***C. similis*** Schenck

*Achillea, Leucanthemum, Tanacetum, Tripleurospermum* / 0

\****Hylaeus nigrinus*** (Fabricius)

*Achillea, Centaurea, Leucanthemum* / 6

***Andrena denticulata*** (Kirby)

*Achillea, Aster, Bidens, Calendula, Centaurea, Cichorium, Cirsium, Erigeron, Hieracium, Hypochoeris, Inula, Leontodon, Solidago, Sonchus, Tanacetum, Tripleurospermum* / 11

\****A. fulvago*** (Christ)

- / 0

\****A. humilis*** Imhoff

*Hieracium, Leontodon* / 2

***Panurgus calcaratus*** (Scopoli)

*Achillea, Calendula, Crepis, Hieracium, Lactuca, Lapsana, Leontodon, Pilosella, Sonchus, Tragopogon* / 1

\****Dufourea vulgaris*** (Schenck)

*Hieracium, Leontodon* / 0

***Dasygaster altercator*** (Harris) [*hirtipes* (Latreille)]

*Centaurea, Hieracium, Leontodon* / 1

***Heriades truncorum*** (L.)

*Achillea, Arnica, Aster, Anthemis, Bidens, Calendula, Centaurea, Cirsium, Crepis, Erigeron, Hieracium, Inula, Lapsana, Leontodon, Leucanthemum, Matricaria, Taraxacum, Tripleurospermum* / 16

\****Megachile bombycina*** Radoszkowski

*Centaurea, Cirsium, Hieracium* / 0

***Osmia leaiana*** (Kirby)

*Centaurea, Pilosella, Leontodon, Taraxacum* / 0

Campanulaceae

***Dufourea dentiventris*** (Nylander)

*Campanula* / 2

\****D. inermis*** (Nylander)

*Campanula* / 0

***Melitta haemorrhoidalis*** (Fabricius)

*Campanula* / 3

***Chelostoma campanularum*** (Kirby)

*Campanula* / 10

***C. rapunculi*** (Lepelletier)

*Campanula* / 17

Dipsacaceae

***Andrena hattorfiana*** (Fabricius)

*Knautia* / 4

\****A. marginata*** Fabricius

*Knautia* / 1

*Continues ...*

Table 2. Continued.

## Ericaceae

**Colletes succinctus** (L.)*Calluna* / 3**Andrena fuscipes** (Kirby)*Calluna* / 1; principally on *C. vulgaris* (Niemelä 1934)**A. lapponica** Zetterstedt*Andromeda*, *Arctostaphylos*, *Chamaedaphne*, *Vaccinium* / 12; *V. vitis-idaea* especially favoured (Niemelä 1934, Viramo 1978)

## Fabaceae

**A. gelriae** van der Vecht*Lathyrus*, *Trifolium*, *Vicia* / 8**A. intermedia** Thomson*Anthyllis*, *Astragalus*, *Lathyrus*, *Medicago*, *Trifolium*, *Vicia* / 9\***A. labialis** (Kirby)*Trifolium*, *Vicia* / 7\***A. lathyri** Alfken*Lathyrus* / 0**A. wilkella** Kirby*Lathyrus*, *Lotus*, *Trifolium*, *Vicia* / 19**Chalicodoma ericetorum** Lepelletier*Astragalus*, *Lathyrus*, *Lotus*, *Ononis*, *Phaseolus*, *Pisum*, *Trifolium*, *Vicia* / 25\***Melitta leporina** (Panzer)*Medicago*, *Ononis*, *Trifolium*, *Vicia* / 1**Trachysa byssina** (Panzer)*Lathyrus*, *Trifolium*, *Vicia* / 7**Megachile nigriventris** Schenck*Lathyrus*, *Trifolium*, *Vicia* / 2**Eucera longicornis** (L.)*Caragana*, *Lathyrus*, *Pisum*, *Trifolium*, *Vicia* / 11; principally on *L. pratensis* (Niemelä 1934)

## Lamiaceae

**Anthophora furcata** (Panzer)*Ballota*, *Galeopsis*, *Hyssopus*, *Lamium*, *Prunella*, *Satureija*, *Scutellaria*, *Stachys* / 16

## Onagraceae

**Megachile lapponica** Thomson*Chamaenerion* / 5; principally on *C. angustifolium* (Niemelä 1934, 1936)

## Primulaceae

**Macropis europaea** Warncke (*labiata* auct.)*Lysimachia* / 23**M. fulvipes** (Fabricius)*Lysimachia* / 10

## Ranunculaceae

**Chelostoma florisomne** (L.) [*maxillosum* (L.)]*Ranunculus* / 19**Bombus consobrinus** Dahlbom*Aconitum* / 8

## Resedaceae

\***Hylaeus signatus** (Panzer)- / 0 (*Reseda*)

## Rosaceae

**Andrena tarsata** Nylander*Potentilla*, *Rubus*, *Sorbaria* / 10

Continues ...

