

A TIGHT RELATIONSHIP BETWEEN THE SOLITARY BEE *CALLIOPSIS* (*CEROLIOPOEUM*) *LAETA* (ANDRENIDAE, PANURGINAE) AND *PROSOPIS* POLLEN HOSTS (FABACEAE, MIMOSOIDEAE) IN XERIC SOUTH AMERICAN WOODLANDS

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Abstract—The large genus *Calliopsis* (Andrenidae, Panurginae) is composed of ten subgenera with polylectic and presumably oligolectic species. These categories have been mainly developed from floral visits of female bees collecting pollen. In the present study, pollen analyses of nest provisions and scopal loads from museum specimens of the monotypic subgenus *Ceroliopoeum* were carried out to assess its degree of specialization to pollen host-plants. Despite the great variety of floral resources close to two active nest aggregations in the Chaco sites (83 and 44 melittophilous taxa from 36 and 17 families, respectively), the only host-plant recorded in all nest pollen samples was *Prosopis*. This genus was represented by six species and their hybrids, all having similar pollen morphology. The nesting sites in Monte scrub also contained several *Prosopis* species, some of which had different pollen morphology from those of the Chaco forest. Two different *Prosopis* pollen types were identified in all samples. Since the whole geographic distribution of *C. laeta* matches with the range of *Prosopis*, its strong association with this pollen host seems to be well supported. However, the low number of study populations (four) could erroneously indicate oligolectism. A broader sampling is necessary to ensure the character of specialization. Most *Calliopsis* species have been identified as oligolectic. Yet, this categorization has mainly been based on floral visits and a large diversity of floral hosts has been recorded for each bee species. Further analyses are necessary to confirm the relationship of this genus with its pollen hosts. Moreover, as most of them have short to medium phenologies (up to 4 months) their presumably oligolecty can be due to a local specialization (i.e. variable according to location) typical of polylecty.

Keywords: *Calliopsini*, Chaco forest, emergence, narrow oligolecty, pollen specialization, specialist bee

INTRODUCTION

The legume family (Fabaceae *sensu lato* or Leguminosae) is a mainly bee-pollinated plant group that constitutes a major food source for the entire taxonomic spectrum of bees (Arroyo 1981). The South American Chaco is a forest characterized by the abundance of woody and herbaceous Fabaceae, mainly the woody mimosoids *Prosopis* and *Acacia*, Zygophyllaceae, Anacardiaceae, Celastraceae, Rhamnaceae, Capparidaceae, Santalaceae, Ulmaceae s.l., Cactaceae and Bromeliaceae (Cabrera & Willink 1973). *Prosopis* is a species-rich plant genus and most species are quite uniform in floral and inflorescence phenotypes (Burkart 1937; Palacios & Bravo 1981). The flowers are open with exposed nectar and pollen resources (Arroyo 1981). *Prosopis* contains 45 species and is mainly distributed in arid and semi-arid regions of the world (Burkart 1976; Palacios & Brizuela 2005). However, recent studies showed that it is not a natural group, and that Old world species are not true

Prosopis (Catalano et al. 2008). In the Americas it is distributed from southwestern USA to central Chile and Argentina, mainly in warm and dry regions. The most important centre of differentiation of the genus is found in Argentina (27 species and 19 varieties) (Burkart 1976; Palacios & Brizuela 2005).

Bees are the most important group of pollinators of *Prosopis* and highly attracted to its flowers for both pollen and nectar resources (Moldenke and Neff 1974; Simpson et al. 1977; Keys et al. 1995). The most common bee genera visiting the flowers of *Prosopis* are *Colletes*, *Pygopasiphae*, *Chilicola*, *Calliopsis*, *Megachile*, *Centris*, *Eremapis*, *Exomalopsis*, *Svastrides* and *Xylocopa* in South American deserts and *Lasioglossum*, *Nomia*, *Perdita*, *Megachile*, *Centris* and *Melissodes* in North American deserts (Simpson et al. 1977). Oligolectic bees of *Prosopis* have been recorded for the South American *Colletes*, *Pygopasiphae*, *Chilicola*, one *Megachile* species and *Eremapis parvula* Ogloblin (Neff 1984; Simpson et al. 1977; Vossler 2013). In North America, *Prosopis* specialists include a complex of *Perdita* species, several *Colletes* and *Ashmeadiella prosopidis* (Simpson et al. 1977).

