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Gabriela Cilla [a b], Marta Caccavari [a], Norberto J. Bartoloni [b] & Arturo Roig-Alsina [a]
[a] Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina
[b] Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, Argentina

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# The foraging preferences of two species of *Melissodes* Latreille (Hymenoptera, Apidae, Eucerini) in farmed sunflower in Argentina

GABRIELA CILLA[1,2], MARTA CACCAVARI[1], NORBERTO J. BARTOLONI[2] & ARTURO ROIG-ALSINA[1]

[1]*Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina,* [2]*Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, Argentina*



**Abstract**

The present study addresses the pollen preferences of two species of wild bees of the genus *Melissodes* in the intensively farmed temperate Pampean region of Argentina. The resources used by *M.* (*Ecplectica*) *tintinnans* and *M.* (*Ecplectica*) *rufithorax* were studied in a commercial plot of sunflower and its field margins in the locality of Carlos Casares, province of Buenos Aires. Surveys before, during and after the bloom of sunflower were carried out. The bees emerged synchronously with the beginning of the bloom, but continued foraging for over a month after maturation of the crop. Pollen analyses of scopal loads indicated that sunflower was a major component of the diet. Bees also collected pollen from other Asteraceae during and after the blooming of the sunflowers. Pollen from *Ligustrum* sp. and *Eucalyptus* sp., two trees common in the hedgerows, was also collected in significant amounts. The vegetation on the field margins facilitated maintenance of the populations after the blooming of the sunflower. The two species of native *Melissodes* used pollen of plant taxa that are frequent and widespread in the Pampean agricultural ecosystems. This fact, together with their habit of nesting in aggregations, indicates that these bees represent a valuable resource as crop pollinators.

**Keywords:** Melissodes tintinnans*,* Melissodes rufithorax*, pollen resources, oligolectyc, field margins*

Sexual wild bees provide important pollination services to various crops (Buchmann & Nabhan, 1996; DeGrandi-Hoffman & Watkins, 2000; Delaplane & Mayer, 2000; Kremen et al., 2004; Herrmann et al., 2007). Knowledge of their foraging preferences helps to understand their bearing on the preservation of the local flora in agricultural environments and, together with knowledge on their biology, helps develop strategies for their conservation and use as pollinators (O'Toole, 1993; Stedman, 1994; Corbet, 1996; Kim et al., 2006, Klein et al., 2007). The present study addresses the pollen preferences of two species of wild bees of the genus *Melissodes* in the intensively farmed temperate Pampean region of Argentina.

*Melissodes* is by far the species-richest genus among the New World bees of the tribe Eucerini (Michener, 2007). It is the most diverse in North and Central America, where more than 120 species occur. In South America, *Melissodes* is represented by seven species, most of which belong to the subgenus *Ecplectica* (Urban, 1973). Although few species are present, they form locally abundant populations. These bees are typical solitary soil burrowers that nest in aggregations (Cameron et al., 1996). They are medium-sized bees, 10–12 mm long, that carry their pollen loads on the scopa of the hind tibia and basitarsus. *Melissodes* bees are important sunflower pollinators in the United States (Parker, 1981*a*, 1981*b*; Greenleaf & Kremen, 2006; Ricketts et al., 2008). Due to the large number of species and the abundance of individuals, several authors have stressed the role of many of its species as pollinators of crops (Linsley, 1946; LaBerge, 1956*b*; Hurd et al., 1980; Parker, 1981*a*, 1981*b*). The pollination

Correspondence: Gabriela Cilla, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Ángel Gallardo 470, (C1405DJR) Buenos Aires, Argentina. E-mail: *gcilla@agro.uba.ar*

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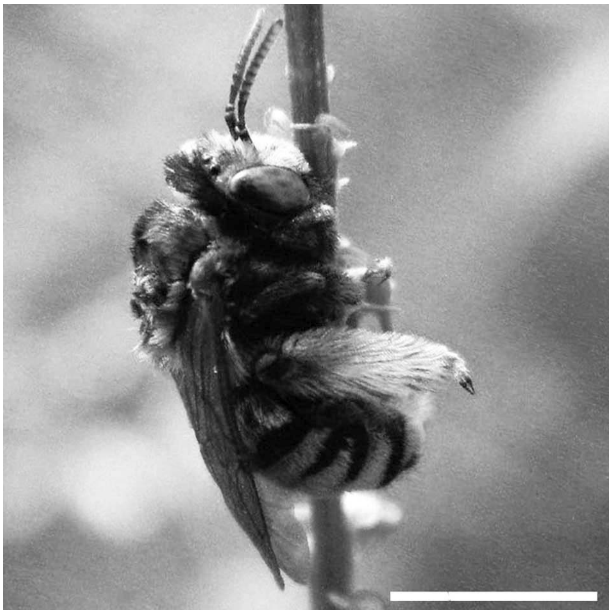


Figure 1. General aspect of *Melissodes rufithorax*. Scale bar – 5 mm.

services of these bees were significantly and positively related to the increase of patches available for nesting (Kremen et al., 2004; Kim et al., 2006).

The flower preferences of many species of *Melissodes* were reported by LaBerge (1956*a*, 1956*b*, 1957, 1961). Some species, such as most members of the subgenus *Melissodes*, are highly polylectic. Other species specialise on Onagraceae, Pontederiaceae, Malvaceae and Asteraceae. Oligolecty of Asteraceae is widespread, particularly in the subgenera *Heliomelissodes*, *Eumelissodes* and *Callimelissodes*. Several detailed studies have confirmed this oligolecty on Asteraceae for *M.* (*Eumelissodes*) *pallidisignata* Cockerell (Thorp & Chemsak, 1964), *M. rustica* (Say) (Clement, 1973; Cameron et al., 1996), *M.* (*Eumelissodes*) *microsticta* Cockerell (Miliczky, 2000) and *M.* (*Eumelissodes*) *agilis* Cresson, which has been indicated as an oligolege of *Helianthus* species (Parker et al., 1981).

