ARE OLIGOLECTIC BEES ALWAYS THE MOST EFFECTIVE POLLINATORS?

In: Freitas, B. M., Pereira, J. O. P. (eds.). 2004.
Solitary bees. Conservation, rearing and management for pollination.
Fortaleza, Imprensa Universitária. 285p.
ISBN 85-7485-049-7

Clemens Schlindwein

Introduction

Bee-plant community studies always reveal a big difference in the number of relationships which the surveyed bee species show to the plant species of the community. While highly eusocial bees seem to not discriminate among melittophilous species - in Brazilian studies worker bees of *Trigona spinipes* and *Apis mellifera* visit flowers of up to more than 50 % of the local melittophilous flora - other bee species show relationships restricted to a few or locally only one plant species (see for example Aguiar *et al.,* 1995; Schlindwein, 1998; Wilms, 1995; Alves-dos-Santos, 1999; Aguiar, 2003; Moura, 2003). It is to be expected that these oligolectic species, which feed their larvae with pollen of only a few plant species of the same genus or family, show morphological and behavioral adaptations to collect pollen from these flowers more efficiently than polylectic species. Then, the oligolectic species would have an advantage over their generalist competitors. When both partners, oligolectic bee and plant, show adaptations and benefit from the close relationship, the interaction may be the result of co-evolution. Effective pollen transfer to stigmas is directly related to the reproductive success of the plant. Therefore, selection may have favored relationships with those pollen collecting bees that are effective pollinators. Are oligolectic bees, in fact, effective pollinators of their specific food plants and better pollinators than polylectic bees? Here is given an overview of the oligolectic bee species of Brazil and information on their effectiveness as pollinators.

Oligolectic bees in Brazil

Information on oligolecty in the Brazilian bee fauna is still riddled with gaps. In most cases it is deduced from bee-plant community studies and detailed information on the relationship between the partners and especially on pollinator effectiveness of the oligolectic species is limited to a few case studies.

Oligolectic bees occur in 12 tribes: especially Andrenidae-Panurginae, non-corbiculate Apidae, and Colletidae-Paracolletini (Table 1). All oligolectic species are solitary. Oligolecty is most common in Onagraceae (*Ludwigia*: 10 bee species), Cactaceae (8 bee spp.), Malvaceae (8), Pontederiaceae (*Eichhornia, Pontederia:* 7), Asteraceae (7), Convolvulaceae (*Ipomoea:* 5), Apiaceae (*Eryngium:* 3), Iridaceae (*Sisyrinchium:* 3), Loasaceae (*Cajophora-Blumenbachia:* 3), Oxalidaceae (*Oxalis:* 3) and Solanaceae (*Petunia-Calibrachoa:* 3). Monocotyledons are only represented by Pontederiaceae and Iridaceae.

The plant species related to oligolectic bees are nearly exclusively herbs and shrubs. The only exceptions are *Jacaranda* and *Tabebuia* trees: their flowers are visited by males and females of the oligolectic monotypic *Niltonia virgilii* (Colletidae, Paracolletini) besides numerous medium- to large-sized polylectic species (Laroca and Almeida, 1985).

Numerous species of food plants of the oligolectic bees are common at ruderal sites in Brazil like *Sida, Ludwigia, Ipomoea, Eryngium, Sisyrinchium, Oxalis, Petunia, Turnera* and Asteraceae species. An adequate habitat management, therefore, may increase the local bee diversity.

