

# A COMPARISON OF THE DIVERSITY, DENSITY, AND FORAGING BEHAVIOR OF BEES AND WASPS ON AUSTRALIAN *ACACIA*<sup>1</sup>

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## ABSTRACT

Twenty-seven bee taxa and 24 wasp taxa were collected on the open inflorescences and/or extra-floral nectaries of eight *Acacia* species in Victoria, Australia. Despite this superficial similarity in taxonomic diversity, bees outnumbered wasp foragers by 88% of the combined catch of winged Hymenoptera. Representatives from five families of bees were recorded, with the short-tongued Halictidae and Colletidae comprising the largest unit of native Apoidea on the *Acacia* species studied. Pollen foraging female bees of the genera *Lasioglossum* (Halictidae) and *Leioproctus* (Colletidae) comprised 83% of the combined catch of the two short-tongued families. The number of bee taxa collected on the *Acacia* species tended to increase from late winter through late autumn. Polylectic foraging bee taxa expanded from mid spring through late summer when the flowering of nectariferous Myrtaceae peaked. There was no correlation between the density and diversity of bees foraging on *Acacia* species bearing secreting extra-floral nectaries and those species that lacked extra-floral nectar while the inflorescences were blossoming. Representatives of seven families of wasps were collected on the eight *Acacia* species. No wasps, however, were collected on var. *retinodes* of *A. retinodes*. Approximately 66% of the wasps collected belonged to the families Sphecidae and Tiphiidae. Wasps repeatedly foraged on extra-floral nectar before foraging on nectarless inflorescences. The density and taxonomic diversity of wasps remained highest on the *Acacia* species that offered the greatest volume of sucrose-rich, extra-floral nectar (i.e., *A. terminalis*). Bees are probably more important pollinators of *Acacia* in southeastern Australia than are wasps. The direct influence of wasps on polyad dispersal appears to be nominal except in those *Acacia* species bearing functional extra-floral nectaries.

Winged Hymenoptera (bees and wasps) have been observed to forage frequently on inflorescences of Australian *Acacia*. In contrast to the Psyllidae and some Coleoptera, bees and non-parasitic wasps are not destructive to the small flowers that comprise an *Acacia* head or spike (Bernhardt, 1982). Instead evidence suggests that Hymenoptera are often pollinators of some *Acacia* species in southeastern Australia (Bernhardt, 1982; Bernhardt et al., 1984; Knox et al., 1985).

The flowers of all Australian *Acacia* examined thus far are nectarless (Bernhardt, 1982; Bernhardt et al., 1984; Bernhardt & Walker, 1984, 1985; J. Kenrick & G. Beresford, pers. comm.). The pollen grains, which are fused together to form polyads, are the primary edible reward. When the anthers dehisce the eight polyads present in each anther are extruded, or partially extruded, from their respective sacs (Kenrick &

Knox, 1979; Knox & Kenrick, 1982). Consequently, bees, wasps, and certain flies easily collect polyads from the synchronously opening florets in an inflorescence.

Female bees are known to collect *Acacia* polyads to feed to their larvae. Foraging bees remove polyads from the anthers via thoracic vibration of whole inflorescences (Buchmann, 1983) or by scraping anthers directly with their forelegs (Vogel, 1978), or both (Bernhardt & Walker, 1984, 1985). *Acacia* species are usually self-incompatible. Seed set tends to occur only when pollinators move between genotypes belonging to the same species (Knox & Kenrick, 1982; Bernhardt et al., 1984; Kenrick et al., 1984b).

Capture records of insects foraging on *Acacia* in southeastern Australia and analyses of their pollen loads suggest that Hymenoptera are often more important as polyad vectors than are either

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beetle or fly taxa. Calliphorid and syrphid flies transport polyads from *Acacia* inflorescence to inflorescence without damage, but they may occur on *Acacia* inflorescences at lower density and diversity than Hymenoptera (Bernhardt et al., 1984; Knox et al., 1985).

Excluding the rare documentation of pollination by birds or marsupials (see review by Turner, 1982; Knox et al., 1985) the flowering behavior, floral presentation, and polyad presentation of most *Acacia* species would be expected to favor a system of generalist entomophily (Bernhardt, 1982; Bernhardt et al., 1984). That is, all insects that forage for polyads have immediate access to the inflorescences of *Acacia* and could effect deposition of polyads on respective stigmas.

