

# The oligolectic solitary bee *Melitta tricinta* Kirby, 1802 (Sw. rödtoppebi) in Sweden (Hymenoptera, Apoidea, Melittidae)\*

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Nilsson, L.A. & Alves-dos-Santos, I.: The oligolectic solitary bee *Melitta tricinta* Kirby, 1802 (Sw. rödtoppebi) in Sweden (Hymenoptera, Apoidea, Melittidae). [**Rödtoppebiet *Melitta tricinta* i Sverige (Hymenoptera, Apoidea, Melittidae).**] – Entomologisk Tidsskrift 130 (2): 85-98 Uppsala, Sweden 2009. ISSN 0013-886x.

In Sweden, the oligolectic solitary bee *Melitta tricinta* Kirby, 1802 has been reported from a few southern provinces and red listed as endangered (EN). In order to explore the conservation status, we studied the reputed and potential material of the species as well as carried out field studies in the area of known modern occurrence, viz. the military training field and Natura 2000-area Revingehed in the southernmost province Skåne. Our results showed that there is no valid Swedish record before 1930, suggesting a fairly recent colonization. There is no evidence that a regional decline during later decades includes Skåne. In Revingehed 2008, the bee was still present on previously detected localities but also occurred on numerous other, hitherto unknown localities that contained the exclusive food plant, the red bartsia, *Odontites vulgaris* (Scrophulariaceae). Nesting sites, on the other hand, seemed not a limiting factor. There was evidence of a metapopulation-like situation, in which bees have a capacity to disperse and occupy even relatively isolated, small and temporary ruderal-type habitats. In total, 25 subpopulations were recorded and the population size estimated to ca. 7000 individuals. Unlike many other red listed bees in Revingehed, *M. tricinta* was largely favoured by the current more-or-less extensive management regime of year-around grazing. Like many, the species was favoured by the considerable military disturbance of the light, largely sandy soils. We conclude that both negative and positive factors have influenced the bee species *M. tricinta* in Sweden during the 80 years of known occurrence and that the current conservation status is promising in spite of a single known large population.

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Of the 17,553 known bee species, the Melittidae s. lat. constitutes a small (157 species) but in the specialization for foraging on flowers unusually diverse family (Michener 2007). Considering today's enforced environmental destruction from land use intensification, no doubt the melittid

specializations including oligolecty (pollen collection from a single plant family) have turned into a formidable threat to survival. For example, in Sweden the melittid fauna numbers eight species (Nilsson 2003), all of which are oligolectic (Michez & al. 2008). Of these, six have been red

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\*This paper commemorates the ninetieth birthday of Charles D. Michener, the power source of modern bee research.



Figure 1. *Melitta tricinta* ♂ and ♀. Photo: L. Anders Nilsson.  
Rödtoppebi ♂ och ♀.

listed, viz. as RE nationally extinct (*Dasyopda argentata* and *D. aurata* (= *D. suripes*, see Baker 2002), EN endangered (*Melitta melanura* (= *M. wankowiczi*, see Nilsson 2007) and *M. tricinta*), and NT near threatened (*Dasyopda hirtipes*, and formerly also *Melitta leporina*) (Gärdenfors 2000, 2005). Only *Melitta haemorrhoidalis* and *Macropis europaea* are yet wide-spread (LAN pers. obs.).

The purpose of the present study was to clarify the history, distribution, and conservation status of *M. tricinta* in Sweden. This endangered species has been recorded from a few southeastern provinces (Gärdenfors 2005). It has not been found in Norway (Ø. Berg unpubl. checklist 2001) and Finland but as close as in the St. Petersburg area in Russia and Estonia (Söderman & Leinonen 2003), and is (probably mostly under the name *M. nigricans*) known from several parts of Denmark (Jørgensen 1921, H.B. Madsen pers. comm.). The species occurs widely across Europe, from southern England in the west, Spain, Sicily (Italy) and Greece in the south, and Romania in the east, and further eastward to Udmurtia and Yakut in Russian Asia (Warncke 1973, 1981, Else 1998, Celary 2005, Michez & Eardley 2007). It is a Euro-Siberian element.

The species epithet *tricinta* refers to the sharp bands of dense whitish filtry hairs at the terminal border of the tergites (Fig. 1). The Swedish vernacular name “rödtoppebi” (Nilsson & Ced-

erberg 2008) refers to the distinctive specialization to collect pollen from “rödtoppa”, i.e. red bartsia *Odontites vulgaris* (Scrophulariaceae), a unique adaptation among Swedish bee species.

#### Material and Methods

The work consisted of both museum studies and field observation. We investigated the scientific literature, museums and private collections for all Swedish actual, reputed or potential material of *Melitta tricinta* Kirby, 1802. Material was found in the Swedish Museum of Natural History, Stockholm (NHRS) and the Zoological Museum, Lund (ZML). Information on potential specimens was also available from the Zoological Museum Helsinki (ZMH), Finland. Specimens in the private collections of M. Franzén, M. Larsson, B.G. Svensson and J. Tengö were studied. We have not seen the name-bearing type of *Melitta tricinta* Kirby, 1802 (in the Natural History Museum, London (former British Museum)), but conform to the stable interpretation of current authors in identification of the species (as in Warncke 1973, Scheuchl 1996, 2006, Celary 2005, Michez & Eardley 2007).