However, the flower preferences of the species of the subgenus *Ecplectica* are little known. Flower visitation is mentioned for some species, but without indication of whether pollen or nectar was collected (Holmberg, 1884; LaBerge, 1956*b*). Silveira et al. (1993) suggest that *Melissodes* (*Ecplectica*) *sexcincta* Lepeletier depends upon species of *Triumfetta* (Tiliaceae) in Minas Geraies, Brazil. Cilla et al. (2007) indicate that *M.* (*Ecplectica*) *tintinnans* Holmberg and M. (*Ecplectica*) *rufithorax* Brèthes could be considered potential sunflower pollinators. In this contribution we study pollen resources used by the latter two species in a commercial plot of sunflower and its field margins.

## Material and methods

### *Study site*

The field surveys were carried out in the province of Buenos Aires, Argentina, near the locality of Carlos Casares (Estancia San Claudio, 35° 56′ S and 61° 11′ W). The commercial field of sunflower studied measured 54.2 ha. On one side, a dirt road separated it from a pasture. The other three sides had herbaceous field margins, mostly 4 m wide, but at some points as narrow as 0.5 m up to as wide as 8 m. These three sides were bordered by hedgerows composed of *Eucalyptus* sp. (Myrtaceae), *Ligustrum lucidum* W.T. Aiton (Oleaceae) and *Gleditsia triacanthos* L. (Fabaceae). There was no wild sunflowers in the sampling area or in nearby lots.

### *Field sampling*

Sampling was performed monthly between November 2006 and March 2007. Bees (Figure 1) were collected on flowers of sunflower, on weeds within the field and on the herbaceous vegetation of the field margins with the aid of an insect net. Each specimen was placed in an individual vial. A survey of the flowering plants that could serve as pollen hosts was performed, both within the crop and the field margins. Plant specimens were collected at the site to prepare reference pollen slides.

The sampling in the field margins consisted of a comprehensive census of the weeds in flower and the capture of visiting bees along the four edges. The sampling effort was 90 minutes on average per edge. The censuses were performed before the flowering of sunflower (14 and 16 November 2006; 4 and 6 December 2006), during flowering (3, 6, 9 and 13 January 2007), and after flowering (20 and 22 February 2007; 6 and 8 March 2007). The total sampling effort in the field margins was 72 hours. The area of cultivation was also sampled during the flowering period. Transects four rows wide were randomly chosen parallel to each surveyed field margin.

### *Pollen analyses*

Pollen counts of scopal loads were made to identify the importance of each plant host in the diet. One hind leg from each female was removed, avoiding contamination from pollen deposited on other parts of the body. The scopa was treated with a 10% potassium hydroxide (KOH) solution in a double boiler (water bath) for 10 minutes. This treatment, applied for pollen by von Post (1933), removes the intine and cell content without damaging the exine. The deflocculant properties of KOH (Fægri & Iversen, 1975) allow the successful separation of the pollen attached to the scopae. Since pollen grains treated in this way decolourise, staining with Fuchsin was used (Reitsma, 1969). The treated pollen was mounted in 80% glycerine on a slide. The slide was first scanned under low magnification to verify that pollen was well mixed and that a sufficient number of grains were present. For taxonomic recognition, the pollen reference collection of the Museo Argentino de Ciencias Naturales, Buenos Aires (BAPa) and pollen from specimens collected around the study area were used. To determine the relative frequency of taxa in pollen loads, five parallel and equidistant transects across the slide were counted, with at least 500 pollen grains counted (von der Ohe, 2004). When the relative frequencies did not stabilise, counts were continued for another five parallel lines situated between the first five. In some specimens that had partially loaded scopae, the number of pollen grains considered for the assessment of the frequency was 200 grains (Sipes & Tepedino, 2005). When the number of grains was less than 200, the total pollen grains were counted.

Pollen passively deposited on the body of the bees was studied to detect plants that may have been visited as nectar sources. Previous to body treatment, the remaining hind leg was removed and then the body was treated as mentioned earlier for scopal pollen loads.

### *Statistical analyses*

In order to look for possible interactions between the visited plant taxa and the two species of *Melissodes*, a log-linear analysis (Agresti, 1996) was performed on the matrix of plant/insect interactions (Table I). A log-linear analysis allows the testing of the null hypothesis of no interaction among main effects (plant species and insect species), which means in our case that we may find no special amount of pollen apart from what is expected from the marginal frequencies corresponding to each cell of Table I. This implies that if the rows and columns in a table are completely independent of each other, the entries in the table (distribution of mass) can be reproduced from the row and column totals alone. Any deviations from the expected values (expected under the hypothesis of complete independence of the row and column variables) will contribute to the overall Chi-square statistic. Maximum likelihood Chi-square tests of marginal association were computed. In order to assess whether the visited taxa in search of pollen were represented among those visited in search of nectar, a non-parametric correlation test (Spearman $R$ test) was also performed. Proportions of the same pollen type in the scopal loads and in the loads resulting from the survey of the retained pollen in the hairs of other body parts for each specimen from both species of *Melissodes* were compared. Analyses were run with the STATISTICA software (StatSoft Inc., 1999).