Therefore the purpose of this study was to determine which groups within the Hymenoptera were major vectors of *Acacia* polyads with sufficient fidelity to regularly effect seed set. To accomplish this end the density and taxonomic diversity of polyad foragers were compared to their respective activities on *Acacia* inflorescences.

#### MATERIALS AND METHODS

*Acacia* species and study sites. Eight *Acacia* were selected to determine interspecific and intraspecific foraging preferences of Hymenoptera. The species of *Acacia* may be found in flower throughout the year (Kenrick et al. 1984a, 1984b; Bernhardt, 1982) with the majority flowering from August through October (Costermans, 1983). Therefore the eight selected species represented the 12-month flowering season of the genus but emphasized the period of intensively overlapping floral phenology from the last month of winter (August) until the second month of spring (October). The periods of fieldwork, study sites, and habitats of each *Acacia* species are listed below. Descriptions of floristic alliances follow Specht and colleagues (1979).

- 1) *Acacia longifolia* Willd. 31/viii/84–28/ix/84. Langwarren Reserve: Tall shrubland with disrupted epacrid heath (Bernhardt, 1986).
- 2) *A. mearnsii* De. Wild. 8/xi/84–21/xi/84. Coranderrk Reserve: Moist sclerophyll woodland/shrubland (see Bernhardt & Calder, 1981).
- 3) *A. mitchellii* Benth. 16/vii/82–21/i/83. Brisbane Ranges National Park: Dry sclerophyll woodland/shrubland (see Bernhardt & Walker, 1984).
- 4) *A. myrtifolia* Willd. 19/viii/82–7/x/82. Brisbane Ranges National Park: Dry sclerophyll woodland/shrubland (see Bernhardt & Walker, 1984).
- 5) *A. paradoxa* DC. (syn. *A. armata* R. Br.). 12/ix/84–31/x/84. Brisbane Ranges National Park: Dry sclerophyll woodland/shrubland (see Bernhardt and Walker, 1984).
- 6) *A. pycnantha* Benth. 11/viii/82–16/ix/82. Brisbane Ranges National Park: Dry sclerophyll woodland/shrubland (see Bernhardt & Walker, 1984).
- 7) *A. retinodes* var. *retinodes* Schdl. 16/i/82–17/i/82. Grampians National Park: Montane and valley dry sclerophyll forest/shrubland with adjacent epacrid heaths (see Bernhardt & Walker, 1985).
- 8) *A. retinodes* var. *uncifolia* J. Black. 15/xi/81–5/iii/82. Cape Schanck National Park: Coastal calcareous dune flora consisting of tall shrubland and invasive, naturalized shrubs and herbs (see Bernhardt et al., 1984).
- 9) *A. terminalis* Macbr. 18/iii/83–28/iv/83. Erica-Moe (south Gippsland) and Boolah Boolah State Forest. Moist sclerophyll woodland/forest with a rain forest element (see Knox et al., 1985).

*Analysis of Hymenoptera.* The foraging behavior of Hymenoptera was observed and recorded over the respective periods of fieldwork every day or every other day. Insects were collected selectively from 8 A.M. until 2 P.M. as foraging behavior becomes negligible by mid afternoon.

Insects were collected only if they were observed foraging on the open inflorescences of *Acacia* and/or taking nectar from extra-floral nectaries on the leaves or phyllodes of *A. longifolia*, *A. myrtifolia*, *A. pycnantha* (Bernhardt & Walker, 1984), and *A. terminalis* (Knox et al., 1985). Foraging is defined here as the active removal of polyads from anthers or the probing of flowers and extra-floral nectaries with mouthparts (Bernhardt et al., 1984). Terminology for bouts of foraging by bee taxa follows Michener (1979).

Insects were killed communally in jars containing fumes of ethyl acetate. To determine the presence of pollen, each insect was observed under a dissecting microscope. To analyze pollen species carried by insects, each insect was placed on a clean glass slide and "bathed" in a couple of drops of 100% ethanol. When ethanol had evaporated, the white residue remaining on the

TABLE 1. Bee taxa collected on the inflorescences of *Acacia*.

