

## Distribution and co-existence of the *Macropis* species and their cleptoparasite *Epeoloides coecutiens* (Fabr.) in NW Europe (Hymenoptera: Apoidea, Melittidae and Apidae)

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The *Macropis* species collect pollen and fatty oil secreted by flowers of loosestrifes (*Lysimachia*, Primulaceae) and are the only known oil-collecting bees in the Holarctic. In NW Europe, *L. vulgaris* is the main or (in large areas) sole pollen and oil source for *M. europaea* Warncke (*labiata* auct.) and *M. fulvipes* (Fabr.). The species are largely sympatric in southern Finland and the Baltic countries, while in Scandinavia and most of Denmark only *M. europaea* has been recorded. The ranges of the *Macropis* species are restricted to the areas of common occurrence of *L. vulgaris*. Presumably, *Epeoloides coecutiens* has colonized Finland and Estonia since about 1970. The phenology of *M. fulvipes* is some days earlier than that of *M. europaea*, and this temporal difference may decrease resource competition in the co-existing populations.

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### 1. Introduction

The Holarctic genus *Macropis* Panzer comprises 16 recognized species of bees (Michener 2000). All species of the genus are believed to be strictly

oligolectic and are specialized in collecting pollen exclusively from flowers of loosestrife (*Lysimachia*, Primulaceae). Three species of *Macropis* occur in the western Palaearctic region: *M. fulvipes* (Fabricius, 1804) (syn. *M. labiata*

[Fabricius, 1804]), *M. europaea* Warncke, 1973 (*M. labiata* auct.) and *M. frivaldskyi* Mocsary, 1876 (see Warncke 1973). The two first-mentioned species occur in most of Europe, whereas *M. frivaldskyi* is found only in southern and south-eastern Europe.

The oligolecty of *Macropis* species for loosestrife (*Lysimachia*) and the flowers being nectarless have long been known. However, fairly recently, the flowers of loosestrife have been discovered to secrete fatty oil as a floral reward. Oil-producing glandular hairs densely cover the connate base of the pistil and stamens of loosestrife flowers. The female bees collect the oil by absorption in specialized hairs situated on the tarsal segments of the fore and middle legs. The oil is mixed with pollen for nourishment of offspring (Vogel 1976, 1986).

Among several subgenera of the large and cosmopolitan genus *Lysimachia*, only the mainly Holarctic species of subgenus *Lysimachia* produce floral oil whereas the majority of species in other subgenera offer nectar as a floral reward. The range of the oil-producing species in Eurasia and North America covers that of the *Macropis* species. Southern China and neighbouring subtropical eastern Asia are especially rich in *Lysimachia* (s. str.) species; most of the approximately 85 species of the subgenus occur there, and many of them are oil producing (Vogel 1986). In subfamily Melittinae floral oil-collecting bees have been recorded apart from the *Macropis* species, in the South African genus *Rediviva* Friese and in subfamily Apinae among some Palaeo- and Neotropical tribes (Vogel 1986, Michener 2000).

*Epeoloides* species are nest parasites of the *Macropis* species (Michener 2000). *Epeoloides coecutiens* is the only Palaearctic species of the genus (Popov 1958) with a second species recorded in North America (Michener 2000).

## 2. Material

The material originates from the collections of museums of the Universities of Helsinki, Turku, Oulu, Lund, Oslo, Bergen, Copenhagen and Tartu, the Swedish Museum of Natural History, and private collections of the persons mentioned in the acknowledgements and those of the authors. The records from Latvia and Lithuania are based on the respective publications of Monsevičius (1995) and Tumss (1973, 1975).

## 3. Food plants and nesting

The main pollen and oil plant of the *Macropis* species in north-western Europe is *L. (L.) vulgaris*. The native (in southern Sweden, Denmark and the Baltic countries), partially cultivated and naturalized *L. (L.) nummularia* and the cultivated *L. (L.) punctata* are other pollen and oil sources in the area. In NW Europe the widely distributed *L. (Naumburgia) thyrsiflora* and in southern Sweden and Denmark *L. (L.) nemorum* do not secrete floral oil and produce only small amounts of pollen (Vogel 1986); *Macropis* species do not forage these, and the note by Snelling & Stage (1995) concerning *M. nuda* (Provancher) visiting *L. thyrsiflora* is dubious (see also Simpson *et al.* 1983). The energy source for adult bees is nectar, which they collect from many plant species mainly with open corolla (Vogel 1986, Pekkarinen *et al.* 2000). The males collect only nectar, but they seem to fly in more or less regular routes around the loosestrife flowers. The routes are rather short, often not more than one metre on each side of the triangle or quadrat route. The males usually stop and sit at a particular place on a leaf where they wait for arriving females. When a female arrives, the male approaches her, lands and copulation proceeds on flowers. The males are attracted not only by female pheromones (Kullenberg 1956, Rozen & Jacobson 1980) but also by appearance.