Distribution of oligolectic bees in Brazil

The surveys of bee-plant communities in Brazil indicate that the number of oligolectic species increases from Northern to Southern Brazil. In various regions with a short favorable season, oligolectic bees are species-rich (Michener, 1979; Feinsinger, 1983; Westrich, 1989). Partitioning of the abundant pollen resources among specialized bees, which are able to locate and explore the floral resources more efficiently than polylectic species, may be a reason for the high diversity of oligolectic species in these regions. However, this is not the case for the highly seasonal *caatinga*, a succulent, thorn-shrub savannah with deciduous leaves occurring in NE-Brazil and the Central Brazilian *cerrado*, a tree-grass savannah with evergreen sclerophyllous leaves (see compilation of bee species in Silveira and Campos, 1995; Zanella, 2000; Zanella and Martins, 2003). Tropical rainforests seem to house only a few species of oligolectic bees. However, there have been only a few studies and information on the bee fauna, especially in the canopy, is scarce. In these habitats, bees of the genera *Centris* and *Euglossa* (Apidae) are very common. They are not oligolectic but show preferences to collect pollen from poricidal anthers (Buchmann, 1983) and nectar from flowers with long corolla tubes, as well as visit oil flowers, perfume flowers and resin flowers. These bees are highly effective pollinators of numerous plant species and may have a key role as pollinators in neotropical ecosystems (Schlindwein, 2000). In addition, stingless bees are very abundant in these tropical ecosystems. This could be the reason for the small number of oligolectic species. In Southern Brazil, the apifauna shows a strong influence of temperate elements: Paracolletini and Panurginae, which are mainly oligolectic, are common in Southern South America and various species show their northern distributional limits in Southern Brazil (Schlindwein, 1998; Alves-dos-Santos, 1999).

Oligolectic bees as pollinators

With the exception of *Sisyrinchium*, which in addition to pollen offers floral oil to the females of *Lanthanomelissa*, all plants that attract oligolectic species are also nectar resources (Table 1). This might prevent the pollen-collecting females from looking for nectar in other flowers, thereby enhancing their flower constancy and, furthermore, also attracting the males to visit these flowers. In almost all cases the male bees patrol the flowers searching for females (Table 1). Alves-dos-Santos (2002) stresses the contribution of patrolling males of oligolectic bees to cross pollination: the males are highly flower-constant, visit often just a few flowers on an individual plant, carry pollen in small quantities, generally touch the stigmas during their legitimate visits, show higher frequencies of flower visits than females, and often perform large transects during their patrolling trips.

In several species, however, *e.g.* in the Emphorini *Ptilothrix fructifera, P. plumata, Ancyloscelis apiformis, A. fiebrigi, A. gigas, Melitoma segmentaria,* and *Melitomella grisescens*, copulation in the flowers is extremely rare in spite of the abundant presence of females. Perhaps females of these species copulate only during a short period after hatching. Alternatively, males of these species may look for females at their nesting sites.

Numerous plant species visited by oligolectic bees have extraordinarily large pollen grains, *e.g.* those of *Ludwigia, Pavonia, Sida, Opuntia* and *Ipomoea* which require a specialized scopa of long, unbranched bristles (Thorp, 1979; Gimenes, 1991) and adapted pollen handling. In the flowers of two *Opuntia* species in S-Brazil, for instance, females of most of the numerous polylectic species collected exclusively nectar, while the oligolectic bees *Ptilothrix fructifera* and *Lithurgus rufiventris* collected most of the produced *Opuntia* pollen and were the most effective pollinators (Schlindwein and Wittmann, 1997a).

Other morphological adaptations are found in females of *Ancyloscelis gigas, A. ursinus* and *A. turmalis* which show hooked hairs on their proboscis, appropriate to collect hidden pollen from short-level anthers in the long flower tubes of tristylous *Eichhornia* and *Pontederia* spp. (Alves-dos-Santos and Wittmann, 1999, 2000; Alves-dos-Santos, 2003). These oligolectic bees are the most effective pollinators of these flowers, especially for the short-styled morphs. Moreover, with their extraordinarily long proboscides these bees reach the nectar in the long flower tubes. Very long mouthparts occur also in the "short-tongued" *Niltonia* bees who show unusual prolonged labial palpi involved in nectar uptake from the base of the nectar chamber of *Jacaranda* and *Tabebuia* flowers. Prolonged labial palpi are also found in the related *Hexantheda missionica, H. eneomera* and *Albinapis gracilis* which also are oligolectic on flowers with nectar chambers (*Petunia* spp., *Calibrachoa* spp.) or a deep, funnel-shaped corolla (*Oxalis* spp.), respectively.