## Results

### *Bee activities*

No specimens of the studied *Melissodes* were detected during November and December, neither in the sunflower field nor in the field margins. Bees were first sighted at the beginning of the flowering of sunflower in January; they were present during all of the flowering period (first to third week of January). After the cultivated sunflowers wilted, the bees continued to forage on herbaceous plants within the field and in the field margins until March.

The highest abundance of individuals was coincident with the flowering of sunflower. During this period, 77% of the specimens caught were *Melissodes tintinnans*. After the flowering of cultivated sunflower was over, the abundance of individuals observed on flowering herbaceous plants was low ($n$ = 10) and *M. rufithorax* made up 70% of the specimens caught.

### *Available flora*

A survey of the flowering plants that could serve as pollen sources was made, both within the crop and in the field margins. We recorded a total of 36 herbaceous plants and two trees in bloom (Table II). Only a fraction of these plants was visited for pollen by the two studied species (indicated by an asterisk in Table II).

### *Pollen analyses*

*Scopal loads.* — A total of 58 female specimens were collected for pollen analysis, 40 of *Melissodes tintinnans* and 18 of *M. rufithorax* (Tables III, IV, see Appendix, Tables AI, AII). All pollen loads analysed of specimens of *M. tintinnans* collected during

Table I. Matrix of plant/insect interactions.

| | Number of pollen grains | | |
|---|---|---|---|
| Plant taxa | *Melissodes tintinnans* | *Melissodes rufithorax* | Total |
| *Helianthus annuus* | 26 137 | 9102 | 35 239 |
| *Ligustrum* sp. | 7292 | 346 | 7638 |
| *Carduus* sp. | 318 | 20 | 338 |
| *Polygonum* sp. | 134 | 11 | 145 |
| *Crepis* sp. | 67 | 0 | 67 |
| *Eucalyptus* sp. | 1321 | 0 | 1321 |
| *Bidens* sp. | 1935 | 3157 | 5092 |
| *Baccharis* sp. | 0 | 549 | 549 |
| Total | 37 204 | 13 183 | 50 389 |

Table II. Plant taxa in bloom in the field margins, hedgerows and within the crop during November–March.

| Family | Species | Nov | Dec | Jan | Feb | Mar |
|---|---|---|---|---|---|---|
| Amaranthaceae | *Alternanthera philoxeroides* (Mart.) Griseb. | | | — | — | — |
| Apiaceae | *Ammi majus* L. | | | — | | |
| | *Conium maculatum* L. | — | — | — | — | — |
| Asteraceae | *Anthemis cotula* L. | — | — | — | — | — |
| | *Carduus acanthoides* L.* | | — | — | — | — |
| | *Cirsiun vulgare* (Savi) Ten. | | — | — | — | — |
| | *Bidens laevis* (L.)* | | — | — | — | — |
| | *Crepis setosa* Haller* | | — | — | — | — |
| | *Lactuca serriola* L. | | — | — | — | — |
| | *Sonchus oleraceus* L. | | — | — | — | — |
| | *Taraxacum officinale* Weber ex F.H. Wigg. | | — | — | — | — |
| | *Baccharis pingraea* DC* | | — | — | — | — |
| | *Eclipta postrata* (L.) L. | | | — | — | — |
| | *Pluchea sagittalis* (Lam.) Cabrera | | | | — | — |
| | *Tagetes minuta* L. | | | | — | — |
| Brassicaceae | *Hirschfeldia incana* (L.) Lagr.-Fossat | — | — | — | — | — |
| | *Sisymbrium officinale* (L.) Scop. | | | — | — | — |
| Commelinaceae | *Commelina erecta* L. | | — | — | — | — |
| Cucurbitaceae | *Cucurbita maxima Duchesne ssp. andreana* (Naudin) Filov | | | — | — | — |
| Fabaceae | *Trifolium pratense* L. | | | | — | — |
| | *Trifolium repens* L. | — | — | — | — | — |
| | *Medicago lupulina* L. | — | | | | |
| Gentianaceae | *Centaurium pulchellum* (Sw.) Druce | | — | — | — | |
| Lamiaceae | *Lamium amplexicaule* L. | | | — | | |
| Lythraceae | *Lythrum hyssopifolia* L. | | — | — | | |
| Malvaceae | *Malva nicaensis* All. | | — | — | | |
| Onagraceae | *Ludwigia peploides* (Kunth) P.H. Raven | | | — | — | — |
| Polygonaceae | *Polygonum aviculare* L. | | | — | — | — |
| | *Polygonum persicaria* L.* | — | — | — | — | — |
| Portulacaceae | *Portulaca oleracea* L. | | | — | — | |
| Solanaceae | *Physalis viscosa* L. | | | — | — | |
| | *Solanum glaucophyllum* Desf. | — | — | — | — | |
| | *Solanum sisymbriifolium* Lam. | — | — | — | — | |
| | *Solanum sublobatum* Willd. | — | — | — | — | |
| Verbenaceae | *Verbena gracilescens* (Cham.) Verter | — | — | — | — | — |
| | *Verbena intermedia* Gillies et Hook. | — | — | — | — | — |
| Oleaceae | *Ligustrum lucidum* Ait.* | | — | — | — | |
| Myrtaceae | *Eucalyptus* sp.* | | — | — | — | |

*Plants visited for pollen by both species of *Melissodes*.

flowering of the cultivated sunflowers ($n = 37$) had pollen of *Helianthus annuus* L. in various proportions (Figure 2A–D). Of these, 18 scopal loads consisted of pure sunflower pollen. Other scopal loads had variable proportions of five pollen types, belonging to four different families: Oleaceae (*Ligustrum* sp.; Figure 2A), Myrtaceae (*Eucalyptus* sp.; Figure 2B), Asteraceae (*Crepis* sp. and *Carduus* sp.; Figure 2C, D) and Polygonaceae (*Polygonum* sp.). When the flowering of cultivated sunflowers was over, the pollen loads examined ($n = 3$) were pure loads of *Bidens* sp. (Asteraceae).

