

The oligolecty status of a specialist bee of South American *Prosopis* (Fabaceae) supported by pollen analysis and floral visitation methods

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Abstract Despite the nest pollen provisions in Western Argentina are composed only of *Prosopis*, the fact that the ground-nesting bee *Eremapis parvula* visits several floral hosts suggested that it is a generalist bee species. In the South American Dry Chaco forest, seven nest aggregations of *E. parvula* were found during three different spring periods. From 34 to 73 species of floral hosts were recorded around each nest aggregation. However, all nest pollen samples were composed of *Prosopis* pollen alone, as previously found in nests from Western Argentina. Thus, pollen analysis proved that *E. parvula* is a specialist bee of *Prosopis*. The “monolecty” and “narrow oligolecty” pollen specialization categories cannot be differentiated using pollen analysis alone. For this reason, a complementary floral visitation method was used. As several *Prosopis* species have been reported in floral records, the narrow oligolecty category for *E. parvula* is supported here. Considering that this exomalopsine is a multivoltine bee, and that flowers of some of the more than seven *Prosopis* species are always available during spring, synchronization between them in rainy periods is highly probable. Thus, it is unlikely that *E. parvula* has to forage on alternative pollen hosts.

Keywords Bee diet · Dry Chaco · *Eremapis* · Exomalopsini · Ground nesting · Solitary bee · Specialist bee

Introduction

Pollen analysis of bee nest provisions was highlighted by Cane and Sipes (2006) as being a more direct and quantitative method to elucidate the pollen breadth of bees than floral visitation. However, in cases where plants with pollen of

similar morphology are found as components of pollen provisions, both methods are necessary to complement the partial information obtained from each method alone (Cane and Sipes 2006) and to assess the true category of pollen specialization of a given bee species.

Isolated flower visits have been recorded for members of the New World bee tribe Exomalopsini. For instance, several species of *Exomalopsis* (*E. biliottii* Torre-Grossa, *E. analis* Spinola, *E. fulvofasciata* Smith, *E. auropilosa* Spinola and others) were recorded as flower visitors of many *Solanum* (Solanaceae), *Prosopis* (Fabaceae, Mimosoideae), *Bidens* (Asteraceae), *Jacaranda oxyphylla* Cham. (Bignoniaceae), *Cassia* (Fabaceae, Caesalpinioideae) and *Capparis atamisquea* Kuntze (Capparidaceae) (Aguiar 2003; Grombone-Guaratini et al. 2004; Guimarães et al. 2008; Simpson et al. 1977; Torre-Grossa 1980; Wille 1963), and *Anthophorula* (*Isomalopsis*) *niveata* (Friese) was recorded in flowers of *Capparis atamisquea*, *Prosopis strombulifera* (Lam.) Benth. (Fabaceae, Mimosoideae), *Cassia aphylla* Cav. (Fabaceae, Caesalpinioideae), *Larrea divaricata* Cav. (Zygophyllaceae) and *Baccharis salicifolia* (Ruiz and Pav.) Pers. (Asteraceae) in Western Argentina (Michelette and Camargo 2000).

The tiny exomalopsine ground-nesting bee *Eremapis parvula* Ogloblin is endemic to Argentina, where it has been recorded in dry areas from Catamarca and Santiago del Estero to Río Negro provinces (Michener 2007; Neff 1984; Ogloblin 1956). For *E. parvula*, pollen provisions were studied from nests found in the Monte phytogeographical province in Catamarca, Western Argentina (Neff 1984). All nests were composed solely of *Prosopis*, indicating that it is likely an oligolectic bee. However, floral visitation documented several floral hosts in these same areas: *Prosopis chilensis* (Molina) Stuntz, *P. flexuosa* DC. and *P. torquata* (Cav. ex Lag.) DC., *Mimozyanthus carinatus* (Griseb.) Burkart, *Ziziphus mistol* Griseb., *Capparis atamisquea*, *Ximenia americana* L., *Jatropha excisa* Griseb., *Larrea divaricata* and *L. cuneifolia*

