

NEST PROVISION AND POLLEN FORAGING IN THREE MEXICAN SPECIES OF SOLITARY BEES (HYMENOPTERA: APOIDEA)

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Abstract.—Pollen selection was determined by two methods for three ground-nesting bees: analysis of nest cell contents (provisions or feces), and of female pollen foraging records. *Ancylloscelis wheeleri* Cockerell and *Melitoma marginella* Cresson (Anthophoridae) were oligolectic on different genera of Convolvulaceae. The two methods differed in emphasis of particular hosts. *Mesoxaea nigerrima* Friese (Oxaeidae) had unrelated hosts in different months. As many as nine pollen species were found in a single cell, but the dominant pollen comprised at least 95% in most cells for all three bee species. Not all minor pollen species were clearly contaminants.

Resumen.—La selección de polen fue determinada por dos métodos para abejas que anidan en el suelo: el análisis del contenido de las celdas de los nidos (provisión o excremento), y la observación de hembras en pecoreo de polen. *Ancylloscelis wheeleri* Cockerell y *Melitoma marginella* Cresson (Anthophoridae), fueron oligolécticos sobre diferentes géneros de Convolvulaceae. Los dos métodos enfatizaron diferentes hospederos. *Mesoxaea nigerrima* Friese (Oxaeidae) tenía plantas hospederas no emparentadas en los diferentes meses. Se encontraron hasta nueve especies de polen por celda, pero el polen dominante comprendió al menos un 95% en la mayoría de las celdas para las tres especies de abejas. No todas las minoritarias parecieron ser contaminantes.

Key Words.—Insecta, feeding specialization, tropical deciduous forest, Convolvulaceae, Leguminosae, Tiliaceae

Pollen is a major nutritional source for most larval bees. The eusocial Apidae in general are highly polylectic (Kleinert-Giovannini & Imperatriz-Fonseca 1987, Lobreau-Callen et al. 1986) and their selection of pollen may be greatly affected by its abundance (Roubik et al. 1986). However, pollen from various plant species may vary demonstrably in nutritional value, as shown for *Apis mellifera* L. (Herbert et al. 1970) and for the solitary bee *Osmia lignaria* Say (Levin & Haydack 1957). The vast majority of bee species are solitary (Linsley 1958), and their host selection evolves quite distinctly from that of eusocial bees (Lobreau-Callen & Coutin 1987). In solitary species the repetition of particular host relations across isolated generations may represent a physiological link. For example, *Colletes fulgidus longiplumosus* Stephen females show a preference for the surface oils of the pollen on which they were reared (Dobson 1987).

The diversity of hosts varies greatly between species of solitary bees (Linsley 1958), and to a lesser extent among their populations (Linsley et al. 1963, Tasei

1976), among individuals (Michener & Rettermeyer 1956), and during or between seasons (Rust 1990). These variations are particularly difficult to quantify in habitats with low visibility of nesting areas, flight patterns and hosts. Hosts for pollen are usually described from observation of foraging females, and not from direct quantitative assessments of pollen types in the nest cells; the latter is an important tool for studying feeding specialization (Cripps & Rust 1989). In this paper, we apply both of these approaches to evaluate the pollen selectivity of populations of three solitary species from a single locality in neotropical deciduous forest.

MATERIALS AND METHODS

The site of this study was the Estación de Biología Chamela (19°30' N, 105°03' W) in the Pacific lowlands (10–150 m) of Mexico, where the rainy season is typically four months long (Bullock 1986) and the mean annual rainfall is 714 mm (1977–1990). The vegetation at this site is principally tropical deciduous forest, with a floristically distinct semideciduous forest along the larger seasonal watercourses (Lott et al. 1987). General collection of bees on flowers has been made sporadically since 1980 by resident and visiting scientists (principally SHB and RA). Tree phenology was reported by Bullock & Solis (1990); other plants were observed while collecting the flora and fauna.

The bees studied were *Ancyloscelis wheeleri* Cockerell and *Melitoma marginella* Cresson (Anthophoridae), and *Mesoxaea nigerrima* Friese (Oxaeidae). Closed nest cells of each species were collected in November 1986. *Ancyloscelis* and *Melitoma* were nesting in dense aggregations, so the individual cells collected may have been from various nests. The *Mesoxaea* nests were solitary. *Ancyloscelis* and *Mesoxaea* nests were active but *Melitoma* nests were already closed; the respective samples were 17 cells, five cells from two nests, and 11 cells. In October 1988, 15 cells were collected from closed nests of *Melitoma* and one from a closed nest of *Mesoxaea*.