Bee Taxon	Acacia Species on Which Bee Taxon Was Captured <sup>a</sup>									No. Bees	
	LO	ME	MI	MY	PA	PY	RR	RU	TE		
Anthophoridae:											
<i>Exoneura (Brevineura) spp.</i>	0	4	0	0	0	0	0	0	0	4	
<i>Exoneura (Exoneura) spp.</i>	0	18	0	0	0	0	2	0	11	31	
										35	
Apidae:											
<i>Apis mellifera</i> <sup>b</sup>	A	1	1	5	4	A	A	A	A		
Colletidae:											
<i>Amphylaeus sp.</i>	0	0	0	0	0	0	0	0	1	1	
<i>Callomelitta perpicta</i>	0	0	0	0	0	0	0	0	4	4	
<i>Callomelitta spp.</i>	0	0	1	2	0	0	1	0	1	5	
<i>Euhesma spp.</i>	0	0	0	0	0	3	8	0	0	11	
<i>Euryglossa spp.</i>	1	0	0	0	2	0	0	0	0	3	
<i>Hylaeus sp.</i>	0	0	0	0	0	0	1	0	0	1	
<i>Leioproctus metallescens</i>	0	0	0	0	0	0	0	14	0	14	
<i>L. plumosus</i>	0	0	0	0	0	0	0	1	0	1	
<i>Leioproctus (Euryglossidia) spp.</i>	0	0	0	0	42	0	2	0	0	44	
<i>Leioproctus (Leioproctus) spp.</i>	3	0	2	12	7	23	19	0	2	79	
<i>Trichocolletes sp.</i>	0	0	0	0	1	0	0	0	0	1	
										164	
Halictidae:											
<i>Homalictus brisbanensis</i>	0	2	0	0	0	0	0	10	0	12	
<i>H. demissus</i>	0	0	0	0	0	0	1	0	0	1	
<i>H. dixonii</i>	0	0	0	0	0	0	0	0	5	5	
<i>H. holochorus</i>	1	0	0	0	0	0	0	0	0	1	
<i>H. megastigmus</i>	0	0	2	0	7	0	1	0	0	9	
<i>H. oxoniellus</i>	0	0	0	0	0	0	0	4	0	4	
<i>H. punctatus</i>	0	0	0	1	0	0	1	0	0	2	
<i>Lasioglossum (Australictus) spp.</i>	0	12	0	0	0	0	0	0	0	12	
<i>La. (Austrevylaeus) spp.</i>	0	0	0	0	0	0	0	0	1	1	
<i>La. (Chilalictus) spp.</i>	0	9	12	5	2	2	6	1	4	41	
<i>La. (Parasphecodes) spp.</i>	2	1	9	9	22	6	16	71	22	158	
<i>Nomia spp.</i>	0	5	5	0	0	0	0	0	0	10	
										256	
Megachilidae:											
<i>Megachile sp.</i>	0	0	0	0	0	0	0	2	0	2	
										2	
Grand Total	7	51	31	29	83	34	58	103	51	457	

<sup>a</sup> LO = *A. longifolia*; ME = *A. mearnsii*; MI = *A. mitchellii*; MY = *A. myrtifolia*; PA = *A. paradoxa*; PY = *A. pycnantha*; RR = *A. retinodes* var. *retinodes*; RU = *A. ret.* var. *uncifolia*; TE = *A. terminalis*.

<sup>b</sup> A = Abundant (no more than five bees caught but far more than that number were identified on sight on this *Acacia* species).

slide was mounted in one or two drops of Calberla's fluid (Ogden et al., 1974). Identification of pollen was made under light microscopy. However, since insects were killed in the same jar, contamination of pollen species was possible. Therefore an *Acacia* species or species of Eparcridaceae was not counted as present on an in-

dividual unless 25 polyads could be counted in that single sample. Taxa producing monad pollen were not counted as present in a sample unless 25 individual grains were identified on a single slide (Bernhardt et al., 1984). Insects washed of pollen were air dried, numbered, placed in individual glassine bags, and identified.