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Cav. (in Catamarca province of Western Argentina) (Simpson et al. 1977; Neff 1984). Other flower visits have been recorded on *Prosopis strombulifera*, *Capparis atamisquea*, *Larrea divaricata* and *Cassia aphylla* in an arid area of San Juan province in Western Argentina (Michelette and Camargo 2000). Although Neff (1984) distinguished between males and females of *E. parvula* when recording floral visitation, the other studies did not. For that reason, the fact that *E. parvula* is associated with several floral hosts suggests that it could be a generalist bee species. However, it is known that specialist bees can obtain nectar from many plants but pollen from only a few (Robertson 1925, 1926). Moreover, the flower visit method does not always discriminate between nectar gathering and pollen foraging. For this reason, the pollen specialization category of *E. parvula* remains dubious.

Material and methods

Climate and vegetation of the study area

The climate of the Chaco region is strongly seasonal and consists of a very hot summer (December–March) with maxima of up to 48.9 °C and low temperatures and frost during winter (July–September) (Prado 1993); there is a manifest yearly variation in rainfall, with a hard, marked dry season in winter–spring, and a rainy season from October to April (Papadakis 1973). The vegetation unit of the study area is the “Quebrachal” of three “quebrachos” (sensu Prado 1993), which is characterized by the shared dominance of *Schinopsis*

lorentzii Engl. (Anacardiaceae), *Schinopsis balansae* Engl. and *Aspidosperma quebracho-blanco* Schldtl. (Apocynaceae). Other floristic elements are *Ziziphus mistol* (Rhamnaceae), *Sideroxylon obtusifolium* (Roem. & Schult.) T.D. Penn. (Sapotaceae), several species of *Prosopis* (Fabaceae, Mimosoideae), *Caesalpinia paraguariensis* (D. Parodi) Burkart (Fabaceae, Caesalpinioideae), *Pterogyne nitens* Tul. (Fabaceae, Caesalpinioideae), *Trithrinax schizophylla* Drude (Arecaceae), *Castela coccinea* Griseb. (Simaroubaceae), *Achatocarpus praecox* Griseb. (Achatocarpaceae), *Celtis* spp. (Celtidaceae), *Schinus fasciculatus* (Griseb.) I.M. Johnst. var. *arenicola* (Hauman) F.A. Barkley (Anacardiaceae), *Maytenus vitis-idaea* Griseb. (Celastraceae), *Moya spinosa* Griseb. (Celastraceae), *Mimosa detinens* Benth. (Fabaceae, Mimosoideae) and several species of *Capparis* (Capparidaceae) and *Acacia* (Fabaceae, Mimosoideae) (Prado 1993; F.G.V. personal observation).

Nest pollen sampling and pollen analysis

Nest pollen samples were obtained from Villa Río Bermejito (25° 37' S, 60° 15' W) and Juan José Castelli (25° 56' S, 60° 37' W) in the Chaco province of Argentina, which belongs to the Chaquénian phytogeographical province (sensu Cabrera 1971) (Fig. 1, Table 1). On sandy soil, many nest aggregations of *E. parvula* were found during three different spring periods (Table 1). A total of 50 pollen samples were studied from seven nest aggregations including brood provisions, stomach content of larvae and scopal pollen from adults caught arriving at nest entrances (Table 2). Each sample was dissolved in