Field observations of *M. tricinta* were carried out in 2002, 2004, 2006 (by LAN) and 2008 (by IAS and LAN) in the only known Swedish area still containing a population, viz. the military training field and Natura 2000-area Revingehed in the province of Skåne. In 2008 in Revingehed, we carried out an inventory of the previ-

ously detected localities/subpopulations and also of all other potential localities where we saw the food plant (*Odontites vulgaris*). We defined a *subpopulation* as a distinctly delimited occurrence of the bee species due to a clump of food plant patches separated from other such clumps by ca. 200 m; the spatial distribution of the patches and sparsely vegetated ground suggested that pollen collecting females hardly fly longer than 150 m between foraging area and potential nesting areas. The presence/absence and quantity of bees were obtained from one or more census walks through the food plant patches in each subpopulation. The observed size of a subpopulation (number of individuals) was the sum of the highest number of observed bees of each sex in the walked area. We made an approximate estimation of the total subpopulation size by considering the amount of food plant, the stage of flight period at the census walk, and the size of the habitat. The floral resource in terms of *O. vulgaris* plants, the availability of seemingly possible nesting sites, and threats for the subpopulation of the bee were also estimated during the census walk. We used a 4-scale quantification of the amount of food plant: "Large" corresponds to >100 m<sup>2</sup>, "medium" to >5 m<sup>2</sup> (but <100 m<sup>2</sup>), "small" to <5 m<sup>2</sup> (but >2 m<sup>2</sup>), and "very small" to <2 m<sup>2</sup> covered by *O. vulgaris*.

In order to explore the *M. tricincta* – *O. vulgaris* interaction also from the principal point of possible mutualism and interdependence, we conducted experiments with three different sets of flowers: isolated (bagged) during flowering, isolated after subjected to single visits from *M. tricincta*, and open-visited control. Seed production was used as the measure of pollination success.

The inventory was conducted during the period 21 July – 16 August 2008. The first 11 days were very dry and warm, with temperatures reaching 30°C, and no clouds. Then the weather changed to very windy conditions and strong rains (esp. 3 – 5 August), with largely unstable weather altering between cloudy and partly cloudy.

Each subpopulation was assigned to the actual management area according to the subdivision in 32 such areas stated in ÖMAS (2003), i.e. the present overall management plan for

Revingehed. Most of the areas are subject to grazing, some to haymaking and only a few are excluded from farming practices. The exact geographical positions of subpopulations of this red listed species have been deposited at the Swedish Species Information Centre (ArtDatabanken, SLU, Uppsala).

## Results

### *History and distribution*

Kirby's species epithet *tricincta* was used on Swedish bee material first by the young Finnish, later famous botanist William Nylander (1824–1899). He referred to "*Kirbya tricincta*" from Ystad (Skåne) in NHRS (1852a) and "*Cilissa tricincta*" collected on Gotland by Carl Henrik Boheman (1852b). In coll. Nylander (ZMH) and NHRS including coll. Boheman, however, there was no specimen of *M. tricincta* sensu Kirby from Ystad or Gotland. In coll. Nylander there is a male specimen of *Melitta leporina* (Panzer, 1799) with the pinned labels "Gl." (= Gotland), "Bhn" (= leg. C.H. Boheman) and "*Kirbya tricincta*" (L. Norén pers. obs. & det. 2003). In the revision of the Swedish bee fauna by Thomson (1872), Nylander's *Cilissa 3-cincta* (as well as *Melitta 3-cincta* Kirby) was listed as a synonym of *Cilissa leporina* (Panzer) (now *Melitta* l.). In coll. Thomson (ZML) there was no Swedish specimen of *M. tricincta* sensu Kirby.

In the treatment of the Swedish bee fauna by Aurivillius (1903), the epithet *tricincta* was not mentioned. Perkins (1917) presumed that *M. tricincta* Kirby was a (senior) synonym of *Kirbya melanura* Nylander, a taxon described from Gotland. For a period of 90 years this synonymy was taken for granted by many authors (namely Blüthgen 1930, Stoeckhert 1933, Erlandsson 1960, Warncke 1973, Richards 1978, Erlandsson & al. 1988, Scheuchl 1996, 2006, Schwarz & al. 1996, Celary 2005). Nevertheless, it was erroneous: *Melitta melanura* is another species (Nilsson 2007). Erlandsson (1960) reported that a male of "*M. tricincta* Kirby (= *melanura* Nyl.)" had been found at Löderup sea-resort (Ystads kn) in Skåne 1958. In coll. Erlandsson (NHRS), we found no such specimen of *M. tricincta* sensu Kirby but, on the other hand, six males of *M. leporina* (Panzer) collected by Erlandsson on the locality in question on 19 July 1958. Michez

& Eardley (2007) listed Erlandsson's record from Löderup as correct under *M. tricinta* Kirby. Apparently, however, Erlandsson's record was due to misidentification of *M. leporina*.

In conclusion, Nylander's Swedish record of the species *M. tricinta*, later writers' misinterpretation of his *M. melanura* as this species as well as Erlandsson's 1958 record, were all erroneous. Unexpectedly, more than 130 years after Nylander had mentioned the epithet *tricinta* for a Swedish bee, the bee species *Melitta tricinta* sensu Kirby (and present) had not yet been reported from this country. Material of the actual species was (in part, viz. from the provinces Skåne, Blekinge, Småland and Öland) first reported by Erlandsson & al. (1988), a fact that was not annotated by and thus evidently unknown to these authors. We found that the oldest Swedish specimens are from Kalmar in East Småland 29–30 July 1930 (ZML), a material due to the notoriously insect collecting brothers Daniel Gaunitz (1894–1955) and Carl Bertil Gaunitz (1895–1969). Only a recent (<80 years) presence of the species in Sweden has any support from documentation.

The valid material of *M. tricinta* in the museums and private collections or field notes (+OBS= observed further individuals) known to us per October 2008 is here listed geographically S to N:

**M, Sk:** Lunds kn, Revingehed, Ekskogen SO 8.VIII. & 9.VIII. 2002 2♀+OBS freq. on *Odontites vulgaris*, 13.VIII. 2004 2♂♂1♀+OBS freq. on *O. vulgaris* leg. & det. L.A. Nilsson (coll. Nilsson); Silvåkra V 8.VIII. 2002 1♂1♀+OBS freq. on *O. vulgaris* leg. & det. L.A. Nilsson (coll. Nilsson); Tvedöra sandtag 22.VII. 1992 1♂ leg. M. Sörensson/ det. J. v.d. Smissen (coll. Sörensson); Tvedöra N 8.VIII. & 9.VIII. 2002 1♂3♀+OBS very freq. on *O. vulgaris* leg. & det. L.A. Nilsson (coll. Nilsson, coll. Norén); Sjöstorps ängar V 25.VII. 2007 1♂ leg. M. Franzén/ det. L. Norén (coll. Franzén); Lottagården 6.VIII. 2005 2♂♂2♀♀ leg. M. Franzén/ det. L. Norén (coll. Franzén); Krankesjön V 28.VII. & 1.VIII. 2002 3♂♂ on *O. vulgaris* leg. & det. M. Larsson (coll. Larsson); Krankesjön N 1.VIII. 2006 1♀ rests on *Scabiosa canescens* leg. & det. L.A. Nilsson (coll. Nilsson); Vinterbo NO 8.VIII. 2002 1♂1♀+OBS freq. on *O. vulgaris* leg. & det. L.A. Nilsson (coll. Nilsson); Svarta hål 20.VIII. 2001 2♀♀+OBS freq. on *O. vulgaris* leg. & det. M. Sörensson (coll. Sörensson); 27.VII. & 31.VII. 2002 3♂♂1♀ on *O. vulgaris*

leg. & det. M. Larsson (coll. Larsson); 7.VIII. 2002 4♂♂1♀+OBS freq. on *O. vulgaris* leg. & det. L.A. Nilsson (coll. Nilsson); Kristianstads kn, Ivö 19.VIII. 1954 1♀ leg. O. Lundblad/ det. L.A. Nilsson (NHRS). **K, Bl:** Karlskrona kn, Karlskrona 2.VIII. 1958 1♂ leg. S. Erlandsson/ det. K. Warncke (NHRS).

**H, Sm:** Kalmar kn, Kalmar stad 29–30.VII. 1930 1♂ leg. D. Gaunitz/ det. H. Wolf (ZML); Kalmar, Pilgatan 1, 29–30.VII. 1930 8♂♂1♀ leg. C.B. Gaunitz/ det. H. Wolf (ZML).

**H, ÖI:** Mörbylånga kn, Resmo fg, Resmo, landborgen 10.VIII. 1932 3♂♂ leg. D. Gaunitz/ det. L. Norén (ZML); Vickleby fg, Lilla Vickleby 5.VIII. & 9.VIII. 1945 1♀4♂♂(1♂ "Odontites") leg. S. Selander (acc. to hand)/ det. L.-Å. Janzon (NHRS); Torslunda fg, Tävelsrum 3.VIII. 1974 1♂ leg. J. Tengö/ det. L.A. Nilsson (coll. Tengö); Böda fg, Böda 7.VIII. 1976 1♂ leg. B.G. Svensson/ det. L.A. Nilsson (coll. Svensson); Öland 1971 1♂ leg. J. Tengö/ det. L.A. Nilsson (coll. Tengö).

The provinces, number of localities and year span (in parenthesis) are: Skåne 10 (1954–2007), Blekinge 1 (1958), Småland 1 (1930) and Öland 4 (1932–1976). Evidently, any record from Gotland (Erlandsson & al. 1988, Gårdenfors 2000, 2005) is erroneous and stems from the old misidentifications. In Skåne, the record in 1954 consists of a single female found at Ivö in the NE part. During the last 32 years in Sweden, the bee has only been found in a single but novel area, viz. Revingehed (Lunds kn) in Skåne. The discovery of the population dates back to a male collected in Tvedöra sand pit 1992, and more bees were recorded at Svarta hål in 2001 (M. Sörensson leg. & pers. comm.). During the period 2002–2007 another 8 localities were found at Revingehed, indicating a complex of subpopulations (LAN pers. obs.).

In our inventory in 2008, a total of 25 subpopulations were recorded at Revingehed (Table 1). These were scattered in principal over the whole of Revingehed: from Mossavägen far in the W to Turemårtensvägen in the E (viz. W–E over a distance of ca. 6 km), and from Revingehed in the N to Klingvall NE in the S (viz. N–S over a distance of ca. 7 km). The bee was found to be still present in those subpopulations that had been detected prior to our inventory (we did not visit the Tvedöra sand pit however). We estimated that the 25 observed subpopulations altogether contained some 3500 bees.

Table 1. Subpopulations of *M. tricincta* in Revingehed 2008 (arranged W to E). Columns denote their management (G=grazed, UG=ungrazed), threat (0=not obvious, 1=plant succession, 2=too little grazing, 3=too intensive grazing, 4=human activity, 5=competition from honeybees), amount of (seemingly possible) nesting sites (+=small, +=many, +++=plentiful or virtually unlimited), amount of *Odontites vulgaris* food plants ((+)=very small, +=small, +=medium, +++=large, see Material and methods) and No of bees: "Obs" is the sum of the highest number of each sex seen during a census walk, "Est" an approximate estimation of the subpopulation size.

Delpopulationer av *M. tricincta* på Revingehed 2008 ordnade från V till Ö. Kolumnerna beskriver skötselregim (G=betad, UG=ej betad), hot mot populationen (0= inget uppenbart hot, 1=igenväxning, 2=för lågintensivt bete, 3= för intensivt bete, 4=mänsklig aktivitet, 5=konkurrens från honungsbin), tillgång på boplatser (+=liten, +=god, +++=stor eller obegränsad), tillgång på värdväxten rödtoppa ((+)=mycket liten, +=liten, +=in-termediär, +++=stor, se Material and methods) och antalet bin: "Obs" =summan av det högsta antalet av varje kön som sågs under ett inventeringstillfälle, "Est" =en uppskattning av totala subpopulationens storlek.