A highly specialized foraging strategy characterizes the oligolectic females of *Bicolletes pampeana* in S-Brazil. They establish micro-foraging routes among annual herbs of *Blumenbachia* and *Cajophora* (Loasaceae) to collect pollen liberated in small portions after stimulation of unique nectar scales during the previous flower visit (Schlindwein and Wittmann 1997b; Schlindwein, 2000b). *Bicolletes pampeana* is the most effective pollinator of these Loasaceae species and competes only with females from a second species of the genus (B. franki). Polylectic competitors do not occur.

The pollination studies performed in Brazil that involve oligolectic species show that these bees are always effective pollinators. Several case studies carried out in species of *Opuntia, Parodia, Gymnocalycium, Pavonia, Eichhornia, Pontederia, Ipomoea, Merremia, Ludwigia* and *Petunia* (see references in Table 1) point out that oligoleges are the most effective pollinators. This corroborates the experiences of Neff and Simpson (1992). Nevertheless, in some cases oligolectic bees are not better pollinators than polylectic bees (Feinsinger, 1983; Neff and Simpson, 1992; Michener, 2000). In Paraíba, NE-Brazil, the seed- and fruit-set of a population of distylic *Turnera subulata* remained high in the absence of its narrowly oligolectic pollinator *Protomeliturga turnerae.* The introduced *Apis mellifera* and other polylectic species were no worse pollinators than *P.turnerae* (Medeiros and Schlindwein, n. publ.). Oligolectic pollen-thieves like those visiting sphingophilous flowers of *Oenothera* (Onagraceae) (Gregory, 1963-64 *apud* Feinsinger, 1983), or females of *Perdita texana* (Andrenidae) which complete a pollen load in one flower visit (Barrows *et al.*, 1976; Neff and Danforth, 1992) are not yet reported among Brazilian oligolectic species.

Acknowledgements

I thank Scott Heald (Cornell University) for revising the text.

Table 1. Oligolectic species recorded in Brazil and their related food plants
(Aguiar and Martins, 1994 (1); Alves-dos-Santos, 1999 (2) - *Actenosigynes fulvoniger* as *Leioproctus fulvoniger*, *Hexantheda eneomera* as *H. petuniae;* Alves-dos-Santos, 2002 (3); Alves-dos-Santos and Wittmann, 1999 (4); Alves-dos-Santos and Wittmann, 2000 (5); Ducke, 1912 (6); Gaglianone, 1999 (7); Gaglianone, 2000 (8); Gimenes, 1991 (9); Hurd and Linsley, 1966 (10); Laroca and Almeida, 1985 (11); Medeiros and Schlindwein, 2003 (12); Morato and Campos, 2000 (13); Pinheiro and Schlindwein, 1998 (14); Schlindwein, 1998 (15) - *Albinapis gracilis* as *"Pentantheda"* sp.; Schlindwein n. publ. (16); Schlindwein, 2000b (17); Schlindwein and Martins, 2000 (18); Schlindwein and Moure, 1998 (19); Schlindwein and Wittmann, 1995 (20); Schlindwein and Wittmann, 1997a (21); Schlindwein and Wittmann, 1997b (22); Silva-Pereira *et al.*, 2003 (23); Silveira *et al.*, 2002 (24); Stehmann and Semir, 2001 (25); Vieira and Lima, 1997 (26); Wittmann *et al.*, 1990 (27); Wittmann and Schlindwein, 1995 (28); Zanella, 2000 (29).