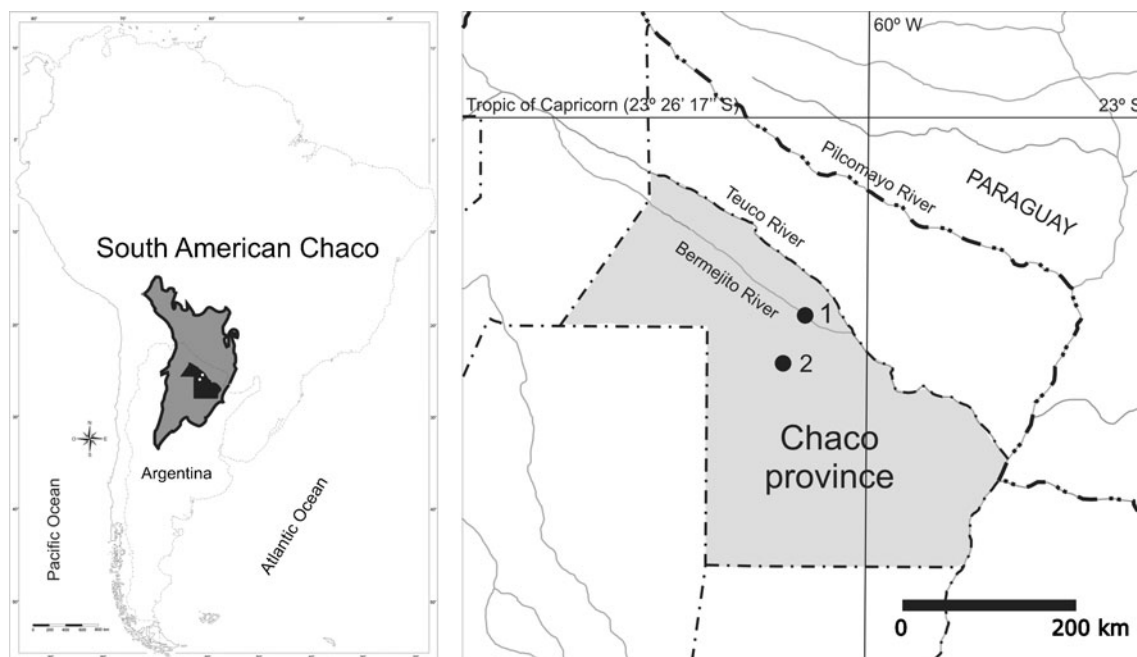


Fig. 1 South American Chaco region indicating the Chaco province of Argentina and localities where nests and pollen samples were obtained. 1 Villa Río Bermejito (25° 37' S, 60° 15' W); 2 Juan José Castelli (25° 56' S, 60° 37' W)

Table 1 Floral availability around the seven nest aggregations of *Eremapis parvula* in the sampling period (late September–early December). Localities and collection date are provided. *Prosopis* richness, abundance of individuals and flowers of *Prosopis* around each nest aggregation of *Eremapis parvula* are also provided

Nest aggregation (nesting area)	Collection date	Locality (for reference see Fig. 1)	Number of available flowering species around nesting area of <i>E. parvula</i>	<i>Prosopis</i> richness	Abundance of <i>Prosopis</i> individuals and their distance from nests	Abundance of <i>Prosopis</i> flowers
1	Late September 2011	2 (open areas with woody-colonized forest)	34 species from 10 families	7 species plus hybrids	Highly abundant / nests under trees	Highly abundant flowers (flowering peak)
2, 3	Late September 2008	1 (riparian forest)	37 species from 12 families	3 species	Highly abundant / nests 1–50 m away	Highly abundant flowers (flowering peak)
4	Late October 2008	1 (riparian forest)	No recorded	?	Abundant / nests 20–50 m away	Scarce inflorescences among leaves
5	Late November 2010	1 (riparian forest)	73 species from 30 families	3 species	Abundant / nests 20–50 m away	Scarce inflorescences among leaves
6, 7	Early December 2010	1 (xerophilous forest)	73 species from 30 families	3 species	Abundant / approximately 100 m away	Scarce inflorescences among leaves
7 nest aggregations	4 months in 3 years	2 localities				

distilled water at 80–90 °C for 10–15 min, pressed when necessary using a glass rod, stirred by hand or, when necessary, using a magnetic stirrer for 5–10 min and then filtered. Finally, to obtain pollen sediment, samples were centrifuged at 472g for 5 min. Processing included Wodehouse (1935) and Acetolysis methods (Erdtman 1960). Slides containing reference pollen grains were prepared from flowers of herbarium plants collected in the study area and deposited in the Herbaria of La Plata (LP) and of Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (BA), Argentina. To observe the detailed wall sculpture of pollen, acetolysed grains were examined in a JEOL JSM-T-100 scanning electron microscopy (Fig. 2b). To avoid undersampling and therefore to correctly identify pollen specialization status of this bee species, nest pollen samples were taken in different months during 3 years and in different sites [in September 2008 and 2011, late October 2008, and November–December 2010, from seven nest aggregations (seven nest populations) in two localities; Fig. 1, Table 1]. Bees were caught from their nests by hand and in nets, identified by A. Roig-Alsina and deposited in the Entomology collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”.