Subpopulation (and management area No.)	Management	Threat	Nesting sites	Food plant	Number of bees	
					Obs	Est
Mossavägen (MA 5/7)	G	3	+++	++	5	50
Björkhaga (MA 2)	G	3	+	+	4	30
Tvedöra N (MA 4)	G	0	+++	++	5	100
Svarta håll 1 (MA 12)	G	0	+++	+++	35	250
Svarta håll 2 (MA 12)	G	0	+++	+	19	100
Ängstorp (MA 4)	G	0	+++	+	6	30
Fredrikslund SV (MA 5)	G	3	++	+	1	20
Svartahållsvägen (MA 12/13)	G	0	+++	+	3	20
Farm 1 (MA 4)	G	0	+++	++	19	100
Farm 2 (MA 4)	UG	1	+++	+++	20	300
Stigsåkravägen 2 (MA 30)	G	2	+++	++	9	150
Ellagård NV (MA 15)	UG	0	+++	(+)	1	5
Stigsåkravägen 1 (MA 23)	G	2	+++	++	15	150
Revingeby S (MA 15)	UG	4	+++	(+)	3	10
Kopparpsvägen (MA 28)	G	2,5	+++	+++	9	100
Vaselundsvägen (MA 29)	G	0	+++	+++	20	200
Krankesjön N 1 (MA 18)	UG	1	+++	+	15	100
Krankesjön N 2 (MA 20)	UG	4	+++	+	17	50
Stigsåkravägen 3 (MA 30)	G	2	+++	++	11	100
Silvåkra V (MA 22)	G	2,5	+++	+++	33	1000
Lottagården V (MA 19)	UG	1	+++	+	12	100
Oxavägen (MA 26)	G	0	+++	+++	32	200
Klingvalla NE (MA 26)	G	0	+++	+++	30	300
Turemårtensvägen 1 (MA 21)	UG	1	+++	+	5	20
Turemårtensvägen 2 (MA 21)	UG	1	+++	+	7	30
Total					336	3515

### Phenology

The flight period in Sweden according to the 1930 – 2007 data was 22 July – 20 August, with median date 7 August (N= 26 occasions of records). This reflects, in terms of basic life cycle, that the bee hibernates as larva and is univoltine. In 2008, we saw the first individuals on 22 July at the most exposed site Silvåkra V, which is mainly a large S-facing slope. Since one of them was

a pollen-collecting female, the flight period had probably started a few days earlier. The flight period was observed to coincide with flowering of the exclusive food plant *O. vulgaris*. On 16 August, when we stopped the inventory, bees were still flying and flowering food plants were abundant. From the phenological stages of bees and plants we expected the flight period to last for another 2 – 4 weeks, thus until September.



Figure 2. The habitat of *M. tricincta* at – a) Svarta håll 1 and – b) Kopparpsvägen with tank tracks and open grassland (purple patches= *Odontites vulgaris*), respectively. Photo: I. Alves-dos-Santos 1.VIII. and 9.VIII.

Rödtoppebiets habitat vid – a) Svarta håll 1 och – b) Kopparpsvägen, med körspår efter tanks på sandmark invid videhåll respektive öppen gräsmark (purpurfärgade bestånd= rödtoppa).

### Habitat

The museum specimen from Blekinge 1958 indicated “Karlskrona”, the name of a town, and specimens from the mainland of Småland 1930 “Kalmar stad” (= Kalmar town) and “Kalmar, Pilgatan 1” (a street name and even address). This suggests that habitats were urban ruderal

places. The habitats of specimens from Öland 1932–1976 probably consisted of open dry pasture (Resmo, Böda), a fallow field (Lilla Vickleby) and a ruderal place (Tävelsrum), at least judging from the conditions at the respective villages in later decades (LAN pers. obs.). The specimen from Ivö in NE Skåne 1954 probably

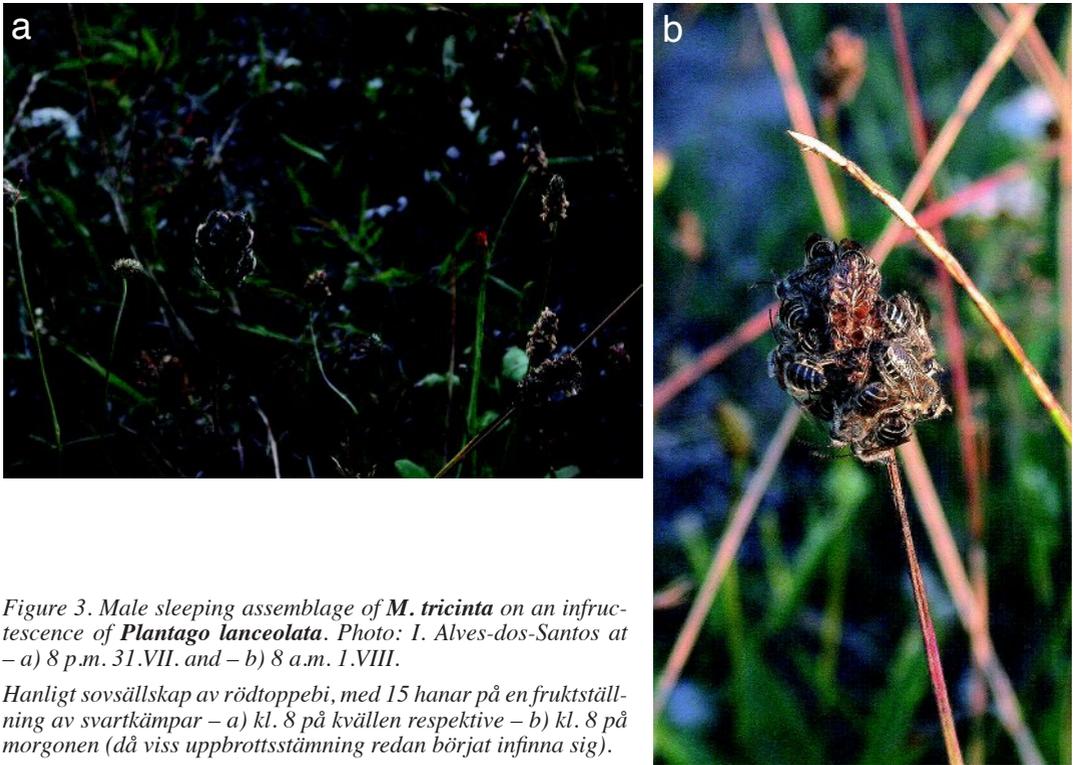


Figure 3. Male sleeping assemblage of *M. tricincta* on an infructescence of *Plantago lanceolata*. Photo: I. Alves-dos-Santos at – a) 8 p.m. 31.VII. and – b) 8 a.m. 1.VIII.