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In South America, the relationship between the bee fauna and *Prosopis* has been studied using flower visits (Simpson et al. 1977; Genise et al. 1990, 1991; Michelette & Camargo 2000). Flower visits allow identifying the association of bees with particular flowering plants, but may miss other host plants. The analysis of pollen from nest provisions is a reliable method to reveal the degree of pollen specialization (as shown by Neff (1984) and Vossler (2013) for *Eremapis parvula*, an oligolectic bee on *Prosopis*). Further advantages of pollen analysis from nest provisions compared to field observations is the unbiased representation of inaccessible or unanticipated pollen hosts, such as forest canopy species or alternative hosts of presumed oligolectic species (Cane & Sipes 2006). However, stenopalynous plant taxa (Erdtman 1952), that show only marginal or no morphological pollen variation can be identified only to a certain taxonomic level (i.e. genus, tribe, subfamily or family). In such cases, field observations will be necessary to identify the specialization status of a presumably oligolectic bee (Cane & Sipes 2006; Vossler 2013).

The genus *Calliopsis* consists of 10 subgenera and approximately 80 species and is found in temperate zones of Western Hemisphere, mainly in xeric areas (Michener 2007). It seems that each subgenus of *Calliopsis* has species specialized in different taxa of pollen host-plants, mostly Fabaceae (Mimosoideae and Papilionoideae, Tab. 1). For the three South American subgenera of *Calliopsis* (i.e. *Ceroliopoeum*, *Liopoeodes* and *Liopoeum*), floral hosts of only three *Liopoeum* species have been identified (Tab. 1).

Calliopsis (Ceroliopoeum) laeta (Vachal) is endemic to Argentina, where it has been recorded in dry areas of La Rioja, Santiago del Estero and Chaco provinces (Jørgensen 1912; Ruz 1991; Michener 2007; Moure & Dal Molin 2012). Biological data of this monotypic subgenus has not yet been documented. The objectives of this survey were to identify the botanical origin of pollen samples from nests and museum specimens of the solitary bee *Calliopsis laeta* and reveal its degree of pollen specialization, using mainly the pollen analysis method. This study further aimed at documenting its phenology and its global geographic distribution.

MATERIALS AND METHODS

Study sites of field observations and museum specimen

To identify pollen specialization of *Calliopsis laeta*, pollen samples were taken from two nesting sites (1-Villa Río Bermejito, 25° 37' S, 60° 15' W and 2-Juan José Castelli, 25° 56' S, 60° 37' W) in Chaco forest (Fig. 1), from 22nd to 26th of September 2008 (for 1) and from 19th to 20th of September 2011 (for 2). Notes on nesting were taken from these same sites and dates. Nests aggregated in horizontal hard packed soils along dirt roads. Cells occurred up to a depth of 10 cm from the soil surface where the soil texture was sandy loam. The presence of clay probably prevented deeper nests. The soil was moist during the nesting period. Nest initiation occurred during a short period of two days after copious rain (96 mm), and before

the soil dried out and hardened. Neither nest building nor flight activity around nest entrances was observed after this period. However, five females and eight males were recorded foraging on *P. alba* on a site 3 km away from this nesting area and five days after the rainfalls. Similar to the statement of Rozen (1967) for many panurgines, there was no indication that a female of *Calliopsis laeta* uses water in building her nest.

Further, two museum specimens from different sites in Monte scrub (3-Amaichá del Valle (Tucumán) and 4-San Fernando del Valle de Catamarca (Catamarca)), captured in early November 2004 (for 3) and 1989 (for 4) could be examined for scopal pollen loads.