Table 2. Continued.

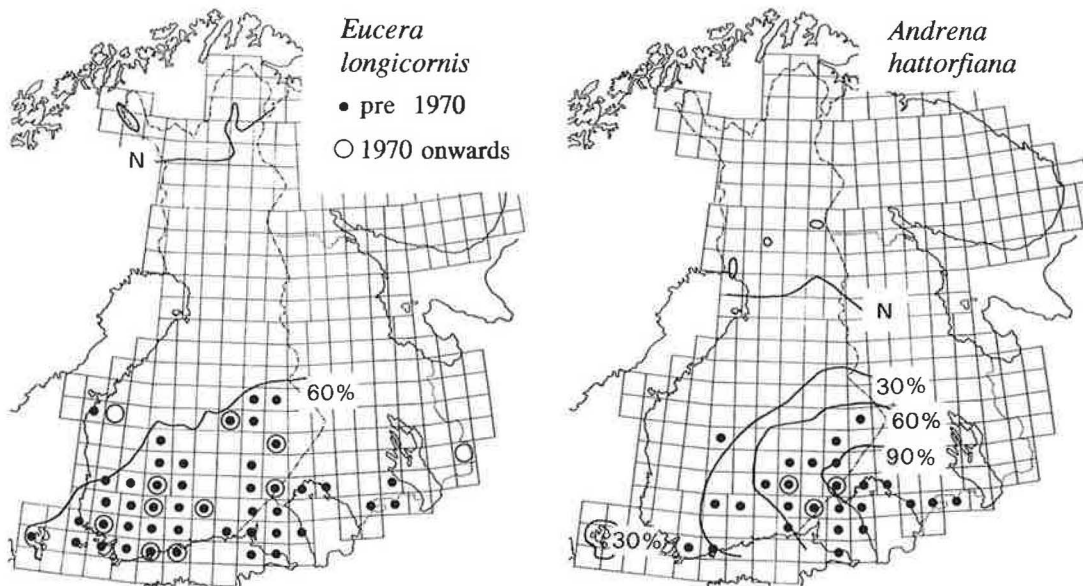
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Salicaceae	
<b>Colletes cunicularius</b> (L.)	<i>Salix</i> / 4
<b>Andrena clarkella</b> (Kirby)	<i>Salix</i> / 3
<b>A. praecox</b> (Scopoli)	<i>Salix</i> / 3
<b>A. ruficus</b> Nylander	<i>Salix</i> / 16
<b>A. vaga</b> Panzer	<i>Salix</i> / 2

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*panula*, *Potentilla*, *Ranunculus*, *Salix*) or markedly more northwards (*Knautia*, *Lathyrus*, *Lysimachia*, *Tanacetum*) than their oligoleges. The northern limits of these narrow oligoleges are thus possibly determined also by some other factors than occurrence of pollen plants, e.g. temperature and length of a suitable season. Furthermore, local frequency of the pollen plants is important and e.g. the uttermost records of *E. longicornis* and *A. hattorfiana* approximately follow certain frequency limits of their main pollen plants in Finland (Figs. 2 and 3). In Sweden, the provinces from which the last-mentioned bee species have

been recorded (Janzon *et al.* 1991, Svensson *et al.* 1990) also fairly well cover the area of the common occurrence of *L. pratensis* and *Knautia*, respectively, given by Hultén (1971). A similar relationship is also obvious in Finland and Sweden between the two *Macropis* species and *C. daviesanus* and their pollen plants *Lysimachia vulgaris* and *Tanacetum*, respectively (Pekkarinen *et al.* 1998). Apparently, pollen and nectar foraging bees, especially oligolectic species, are dependent on much larger associations of their food plants and are thus more sensitive to impoverishment of vegetation than e.g. leaf-eating insect species.