All scopal loads analysed of specimens of *Melissodes rufithorax* collected during blooming of the field of sunflowers ($n = 11$) had pollen of *Helianthus annuus*. Eight scopal loads consisted of pure sunflower pollen. The other samples ($n = 3$) had pollen of *Ligustrum* sp. and a low proportion of pollen of *Carduus* sp. and *Polygonum* sp. After the blooming of sunflower, the scopal loads analysed had pure loads of *Bidens* sp. ($n = 3$) and mixed loads of *Biden*s sp. and *Baccharis* sp. ($n = 4$).

For both species of bees, *Bidens* sp. and *Baccharis* sp. only appear in the scopal loads when there is no sunflower in bloom, while *Ligustrum* sp., *Eucalyptus* sp., *Crepis* sp., *Carduus* sp. and *Polygonum* sp. occur when sunflower is present as well.

*Pollen on the body hairs.* — The pollen carried by the body hairs (hind legs removed) was analysed from 58 female bees. This pollen was not actively collected by the bees and reflects all the visits paid to flowers, both for nectar and pollen (Table IV, see Appendix, Table AII).

All the specimens analysed of *Melissodes tintinnans* that were collected during the blooming of sunflower ($n = 37$) had pollen of *Helianthus annuus* on them, 17 of which had exclusively this type of pollen. The

Table III. Number of samples and percentage of pollen in each sample of the plant taxa present in scopal loads (S) and body hair loads (C) of *Melissodes tintinnans* during and after the sunflower bloom.

| | | Bloom | | | | | | | | After bloom | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ($n = 37$) | | | | | | | | ($n = 3$) | |
| | | <5% | | 5–50% | | >50% | | 100% | | 100% | |
| Habit | Taxa | S | C | S | C | S | C | S | C | S | C |
| Herb | Asteraceae | | | | | | | | | | |
| | *Baccharis* sp. | | | | | | | | | | |
| | *Bidens* sp. | | | | | | | | | 3 | 3 |
| | *Carduus* sp. | 1 | | 1 | 1 | | | | | | |
| | *Crepis* sp. | 4 | 3 | 1 | 1 | | | | | | |
| | *Helianthus annuus* | 1 | 1 | 3 | 4 | 15 | 17 | 18 | 17 | | |
| | Polygonaceae | | | | | | | | | | |
| | *Polygonum* sp. | 1 | | 1 | 1 | | | | | | |
| Tree | Oleaceae | | | | | | | | | | |
| | *Ligustrum* sp. | 16 | 17 | 6 | 5 | 2 | 1 | | | | |
| | Myrtaceae | | | | | | | | | | |
| | *Eucalyptus* sp. | 5 | 6 | 7 | 6 | 1 | 2 | | | | |

20 mixed samples had various proportions of the same six major pollen types present in scopal loads that is, in decreasing importance: *Helianthus annuus*, *Ligustrum* sp., *Eucalyptus* sp., *Carduus* sp., *Polygonum* sp. and *Crepis* sp. When the flowering of cultivated sunflowers was over, the pollen on the body hairs ($n = 3$) was exclusively pollen of *Bidens* sp.

All the *Melissodes rufithorax* bees collected during the blooming of sunflowers ($n = 11$) had pollen of *Helianthus annuus* on them, seven of which bees had exclusively this type of pollen. The other specimens had low proportions of pollen of *Ligustrum* sp. and *Carduus* sp. accompanying the *H. annuus* pollen. After the blooming of sunflowers, the bodies analysed showed pure loads of *Bidens* sp. ($n = 3$) and mixed loads of *Bidens* sp. and *Baccharis* sp. ($n = 4$).

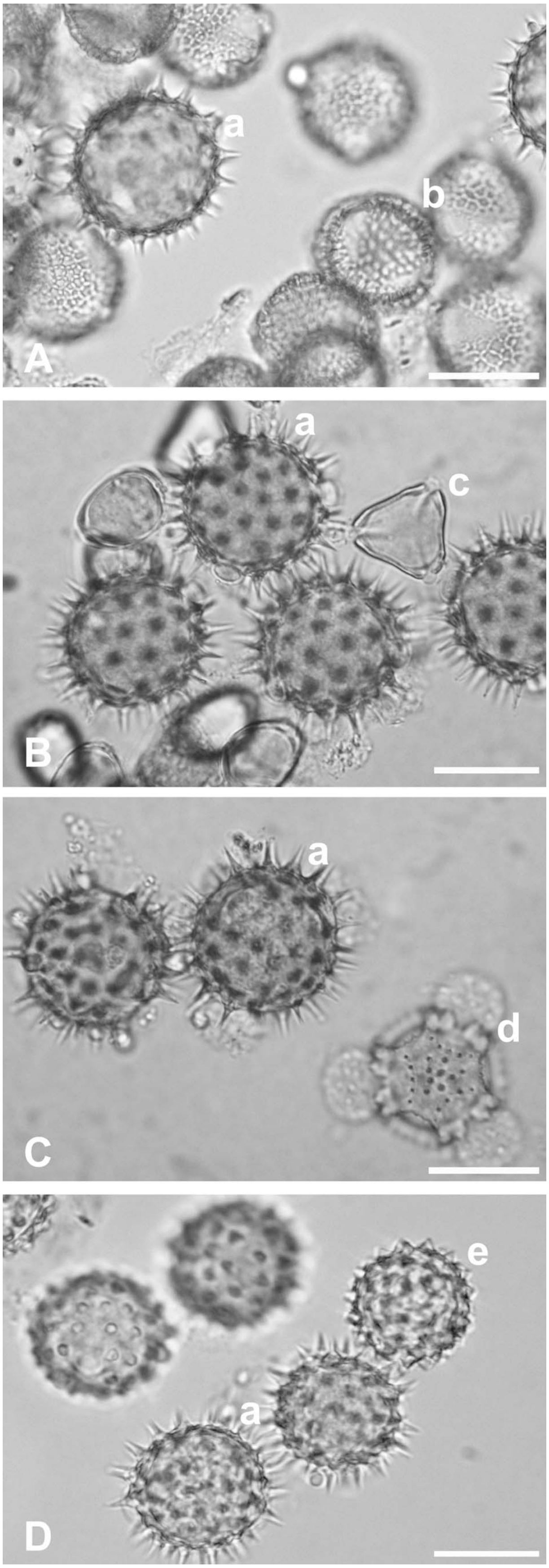
For both species of bees, *Bidens* sp. and *Baccharis* sp. appear on the body hairs only when there is no sunflower in bloom, while all other plant taxa occur in the presence of it.