The pollen samples were prepared by standard acetolysis methods. Percentage composition was determined from counts of 1000 grains from three mounts (Ramalho & Kleinert-Giovannini 1986). Volumetric measurements are not a clear solution to the related problem of nutritional values.

RESULTS

Ancyloscelis wheeleri. — Pollen of five plant species was found in nest provisions, including three species of Convolvulaceae. *Merremia quinquefolia* (L.) Hallier f. contributed 99.67%, and there were small amounts of an *Ipomoea* sp. (0.28%) and of *Jacquemontia nodiflora* (Desrousseaux) G. Don (0.05%). The other two pollen types were *Heliocarpus pallidus* Rose (Tiliaceae), 0.09%, and an unidentified Compositae, 0.02%. The latter two may have come from exploratory or nectar foraging, or may have been introduced as contaminants by the bees because these forms are commonly airborne (RPC & SHB, unpublished data).

The nesting and principal flight period is October and November, but we have found occasional individuals as late as April. Pollen-foraging females were collected on only three plant species: *M. quinquefolia*, *J. nodiflora* and *Ipomoea crinicalyx* Moore. Nectar-foraging individuals of one or both sexes were collected on five Convolvulaceae, one Acanthaceae and one Boraginaceae species.

Melitoma marginella.—The 1986 nest samples all showed only one form of pollen, most closely resembling reference material of *Ipomoea pedicellaris* Ben-tham.

In the 1988 sample, three species of *Ipomoea* were predominant: *I. pedicellaris*, *I. clavata* (G. Don) Oostroom and *I. wolcottiana* Rose. The most abundant species comprised 99% to 100% in eight cells (monospecific in *Ipomoea*), 87% to 97% in four cells, and 53.6% to 70.5% in three cells. As many as three *Ipomoea* species were present in only three cells. *Ipomoea nil* (L.) occurred only once (2.1%). Non-*Ipomoea* constituents in four cells were probably all contaminants introduced by the bees, including *Poeppigia procera* Presl (Leguminosae), an unidentified Po-aceae, and two species not present in the area of the Chamela station, *Alnus* sp. (Betulaceae) and *Pteris* sp. (Adiantaceae), which are distributed by wind. In all the samples of fecal material, the pollen grains were broken into many pieces.

The flight season was September and October, and again February and March; the life cycle remains problematic (GRG, unpublished data). Pollen-foraging females were collected on *Ipomoea muricata* Cavanillas, *I. nil* and *I. pedicellaris*. Nectar-foraging males were collected on *I. muricata*, *I. trifida* (HBK) G. Don, and on *I. wolcottiana* (Bullock et al. 1987).

Mesoxaea nigerrima.—A single pollen type dominated the November 1986 nest samples: *Heliocarpus pallidus* comprised 99.9%, although trace amounts of *Phaseolus* sp. and *Apoplanesia paniculata* Presl (both Leguminosae) appeared also. The 1988 sample was collected before *Heliocarpus* began to flower: the contents were dominated by *Schrankia diffusa* Rose (Leguminosae, 95.6%), which is a common vine and the most frequently observed host of foraging *Mesoxaea* females. Eight other species were present in this single cell provision: *Poeppigia procera* (1%), *Cassia* sp. (0.8%), and *Senna* sp. (0.8%) (all Leguminosae), *Doyerea emetocathartica* Grosourdy (Cucurbitaceae, 0.7%), *Serjania brachycarpa* A. Gray (Sapindaceae, 0.6%) and trace amounts of *Psidium sartorianum* (Berg) Niedenzu (Myrtaceae, 0.2%), *Cleome* sp. (Capparidaceae, 0.1%), and *Pedilanthus calcaratus* Schlechtendal (Euphorbiaceae, 0.1%).

The flight season extended from July through November. *Mesoxaea* was collected foraging on 11 species from four families (Leguminosae, Malpighiaceae, Sapindaceae and Tiliaceae). Females were observed collecting pollen from four mimosoid and one caesalpinoid legume species (*Mimosa brandegei* B. L. Robinson, *M. leptocarpa* Rose, *Piptadenia obliqua* (Persoon) MacBride, *Schrankia diffusa*, and *Apoplanesia paniculata*) and from *Heliocarpus pallidus*.