TABLE 2. Characteristics of the secretion of extra-floral nectar in four *Acacia* species.<sup>a</sup>

Characteristics of the Nectary or Nectar	LO	MY	PY	TE
Nectary secretes throughout the flowering seasons	+	+	+	+
Nectary secretes ≥ 1 ml every morning <sup>b</sup>	—	—	—	+
Nectar hexose rich	?	—	+	—
Nectar sucrose rich or sucrose dominant	?	+	—	+

<sup>a</sup> Derived from Bernhardt (1982), Bernhardt and Walker (1985) and Knox et al. (1985).

<sup>b</sup> Observations and collections of nectar made between 7–9 A.M.

LO = *A. longifolia*; MY = *A. myrtifolia*; PY = *A. pycnantha*; TE = *A. terminalis*.

RESULTS

BEES

Bees foraged for polyads on each of the eight *Acacia* species (Table 1). A total of 457 bees were caught on the eight *Acacia* species. The greatest numbers of bees collected belonged to the short-tongued family of Halictidae. Of all five families the Halictidae offered the greatest number of genera collected. *Lasioglossum* (subgenus *Parasphecodes*; Halictidae) species were collected in greater numbers on *Acacia* compared to all other genera and subgenera of native Apoidea.

The naturalized honeybee, *A. mellifera*, was locally abundant on half of the *Acacia* species studied and could be identified effortlessly on sight (Table 1). This bee was the dominant forager on *A. longifolia*.

Five bee families were identified on eight *Acacia* species. However, seven out of the 27 bee taxa represented single captures. The long-tongued families Apidae and Megachilidae were represented by only one taxon each. The third long-tongued family, Anthophoridae, was represented by two subgenera of *Exoneura* (Table 1). All remaining bee taxa belonged to the short-tongued families Halictidae and Colletidae. Eighty-four percent of the Colletidae collected belonged to the genus *Leioproctus* s.l. Eighty-three percent of the Halictidae belonged to the genus *Lasioglossum* s.l. (Table 1). *Lasioglossum* (subgenus *Parasphecodes*) species and *A. mellifera* were the only bee taxa collected on each of the eight *Acacia* species (Table 1). *Leioproctus* (subgenus *Leioproctus*) species were caught on seven out of eight *Acacia* species.

Representatives from the families Anthophoridae, Apidae, Colletidae, and Halictidae were recorded as foraging on the extra-floral nectaries of *A. longifolia*, *A. myrtifolia*, *A. pycnantha*, and *A. terminalis* (Tables 1, 2). There was no evidence that *Acacia* inflorescences growing on

shoots bearing extra-floral nectar received greater numbers of bees (or more bee taxa) compared to those *Acacia* species lacking extra-floral nectar (Table 1).

There was no obvious correlation between the number of bee taxa collected on an *Acacia* species and the habitat in which the species was studied (Table 3). At the intraspecific level, though, the dry sclerophyll woodlands and heaths of the Grampians National Park offered a wider fauna for *A. retinodes* var. *retinodes* than did the coastal dunes of Cape Schanck (Table 3). The number of bee taxa below the family level collected on four *Acacia* species sympatric through the Brisbane Ranges National Park varied from five to eight. No more than four families of bees were collected on any *Acacia* species (Tables 1, 3).

Variation in the number of bee taxa on an *Acacia* species did correlate positively with the flowering seasons of the plants and increased from mid winter (July) until the end of autumn (May; see Table 4). The number of bee taxa collected from mid winter to early spring (September) on *A. longifolia* and *A. pycnantha* doubled from early autumn (March) to early winter (June) on *A. terminalis* (Table 4). The greatest number of bee taxa was collected on the summer-flowering *A. retinodes* var. *uncifolia* (Table 4).

The majority of bee taxa foraging on the eight *Acacia* species visited a wide range of plants for pollen and/or nectar (Tables 4, 5). Technically these bees must be classified as polylectic foragers (Armstrong, 1979; Michener, 1979). From mid winter until late spring, and then from autumn to early winter, 21–55% of the bees captured on any *Acacia* species carried the polyads of that species mixed with the pollen of one or more sympatric species. Furthermore 63–91% of the bees captured on *Acacia* from late spring to late summer carried the pollen of one or more sympatric plants mixed with *Acacia* polyads (Table 4). Bees collected on *A. pycnantha* showed

TABLE 3. Variation in the number of bee taxa collected at different sites.