Availability of floral resources around nest aggregations and floral visitation

Floral availability was recorded in a radius of more than 100 m around the nesting areas during 1–4 weeks per site (Table 1). The vegetation around the nests belonged to riparian and xerophilous forests (site 1) and open areas with woody-colonized forests (site 2) (Fig. 1, Table 1). Floral visitations of *E. parvula* were also recorded, these bees were caught using nets during a whole day.

Results

All nest pollen samples of *E. parvula* were composed of pollen of *Prosopis* alone (Table 2; Fig. 2a, b). The chaquenian *Prosopis* species found in the study area belong to *Prosopis* section *Algarobia* (Burkart 1976). These species have morphologically similar pollen grains characterized by a thin exine (<2 µm) and scabrate or smooth wall sculpture (Fig. 2b) (Caccavari 1972). As stressed by Burkart (1937, 1976) and Palacios and Bravo (1981), natural hybridization is very common among the Chaquenian sympatric species of this section [i.e., serie *Chilenses*: *P. alba* Griseb. and *P. nigra* (Griseb.) Hieron., and serie *Ruscifoliae*: *P. ruscifolia* Griseb., *P. fiebrigii* Harms, *P. hassleri* Harms and *P. vinalillo* Stuck.]. This fact might contribute to making their pollen grains undistinguishable under light and scanning microscopy. Their protein content ranges from 20 % to 30 % of the total pollen grain biomass (Vossler 2012).

Table 2 Number of pollen samples and their content analyzed per type of nest sample (new and old brood pollen masses, stomach content of larvae, and scopal pollen from incoming adults). Pollen content of all nest samples was composed of *Prosopis* alone

Type of nest pollen sample	Number of pollen samples analyzed	Pollen content of samples
New brood pollen masses with very small larvae	31	100 % <i>Prosopis</i>
Old brood pollen masses (dry or moldy)	6	100 % <i>Prosopis</i> (very scarce pollen grains)
Stomach content of larvae	3	100 % <i>Prosopis</i> (very scarce pollen grains)
Scopal pollen of incoming adults	10	100 % <i>Prosopis</i>
Total	50 pollen samples	

Floral host availability from September to early December included many species (34–73) of diverse plant families (10–30) (Table 1). During early spring (late September), abundant blooming of all *Prosopis* species was recorded [*P. alba*, *P. nigra*, *P. ruscifolia*, *P. vinalillo*, *P. elata* (Burkart) Burkart, *P. kuntzei* Harms and hybrids]. In the following months, only *P. elata* and *P. kuntzei*, and a few branches with scarce inflorescences of *P. alba* were found blooming (Fig. 3). Therefore, in the whole sampled period, flowers of *Prosopis* were always available in the field (Table 1).

Floral visitation was recorded on *P. alba* and *P. ruscifolia* bloomings, but *E. parvula* was detected only in *P. alba*.