Pollen analysis of nest samples and museum specimens

Pollen samples from nests included brood provisions ($N = 3$ from 2008 and 2 from 2011), stomach contents of larvae ($N = 10$ from 2008), feces of post-defecating larvae ($N = 11$ from 2008), and scopal pollen from adults caught returning to nest entrances ($N = 3$ from 2008). Bees were caught at nests by hand and in nets, identified by Arturo Roig-Alsina and deposited in the Entomology collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN). Nest pollen samples were dissolved in distilled water at 80-90 °C for 10-15 minutes, pressed when necessary using a glass rod, stirred by hand or, when necessary, by a magnetic stirrer for 5-10 minutes, and filtered. Finally, to obtain pollen sediment, samples were centrifuged at $472 \times g$ for 5 minutes. Processing included Wodehouse (1935) and acetolysis methods (Erdtman 1960; Lieux 1980).

Sixty-six museum specimens of female *C. laeta* were examined but only two bore pollen loads. These are very moist and may get lost during handling (netting, pan trapping). The discovered samples stemmed from two localities in western Argentina (Tucumán and Catamarca provinces). One leg per individual was mounted on a slide, immersed in acetolysis fluid and heated directly over a flame for 20 seconds. This sediment was mounted using a glycerine-jelly mixture. A cover glass was added and sealed with paraffin. After this short process, pollen grains acquired a brownish colour similar to that obtained via the acetolysis method of Erdtman (1960). Pollen types were identified using a Nikon Eclipse E200 light microscope at $1000 \times$ magnification. Pollen grains from flowers of herbarium plants collected in the study area and deposited in the Herbaria of La Plata (LP) and of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (BA), Argentina served as reference collection. The classification of host-plant specialization by bees follows Cane & Sipes (2006) and Müller & Kuhlmann (2008).

Additional data on the phenology and geographic distribution of *Calliopsis laeta* were taken from specimens examined from MACN collection (see Appendix 1).

Availability of floral resources

The availability of floral resources next to the two nest aggregations was recorded, as stressed by Cane & Sipes

TABLE I. Host-plant associations of the ten *Calliopsis* subgenera and specialization degree as suggested by different authors. Literature references: 1_ this article; 2_ Michelette & Camargo (2000); 3_ Simpson et al. (1977); 4_ Dumesh & Packer (2011); 5_ page 309 in Michener (2007); 6_ Shinn (1967); 7_ page 264 in Wcislo & Cane (1996); 8_ Rozen (1970); 9_ Danforth (1990); 10_ Rozen (2008); 11_ Rozen (1963); 12_ Wcislo (1999); 13_ Vossler (*in prep.*); 14_ Michener (1954); 15_ Robertson (1929). References: Pollen collection (P); nectar collection (N).