Bee species	Related plants	Nectar collection	Patrolling males	effective pollinator	Reference
ANDRENIDAE					
PROTANDRENINI					
Anthrenoides meridionalis (Schrottky, 1906)	*Oxalis* (Oxalidaceae)	yes	yes	?	2,15
Cephalurgus anomalus Moure and Oliveira, 1962	*Gaya, Modiolastrum, Sida, Wissadula* (Malvaceae)	yes	yes	yes	7
Panurgillus flavitarsis Schlindwein and Moure, 1998	*Ludwigia* (Onagraceae)	yes	?	?	2, 19
Panurgillus formosus Schlindwein and Moure, 1998	*Eryngium* (Apiaceae)	yes	no	?	15,19
Panurgillus hamatus Schlindwein and Moure, 1998	*Acicarpha* (Calyceraceae)	yes	?	?	2,19
Panurgillus malvacearum Schlindwein and Moure, 1998	*Abutilon, Modiolastrum* (Malvaceae)	yes	no	?	15,19
Panurgillus minutus Schlindwein and Moure, 1998	*Eryngium* (Apiaceae)	yes	no	?	2,19
Panurgillus pereziae Schlindwein and Moure, 1998	*Pamphalea, Perezia* (Asteraceae)	yes	yes	?	15,19
Panurgillus plumosulus Schlindwein and Moure, 1998	*Oxalis* (Oxalidaceae)	yes	no	?	15,19
Panurgillus reticulatus Schlindwein and Moure, 1998	*Oxalis* (Oxalidaceae)	yes	no	?	2,15,19
Panurgillus vagabundus (Cockerell, 1918)	*Abutilon, Modiolastrum Sida* (Malvaceae)	yes	no	?	15,19
PROTOMELITURGINI					
Protomeliturga turnerae (Ducke, 1907)	*Turnera* (Turneraceae)	yes	yes	yes	6,12
CALLIOPSINI					
Arhysosage cactorum Moure, 1999	*Parodia, Gymnocalycium, Opuntia* (Cactaceae)	yes	yes	yes	15,20,21
Callonychium petuniae Cure and Wittmann 1990	*Petunia* (Solanaceae)	yes	yes	yes	2,15,27
APIDAE					
EMPHORINI					
Ancyloscelis apiformis (Fabricius, 1793)	*Ipomoea, Merremia* (Convolvulaceae)	yes	yes	yes	2,3,4,15
Ancyloscelis fiebrigi Brèthes, 1909	*Gymnocalycium, Opuntia, Parodia,* (Cactaceae)	yes	yes	yes	2,4,15,20
Ancyloscelis gigas Friese, 1904	*Eichhornia* (Pontederiaceae)	yes	yes	yes	2,3,4,5,15