### *Statistical analyses*

Chi-square marginal tests showed very highly significant interactions among the visited plant taxa and species of *Melissodes*, (ML $\chi^2 = 6953.8$, $p < 0.00001$; Figure 3). In the absence of sunflower, *Baccharis* sp. and *Bidens* sp. change their predominance according

Table IV. Number of samples and percentage of pollen in each sample of the plant taxa present in scopal loads (S) and body hair loads (C) of *Melissodes rufithorax* during and after the sunflower bloom.

| | | Bloom | | | | | | | | After bloom | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ($n = 11$) | | | | | | | | ($n = 7$) | | | | | |
| | | <5% | | 5–50% | | >50% | | 100% | | 5–50% | | >50% | | 100% | |
| Habit | Taxa | S | C | S | C | S | C | S | C | S | C | S | C | S | C |
| Herb | Asteraceae | | | | | | | | | | | | | | |
| | *Baccharis* sp. | | | | | | | | | | | 4 | 4 | | |
| | *Bidens* sp. | | | | | | | | | 4 | 4 | | | 3 | 3 |
| | *Carduus* sp. | | 2 | 2 | | | | | | | | | | | |
| | *Crepis* sp. | | | | | | | | | | | | | | |
| | *Helianthus annuus* | | | | | 3 | 4 | 8 | 7 | | | | | | |
| | Polygonaceae | | | | | | | | | | | | | | |
| | *Polygonum* sp. | 2 | | | | | | | | | | | | | |
| Tree | Oleaceae | | | | | | | | | | | | | | |
| | *Ligustrum* sp. | 1 | 1 | 2 | 3 | | | | | | | | | | |




to the insect species bearing their pollen, *Melissodes tintinnans* bearing, on the average, the most of *Bidens* sp. pollen and *M. rufithorax* the most of *Baccharis* sp. pollen. When sunflower is present, *M. rufithorax* bore the most of the *Helianthus annuus* pollen whereas *M. tintinnans* bore the most of *Ligustrum* sp. pollen. Considering all the other species, *M. tintinnans* was the species collecting most of the pollen. Correlation analyses showed that the proportions of each pollen type loaded on the scopae and hairs were similar for both *Melissodes* species. Spearman correlation coefficients were 0.81 ($p < 0.000001$) for *M. tintinnans* and 1.00 ($p < 0.000001$) for *M. rufithorax*.

## Discussion

Pollen of *Helianthus annuus* represents a major component of the diet of *Melissodes tintinnans* and *M. rufithorax* in the studied area. The emergence of the two species synchronously with the beginning of the flowering of the cultivated sunflower and the concordance of the decline of their abundance with the end of the flowering period of the crop is a striking fact. This synchrony was closer in *M. tintinnans*, but less evident at the end of the period in *M. rufithorax*, although both species continued foraging for over a month after the sunflower crop wilted. The two species are aestival bees in the temperate region of Argentina. Further studies may reveal whether local populations may have become synchronised with the bloom of sunflowers.

Both species showed a strong tendency to collect pollen of Asteraceae, but they also gathered pollen from plants in other families. Pollen from *Ligustrum* (Oleaceae) and *Eucalyptus* (Myrtaceae) was also gathered in significant amounts at the same time of the sunflower bloom. Bees collected pollen from other Asteraceae during and after the bloom of sunflowers, but in different tribes of this large family (Astereae, Cichoreae, Cynareae and Heliantheae). *Melissodes tintinnans* would be classified as eclectic oligolectic and *M. rufithorax* as broadly oligolectic, following the classification of pollen host specialisation of Cane and Sipes (2006) and the modifications proposed by Müller and Kuhlmann (2008).