No. of species	Bee species	Host-plant genus (plant family)	Pollen samples (PS)/ floral visits (FV) and study sites	Specialization suggested by authors
South American subgenus				
<i>Ceroliopoeum</i> (1 species endemic to Argentina)	<i>C. (Ceroliopoeum) laeta</i> (Vachal)	<i>Prosopis</i> (Fabaceae, Mimosoideae) ¹	29 PS (Dry Chaco forest) and 2 PS (Monte desert) ¹	Possibly narrowly oligolectic ¹
<i>Liopoeodes</i> (1 species endemic to Argentina)	<i>C. (Liopoeodes) xenopous</i> Ruz	Unknown	No data	
<i>Liopoeum</i> (5 species from Chile and Argentina ^{4,5})	<i>C. (Liopoeum) argentina</i> (Jørgensen)	<i>Larrea</i> and <i>Bulnesia</i> (Zygophyllaceae) ²	FV (two Argentinean sites from Catamarca and La Rioja provinces, Monte desert) ^{2,3}	Polylectic ³
	<i>C. (Liopoeum) rigormortis</i> Dumesh & Packer	<i>Adesmia</i> (Fabaceae, Papilionoideae) ⁴		Apparently specialist ⁴
	<i>C. (Liopoeum) mendocina</i> (Jørgensen)	<i>Prosopis</i> , <i>Solanum</i> (Solanaceae) and <i>Brassicaceae</i> ¹³	31 PS (Dry Chaco forest), 3 PS (Monte desert) and 2 PS (Wet Chaco forest) ¹³	Polylectic with strong preference for <i>Prosopis</i> ¹³
North and Central American subgenus				
<i>Calliopsis s. str.</i> (12 species, North and Central America to Panama)				Subgenus narrowly polylectic ⁵ . Subgenus widely polylectic, mostly on Fabaceae, especially the small-flowered clovers <i>Trifolium</i> and <i>Melilotus</i> ⁶
	<i>C. (Calliopsis) andreniformis</i> Smith	<i>Trifolium</i> and <i>Melilotus</i> (Fabaceae, Papilionoideae) ^{5,6} , <i>Malva</i> (Malvaceae) (P) ⁶ . Fabaceae, Asteraceae, Verbenaceae and Malvaceae (P and N) ⁶	17 PS (pure Fabaceae, pure Malvaceae or mixed Asteraceae and Malvaceae) ⁶ and 98 FV ⁶	
	<i>C. (Calliopsis) hondurasica</i> Cockerell	<i>Aeschynomene americana</i> (Fabaceae, Papilionoideae) in Panamá ¹²	PS (a nest population near Veracruz, Panamá, open field regularly mowed surrounded by deciduous tropical forest) ¹² ; FV (Panamá) ¹⁴	Possibly pollen specialist ¹²
	Other species	Apocynaceae, Convolvulaceae, Asteraceae, Fabaceae, Oxalidaceae, Lamiaceae, Verbenaceae, etc ⁶	FV ⁶	
<i>Calliopsima</i> (15 species, Canada, USA and Mexico)	Most species	<i>Heterotheca</i> , <i>Gutierrezia</i> , <i>Baileya</i> , <i>Senecio</i> , <i>Solidago</i> , <i>Bidens</i> , <i>Boltonia</i> , <i>Coreopsis</i> , <i>Rudbeckia</i> , <i>Cirsium</i> , <i>Encelia</i> , <i>Hemizonia</i> , <i>Haplopappus</i> , <i>Grindelia</i> , <i>Verbesina</i> , etc. (Asteraceae), <i>Melilotus albus</i> and <i>Medicago sativa</i> (Fabaceae) ⁶	FV ⁶	Primarily on the Asteraceae, particularly tribes Heliantheae and Astereae ⁶
	<i>C. (Calliopsima) coloradensis</i> Cresson	<i>Boltonia</i> , <i>Solidago</i> , <i>Bidens</i> , <i>Rudbeckia</i> and <i>Coreopsis</i> (P) ^{6,15}	FV (Carlinville, Illinois, USA) ¹⁵	
	<i>C. (Calliopsima) rozeni</i> Shinn	Primarily on <i>Heterotheca subaxillaris</i> ⁶	FV ⁶	

TABLE I. continued.