Ancyloscelis turmalis Vachal, 1904	*Pontederia* (Pontederiaceae)	yes	yes	yes	2,4,15
Ancyloscelis ursinus Haliday, 1836	*Pontederia* (Pontederiaceae)	yes	yes	yes	2,4,15
Diadasina distincta (Holmberg, 1903)	*Ludwigia* (Onagraceae)	yes	?	?	2
Diadasina riparia (Ducke, 1908)	*Ludwigia* (Onagraceae)	yes	?	?	2,15
Melitoma ipomoearum (Ducke, 1913)	*Ipomoea* (Convolvulaceae)	yes	?	?	29
Melitoma segmentaria (Fabricius, 1804)	*Ipomoea* (Convolvulaceae)	yes	yes	yes	2,3,14,15
Melitomella grisescens (Ducke, 1907)	*Ipomoea* (Convolvulaceae)	yes	?	?	29
Melitomella murihirta (Cockerell, 1912)	*Ipomoea* (Convolvulaceae)	yes	?	?	29
Ptilothrix fructifera (Holmberg, 1903)	*Opuntia* (Cactaceae)	yes	yes	yes	15,17,21
Ptilothrix plumata Smith, 1853	*Pavonia* (Cactaceae)	yes	yes	yes	3,18
Ptilothrix relata (Holmberg, 1903)	*Ludwigia* (Cactaceae)	yes	?	?	2,15
EUCERINI					
Florilegus condignus (Cresson, 1878)	*Pontederia* (Pontederiaceae)	yes	?	?	15
Florilegus festivus (Smith, 1854)	*Pontederia* (Pontederiaceae)	yes	yes	yes	2,3
Florilegus fulvipes (Smith, 1854)	*Eichhornia*, *Pontederia* (Pontederiaceae)	yes	yes	yes	2,3,5,15
Florilegus riparius Ogloblin, 1955	*Pontederia* (Pontederiaceae)	yes	yes	yes	2,
Gaesischia fulgurans (Homberg, 1903)	*Vernonia* (Asteraceae)	yes	?	?	2
Gaesischia nigra Moure, 1948	*Vernonia* (Asteraceae)	yes	?	?	2
Gaesischia sparsa (Brèthes, 1910)	*Vernonia* (Asteraceae)	yes	?	?	2
Gaesischia trifasciata Urban, 1968	*Vernonia* (Asteraceae)	yes	?	?	2,15
Melissoptila bonaerensis (Holmberg, 1903)	*Abutilon*, *Modiola*, *Modiolastrum* *Wissadula* (Malvaceae)	yes	?	?	2,15
Melissoptila fiebrigi Brèthes, 1909	*Abutilon* (Onagraceae)	yes	?	?	2
Melissoptila paraguayensis (Brèthes, 1909)	*Ludwigia* (Onagraceae)	yes	?	?	2
Melissoptila thoracica Smith, 1854	*Sida* (Malvaceae)	yes	yes	yes	8,23
Melissoptila cnecomala (Moure, 1944)	*Sida*, *Malvastrum* (Malvaceae)	yes	no	yes	13
Peponapis fervens (Smith, 1879)	*Cucurbita* (Cucurbitaceae)	yes	?	yes	10
Santiago mourei Urban, 1989	*Vochysia* (Vochysiaceae)	?	?	?	24
TAPINOTASPIDINI					
Lanthanomelissa clementis Urban, 1995	*Sisyrinchium* (Iridaceae)	no	no	yes	15
Lanthanomelissa discrepans Holmberg, 1903	*Sisyrinchium* (Iridaceae)	no	no	yes	15
Lanthanomelissa pampicola Urban, 1995	*Sisyrinchium* (Iridaceae)	no	?	?	15
COLLETIDAE					
PARACOLLETINI					
Actenosigynes fulvoniger (Michener, 1989)	*Cajophora* (Loasaceae)	yes	yes	yes	2,17,28
Albinapis gracilis Urban and Graf, 2000	*Oxalis* (Oxalidaceae)	yes	yes	yes	15
Bicolletes pampeana Urban, 1995	*Blumenbachia*, *Cajophora* (Loasaceae)	yes	yes	yes	15,22,28
Bicolletes franki (Friese, 1908)	*Blumenbachia*, *Cajophora* (Loasaceae)	yes	yes	yes	15,22,28
Cephalocolletes isabelae Urban, 1995	*Opuntia* (Cactaceae)	yes	yes	?	2,17
Cephalocolletes rugata Urban, 1995	*Opuntia* (Cactaceae)	yes	yes	yes	15,21
Hexantheda eneomera Urban and Graf, 2000	*Petunia* (Solanaceae)	yes	yes	?	2,16
Hexantheda missionica Ogloblin, 1948	*Calibrachoa*, *Petunia* (Solanaceae)	yes	yes	yes	2,25