Hanligt sovsällskap av rödtoppebi, med 15 hanar på en fruktställning av svartkämpar – a) kl. 8 på kvällen respektive – b) kl. 8 på morgonen (då viss uppbrottsstämning redan börjat infinna sig).

originated from pasture. Ivö is a village on an island in a lake.

On Revingehed, the species was found to mainly occur on unfertilized open pasture with often slightly moist depressions or gentle slopes but also in ungrazed areas along ditches, small gravel roads and ground tracks, and in old sand pits (Fig. 2). We found the bee in 17 management areas, most of which were grazed. Based on the total maximum number of bees recorded on census walks (Table 1), 76% of the bees occurred in grazed habitats. Based on the approximately estimated total numbers in subpopulations, the proportion was 82%. Eight of the 25 recorded subpopulations had ungrazed habitats with intensive encroachment of grasses and rank herbs. In these cases there was always a distinct component of ruderal condition due to disturbance either from military vehicles, mammals (esp. moles) or trampling by humans. In one case (Revingeby S), the habitat consisted of a motocross training area in an old sand pit.

#### Mating system

In all subpopulations observed in Revingehed, sexual activity of the bee was exclusively associated with the flowering food plant *O. vulgaris*. With a fast, erratic undulating flight the males were patrolling flowering patches, and most intensively so the largest such patches. No active male perfuming behaviour on the plants or elsewhere was seen. At 15.00h on 23 July 2008 in subpopulation Svarta håll 1 we saw a fresh female on an inflorescence when two males approached. Copulation immediately took place with one of them, the pair sitting on flowers and bracts. That we only witnessed this once while many foraging young and old females were seen to be unattractive to males indicated that the females are monogamous. Clearly, the mating system relies on the fact that the virgin females with a high probability are immediately attracted to the food plant.

In 2008, we observed at least a total of 230 males and 106 females, thus a sex ratio of 2.1.

However, the sex ratio was strongly male-biased early and female-biased late, indicating a strong protandry (i.e. males peak before females). For example, the sex ratio on 25 July was 47.7 (N=146) but on 15 August 0.5 (N=63). Evidently, the system utilizes male reconnaissance of the foraging environment as well as competition for females. Considering the observed sex ratios and also that males can be readily observed when active (patrolling or foraging) but females only so during foraging suggest that the species at least has no overall markedly skewed sex ratio.

#### Male sleeping

In the middle of a grazed meadow in the subpopulation Farm 1 at 7 p.m. on 31 July we discovered a male sleeping assemblage (Fig. 3). Fifteen males were sitting more-or-less head-down tightly together on an infructescence of *Plantago lanceolata*. Some movement with inter-positioning among them occurred now and then until 8 p.m. In the next day at 7 a.m. they were still motionless but covered by dew. By 8 a.m. they had all started grooming and warming up. They then left one by one. For the next evening between 6 and 7 p.m. males appeared on the same infructescence to sleep but were fewer in number. On 2 August the weather changed to rain and windy conditions, and the males did not show up in the evening. On 5 August the weather improved a little, but still we found no males sleeping on any of the many infructescences at the site.

#### Nesting

On Revingshed, nesting must occur in sandy or at least markedly minerogenous soil. From the coming and going of pollen-collecting females in relation to the food plant patches we had the impression that nesting usually occurred within 100 m. There was seemingly no real shortage of nesting sites for any subpopulation (Table 1). Rather, such sites were plentiful or virtually unlimited as the largely sandy soils were much disturbed by military vehicles, cattle and wild mammals (esp. moles). In the subpopulation Farm 1 we saw females of the assumed nest parasite *Nomada flavopicta* (Kirby) seeking over strongly grazed, somewhat sparsely vegetated spots that probably contained *M. tricincta* nests.

#### Foraging

Museum specimens yielded but a single hint on floral food: the label of a male specimen (NHRS) collected in Vickleby on Öland 1945 includes “*Odontites*”. Nevertheless, in all subpopulations and years in Revingshed the species was by us and others observed to forage only on *Odontites vulgaris*: both sexes feed on the nectar and the females collect the pollen. Thus, the bee in Sweden is oligolectic on Scrophulariaceae, in practice extremely so, viz. monolectic, on *O. vulgaris*. In the subpopulation Krankesjön N 2 under somewhat cool weather in 2006, an inactive fresh female was observed to sit on an inflorescence of *Scabiosa canescens* (Dipsacaceae). The amount of *O. vulgaris* for the subpopulation in question was small and consisted of just a few aggregated patches ca. 40 m away. That the young female had no nest and a low site affiliation may explain why she visited another nectar plant. During dispersal or food shortage individuals may thus explore other plants.

In Revingshed, wherever the food plant *Odontites vulgaris* occurred in an appreciable amount the bee was present. In many subpopulations we saw many bees and this almost always coincided with a large or rather large local amount of food plant (Table 1). In a number of places during August, *O. vulgaris* formed a considerable, more-or-less dominating, part of the vegetation (Fig. 2). Still, in the bee subpopulations at Ellagård NV and Revingsby S there were only a few plants available as a resource. Both habitats were ruderal places.

Our experiments with virgin flowers showed that foraging *M. tricincta* bees acted as good pollinators of their food plant *O. vulgaris*, viz. on average 16 seeds were produced from a single visit (N=23) compared to 2.7 seeds in isolated (N=78) and 18.1 seeds in open-visited control flowers (N=135). In the beginning of the flowering period *M. tricincta* was virtually the only visitor and pollinator but later both bumblebees and on two sites honeybees were seen to largely shift to *O. vulgaris*. Therefore, *M. tricincta* and the other bees were competitors as well as pollinators and these interactions varied greatly in time and space. Elsewhere in Sweden, in the absence of *M. tricincta* bumblebees have readily been seen as the regular pollinators over the

main distribution area of *O. vulgaris* (LAN pers. obs.).

#### Parasites

On many occasions in Revingehed, we saw the cuckoo bee *Nomada flavopicta* flying on the same localities as *M. tricincta* which constituted the most-likely host. Both *Melitta leporina* and *M. haemorrhoidalis*, known hosts of *N. flavopicta*, occurred as well however. The cuckoo bee did not visit *Odontites* but other nectar plants, mainly *Knautia arvensis* and *Senecio jacobaea*.