No. of species	Bee species	Host-plant genus (plant family)	Pollen samples (PS)/ floral visits (FV) and study sites	Specialization suggested by authors	
<i>Hypomacrotera</i> (3 species, SW USA to Mexico)	<i>C. (Hypomacrotera) persimilis</i> (Cockerell)	<i>Physalis</i> (Solanaceae) (P) ^{8,9}	PS (Animas, New Mexico, USA, mixed grassland adjacent to a cotton field) ⁹		
	<i>C. (Hypomacrotera) subalpina</i> (Cockerell)	<i>Sphaeralcea</i> (Malvaceae) ^{8,5}	FV (Douglas, Arizona, USA) ⁸		
<i>Micronomadopsis</i> (20 species, Western North America)	<i>C. (Micronomadopsis) snellingi</i> (Rozen)	<i>Salvia</i> (Lamiaceae) ¹¹	FV ¹¹	Subgenus oligolectic of <i>Trifolium</i> ⁷ . Many species are oligolectic ⁵	
	<i>C. beamerorum</i> (Rozen)	<i>Prosopis</i> ¹¹	FV ¹¹		
	<i>C. fracta</i> (Rozen)	<i>Eriodictyon</i> (Boraginaceae) ¹¹	FV ¹¹		
<i>Nomadopsis s.s.</i> (8 species) (the 5 species of <i>Macronomadopsis</i> were separately analyzed in this article) (Western North America)	<i>C. (Macronomadopsis) micheneri</i> (Rozen), <i>C. anthidia</i> Fowler, and <i>C. filiorum</i> (Rozen)	<i>Trifolium</i> (Fabaceae) (P) ¹¹	FV ¹¹	All <i>Macronomadopsis</i> species appear to be oligolectic of Fabaceae ¹⁰	
	<i>C. zebrata</i> Cresson	<i>Astragalus</i> (Fabaceae) (P) ¹¹	FV ¹¹		
	<i>C. (Nomadopsis) trifolii</i> (Timberlake)	<i>Mimulus</i> (Phrymaceae or Scrophulariaceae s.l.) (P) ¹¹	FV ¹¹		
<i>Perissander</i> (7 species, (SW USA to NW Mexico)	<i>C. zonalis sierrae</i> Cresson	<i>Monardella</i> (Lamiaceae) ¹¹	FV ¹¹	Subgenus oligolectic of <i>Euphorbia</i> ⁷	
	<i>C. (Perissander) anomoptera</i> Michener	<i>Euphorbia</i> (Euphorbiaceae) (six species), <i>Cladotrix</i> (Amaranthaceae), <i>Eriogonum</i> (Polygonaceae), <i>Lepidium</i> (Brassicaceae) and <i>Tidestromia</i> (Amaranthaceae) ⁶	2 PS (<i>Euphorbia</i>) ⁶ ; most FV on <i>Euphorbia</i> ⁶		Species principally on Euphorbiaceae ⁶
<i>Verbenapis</i> (4 species, USA and Mexico)	Other species	<i>Euphorbia</i> , <i>Tidestromia</i> and <i>Verbesina</i> ⁶	FV ⁶	Subgenus oligolectic of <i>Verbena</i> ⁷	
	<i>C. (Verbenapis) verbenae</i> Cockerell and Porter	<i>Verbena</i> (Verbenaceae), <i>Sphaeralcea</i> (Malvaceae) and <i>Chamaesaracha</i> (Solanaceae) ⁶	Most FV on <i>Verbena</i> ⁶ ; PS (mixed Verbenaceae and Fabaceae) ⁶		Species oligolectic of <i>Verbena</i> ⁶
	<i>C. (Verbenapis) hirsutifrons</i> Cockerell	<i>Verbena</i> , <i>Vernonia</i> (Asteraceae), <i>Ambrosia</i> (Asteraceae), <i>Asclepias</i> (Apocynaceae) and <i>Medicago sativa</i> (Fabaceae) ⁶	Most FV on <i>Verbena</i> ⁶		