Site <sup>a</sup>	<i>Acacia</i> Taxon	No. Bee Taxa (No. Families)
Brisbane Ranges	MI	7 (3)
	MY	6 (3)
	PA	8 (3)
	PY	5 (3)
Cape Schanck	RU	8 (4)
Coranderrk Reserve	ME	8 (3)
Erica-Moe; Boolah Boolah	TE	10 (4)
Grampians	RR	12 (4)
Langwarren Reserve	LO	5 (3)

<sup>a</sup> See study sites for description of habitat.

MI = *A. mitchellii*; MY = *A. myrtifolia*; PA = *A. paradoxa*; PY = *A. pycnantha*; RU = *A. ret.* var. *uncifolia*; ME = *A. mearnsii*; TE = *A. terminalis*; RR = *A. retinodes* var. *retinodes*; LO = *A. longifolia*.

the lowest level of polylectic foragers, whereas bees collected on *A. mearnsii* showed the highest (Table 4).

Sixty-three percent of the bees bearing loads of *Acacia* polyads that were mixed with the pollen of other plants carried monads of one or more genera of Myrtaceae (Table 5). Ninety-two percent of the bees carrying mixed pollen loads carried the pollen of plants that bear floral nectaries (Table 5).

#### WASPS

Wasps were collected on all *Acacia* species excluding *A. retinodes* var. *retinodes*. Only 58 wasps were collected on the *Acacia* species representing seven wasp families (Table 6). Sixty-four percent of the wasps were divided equally between the Sphecidae and Tiphiidae. The greatest numbers belonged to *Cerceris* s.l., but these insects were collected only on *A. paradoxa* and *A. terminalis* (Table 6).

A total of 24 wasp taxa below the family level were collected on *Acacia*. Eleven of these represented single captures. No wasp taxon was recorded on more than two *Acacia* species. *Acacia* species offering extra-floral nectar appeared to attract a minimum of twice as many wasp taxa as those lacking extra-floral nectar (Tables 2, 6). Wasps observed and collected on *A. longifolia*, *A. myrtifolia*, and *A. terminalis* consistently flew to the extra-floral nectary before attempting to forage on the nectarless florets.

TABLE 4. Flowering patterns of *Acacia* species as correlated with the taxonomic diversity and foraging behavior of the bees.

Flowering Period and <i>Acacia</i> Species	No. Bee Taxa on <i>Acacia</i> sp.	No. Bees Bearing <sup>a</sup> <i>Acacia</i> Polyads	Ratio <sup>b</sup>
Mid Winter–Early Spring			
<i>A. longifolia</i>	5	22 (9)	0.40
<i>A. pycnantha</i>	5	41 (9)	0.21
Mid Winter–Mid Spring			
<i>A. myrtifolia</i>	6	29 (16)	0.55
Early Spring–Late Spring			
<i>A. paradoxa</i>	8	96 (50)	0.52
Late Spring			
<i>A. mearnsii</i>	8	59 (45)	0.91
Early Summer–Mid Summer			
<i>A. mitchellii</i>	7	32 (25)	0.78
Early Summer–Late Summer			
<i>A. retinodes</i> var. <i>retinodes</i>	12	67 (56)	0.8
<i>A. retinodes</i> var. <i>uncifolia</i>	8	121 (77)	0.63
Autumn–Early Winter			
<i>A. terminalis</i>	10	50 (16)	0.32

<sup>a</sup> The first number in the column refers to the total number of bees caught on the particular *Acacia* sp. that carried polyads of *Acacia* on their bodies. The second number, in parentheses, refers to the total number of bees that carried *Acacia* polyads plus the pollen of other genera.

<sup>b</sup> The ratio = number of bees that carried *Acacia* polyads plus pollen of other genera divided by total number of bees that carried *Acacia* polyads.

*Acacia terminalis* offered more extra-floral nectar per gland on a daily basis than did the three other nectariferous species (Table 2). *Acacia terminalis* received 33–66% more wasp taxa than were captured on the other three nectariferous species.

Wasps foraged selectively on *Acacia* species with functional, extra-floral nectaries. These *Acacia* species flowered during mid winter to mid spring and from autumn to early winter (Tables 4, 6). Consequently the density and diversity of wasps on *Acacia* was heaviest during the coldest seasons.

