A TIGHT RELATIONSHIP BETWEEN THE SOLITARY BEE CALLIOPSIS (CEROLIPOEUM) 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 oligolectic 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 Lasiosglossum, 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 Ogbobin (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).
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; Michelerre & 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 *Erenapis 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 parts 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, Liopoecoed and Liopoenum*), floral hosts of only three *Liopoenum* 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 (Jörgensen 1912; Ruiz 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-Amachá 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 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 × g for 5 minutes. Processing included Wiecholde (1935) and acetolysis methods (Erdtman 1960; Lieu 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 color similar to that obtained via the acetolysis method of Erdtman (1960). Pollen types were identified using a Nikon Eclipse E200 light microscope at 1000 × 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 1. 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 Weislo & Cane (1996); 8_ Rozen (1970); 9_ Danforth (1990); 10_ Rozen (2008); 11_ Rozen (1963); 12_ Weislo (1999); 13_ Vossler (in prep.); 14_ Michener (1954); 15_Robertson (1929). References: Pollen collection (P); nectar collection (N).

<table>
<thead>
<tr>
<th>No. of species</th>
<th>Bee species</th>
<th>Host-plant genus (plant family)</th>
<th>Pollen samples (PS)/floral visits (FV) and study sites</th>
<th>Specialization suggested by authors</th>
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<tbody>
<tr>
<td><strong>South American subgenus</strong></td>
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<tr>
<td>Ceroliopoeum (1 species endemic to Argentina)</td>
<td><em>C.</em> (<em>Ceroliopoeum</em>) <em>laeta</em> (Vachal)</td>
<td><em>Prosopis</em> (Fabaceae, Mimosoideae)</td>
<td>29 PS (Dry Chaco forest) and 2 PS (Monte desert)</td>
<td>Possibly narrowly oligolectic</td>
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<tr>
<td>Liopoeodes (1 species endemic to Argentina)</td>
<td><em>C.</em> (<em>Liopoeodes</em>) <em>xenopus</em> Ruz</td>
<td><em>Larrea</em> and <em>Bidensia</em> (Zygophyllaceae)</td>
<td>FV (two Argentinean sites from Catamarca and La Rioja provinces, Monte desert)</td>
<td>Polylectic</td>
</tr>
<tr>
<td>Liopoeum (5 species from Chile and Argentina)</td>
<td><em>C.</em> (<em>Liopoeum</em>) <em>argentina</em> (Jörgensen)</td>
<td><em>Adesmia</em> (Fabaceae, Papilionoideae)</td>
<td>31 PS (Dry Chaco forest), 3 PS (Monte desert) and 2 PS (Wet Chaco forest)</td>
<td>Polylectic with strong preference for <em>Prosopis</em></td>
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<td><strong>North and Central American subgenus</strong></td>
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<td><em>Calliopsis s. str.</em> (12 species, North and Central America to Panama)</td>
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<td></td>
<td>Subgenus narrowly polylectic. Subgenus widely polylectic, mostly on Fabaceae, especially the small-flowered clovers <em>Trifolium</em> and <em>Melilotus</em></td>
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<tr>
<td><em>C.</em> (<em>Calliopsis</em>) <em>andreniformis</em> Smith</td>
<td><em>Trifolium</em> and <em>Melilotus</em> (Fabaceae, Papilionoideae), <em>Malva</em> (Malvaceae) (P), Fabaceae, Asteraceae, Verbenaceae and Malvaceae (P and N)</td>
<td>17 PS (pure Fabaceae, pure Malvaceae or mixed Asteraceae and Malvaceae) and 98 FV</td>
<td>Possibly pollen specialist</td>
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<tr>
<td><em>C.</em> (<em>Calliopsis</em>) <em>honduristica</em> Cockerell</td>
<td><em>Aescyphonyme americana</em> (Fabaceae, Papilionoideae) in Panamá</td>
<td>PS (a nest population near Veracruz, Panamá, open field regularly mowed surrounded by deciduous tropical forest)</td>
<td>15 FV</td>
<td></td>
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<tr>
<td><strong>Other species</strong></td>
<td><em>Apocynaceae, Convolvulaceae, Asteraceae, Fabaceae, Oxalidaceae, Lamiaceae, Verbenaceae, etc.</em></td>
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<tr>
<td><em>Calliopsima</em> (15 species, Canada, USA and Mexico)</td>
<td><em>Heterotheca</em>, <em>Gasterariza</em>, <em>Baileya</em>, <em>Senecio</em>, <em>Solidago</em>, <em>Bidens</em>, <em>Boltonia</em>, <em>Coreopsis</em>, <em>Rudbeckia</em>, <em>Cirsium</em>, <em>Encelia</em>, <em>Hemizonia</em>, <em>Haplopappus</em>, <em>Grindelia</em>, <em>Verbena</em>, etc. (Asteraceae), <em>Melilotus albus</em> and <em>Medicago sativa</em> (Fabaceae)</td>
<td>FV</td>
<td>Primarily on the Asteraceae, particularly tribes Heliantheae and Astereae</td>
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<td><em>C.</em> (<em>Calliopsima</em>) <em>coloradensis</em> Cresson</td>
<td><em>Boltonia</em>, <em>Solidago</em>, <em>Bidens</em>, <em>Rudbeckia</em> and <em>Coreopsis</em> (P)</td>
<td>FV (Carlinville, Illinois, USA)</td>
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<td><em>C.</em> (<em>Calliopsima</em>) <em>rozenni</em> Shinn</td>
<td>Primarily on <em>Heterotheca subaxillaris</em></td>
<td>FV</td>
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TABLE 1, continued.