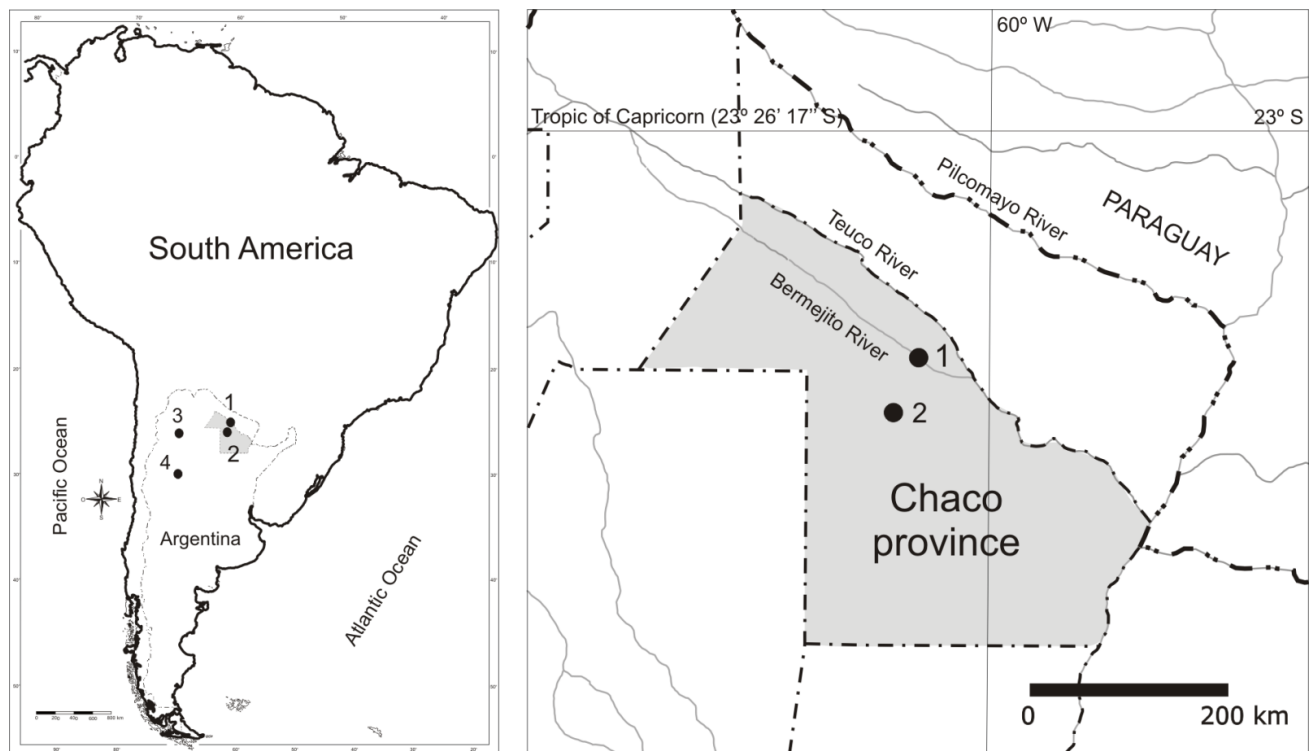


FIGURE 1. Study sites where pollen samples from nests (1-Villa Río Bermejito and 2-Juan José Castelli, both Chaco) and bee specimens of museum collections were taken (3-Amaichá del Valle (Tucumán) and 4-San Fernando del Valle de Catamarca (Catamarca)).

(2006). The relative abundance of flowers and flowering individuals as a whole was estimated and simply classified as I = rare, 2 = common, and 3 = highly abundant (Appendix II). All the entomophilous plants flowering within a radius of up to 100 m of the two nesting aggregations from the Chaco forest were recorded (Appendix II). Plants around the nests mainly belonged to riparian (site 1) and xerophilous forest vegetation (site 2), accompanied by alien plants (Fig. 1; Appendix II).

RESULTS

A total of 31 pollen samples from two nest aggregations and two museum specimens were analyzed. All samples consisted only of *Prosopis* pollen. Using light microscopy, two pollen types belonging to *Prosopis* could be distinguished: *Prosopis* type 1 had an exine <math><2</math> (mainly from 1 to 1.5) μm thick and a smooth or slightly scabrate wall sculpture (all Chaco and Tucumán samples) while *Prosopis* type 2 had an exine 1.5–3 μm thick and a strongly scabrate wall sculpture (the Catamarca sample). These two pollen morphologies belong to different sections of the genus *Prosopis* according to Caccavari (1972): pollen type 1 to *Algarobia* and type 2 to sections *Strombocarpa* (*P. abbreviata* Benth., *P. reptans* Benth., *P. strombulifera* (Lam.) Benth. and *P. torquata* (Lag.) DC.), *Cavenicarpa* (*P. ferox* Gris.) and *Monilicarpa* (*P. argentina* Burk.) (following the taxonomical classification of Burkart (1976)).

The fecal pollen of post-defecating larvae, found at the end of brood cells, consisted of collapsed *Prosopis* pollen grains (Fig. 2a).

A total of 83 and 44 melittophilous plant taxa belonging to 36 and 17 families were recorded around nesting areas during September 2008 and 2011, respectively (Appendix II). In the riparian forest at study site 1, most blooming species belonged to the families Asteraceae (20 taxa, mainly from tribe Heliantheae), Fabaceae (8 taxa, mainly from subfamily Mimosoideae), Verbenaceae (6 taxa), Solanaceae (5 taxa) and Bignoniaceae (4 taxa). In the xerophilous forest at study site 2, the major families were Fabaceae (14 taxa), Asteraceae (7 taxa), Capparidaceae (3 taxa), Verbenaceae (3 taxa) and Bignoniaceae (3 taxa). The most frequent growth habits were herbs in locality 1 (47 taxa), while trees or shrub-trees (17) were equally abundant as herbs (16) in locality 2. During the nesting period, flowers of *Prosopis alba*, *Albizia inundata*, *Leucaena leucocephala*, *Ziziphus mistol*, *Cissampelos pareira* and *Clematis montevidensis* were highly abundant in locality 1 within 20 to 50 m from the nests (Appendix II). In the xerophilous forest of locality 2, flowers of all *Prosopis* species (*P. alba*, *P. nigra*, *P. ruscifolia*, *P. vinalillo*, *P. elata* and *P. kuntzei*) and hybrids, as well as of three *Capparis* species, two Celastraceae, *Cercidium praecox*, *Castela coccinea* and *Ziziphus mistol* were abundant in close proximity to the nests (5 to 10 m) (Fig. 2b). A crop of *Melilotus albus* at flowering peak was also found in 4 m distance to the nests of locality 2. The *Prosopis* species found close to the nesting sites belong to section *Algarobia* (Burkart 1976) and have pollen grains of similar morphology (Caccavari 1972). Floral visits were recorded on *P. ruscifolia* and *P. alba* during a whole day (22nd September 2011), but *Calliopsis laeta* was only observed on *Prosopis alba*.