The nests occur in soil as small aggregations near loosestrife. The nest consists of a short burrow leading to a nest cavity from which some cells radiate. The cells are lined with a greenish-yellow waterproof substance, which is derived from *Lysimachia* floral oil. The lining ensures constant humidity for the pollen and prevents water entrance into the nest. As far as we know, all *Macropis* species are univoltine (Malyshev 1929, Phipps 1948, Rozen & Jacobson 1980, Cane *et al.* 1983).

## 4. Distribution

*M. europaea* is recorded mainly from Europe and eastwards to Kazakh (Vogel 1986). *M. fulvipes* has a Transpalaearctic range and the form occurring in the Amur and Ussuriisk areas is regarded as a separate subspecies, *M. f. amurensis* Popov

(Romankova 1995). Presumably, *M. fulvipes* has dispersed fairly late to western Europe from the east and has not reached Scandinavia or the British Isles.

In Finland, the two *Macropis* species have rather similar distributions. The species are also largely sympatric in the Baltic countries, while in Scandinavia and most of Denmark, only *M. europaea* has been recorded (only a few old records exist from the beginning of the last century of *M. fulvipes* on the Danish island of Lolland). In the Fennoscandian area, *L. vulgaris* has a large distribution, reaching as far as southern Lapland (Fig. 1). However, the ranges of the two bee species in Finland are mainly restricted to areas where *L. vulgaris* is common, i.e. shows a frequency of 40% (Fig. 1). Similarly, *M. europaea* occurs in Sweden and Norway only in the southern range of the distribution of *L. vulgaris*, approximately in the area where Hultén (1971) considered the plant to be common or very common (Fig. 1). In Russian Karelia, the records of *Macropis* species are scanty and their northernmost distribution is poorly documented.

Many oligolectic bee species in Europe have suffered from a decline in their pollen and nectar resources (e.g. Westrich 1990, Falk 1991, Pekkarinen 1998, 1999). *L. vulgaris*, a hygrophyte often growing abundantly at the edge of waters or in other damp places, has not been greatly impacted by changes in agriculture as have many other food flowers of bees. Consequently, the *Macropis* species are often locally abundant in the area in question.

Two old records of *Epeoloides coecutiens* are available from the Karelian Isthmus (Sahlberg 1889, Niemelä 1935). The species has been found on the Hanko Peninsula in southernmost Finland since 1970, and about thirty specimens have subsequently later been collected in several localities in southern Finland (even in Åland in 2002) (Viitasaari 1975, Ranta 1994, Pekkarinen *et al.* 2000; personal communications of J. Pöyry, J. Paukkunen, G. Söderman and I. Teräs) (Fig. 1). While Sagemehl (1882) did not note the species in the Baltic countries, it has been reported in a few localities in Lithuania since 1930 (Monsevičius 1995), and in Estonia since 1973. The species has not been recorded from Denmark or Scandinavia. The lack of old records and many

new findings of *E. coecutiens* in Finland and Estonia imply a recent dispersal of this conspicuous species in NW Europe. Moreover, Schmiedeknecht (1930:834) characterized the species to be one of the rarest bee species in central Europe but, Westrich (1990), for example, regarded the species as fairly common locally in south-western Germany. By contrast, the American species *E. pilosula* (Cresson) may be extinct since no records have been made after 1942 (Michener 2000).

## 5. Phenology

*L. vulgaris* is the only native pollen and oil resource for the *Macropis* species in Finland. The main flight periods of the two bee species coincides with the height of the flowering of *L. vulgaris* in July. *M. fulvipes* has a slightly earlier occurrence, and the medians of flight dates (see large histograms in Fig. 2) and their differences (in days) between the species and the sexes are shown in Table 1.

The flight-date records (Table 1) originate over several decades and different sampling years, and variation in general phenology may be even some weeks during more extreme summers in southern Finland. Thus, a flight period of a single season is considerably shorter than indicated by the large multi-year histograms in Fig. 2. The small (black) histograms, indicating one flight season, imply that a maximal local flight period may be about one month (see also Rozen & Jacobson 1980). In the (fairly small) Estonian material, the medians of the flight dates are as follows: *M. fulvipes* males 15.VII (−0.4) ( $n = 12$ ), females 17.VII (+0.1) ( $n = 15$ ); *M. europaea* males 18.VII (+0.5) ( $n = 22$ ), females 1.VIII (−0.2) ( $n = 17$ ).