Niltonia virgilii Moure, 1964	*Jacaranda, Tibouchina* (Bignoniaceae)	yes	?	?	11
Nomiocolletes arnaui Moure, 1949	*Eryngium* (Apiaceae)	?	no	?	15
Perditomorpha brunerii Ashmead, 1899	*Abutilon, Sida, Malvastrum* (Malvaceae)	yes	yes	yes	7,15
Protodiscelis echinodori Melo, 1996	*Echinodorus* (Alismataceae)	?	?	?	26
Sarocolletes guaritarum Urban, 1995	*Abutilon, Modiolastrum* (Malvaceae)	yes	yes	?	15
Tetraglossula anthracina (Michener, 1989)	*Ludwigia* (Onagraceae)	?	?	?	2
Tetraglossula bigamica (Strand, 1910)	*Ludwigia* (Onagraceae)	yes	yes	yes	2,9,15
HALICTIDAE					
HALICTINI					
Pseudagapostemon brasiliensis Cure, 1989	*Ludwigia* (Onagraceae)	yes	yes	?	2,3
Pseudagapostemon pruinosus Moure and	*Ludwigia* (Onagraceae)	yes	yes		
ROPHITINAE					
Ceblurgus longipalpis Urban & Moure, 1993	*Cordia* (Boraginaceae)	yes	yes	?	1
MEGAHILIDAE					
ANTHIDINI					
Gnathanthidium sakagamii Urban, 1992	*Cuphea*, (Lythraceae)	yes	yes	?	15
Hypanthidium flavomarginatum (Smith, 1897)	*Cuphea* (Lythraceae)	yes	yes	?	2,15
LITHURGINI					
Lithurgus rufiventris Friese, 1908	*Opuntia* (Cactaceae)	yes	yes	yes	15
Microthurge pygmaeus (Friese, 1908)	*Abutilon, Krapovickasia, Modiolastrum, Sida, Sphaeralcea* (Malvaceae)	yes	yes	?	15
MEGACHILINI					
Megachile apicipennis Schrottky, 1902	*Senecio, Vernonia* (Asteraceae)	yes	?	?	2,15
Megachile brasiliensis Dalla Torre, 1896	*Ludwigia* (Onagraceae)	yes	?	?	2
Megachile nigropilosa Schrottky, 1902	*Elephantopus, Vernonia* (Asteraceae)	yes	?	?	2,15

Niltonia virgilii Moure, 1964	*Jacaranda, Tibouchina* (Bignoniaceae)	yes	?	?	11
Nomiocolletes arnaui Moure, 1949	*Eryngium* (Apiaceae)	?	no	?	15
Perditomorpha brunerii Ashmead, 1899	*Abutilon, Sida, Malvastrum* (Malvaceae)	yes	yes	yes	7,15
Protodiscelis echinodori Melo, 1996	*Echinodorus* (Alismataceae)	?	?	?	26
Sarocolletes guaritarum Urban, 1995	*Abutilon, Modiolastrum* (Malvaceae)	yes	yes	?	15
Tetraglossula anthracina (Michener, 1989)	*Ludwigia* (Onagraceae)	?	?	?	2
Tetraglossula bigamica (Strand, 1910)	*Ludwigia* (Onagraceae)	yes	yes	yes	2,9,15
HALICTIDAE					
HALICTINI					
Pseudagapostemon brasiliensis Cure, 1989	*Ludwigia* (Onagraceae)	yes	yes	?	2,3
Pseudagapostemon pruinosus Moure and	*Ludwigia* (Onagraceae)	yes	yes		
ROPHITINAE					
Ceblurgus longipalpis Urban & Moure, 1993	*Cordia* (Boraginaceae)	yes	yes	?	1
MEGAHILIDAE					
ANTHIDINI					
Gnathanthidium sakagamii Urban, 1992	*Cuphea*, (Lythraceae)	yes	yes	?	15
Hypanthidium flavomarginatum (Smith, 1897)	*Cuphea* (Lythraceae)	yes	yes	?	2,15
LITHURGINI					
Lithurgus rufiventris Friese, 1908	*Opuntia* (Cactaceae)	yes	yes	yes	15
Microthurge pygmaeus (Friese, 1908)	*Abutilon, Krapovickasia, Modiolastrum, Sida, Sphaeralcea* (Malvaceae)	yes	yes	?	15
MEGACHILINI					
Megachile apicipennis Schrottky, 1902	*Senecio, Vernonia* (Asteraceae)	yes	?	?	2,15
Megachile brasiliensis Dalla Torre, 1896	*Ludwigia* (Onagraceae)	yes	?	?	2
Megachile nigropilosa Schrottky, 1902	*Elephantopus, Vernonia* (Asteraceae)	yes	?	?	2,15

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