The latter authors assigned the different subcategories of oligolecty and inferred bee host ranges by microscopical analysis of scopal pollen loads based

←
Figure 2. Scopal load of *Melissodes tintinnans*. **A.** Pollen of *Helianthus annuus* (a) and *Ligustrum* sp. (b); **B.** *Helianthus annuus* (a) and *Eucalyptus* sp. (c); **C.** *Helianthus annuus* (a) and *Crepis* sp. (d); **D.** *Helianthus annuus* (a) and *Carduus* sp. (e). Scale bars – 20 μm.

on two different methods: (1) on the number of pollen grains counted and (2) the individual composition of the pollen loads. *Melissodes tintinnans* is eclectic oligolectic (pollen collection from two to four plant genera belonging to two or three plant families) according to the first method: 98% of the pollen grains counted belong to the same four plant genera from three plant families: Asteraceae (*Helianthus* and *Bidens*), Oleaceae (*Ligustrum*) and Myrtaceae (*Eucalyptus*). It is also eclectic oligolectic according to the second method: pollen grains of the same four plant genera from three plant families were found in 100% of the pollen loads. *Melissodes rufithorax* is broadly oligolectic (pollen collection from two or more genera of one plant tribe, subfamily or family) according to the first method: 97% of the pollen grains counted belong to one plant family, the Asteraceae, but it is eclectic oligolectic according to the second method as 100% of the pollen loads had pollen of the same four plant genera from two families, Asteraceae (*Helianthus*, *Baccharis* and *Bidens*) and Oleaceae (*Ligustrum*). The two methods resulted in different categorisation. In this case, we assigned the higher degree of specialisation (i.e., broad oligolecty) as the authors suggest when the number of pollen loads analysed is less than 20 ($n = 18$).

The eclectic behaviour of *Melissodes tintinnans* would be reflected in the choice of plant taxa different to the Asteraceae, while *M. rufithorax* shows greater fidelity to species of this family (Figure 3). When sunflower was present, *M. rufithorax* bore the most *Helianthus annuus* pollen, whereas *M. tintinnans* bore the most *Ligustrum* sp. pollen, as well as pollen of all other plant taxa.

Both species collected pollen not only from the herbaceous vegetation, but also from trees. The specimens captured in the morning (9.30–11.00 am) collected pollen of *Ligustrum* sp. and/or *Eucalyptus* sp. The loads were clearly distinguishable by the white colour of part or of the entire load compared to the uniform yellow-orange colour of the pure sunflower loads. Pollen of *Ligustrum* sp. and *Eucalyptus* sp. was present in a large number of specimens and in some scopal loads in a large percentage. Two loads had 50% and 70% of *Ligustrum* sp. pollen, respectively, while one load had 50% of *Eucalyptus* sp. pollen and another one consisted of 98% of *Eucalyptus* sp. pollen. The presence of this pollen may be related to the mass supply of pollen produced by these floriferous trees in the study area (Giscafré & Ragonese, 1946).

Even when a crop is in full bloom, a good nectar or pollen flow from other plants can attract the bees away from the crop (Crane, 1990). A study conducted in Spain with *Apis mellifera* L. (honeybees) in sunflower revealed that foraging activity in the

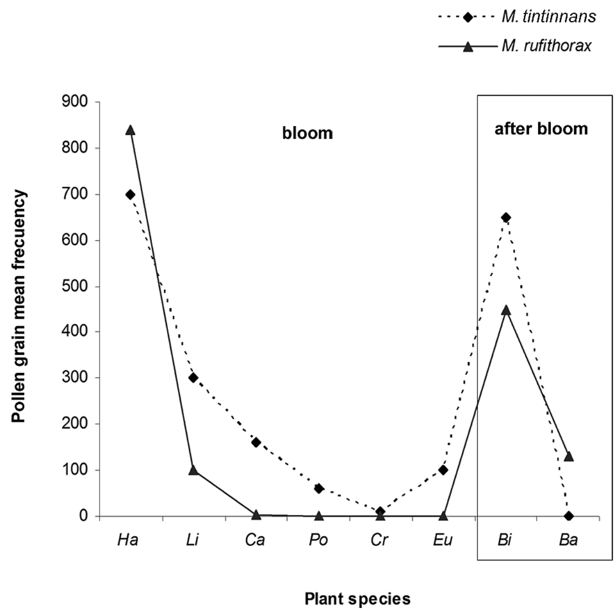



Figure 3. Plot of mean observed pollen grain frequency from *Helianthus annuus* (Ha), *Ligustrum* sp. (Li), *Carduus* sp. (Ca), *Polygonum* sp. (Po), *Crepis* sp. (Cr), *Eucalyptus* sp. (Eu), *Bidens* sp. (Bi) and *Baccharis* sp. (Ba) loaded on *Melissodes tintinnans* and *M. rufithorax*.

crop is related to the dehiscence of other competitive pollen sources (Ortiz-Sanchez & Tinaut, 1994). The pollen sources of nearby sunflower fields in the lower valley of Río Colorado (province of Buenos Aires, Argentina) were highly attractive to bees even when the abundance of those sources was low in the area and the sunflower was in full bloom (Andrada et al., 2004). The answer to why pollen of *Eucalyptus* sp. and *Ligustrum* sp. appears only in loads of bees captured in the morning could lie in the biology of these two arboreal species. The dehiscence or production of nectar with a high concentration of sugars in the morning would make these species alternative sources for the bees. However, in the absence of sunflower, *Melissodes tintinnans* selected *Bidens* sp. as the sole source of pollen, even in the simultaneous presence of *Eucalyptus* sp. and *Ligustrum* sp.

Further studies on a broader geographic range would be desirable to better define the diet of these species. Our results suggest that *Melissodes tintinnans* and *M. rufithorax* of the subgenus *Ecplectica* may be more similar in their foraging behaviour to the species specialised on Asteraceae of widespread occurrence, particularly in the subgenera *Heliomelissodes*, *Eumelissodes* and *Callimelissodes*.