Seventeen wasp taxa carried the polyads of at least one of the *Acacia* species on which they were caught: *Antamenes* sp., *Anthobosca* sp.,

TABLE 5. Comparative frequencies of pollen from other spermatophyte families as identified on bees carrying *Acacia* polyads.

Spermatophyte Family <sup>a</sup>	No. of Bees Bearing <i>Acacia</i> Polyads Mixed with Pollen of Other Families Captured on each <i>Acacia</i> spp.									Total
	LO	ME	MI	MY	PA	PY	RR	RU	TE	
Compositae + -	0	4	0	0	3	1	6	26	0	40
Dilleniaceae -	0	0	3	0	4	1	0	0	0	8
Epacridaceae +	0	0	0	1	3	1	0	0	3	8
Leguminosae (Papilionoidae)+	1	4	0	0	23	0	0	0	0	28
Liliaceae s.l. + -	0	6	0	0	2	0	0	0	0	8
Myrtaceae +	2	47	19	2	26	0	71	43	15	225
Pinaceae -	9	0	0	0	1	1	0	0	0	11
Pittosporaceae +	0	0	0	0	0	0	2	0	0	2
Proteaceae +	0	0	0	4	0	3	0	0	0	7
Rhamnaceae +	0	0	0	12	2	4	0	0	0	18

<sup>a</sup> + = bees bearing pollen of genera with nectariferous flowers; - = bees bearing pollen of genera with nectarless flowers.

LO = *A. longifolia*; ME = *A. mearnsii*; MI = *A. mitchellii*; MY = *A. myrtifolia*; PA = *A. paradoxa*; PY = *A. pycnantha*; RR = *A. retinodes* var. *retinodes*; RU = *A. ret.* var. *uncifolia*; TE = *A. terminalis*.

*Cerceris antipodes*, *Cerceris* sp., *Labium* sp., *Lissopimpla excelsa*, *Lissopimpla* sp., *Lophocheilus anilitatus*, *Neourys* sp., *Phymatothynnus pygidialis*, *P.* sp. near *nonilicornis*, *Podagritus* sp., *Pseudozethus* sp., *Rhagigaster comparatus*, *Sphex* sp., *Tachynomia moerens*, and the unidentified species of Tiphidae. Mixed loads of *Acacia* polyads plus the pollen of sympatric plants were confined to those angiosperm families with nectariferous flowers: Compositae, Epacridaceae, Myrtaceae, Rhamnaceae, and Solanaceae.

#### DISCUSSION

*Wasps versus bees as Acacia pollinators.* The taxonomic diversity of wasps versus bees on Australian *Acacia* appears almost evenly matched. Wasps, however, comprise only 11% of the total population of foraging Hymenoptera. This supports previous reports that bees forage for *Acacia* polyads in far greater numbers than do wasps (Bernhardt, 1982; Bernhardt et al., 1984; Bernhardt & Walker, 1984, 1985; Knox et al., 1985). Female bees appear to forage primarily for polyads and secondarily for extra-floral nectar (Bernhardt & Walker, 1984; Knox et al., 1985). The results presented in this paper indicate that wasps tend to forage preferentially for extra-floral nectar.

Large quantities of extra-floral nectar fail to assure polyad transport by wasp foragers (Knox et al., 1985). Almost equal numbers of bees and wasps foraged for nectar and polyads on valley

populations of *A. terminalis*, but bees consistently carried polyads of *A. terminalis* more often than did wasps (Knox et al., 1985). The low density of wasp populations on flowering *Acacia*, combined with the foraging preferences of these insects, suggests that wasps are of secondary importance to seed set, at best. Under certain circumstances, pollen-eating flies are probably superior polyad vectors compared to wasps (Bernhardt et al., 1984).

This does not mean to suggest that wasps are always nominal pollinators of the Australian flora. Unfortunately few studies have been done to assess the selective pressure of wasp foraging on other angiosperms (Armstrong, 1979). Wasps are important pollinators of nectariferous and nectarless (pseudocopulatory) Orchidaceae in Australia (Beardsell & Bernhardt, 1982). Wasps may also pollinate the nectariferous Epacridaceae (Bernhardt, pers. obs.; Knox et al., 1985). Of course, wasps are important pollinators of *Prosopis* (Simpson et al., 1977), but these mimosoid shrubs bear floral nectaries.