## 6. Co-existence

To date, the *Macropis* species are the only known (regular) floral oil-foraging visitors of *Lysimachia*, and other insect groups, such as hoverflies, have been observed to eat only pollen (Vogel 1986). All *Macropis* species are oil foraging and are the principal pollinators of oil-producing loosestrifes. Thus, a long-continued mutualism between the

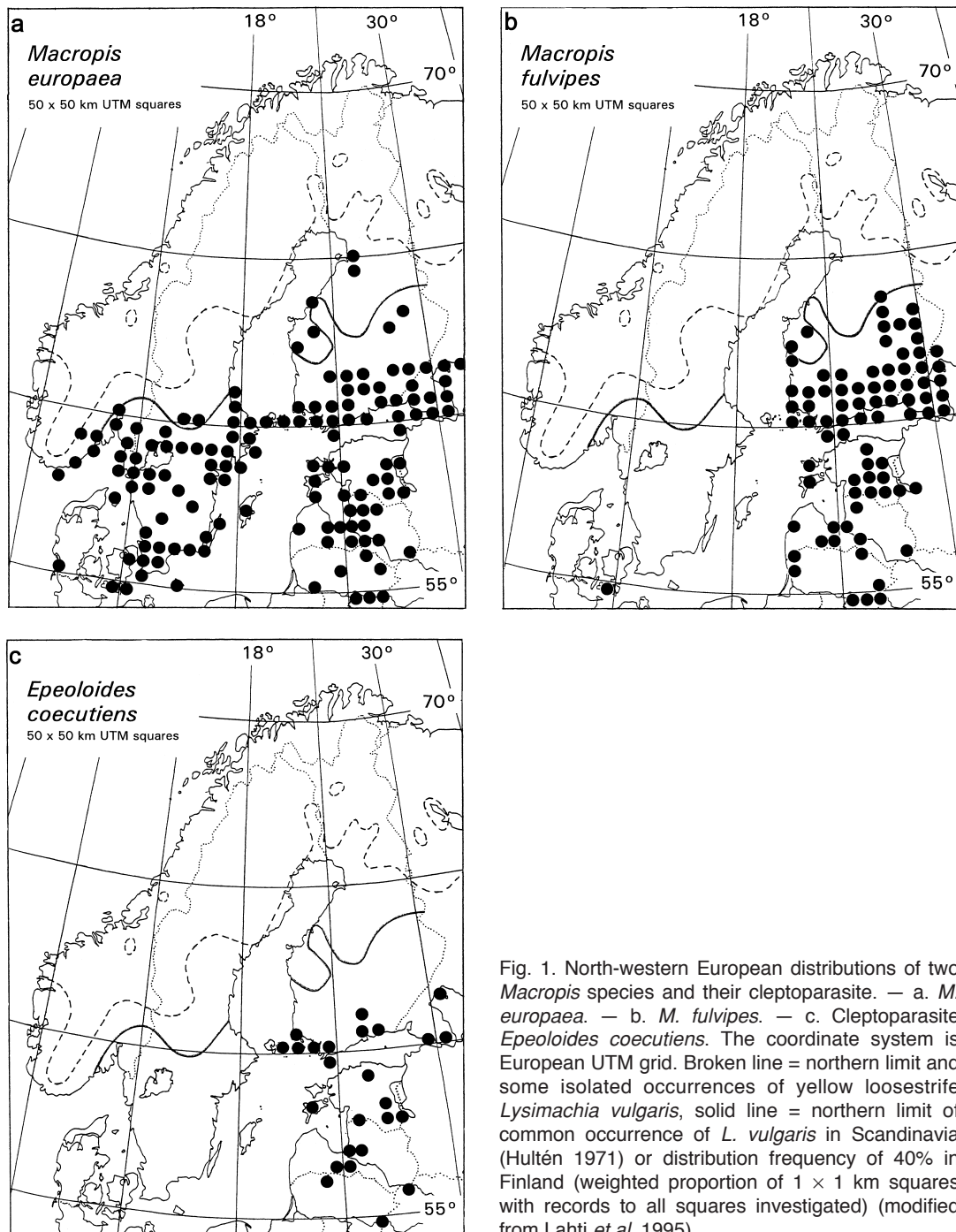


Fig. 1. North-western European distributions of two *Macropis* species and their cleptoparasite. — a. *M. europaea*. — b. *M. fulvipes*. — c. Cleptoparasite *Epeoloides coecutiens*. The coordinate system is European UTM grid. Broken line = northern limit and some isolated occurrences of yellow loosestrife *Lysimachia vulgaris*, solid line = northern limit of common occurrence of *L. vulgaris* in Scandinavia (Hultén 1971) or distribution frequency of 40% in Finland (weighted proportion of  $1 \times 1$  km squares with records to all squares investigated) (modified from Lahti *et al.* 1995).

loosestrifes and the *Macropis* species is evident. An eastern Asiatic species, *M. ussuriana* (Popov), which has been placed in the subgenus *Paramacropis* and regarded as a sister group of all other

*Macropis* species by Wu & Michener (1986), has similar oil-collecting hairs to the other species of the genus, thus indicating old age of the mutualism. However, as Vogel (1986) emphasizes, the

relationship has more likely been between groups of specialized pollinators and plants with specialized floral reward than mutualism between one bee and one plant species.