<table>
<thead>
<tr>
<th>No. of species</th>
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<th>Host-plant genus (plant family)</th>
<th>Pollen samples (PS)/ floral visits (FV) and study sites</th>
<th>Specialization suggested by authors</th>
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<tr>
<td><strong>Hypomacrotera</strong> (3 species, SW USA to Mexico)</td>
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<td></td>
<td>C. (Hypomacrotera) persimilis (Cockerell)</td>
<td>Physalis (Solanaceae) (P_s^{6,6})</td>
<td>PS (Animas, New Mexico, USA, mixed grassland adjacent to a cotton field)(^6)</td>
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<td>C. (Hypomacrotera) subalpina (Cockerell)</td>
<td>Sphaeralcea (Malvaceae)(^{6,6})</td>
<td>FV (Douglas, Arizona, USA)(^6)</td>
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<td><strong>Micronomadopsis</strong> (20 species, Western North America)</td>
<td>C. (Micronomadopsis) snelligi (Rozen)</td>
<td>Salvia (Lamiaceae)(^{7,1})</td>
<td>FV(^{7,1})</td>
<td>Subgenus oligolectic of <em>Trifolium</em>. Many species are oligolectic(^7)</td>
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<td>C. (Micronomadopsis) micheneri (Rozen), C. anthidia Fowler, and C. tiliorum (Rozen)</td>
<td>Trifolium (Fabaceae) (P_s^{7,1})</td>
<td>FV(^{7,1})</td>
<td>All <em>Micronomadopsis</em> species appear to be oligolectic of Fabaceae(^7)</td>
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<td>C. beamerorum (Rozen)</td>
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<td>C. fracta (Rozen)</td>
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<td>C. zebrata Cresson</td>
<td>Astragalus (Fabaceae) (P_s^{7,1})</td>
<td>FV(^{7,1})</td>
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<td>C. (Nomadopsis) trifoli (Timberlake)</td>
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<td></td>
<td>C. (Perissander) anomoptera Michener</td>
<td>Euphorbia (Euphorbiaceae) (six species), Cladostelus (Amaranthaceae), Erodogon (Polygonaceae), Lepidium (Brassicaceae) and Tidestromia (Amaranthaceae)(^8)</td>
<td>2 PS (Euphorbia)(^8); most FV on Euphorbia(^8)</td>
<td>Species principally on Euphorbiaceae(^8)</td>
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<td>FV(^8)</td>
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<td>C. (Nomadopsis s.s.) (8 species)</td>
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<td></td>
<td>C. zebrata Cresson</td>
<td>Monardella (Lamiaceae)(^{7,1})</td>
<td>FV(^{7,1})</td>
<td>Subgenus oligolectic of <em>Euphorbia</em></td>
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<td>C. hirsutifrons Cockerell</td>
<td>Verbena, Tidestromia and Verbesina (P_s)</td>
<td>FV(^8)</td>
<td>Subgenus oligolectic of <em>Verbena</em> (P_s)</td>
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<td>C. (Verbenapis) verbenae Cockerell and Porter</td>
<td>Verbena (Verbenaceae), Sphaeralcea (Malvaceae) and Chamaescarocha (Solanaceae)(^7)</td>
<td>Most FV on <em>Verbena</em>; PS (mixed Verbenaceae and Fabaceae)(^9)</td>
<td>Species oligolectic of <em>Verbena</em> (P_s)</td>
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<td>C. (Verbenapis) merriamis Cockerell</td>
<td>Verbena, Vernonina (Asteraceae), Anebrosis (Asteraceae), Asclepias (Apocynaceae) and Medicago sativa (Fabaceae)(^8)</td>
<td>Most FV on <em>Verbena</em> (P_s)</td>
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(2006). The relative abundance of flowers and flowering individuals as a whole was estimated and simply classified as 1 = 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 xerophylous 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 <2 (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.), Cavencarca (P. ferox Cris.) 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 montevideus 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, Ceridium 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 feaces 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 Medicago, 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, Cavuncarpa 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 oligolectry 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 oligolectry can be due to a local specialization (i.e. variable according to location) typical of polylectry.

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 Salta with Perdita in North America (Rozen 1967; Simpson et al. 1977). Prosopis with Acmatopoecum 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.

**References**


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