#### Threats

For 9 of the 25 subpopulations observed in Revingehed we found no obvious threat in relation to current management. Threats from too intensive grazing were recorded in 3, too low grazing in 5, plant succession in 5, honeybee competition in 2 and direct (non military) human impact in 2. Intensive grazing causes damage from trampling or removal of parts of the flowering food plant. For subpopulations under conditions of low or no grazing there was a potent threat from plant succession with the encroachment of grasses and rank herbs. In such cases there were obvious risks for the loss of both food plant and nesting sites. In the subpopulation Krankesjön N 1, which habitat was in fast succession, we also saw that the bees were facing considerable difficulties in their patrolling and foraging: they had to fly slowly "far down" amongst dense stems of grasses and herbs. Such vegetation strongly intervened with flight and may have caused frequent wing damage. Habitats containing more-or-less fast succession were seemingly maintained largely due to the disturbance from heavy military vehicles.

#### Discussion

Our results show that the species *M. tricincta* Kirby for long was misinterpreted in Sweden. Although mentioned for the fauna already in 1852, the first valid record is from 1930 and report from 1988. The lack of earlier museum records despite the fact that especially Skåne and in particular the Lund area were explored by eminent entomologists already since the beginning of the nineteenth century points to a fairly late colonization, most likely during the

early twentieth century. The species has never been documented from Gotland. Valid records exist from 4 provinces but from the last 30 year period only from Skåne. Our inventory in Revingehed 2008 detected a total of 25 subpopulations and these were scattered over ca. 6x7 km, in principal over the whole area. The bee was found to be still present in 9 subpopulations detected before the inventory. These results indicate that, in Revingehed, the species *M. tricincta* is widely spread, well established, persistent and largely favoured by the present conditions. Furthermore, during the handling of our submitted manuscript, a ♀ specimen was confirmed to have been found at Falsterbo (in Vellinge kn) on 30 July 2008 (leg. M. Franzén, det. L. Norén/LAN). Falsterbo is situated on a small peninsula in Öresund ca. 50 km SW of Revingehed (and 20 km S of the island of Saltholm in Denmark), thus a new tract of known occurrence.

The Swedish phenological data conform to what is known from other parts of Europe: the species has a relatively late flight period (Westrich 1990, Falk 1991). The most obvious explanation is that the bee possesses strict adaptation to, and is under strong selection from, the unusually late-flowering food plant. The habitat data indicate that *M. tricincta*, unlike most other red listed bee species in Revingehed (Nilsson 2008), is favoured by extensive grazing but also occurs on ungrazed ground as long as there are sufficient other activities that hold back plant succession at least here and there. The records largely conform to those from other parts of Europe. In Germany, the species has been reported to occur in a variety of situations, viz. pits for the exploitation of sand, gravel and clay, but also on high water dams, inland dunes, dune sand fields, sheep grazed meadows, fallow fields and urban ruderal places (Westrich 1990). In England, the bee has been recorded from a variety of habitats, including dry chalk and limestone grassland, coastal landslips and soft rock cliffs and, occasionally, heathland, ruderal ground and woodland rides (Falk 1991). It seems to have a preference for pasture on chalk but sometimes occurs in open deciduous forest (Else 1998). In Poland, habitats have been characterized as mainly dry meadows and swards (Celary 2005). Thus, the habitat specialization of *M. tricincta*

fits well landscapes that have been modified by human activity for agriculture, settlement and exploitation.

The mating system is insufficiently known. Also in Germany and Holland males have been observed to patrol flowering *Odontites* plants (Westrich 1990, Peeters & al. 1999). In England, Falk (1991) mentioned that “the males fly fast, and erratically low, over the main forage plant, only briefly pausing”. He apparently described patrolling. Our observations showed that mate seeking, sexual encounters and copulation occur strictly in association with the flowering food plant and not at any other habitat component, e.g. nesting sites. Similar systems are present in the other Swedish *Melitta* species (LAN pers. obs.). Moreover, we found a strong protandry. This suggests the presence of strong sexual selection. Probably this process is driven by the late flight period (and thus initially by the late flowering time of the food plant) that confers stress for a fast reproductive period before fall. Falk (1991) mentioned that “females are usually less plentiful than males”. We found, however, no evidence for an overall male skewed sex ratio.

That the males form sleeping assemblages may have benefits for them individually: heat gain, less night dew, a strong emission of alarm pheromone, etc. On the other hand it may be risky for a subpopulation that occurs on pasture – many males at a time may simply get engulfed or trampled by cattle. The phenomenon of sleeping assemblages is fairly widespread among Swedish bees. It occurs at least in *Chelostoma* spp., *Lasioglossum* spp. (e.g. *L. albipes*) and other *Melitta* spp. such as *M. melanura*; in the latter species usually 2-3 males spend the night together in a flower of *Campanula* (LAN pers. obs.).

We were not able to locate nesting in the species. In Central Europe, nesting has been mentioned to take place in own dug cavities and that any preference for a particular ground is not obvious (Westrich 1990, Schmid-Egger & al. 1995). In Dorset, England, the bee has been observed to nest widely scattered in exposed, hard, compacted soil overlying chalk (Else 1998). The architecture and construction of the nest of the species seem, however, never to have been de-

scribed. Still, due to the frequent spots with exposed soil from military and other disturbance, we conclude that nest site availability is not a limiting factor in Revingehed.