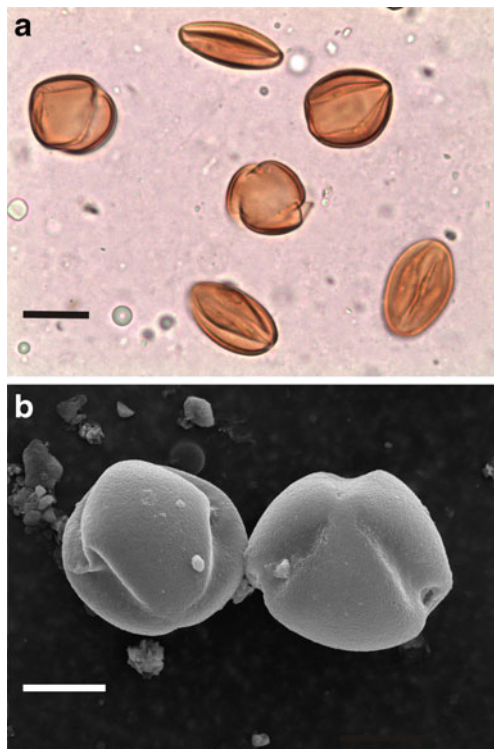


Fig. 2 **a** Acetolyzed pollen grains of *Prosopis* from nest samples, seen in light microscope at 40× magnification. **b** Scanning photomicrograph of pollen grains of *Prosopis alba* in equatorial (left) and polar (right) view, showing scabrate and punctate wall sculpture. Bars **a** 20 μm, **b** 10 μm

Discussion

Eremapis parvula: a narrowly oligolectic bee of *Prosopis*

Taking into account the consistency of the results in the present study, it is highly probable that the data recorded by other authors belong to nectar hosts. It is likely that the mistaken identification of the generalist feeding habit of this bee species is due to the lack of discrimination between male and female foragers and/or nectar versus pollen gathering when recording floral visitation. Moreover, Neff (1984) found that males visited several floral hosts but females visited only *Prosopis* flowers. Pollen analysis of nest pollen samples of *E. parvula* taken from seven nest aggregations at different sites and times showed that it is a bee associated with host plants of the *Prosopis* genus alone. This type of pollen specialization can be classified as monolecty (sensu Robertson 1925) as well as narrow oligolecty (sensu Cane and Sipes 2006) (i.e., the former term was suggested to include bee species that are pollen-specialized in a plant species only while the latter in a genus). However, because *Prosopis* species of the section *Algarobia* found near the nests have pollen of similar morphology, differentiation between the Monolecty and narrow oligolecty categories was not possible using the pollen analysis method alone.

Most oligolectic bees do not discriminate among congeneric hosts, and so they should readily colonize new sister taxa (Wcislo and Cane 1996). This could be the case with



Fig. 3 An inflorescence of *Prosopis alba* among a great quantity of well developed leaves, photographed in late November. The light green-yellowish flowers are densely distributed in the spike-like inflorescence. An unripe fruit is shown

Prosopis—a genus quite uniform in floral and inflorescence phenotype (Burkart 1937; Palacios and Bravo 1981). Examples at population level include a *Vaccinium* (Ericaceae) specialist that readily adopts another *Vaccinium* species outside its native range (Cane and Payne 1993). Moreover, in areas where closely related pollen hosts bloom together (as observed for the seven species of *Prosopis*), specialists typically forage on all of them (Weislo and Cane 1996).

Considering the great availability of floral hosts in the field (Table 1), pollen analysis of nest samples proved that *E. parvula* is a specialist bee of *Prosopis*. Moreover, Neff (1984) found that all nest provisions studied were composed solely of *Prosopis* and suggested that *E. parvula* is apparently oligolectic on this plant genus.

Thus, as many *Prosopis* species were recorded as hosts for *E. parvula* throughout a large geographical area (*P. alba*, *P. chilensis*, *P. flexuosa*, *P. strombulifera* and *P. torquata*), the narrow oligolecty category is supported. In different bee families, others narrowly oligolectic genera have been found, such as *Dufourea* (Halictidae family), *Perdita* and *Andrena* (Andrenidae), *Melitta* (Melittidae), *Proterides* (Megachilidae), and *Diadasia* (Apidae, Emphorini) (Cane and Sipes 2006; Parker 1978; Rust et al. 1974; Torchio et al. 1967).

Synchronization between *Eremapis parvula* emergence and *Prosopis* blooming

During the three spring periods studied, a large and diverse spectrum of floral hosts was available. The constancy of only *Prosopis* pollen in all nest samples suggests that there is a strong correspondence between *E. parvula* and *Prosopis* in the Chaco forest, similar to those found in the Monte desert by Neff (1984).