The pollen carried by the bees on their body hairs did not reveal a different pattern of flower visitation. Pollen on the body may reflect nectar hosts other than those visited for pollen. The similar pollen spectra found in the scopae and on the body for both species suggest that they use the same plants to collect nectar and pollen.

## Conclusion

The pollen analyses allow us to conclude even though the pollen of sunflower represented a major component of the diet at the study site, both *Melissodes* species studied did not present a narrow oligolectic foraging behaviour on *Helianthus annuus*, the bees not only visited herbaceous but also arboreal vegetation, and the herbaceous vegetation in the field margins and the hedgerows facilitated the maintenance of the populations after the bloom of sunflowers.

The plant taxa used as pollen sources by the two studied species of native *Melissodes* occur frequently and widespread in the Pampean agricultural ecosystems (Cabrera, 1963; Parodi, 1964; Cozzo, 1967). This, together with the habit of nesting in aggregations of *M. tintinnans* and *M. rufithorax*, both within the crop and in the field margins, indicate that these bees may represent a valuable resource as crop pollinators in the intensively farmed Pampean region of Argentina.

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**Appendix**

Table AI. Pollen spectrum in all studied scopal loads of *Melissodes tintinnans* and *M. rufithorax* during and after the sunflower bloom.

| | | Herb | | | | | | Tree | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Asteraceae | | | | | Polygonaceae | Oleaceae | Myrtaceae | |
| Taxa | Sample number | *Baccharis* sp. | *Bidens* sp. | *Carduus* sp. | *Crepis* sp. | *Helianthus annuus* | *Polygonum* sp. | *Ligustrum sp.* | *Eucalyptus* sp. | Number of pollen grains |
| *Melissodes tintinnans* | | | | | | | | | | |
| Bloom ($n = 37$) | | | | | | | | | | |
| | 1 | | | | | 30% | | 70% | | 3063 |
| | 2 | | | | | 100% | | <1% | | 1100 |
| | 3 | | | | | 60% | | 40% | | 1302 |
| | 4 | | | 25% | | 71% | | 4% | | 1252 |
| | 5 | | | <1% | | 100% | <1% | <1% | | 1560 |
| | 6 | | | | | 79% | 14% | 7% | | 921 |
| | 7 | | | | | 78% | | 22% | | 431 |
| | 8 | | | | | 99% | | 1% | | 1350 |
| | 9 | | | | | 57% | | 43% | | 569 |
| | 10 | | | | <1% | 100% | | <1% | | 1300 |
| | 11 | | | | | 100% | | <1% | | 1230 |
| | 12 | | | | | 100% | | <1% | | 690 |
| | 13 | | | | | 100% | | <1% | | 2031 |
| | 14 | | | | | 91% | | 9% | | 471 |
| | 15 | | | | | 50% | | 50% | | 7891 |
| | 16 | | | | | 49% | | | 51% | 713 |
| | 17 | | | | | 81% | | | 19% | 672 |
| | 18 | | | | | 91% | | 7.5% | 1.5% | 518 |
| | 19 | | | | | 100% | | | | 110 |
| | 20 | | | | | 100% | | | | 180 |
| | 21 | | | | 28% | 45% | | | 27% | 179 |
| | 22 | | | | | 95% | | | 5% | 138 |
| | 23 | | | | | 95% | | | 5% | 186 |
| | 24 | | | | | 100% | | | <1% | 1320 |
| | 25 | | | | | 2% | | | 98% | 598 |
| | 26 | | | | | 74% | | 2% | 24% | 630 |
| | 27 | | | | | 100% | | | | 130 |
| | 28 | | | | | 100% | | | | 1615 |
| | 29 | | | | 4% | 95% | | 1% | | 258 |
| | 30 | | | | | 100% | | <1% | | 215 |
| | 31 | | | | 2% | 94% | | 4% | | 815 |
| | 32 | | | | | 100% | | <1% | <1% | 311 |
| | 33 | | | | <1% | 100% | | <1% | | 259 |
| | 34 | | | | | 100% | | | <1% | 121 |
| | 35 | | | | | 81% | | 1% | 18% | 330 |
| | 36 | | | | | 100% | | <1% | <1% | 423 |
| | 37 | | | | | 100% | | | | 381 |

Table AI. (*Continued*).

| | | Herb | | | | | | Tree | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Asteraceae | | | | | Polygonaceae | Oleaceae | Myrtaceae | |
| Taxa | Sample number | *Baccharis* sp. | *Bidens* sp. | *Carduus* sp. | *Crepis* sp. | *Helianthus annuus* | *Polygonum* sp. | *Ligustrum sp.* | *Eucalyptus* sp. | Number of pollen grains |
| After bloom ($n = 3$) | | | | | | | | | | |
| | 1 | | 100% | | | | | | | 785 |
| | 2 | | 100% | | | | | | | 876 |
| | 3 | | 100% | | | | | | | 875 |
| *Melissodes rufithorax* | | | | | | | | | | |
| Bloom ($n = 11$) | | | | | | | | | | |
| | 1 | | | | | 100% | <1% | | | 1200 |
| | 2 | | | | | 89% | <1% | 10% | | 175 |
| | 3 | | | | | 100% | | | | 2120 |
| | 4 | | | | | 100% | | | | 2030 |
| | 5 | | | | | 100% | | | | 620 |
| | 6 | | | | | 100% | | | | 956 |
| | 7 | | | <1% | | 87% | | 12% | | 284 |
| | 8 | | | | | 100% | | | | 260 |
| | 9 | | | | | 100% | | | | 680 |
| | 10 | | | | | 95% | | 5% | | 1054 |
| | 11 | | | | | 100% | | | | 201 |
| After bloom ($n = 7$) | | | | | | | | | | |
| | 1 | | 100% | | | | | | | 821 |
| | 2 | | 100% | | | | | | | 980 |
| | 3 | 59% | 41% | | | | | | | 311 |
| | 4 | 57% | 43% | | | | | | | 240 |
| | 5 | 64% | 36% | | | | | | | 172 |
| | 6 | 60% | 40% | | | | | | | 198 |
| | 7 | | 100% | | | | | | | 984 |