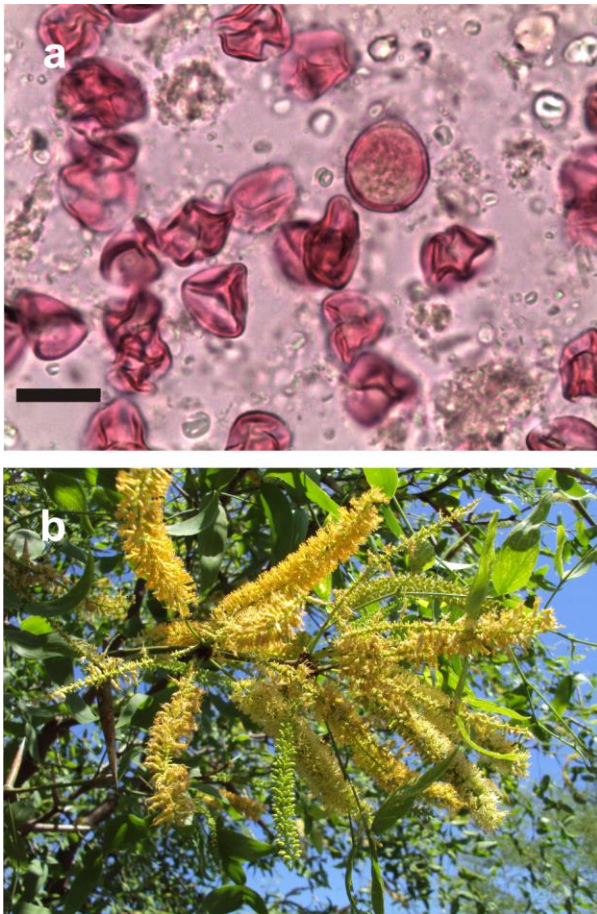


FIGURE 2. a) Collapsed pollen grains of *Prosopis* from feces of bee larvae. Unacetolyzed pollen grains dyed using fuchsine, seen in light microscope at 40 × magnification. Scale bar = 10 μm. b) Flowers of *Prosopis ruscifolia* at its flowering peak in early spring.

The examination of museum specimens revealed that *C. laeta* occurs in the dry Monte and Chaco regions of Argentina, from Salta and Formosa in the north to Mendoza and San Luis provinces in the south and that flight activity lasted less than a month. In Chaco sites, bees were active for two weeks in late September 2008 and only one week in late September 2011 (after 30 mm and 96 mm rain, respectively). From the dates recorded on the museum specimen from the Monte sites, it was concluded that bees were active from mid October to early November for females and up to 22nd November considering only males.

DISCUSSION

Prosopis as the only pollen host of *Calliopsis laeta*

Only *Prosopis* pollen was found in nest samples in spite of the presence of abundant alternative pollen hosts being available, such as *Melilotus*, *Capparis*, *Cercidium*, *Albizia* and others (Appendix II). Taking into account all examined samples throughout the geographic range of *Calliopsis laeta*, two pollen types belonging to *Prosopis* species were well distinguished using light microscopy. One of them belonged to *Prosopis* section *Algarobia* (Chaco and Tucumán samples) and the other to the sections *Strombocarpa*,

Cavenicarpa or *Monilicarpa* (the Catamarca sample). Therefore, pollen analysis of nests and museum specimens showed that *Calliopsis laeta* could be specialized in pollen collection from the genus *Prosopis* alone, suggesting that it is a *narrowly oligolectic* bee species. Although the low number of study populations (two museum specimens and two field studies) could indicate oligolectism, a broader sampling is necessary to ensure the character of specialization. *C. laeta* seems to be quite limited in its geographic distribution (only eight Argentine provinces), but occurs within the range of *Prosopis*, which could add to the hypothesis of oligolecty on this plant-host.