DISCUSSION

Hurd (1979: 2118, 2123) stated that all species of *Ancyloscelis* and *Melitoma* visit flowers of *Ipomoea* for pollen and nectar, but also visit a variety of other flowers for nectar. Our results confirm the *Melitoma*–*Ipomoea* association and extend its generality in terms of species, habitat and geography. *Ancyloscelis wheeleri*, however, is a specialist on Convolvulaceae but not on *Ipomoea* at Chamela, as far as our samples are representative. Both fit the restricted definition of oligolecty—"species that confine their pollen foraging to species within a genus"—suggested by detailed comparative study of provisions in seven *Osmia* species of a montane meadow (Cripps & Rust 1989: 136).

Intermingled nests of *M. marginella* and *A. wheeleri* (Hurd 1979) have not been

observed at Chamela, although large aggregations of each are known. Our finding that virtually all grains in the feces of *M. marginella* are highly fragmented is apparently unique.

Both these anthophorids have relatively brief flight seasons which may not exceed the flowering seasons of single host species. Yet their host specificity is rather remarkable because of the range of closely related plants available simultaneously. October and November are the months of peak flowering of Convolvulaceae at Chamela, typically including six genera and 23 species, with 16 species of *Ipomoea* (as currently revised).

Pollen hosts of oxaeids are reported from Solanaceae, Zygophyllaceae and Leguminosae, especially *Cassia* (Hurd & Linsley 1976, Camargo et al. 1984). Flowers in the former two families are common at Chamela during the flight period of *Mesoxaea nigerrima*, but there are no foraging or provision records. Foraging has not been observed on *Cassia* or *Senna* but these were minor species in one cell provision. The rarity of visits to buzz-pollinated plants at Chamela is conspicuous; the common pollen hosts were mimosoid legumes. Typical of Oxaeidae, *M. nigerrima* is a polylectic species, and several plant families may be present in any cell; however, one species is heavily dominant.

Mesoxaea change principal host within an individual female's (?) flight season. *Schrankia* flowers for several months starting about the same time as the flight season of *Mesoxaea*, but *Heliocarpus* has only a brief abundant flowering in October or November. The flower visitation records and our observations on other plant species clearly show that *Mesoxaea nigerrima* discriminates and is not simply dependent on flower-frequency in its host selection.

Little is known about the means of pollen host recognition in newly emerged solitary bees. Experiments with *Colletes fulgidus* showed that bees can recognize their host plant by the odor of its pollen, suggesting that larvae may be conditioned to volatile oils of pollen in their provision (Dobson 1987). This hypothesis might be appropriate in *M. marginella* and *A. wheeleri*. However, our data suggest that some *M. nigerrima* individuals begin collecting pollen on plants that are unrelated to their larval host.

The actual host range in a bee population at any one time may be significantly greater than we could sample. Certainly the data indicate that generally only one host species is used over several to many foraging trips, over periods of days, and among neighboring females in *Ancyloscelis*. Any one larva of any of these species is unlikely to experience more than a one percent admixture of a second pollen type in its provision, and the combined percentage of secondary species exceeded five percent only in some cells of *M. marginella*.

Both flower visitation records and palynological analysis of nest contents have limitations in terms of optimum sampling—particularly in forests and for ground-nesting bees. In the present case the contribution of pollen analysis is in the quantification of the purity, or lack of it, in the provisions for individual bees. Observation of foraging females had not missed any major hosts. But in a forest habitat, following an individual bee throughout a single foraging trip, or during several trips or days, is virtually impossible.

The presence of pollen species other than the principal hosts may be attributable to several causes. Of considerable importance are the opportunities for contamination of the bee's pollen load. Foreign grains may be added to flowers of a given

species through the visits of more polylectic insects, somewhat analogous to intra-hive inter-bee transfer of pollen (DeGrandi-Hoffman et al. 1986). Also, airborne pollen is ubiquitous and remarkably diverse (Palacios 1985; RPC & SHB, unpublished data) which will also contact the bees via soil, leaves, etc. However, the most important causes are probably the admixture of pollen from plants visited for nectar, and from exploratory visits by bees to potential alternate resources (Heinrich 1979, Cripps & Rust 1989).

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