Oil-producing loosestrifes are also able to multiply vegetatively by means of autogamy or non-specialist pollinators, such as other bees and hoverflies (Cane *et al.* 1983, Simpson *et al.* 1983, Vogel 1986). Yet, few other bee species have been found to visit loosestrifes: *Hylaeus confusus* Nylander, *H. hyalinatus* F. Smith, *Halictus tumulorum* (L.) and four *Bombus* species in Finland (Niemelä 1934, Elfving 1968, pers. obs.); Westrich (1990) notes only *Lasioglossum calceatum* (Scopoli) in Baden Württemberg. Some other bee genera have been recorded as visitors of *Lysimachia*: *Heriades*, *Epeoloides*, *Ceratina*, *Allodape* and *Crocisa* (Haman & Koller 1956, Popov 1958, Wu 1965). Occasionally, some migrating species of hoverflies visit loosestrifes abundantly, including *Episyrphus balteatus* (De Geer) and *Sphaerophoria scripta* (L.) in southern Finland in 1998.

There are two or more sympatric *Macropis* species and several floral oil-producing *Lysimachia* species in a very large part of their common range. In North America, four largely sympatric *Macropis* and up to 17 native oil-producing *Lysimachia* species occur, while in Europe the corresponding figures are three and three (Simpson *et al.* 1983, Vogel 1986, Snelling & Stage 1995). Thus, sympatric *Macropis* species may prefer different species of *Lysimachia* and avoid interspecific competition for pollen and oil resources; *M. fulvipes*, for instance, has been reported to favour early flowering *L. nummularia*, while *M. europaea* prefers later flowering *L. vulgaris* (Malyshev 1929, Westrich 1990).

Finland has only one native oil-producing loosestrife species, and the two *Macropis* species

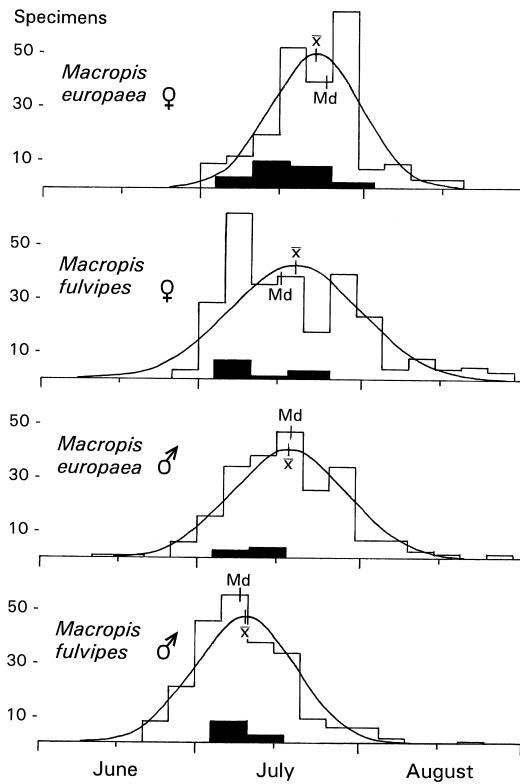


Fig. 2. Large histograms: dates (in five-day periods) of the *Macropis* species in Finland (from public and private collections). Small (black) histograms: dates (in approximately seven-day periods) of specimens collected by Malaise trap in 1983 in southern Finland (N: Sipoo 669:40). Curves of normal distribution have been drawn for large histograms ( $\bar{x}$  = mean; Md = median).

have to share the same larval food resource. They often co-exist in the same localities and may even forage on the same florescences of loosestrife. Moreover, the daily rhythm and the foraging behaviour of the two species seem to be similar and competition for food resources is possible. If the

Table 1. The median flight periods (large histograms in Fig. 2) of two *Macropis* species in Finland, and differences in flight periods (in days) indicated for sexes (right column) and for the species (lower row).

Species	Males	Females	Difference
<i>M. fulvipes</i>	9.VII (+0.2) (n = 227)	16.VII (-0.1) (n = 276)	6.7
<i>M. europaea</i>	18.VII (+0.1) (n = 228)	24.VII (-0.2) (n = 223)	5.7
Difference	8.9	7.9	



flight period is 30 days and species occurrences follow a normal distribution, a median difference of five days between the species reduces temporal overlap by about 30%, and the difference of ten days by about 60%. Actually, the distributions in Fig. 2 are skewed and biased to the early (mean > median; *M. fulvipes*) or the latter (mean < median; *M. europaea*) part of the flight periods, and overlaps are thus even smaller than in normal distributions. Specific differences in flight periods of the coexisting *Macropis* species are therefore meaningful for resource partitioning.

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