Our Swedish records of flower visits conform well to the specialization reported elsewhere. In Denmark, a recent (2006) record from the island of Saltholm in Öresund was made on *Odontites vernus* (H.B. Madsen pers. comm. 2008). Also *Cirsium arvense* and *Lythrum salicaria* have been mentioned as visited (Jörgensen 1921), but this probably reflects some confusion with *Melitta nigricans*. In Holland, the bee has been characterized as specialized on *O. vernus* (Peeters & al. 1999). In Germany, the species has been observed to almost exclusively visit *Odontites* and *Ortantha* (formerly *Odontites*) species, including yellow-flowered ones such as *Ortantha lutea*, but sometimes also *Cichorium*, *Euphrasia officinalis*, *Galeopsis ladanum*, *Lythrum salicaria* (Friese 1901, Alfken 1912 as *melanura*, Blüthgen 1930, Stoeckhert 1933, Warncke 1981). In England, the species has been mentioned to collect pollen exclusively from *O. vernus*; rarely the bee has been seen on *Mentha aquatica* and *Ononis* species for nectar (Else 1998). In Poland and Hungary, most of the visits have been seen on *Odontites serotina* but occasionally (for nectar) on *Centaurea*, *Cirsium acanthoides*, *Daucus carota*, *Hyssopus officinalis*, *Inula britannica*, *Lotus corniculatus*, *Medicago media*, *M. sativa*, *Mentha aquatica*, *Stachys palustris*, *Succisa pratensis*, *Trifolium pratense* (Blüthgen 1919 as *melanura*, Ruszkowski & al. 1988, Celary 2005). In Lithuania, the bee has been mentioned to visit *Galeopsis tetrahit*, *Scabiosa ochroleuca* and *Trifolium repens* (Monsevičius 1995). Like in *Melitta* species in general (Westrich 1990), the female moistens the pollen with some nectar during the transfer of it to the scopa; the transported pollen therefore appears slightly solid and remarkably resistant to falling off.

The bee *M. tricincta* has been mentioned as narrowly (“strictly”) oligolectic on *Odontites* species (Westrich 1990, Schmid-Egger & al. 1995, Scheuchl 1996, 2006, Celary 2005) or even monolectic on *O. vernus* (Else 1998). Miché & al. (2008) used field records including information on specimen labels to calculate the

proportions of the main host plant family for females and obtained the value 97%. Michez & Eardley (2007) also presented the flower visitation data of 187 female specimens: 78% indicated *Odontites* and 19% *Euphrasia*. This suggests that *Euphrasia* may play a buffering role for survival of *M. tricincta* when late-flowering plants of the genus co-occur with *Odontites*.

That *N. flavopicta* is a parasite on *M. tricincta* has been reported from Germany and Holland (Westrich 1990, Peeters & al. 1999). In England, *M. tricincta* has been mentioned as its subsidiary host (Falk 1991). Else (1998) reported *M. tricincta* as probable host and our Swedish circumstantial evidence supports that suggestion.

### Conclusion: Conservation status

In the Swedish red list, the species *M. tricincta* has been classified as EN, endangered, with reference to the categories B2ab (i, ii, iii, iv), i.e. decline in "Geographic range in the form of area of occupancy and fulfilling the two subcriteria a/ severely fragmented or exists at <5 locations and b/ continuing decline in (i) extent of occurrence, (ii) area of occupancy, (iii) area, extent and/or quality of habitat, and (iv) number of locations or subpopulations" (Gärdenfors 2005). At the classification, no estimation of the total number of individuals was made (B. Cederberg pers. comm. 2009). Our 2008 inventory increased the number of known subpopulations of *M. tricincta* by a factor 2.5 in Revingehed. No doubt there are also a hidden number of subpopulations in the area. The level of the hidden number is difficult to ascertain but perhaps a reasonable, or at least not an overestimation, would be a factor 2. With this assumption there would be (cf. Table 1) a total of ca. 50 subpopulations and 7000 individuals making up the current population in Revingehed. Our results indicate that with a management of Revingehed like at present there is no substantial threat to the survival of the bee in the area. Although the pattern of records in time and space suggests that *M. tricincta* has disappeared from Småland and Blekinge decades ago and perhaps from Öland more recently, there is no documented decline of the species in Skåne. Accordingly, there seem to be regionally negative and locally positive factors. Even an increase in the number of individuals in Skåne

cannot be excluded since the military training field of Revingehed, where *M. tricincta* was first sighted as late as in 1992, after 1963 was enlarged from 1123 ha to ca. 4500 ha, i.e. 400% (ÖMAS 2003). Moreover, the basic features and status of the discovered population at Falsterbo in 2008 remain to be studied.

The status of the species elsewhere in Europe is apparently one of decline. In Denmark, there are only ca. 5 localities known of which only one is recent (H.B. Madsen pers. comm. 2008). In Germany, the bee has been nationally classified as "Gefährdet" (Binot & al. 1998). The bee is historically known from 12 nature conservancy regions but since 1980 only from 9 (Dathe & al. 2001). In Thüringen, it has been stated to be "vom Aussterben bedroht" (= ca. critically endangered) (Burger & Winter 2001). In Baden-Württemberg and Rheinland-Pfalz, the species has been classified as "stark Gefährdet" (Westrich 1990, Schmid-Egger & al. 1995). In Sachsen, it has not been seen in the last ca. 100 years (Burger 2005). In Holland, early records were widely spread over the eastern part but records after 1980 are only confined to the southeastern enclave (Peeters & al. 1999). In England, *M. tricincta* has been declining and classified as a Nationally Notable (Nb) species, i.e. estimated to occur within the range of 31–100 modern 10 km squares (Falk 1991, Else 1998). In Poland, some 20 localities have been reported (Celary 2005). In Lithuania, the species is only known from 4 places (Monsevičius 1995). To conclude, the decline has a large-scale dimension.