Table AII. Pollen spectrum of body hair loads of all specimens of *Melissodes tintinnans* and *M. rufithorax* during and after the sunflower bloom.

| | | Herb | | | | | | Tree | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Asteraceae | | | | | Polygonaceae | Oleaceae | Myrtaceae | |
| Taxa | Sample number | *Baccharis* sp. | *Bidens* sp. | *Carduus* sp. | *Crepis* sp. | *Helianthus annuus* | *Polygonum* sp. | *Ligustrum sp.* | *Eucalyptus* sp. | Number of pollen grains |
| *Melissodes tintinnans* | | | | | | | | | | |
| Bloom ($n = 23$) | | | | | | | | | | |
| | 1 | | | | | 10% | | 90% | | 300 |
| | 2 | | | | | 100% | | <1% | | 110 |
| | 3 | | | | | 70% | | 30% | | 340 |
| | 4 | | | 25% | | 71% | | 4% | | 456 |
| | 5 | | | | | 100% | | | | 110 |
| | 6 | | | | | 90% | 7.5% | 3.5% | | 321 |
| | 7 | | | | | 90% | | 10% | | 345 |
| | 8 | | | | | 99% | | 1% | | 109 |
| | 9 | | | | | 98% | | 2% | | 345 |
| | 10 | | | | <1% | 100% | | <1% | | 234 |
| | 11 | | | | | 100% | | <1% | | 178 |
| | 12 | | | | | 100% | | <1% | | 169 |
| | 13 | | | | | 100% | | <1% | | 234 |
| | 14 | | | | | 91% | | 9% | | 102 |
| | 15 | | | | | 50% | | 50% | | 381 |
| | 16 | | | | | 49% | | | 51% | 323 |
| | 17 | | | | | 81% | | | 19% | 223 |
| | 18 | | | | | 90% | | 8% | 2% | 518 |
| | 19 | | | | | 100% | | | | 110 |
| | 20 | | | | | 100% | | | | 180 |
| | 21 | | | | 30% | 40% | | | 30% | 179 |
| | 22 | | | | | 95% | | | 5% | 138 |
| | 23 | | | | | 95% | | | 5% | 186 |
| | 24 | | | | | 100% | | | <1% | 380 |
| | 25 | | | | | 2% | | | 98% | 228 |
| | 26 | | | | | 77% | | 1% | 20% | 230 |
| | 27 | | | | | 100% | | | | 40 |
| | 28 | | | | | 100% | | | | 456 |
| | 29 | | | | 3% | 95% | | 2% | | 118 |
| | 30 | | | | | 100% | | <1% | | 215 |
| | 31 | | | | | 95% | | 3% | 2% | 154 |
| | 32 | | | | | 100% | | <1% | <1% | 174 |
| | 33 | | | | <1% | 100% | | <1% | | 123 |
| | 34 | | | | | 100% | | | <1% | 102 |
| | 35 | | | | | 79% | | 1% | 20% | 175 |
| | 36 | | | | | 100% | | <1% | <1% | 160 |
| | 37 | | | | | 100% | | | | 108 |

Table AII. (*Continued*).

| Taxa | Sample number | Herb | | | | | | Tree | | Number of pollen grains |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Asteraceae | | | | | Polygonaceae | Oleaceae | Myrtaceae | |
| | | *Baccharis* sp. | *Bidens* sp. | *Carduus* sp. | *Crepis* sp. | *Helianthus annuus* | *Polygonum* sp. | *Ligustrum sp.* | *Eucalyptus* sp. | |
| After bloom ($n = 3$) | | | | | | | | | | |
| | 1 | | 100% | | | | | | | 234 |
| | 2 | | 100% | | | | | | | 230 |
| | 3 | | 100% | | | | | | | 185 |
| *Melissodes rufithorax* | | | | | | | | | | |
| Bloom ($n = 9$) | | | | | | | | | | |
| | 1 | | | | | 100% | | | | 220 |
| | 2 | | | | | 87% | | 13% | | 122 |
| | 3 | | | | | 100% | | | | 110 |
| | 4 | | | | | 100% | | | | 350 |
| | 5 | | | | | 100% | | | | 160 |
| | 6 | | | | | 100% | | | | 52 |
| | 7 | | | 1% | | 92% | | 8% | | 80 |
| | 8 | | | | | 98% | | 2% | | 170 |
| | 9 | | | | | 100% | | | | 280 |
| | 10 | | | <1% | | 93% | | 7% | | 280 |
| | 11 | | | | | 100% | | | | 91 |
| After bloom ($n = 7$) | | | | | | | | | | |
| | 1 | | 100% | | | | | | | 210 |
| | 2 | | 100% | | | | | | | 280 |
| | 3 | 60% | 40% | | | | | | | 203 |
| | 4 | 65% | 45% | | | | | | | 139 |
| | 5 | 59% | 41% | | | | | | | 82 |
| | 6 | 60% | 40% | | | | | | | 87 |
| | 7 | | 100% | | | | | | | 345 |