Most *Calliopsis* species have been identified as oligolectic (Tab. I). Yet, this categorization has mainly been based on floral visits. A large diversity of floral hosts has been recorded for each bee species demanding for further analyses to confirm the relationship of this genus with its pollen hosts. Moreover, as most of them have short to medium phenologies (up to 4 months) (Shinn 1967, see page 803) their presumably oligolecty can be due to a local specialization (i.e. variable according to location) typical of polylecty.

In a review of floral relationships of panurgine bees in Northeastern Brazil, Schlindwein (2003) highlighted that they have not been recorded visiting flowers of trees, but only herbs or small shrubs, and only in open areas (but not in tropical rainforest habitats). However, in other regions this bee group has also been associated to arboreal pollen hosts, such as *Prosopis* and *Salix* with *Perdita* in North America (Rozen 1967; Simpson et al. 1977), *Prosopis* with *Acamptopoeum* and *Calliopsis argentina* in South America (Simpson et al. 1977; Rozen & Yanega 1999).

After a 5-month autumn-winter unfavourable period of cold climate and drought, the first heavy rain commonly occurs between August and November (Appendix III). In the Chaco sites, emergence of the ground nesting *Calliopsis laeta* was observed after rain, presumably because of the rain softening the hard packed sandy loam soil making nest excavation possible. The shallow nests of *C. laeta* (of no more than 10 cm) appear to support this hypothesis. When the soil dried out, nest building (and provisioning) stopped even though *Prosopis* was still flowering. On the other hand, foraging activity of females and males was observed on *P. alba* when nesting had already stopped suggesting the presence of active nests outside the study area. This would indicate that soil moisture varies among microsites, such as shadowed areas in the forest vs sunny dirt roads, explaining the differences in duration of provisioning periods observed. Many *Prosopis* species are deep-rooted perennial phreatophytes which do not rely on rainfall but rather on changes in day length as the cue for floral initiation (Peacock & McMillan 1965; Simpson et al. 1977).

As different cues trigger both *Prosopis* blooming and the emergence of the ground nesting *Calliopsis*, synchronization between them might not occur. Nevertheless, even when triggers are different, the bee nesting and peak flowering of their pollen hosts overlap. The museum specimens examined from Tucumán and Catamarca, Western Argentina, had scopal loads composed only of *Prosopis*. These bees were

collected in early November, co-occurring with the single blooming period of *Prosopis flexuosa* and *P. chilensis* and the first flowering of *P. torquata* in this region (Simpson et al. 1977). During five field samplings carried out in the Chaco region during rainy episodes (September 2008 and 2011, late October, late November and early December 2008, see Vossler 2013), nest aggregations of *C. laeta* were only found in September (late winter - early spring) in both years when all *Prosopis* species (including their hybrids) were in their flowering peak. In both areas, bee phenology is triggered by the first rains, which in Western Chaco occur in spring (Appendix III), while in northern Monte first rain falls towards the end of spring but more often in summer (Cabrera 1976). Since all examined specimens were from the whole geographic distribution, its flight activity could be narrowed to a short period of no more than one month (from mid October to mid November in the Monte scrub and during late September in the Chaco forest), indicating its univoltine nature.

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APPENDICES

Additional supporting information may be found in the online version of this article:

APPENDIX I. Museum specimens examined from MACN entomological collection.

APPENDIX II. Available floral resources during the *Calliopsis* nesting period (September 2008 and 2011) in the Chaco forest.

APPENDIX III. Climate diagram from 2008 to 2010 for "Los Frentones" meteorological station (26° 22' 13" S, 61° 27' 34" W), Chaco province, Argentina.

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