The overall Achilles' heel of the bee in Sweden may be the availability of the special pollen plant, i.e. a draw-back caused by the specialization. The fact that the bee is a good pollinator of its food plant is of principal interest here, because it supports mutual survival. Even in small and declining food plant populations seed output will be high as soon as the bee is present. The plant *O. vulgaris* has generally from a botanical (not bee!) point of view been classified as "rather common" (Mossberg & Stenberg 2003) or "rather common to less common" (Jonsell & Jonsell 2003). An exclusive pollen plant fulfilling such a category is unique among Swedish oligolectic bee species – host plants of oligolectic species are normally of the cat-

egory “common” (LAN pers. obs.). Moreover, botanically “rather common or less common” and bearing capacity (i.e. sufficiently large and dense floral resource for bee populations) that is predictable in time and space are two separate things that may seldom coincide. No doubt *O. vulgaris* has declined as weed in pace with the intensification in agriculture (herbicides, fertilizers etc.), overgrazing and urbanization, as well as on the other hand with the pollution-driven faster plant succession in general. Large or even small stands of the plant are now sporadic and mostly rare (LAN pers. obs.). Clearly, the decline in *O. vulgaris* seems to be the factor explaining the regional decline in *M. tricincta* since ca. 1960. In Revingehed, fortunately, any situation of decline is not present and the food plant still occurs in sufficient quantity in many places. Also the new area Falsterbo with adjacent rather extensive coastal grazed meadows may provide potentially favourable conditions (M. Franzén pers. comm.).

Evidently, this narrowly specialized bee species can be protected by means of setting aside and managing, e.g. by moderate grazing, sufficient areas that contain established, predictable fertile stands of *O. vulgaris*. Our observations indicated that the bee has a considerable capacity to disperse to, locate and occupy even small amounts of food plant. Even if food plant occurrence may vary considerably in time and space, the bee seems well suited for handling a food plant metapopulation situation as, e.g., the present one within Revingehed. We conclude that food plant availability is an overall decisive factor for the survival and conservation of *M. tricincta* in Sweden.

### Acknowledgement

This work was made possible partly due to a grant from the Swedish Institute to IAS. Jon Ågren (Dept. of Plant Ecology, Uppsala) helped in interacting with SI. ArtDatabanken, SLU, Uppsala (Björn Cederberg & Hjalmar Croneborg) provided financial support to IAS for transportation. Stenoffa Ecological Research Station (Henrik Smith, Dept. of Ecology, Lund) provided laboratory and lodging facilities. Lars Norén identified bees in coll. Nylander (ZMH). Markus Franzén, Magnus Larsson, Bo G. Svensson, Mikael Sörensson and Jan Tengö put specimens or data from their collections at our disposal. The County Author-

ity in Skåne (Gabrielle Rosquist) and Southern Region office at Revingehed provided authorization for using the non-public roads of the training field. Erik Öckinger and Mats Jonsell gave comments on the manuscript.

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### Sammanfattning

Vi undersökte förekomsthistoria, gjorde biologiska observationer och utvärderade bevarandestatus hos rödtoppebi *Melitta tricinta* i Sverige. Arten, som är euro-sibirisk, når de sydöstra landskapen i landet och samlar här pollen uteslutande från ängsörten rödtoppa *Odontites vulgaris*. Rödtoppebiet är i rödlistan 2005 klassat som starkt hotat (EN). En granskning av museimaterial och litteraturuppgifter visade att *M. tricinta* dokumenterats och rapporterats först så sent som 1930 respektive 1988. Detta tyder främst på att arten har invandrat till Sverige i ganska sen tid, troligen i början av 1900-talet. Uppgifter om förekomst på Gotland visade sig felaktiga, varför den kända historiska utbredningen är Öland, Småland (H län enbart), Blekinge och Skåne. Mönstret av insamlingsdata i tid och rum tycks indikera en regional nedgång i förekomst under senaste halvsekleket men inga bevis finns för att nedgången inkluderar Skåne. Under de senaste drygt 30 åren har förekomst endast påvisats från Skåne och där endast från det militära övningsområdet, numera tillika Natura 2000-området, Revingehed i Lunds kn. År 2008 dokumenterades emellertid förekomst även i Falsterbo, Vellinge kn.

Våra observationer av förekomsten på Revingehed under senare år visade att rödtoppebiets flygtid, habitat, parningsflygning och blombesök är finstämt och hårt knutna till blomningen av den exklusiva pollenväxten rödtoppa. Växten blommar relativt sent, slutet av juli – augusti, vilket förklarar biets motsvarande ovanligt sena flygtid. Habitat utgörs främst av ogödslad småfuktig betesmark men också av obetad, ställvis störd mark av ruderatängskaraktär. Vid flygväder patrullerar hanarna, som i princip är polygama och sinsemellan konkurrerande om parningar, blommande rödtoppebestånd hek-

tiskt för att träffa på nyframkomna, i princip monogama honor. Parningen sker på näringsväxten. Hanarna spenderar natten i sovsällskap i toppen av någon uppstickande stängel på ängsmark (Fig. 3). Boet anläggs sannolikt på varma, glesbevuxna och oftast mineraljordiga ställen.

En inventering som vi gjorde på Revingehed 2008 visade att arten fanns kvar på alla lokaler som upptäckts tidigare under 2000-talet och att den dessutom förekom på ett större antal tidigare okända lokaler. Biet konstaterades på samtliga lokaler som hade en påtaglig förekomst av näringsväxten. Totalt fann vi 25 subpopulationer och uppskattade antalet individer i Revingehed-området till ca. 7000. Inget påtagligt hot noterades för närmare 40% av subpopulationerna medan hot för övriga utgjordes främst av för svagt eller för hårt bete och/eller igenväxning. Arten måste dock generellt ses som starkt betesgynnad: ca. 80% av bina/populationen förekom på betad mark. Revingehed har miljöanpassad varierad skötselplan som omfattar vidsträckt, delvis mosaikartade, både betade och obetade arealer och biarten tycks förekomma i en metapopulationsliknande situation med välfungerande spridning och dynamik i relation till näringsväxten rödtoppa som är vanligt förekommande och ställvis vegetationsbildande. Enligt våra experiment är rödtoppebiet också en god pollinatör av sin näringsväxt. Vi bedömer sammantaget att arten *M. tricinta* (utifrån idag kända faktorer) inte är hotad i Revingehed-området. Detta eftersom en ständig tillgång på näringsväxten rödtoppa inom flyghåll – vilket skötseln ger idag – är den genomgående bestämmande faktorn för överlevnad och bevarande. Vi drar slutsatsen att både negativa och positiva faktorer har påverkat biarten *M. tricinta* i Sverige och att nuvarande bevarandestatus är lovande trots förekomsten av endast en enda känd stor population.