Figs. 2 and 3. Distribution of *Eucera longicornis* and *Andrena hattorfiana* in Finland and northwestern Russia according to the European UTM grid system. Nearly all records from Russian territory are based on samples collected before 1945. The lines show the limits of frequencies (weighted proportion of 1 x 1 km squares with records to all squares investigated) of the main pollen plants *Lathyrus pratensis* (Fig. 2) and *Knautia arvensis* (Fig. 3) and approximate limits of northernmost records in Finland (N) (according to Lahti *et al.* 1995).

In the area of Baden-Württemberg in Germany, 190 pollen-collecting bee species have been estimated to be threatened, of which 74 (about 40%) are oligolectic (Westrich 1990). In England, 96 pollen-collecting bee species have been listed as threatened or notable (Falk 1991), 29 (30%) of which are oligolectic. In Poland, 51 pollen-collecting species have been estimated to be extinct, endangered or vulnerable (including 13 *Bombus* species) (Banaszak 1995), of which 12 (24%) are oligolectic. These three lists include 32 oligolectic species occurring in Finland, of which several have been recorded previously as common and widely distributed in Finland e.g. *Andrena clarkella*, *A. denticulata*, *A. intermedia*, *A. praecox*, *A. ruficornis*, *A. wilkella*, *Anthophora furcata*, *Colletes cunicularius*, *Eucera longicornis*, *Dufourea dentiventris* and *Trachysa byssina*.

The decline of many oligolectic bee species also in Finland is obvious and is correlated with habitat impoverishment of flowering meadows and fields caused mainly by modern agriculture and afforestation. Furthermore, the decrease in suitable nesting sites, e.g. to sun exposed, sparsely vegetated banks and slopes, decaying tree-trunks, old barns and timber houses is evident. However, the decline or total loss of previous rich populations in soil nesting bees have been observed in Finland also in some localities without notable great change of nesting habitats or food plants.

The records of two oligolectic species based mainly on the collections of the Zoological Museums of the Universities of Helsinki, Oulu and Turku, the Department of Applied Zoology of the University of Helsinki and Kuopio Museum of Natural History (some published and unpublished field observations have also been included) are given here as examples of the decline (Figs. 2 and 3). *E. longicornis* is a gregariously nesting species, which has previously occurred as a widely distributed common oligolectic of Fabaceae (preferring *Lathyrus pratensis*; Niemelä 1934) and *A. hattorfiana* as a locally distributed narrow oligolectic of *Knautia*. The sampling activity has been variable during different periods but, on the other hand, both these species are large and conspicuous (especially males of *E. longicornis*) and are also often collected by entomologists other than bee specialists. The numbers of individuals in the

collections (the first number) and numbers of UTM grids with records in Figs. 2 and 3 (the second number) from various periods in Finland (present Russian territory is not included) are as follows:

	<i>E. longicornis</i>		<i>A. hattorfiana</i>	
Pre-1900	43	9	6	4
1900–1919	60	6	3	2
1920–1939	141	17	24	4
1940–1959	137	18	40	6
1960–1979	68	12	94	10
1980–1996	16	6	1	1

The numbers of individuals from the five-year periods after 1949 are as follows:

	<i>E. longicornis</i>	<i>A. hattorfiana</i>
1950–1954	33	19
1955–1959	57	14
1960–1964	52	74
1965–1969	6	17
1970–1974	5	1
1975–1979	5	2
1980–1984	4	–
1985–1989	2	–
1990–1996	10	1

The material of *A. hattorfiana* from 1960–64 has biased by large samples from two localities (K1: Parikkala, Grid 27°E: 682:63 and Kb: Liperi, Grid 27°E: 694:62). The data, however, distinctly imply that a drastic decrease in the two bee species has occurred in Finland and culminated during the sixties. It is also noteworthy that all the three records of *A. hattorfiana* after 1969 originate from the area of the high frequency (> 60%) of *Knautia* (Fig. 3). Obviously, *A. hattorfiana* has completely disappeared from a large area of its former range in Finland, while *E. longicornis* has become only more scarce. On the other hand, it seems that the two *Macropis* species have not remarkably declined in Finland (Pekkarinen *et al.* 1998), since their pollen plant (*L. vulgaris*) is on water-sides growing hygrophyte and not largely dependent on agriculture.

Further studies are urgently needed for elucidating the possible decline in and threats to various bee species, as well as for the management required to maintain threatened oligolectic and other bee species in Northern Europe.



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