Unlike annual plants that rely on rainfall for germinating and flowering, *Prosopis* species are woody perennials and their flowering is a predictable event. Conversely, emergence of *E. parvula* is unpredictable because it seems to be associated with rainy episodes when the soil is optimal for building its nests. Therefore, synchronization between them might occur only in rainy periods. The nest aggregations observed for *E. parvula* in different months suggest that it is a multivoltine bee (i.e., a bee species with emergence several times in a year). As this exomalopsine is a multivoltine bee and flowers of some of the more than seven *Prosopis* species are always available during spring, synchronization between them during spring rainy periods is highly probable. Thus, it is unlikely that *E. parvula* has to forage on alternative pollen hosts. Therefore, it is impossible to prove whether it is a facultative [i.e., a bee species that might turn to alternative pollen taxa, but only when their regular pollen hosts are temporarily absent (Linsley and MacSwain 1958)] or an obligate [i.e., a bee species that refuse to provision or even nest in the absence of their floral

host (Cane and Sipes 2006)] oligolectic bee. Pollen grains of *Prosopis* contain starch in the cytoplasm of the vegetative cell and pollenkit between the intine and exine walls (Hoc et al. 1994) as well as a high percentage of protein (>20 %) (Andrada and Tellería 2005; Vossler 2012). This would mean that *Prosopis* pollen could supply all nutrient requirements for the offspring of any bee species.

Although many monolectic and oligolectic bees appear to depend on a particular plant species or genus, host plants are generally not dependent for pollination on their monoleges or oligoleges (Michener 1979, 2007). Therefore, the lack of synchronization between this specialist bee and *Prosopis* flowering would not have a negative consequence for the reproductive success of *Prosopis* species.

The importance of *Prosopis* for several bee groups

Bees are the most important group of pollinators of *Prosopis*, and several bee groups are highly attracted to *Prosopis* flowers for both pollen and nectar resources wherever their species are found (Genise et al. 1990, 1991; Golubov et al. 2010; Keys et al. 1995; Michelette and Camargo 2000; Neff 1984; Pasiecznik et al. 2001; Simpson et al. 1977). These resources are collected intensively and stored in nests by different bee groups. In South American xeric areas, these are: *Caupolicana mendocina* Jorgensen, *C. ruficollis* Friese (Colletidae, Diphaglossinae, Caupolicanini), *Xylocopa splendidula* Lepeletier (Apidae, Xylocopini) (Genise et al. 1990, 1991), *Apis mellifera* Linnaeus (Apidae, Apini) (Andrada and Tellería 2005; Basilio and Noetinger 2002; Cabrera 2006; Costa et al. 1995; Fagúndez and Caccavari 2003, 2006; Salgado 2006; Salgado and Pire 2000; Tellería 2000; Tellería and Forcone 2000), *Geotrigona argentina* Camargo and Moure (Apidae, Meliponini) (Vossler et al. 2010). However, only *E. parvula* has been associated with *Prosopis* alone using pollen analysis of nest provisions.

Over 80 and 160 bee species have been found visiting flowers of *Prosopis* in the deserts of South and North America, respectively (Moldenke and Neff 1974; Simpson et al. 1977). Among them, the most common bee genera found are *Colletes*, *Bicolletes*, *Oediscelis*, *Liopoeum*, *Megachile*, *Centris*, *Eremapis*, *Exomalopsis*, *Svastrides* and *Xylocopa* in South America and *Dialictus*, *Evyllaesus*, *Nomia*, *Perdita*, *Megachile*, *Chalicodoma*, *Centris* and *Melissodes* in North America (Simpson et al. 1977). Oligolectic bees of *Prosopis* have been recorded only tentatively for the South American *Colletes*, *Bicolletes*, *Oediscelis*, one *Megachile* species and *Eremapis parvula* (Neff 1984; Simpson et al. 1977) and for North American *Perdita* species.

Flowers of *Prosopis* have relatively exposed nectar and pollen resources (Arroyo 1981), being an important source for both generalist and specialist bees. In the Chaco region, diverse bee groups forage on *Prosopis*. It is probable that a

high number of oligolectic bees are waiting to be discovered in this plant genus.

For that reason, analyses of pollen provisions from nests, as was done in the present study for *E. parvula*, are necessary to provide more information about the actual diversity of pollen host plants associated with a bee species and, thus to reveal its pollen specialization category.

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