*Bee diversity on Acacia species.* Although all representatives from all five families of Apoidea found in Australia (Armstrong, 1979) were identified on *Acacia* in this study, some families were more common than others. This is partially explained by biogeography. The Apidae are poorly represented in Australia (Michener, 1979), and the native genus *Trigona* is uncommon south of the Tropic of Capricorn (K. Walker, pers. comm.).

TABLE 6. Wasp taxa collected on the inflorescences of *Acacia* species.

Wasp Taxon	<i>Acacia</i> spp. on Which Wasp Was Captured									No. Wasps
	LO	ME	MI	MY	PA	PY	RR	RU	TE	
Braconidae:										
<i>Apanteles</i> sp.	1	0	0	0	0	0	0	0	0	$\frac{1}{1}$
Eumenidae:										
<i>Antamenes</i> sp.	0	3	0	0	0	0	0	0	0	3
<i>Pseudozethus</i> sp.	0	0	0	0	0	0	0	0	5	5
Unidentified sp.	0	0	1	0	0	0	0	0	0	$\frac{1}{9}$
Ichneumonidae:										
<i>Biconus</i> sp.	0	0	0	1	0	0	0	0	0	1
<i>Labium</i> spp.	1	0	0	0	0	0	0	0	3	4
<i>Lissopimpla excelsa</i>	0	0	0	1	0	0	0	0	0	1
<i>Lissopimpla</i> sp.	0	0	0	0	0	0	0	0	2	$\frac{2}{8}$
Pergidae:										
<i>Neourys</i> sp.	0	0	0	0	0	1	0	0	9	$\frac{1}{1}$
Pompilidae:										
<i>Chirodamus</i> sp.	0	0	0	0	0	0	0	0	1	1
<i>Pompilius</i> sp.	0	0	0	0	0	0	0	0	1	$\frac{1}{2}$
Sphecidae:										
<i>Cerceris antipodes</i>	0	0	0	0	0	0	0	0	7	7
<i>Cerceris</i> spp.	0	0	0	0	1	0	0	0	6	7
<i>Harpactophilus</i> sp.	1	1	0	0	0	0	0	0	0	2
<i>Rhopalum</i> sp.	0	0	0	0	0	0	0	0	1	1
<i>Sphex</i> sp.	0	0	0	1	0	0	0	0	0	$\frac{1}{18}$
Tiphiidae:										
<i>Anthobosca</i> sp.	0	0	0	0	0	0	0	3	2	5
<i>Lophocheilus anilitatus</i>	0	0	0	1	0	1	0	0	0	2
<i>Phymatothynnus pygidalis</i>	0	0	0	0	0	1	0	0	9	1
<i>Phymatothynnus</i> sp. nov. n. <i>nonilicornis</i> <sup>a</sup>	0	0	0	0	0	3	0	0	0	3
<i>Phymatothynnus</i> sp.	0	0	0	1	0	0	0	0	0	1
<i>Rhagigaster comparatus</i> <sup>a</sup>	0	0	0	0	0	2	0	0	0	2
<i>Tachynomia moerens</i> <sup>a</sup>	0	0	0	0	0	2	0	0	0	2
Unidentified spp.	2	0	0	0	1	0	0	0	0	$\frac{3}{19}$
Total No. Wasps/ <i>Acacia</i> species	5	4	1	5	2	10	0	3	28	58
Total No. Wasp Taxa/ <i>Acacia</i> species	4	2	1	5	2	6	0	1	9	

<sup>a</sup> Refers to wasp taxa caught *en copula*.

LO = *A. longifolia*; ME = *A. mearnsii*; MI = *A. mitchelii*; MY = *A. myrtifolia*; PA = *A. paradoxa*; PY = *A. pycnantha*; RR = *A. retinodes* var. *retinodes*; RU = *A. ret.* var. *uncifolia*; TE = *A. terminalis*.

*Trigona* may be important in the pollination of paleotropical *Acacia* through northeastern Australia (Bernhardt, 1982; Armstrong, 1979).

Biogeography alone, however, cannot explain the comparative dearth of anthophorid and megachilid bees on *Acacia* species in southeastern Australia. While it is true that neither family approaches the taxonomic diversity of Colletidae in Australia (Michener, 1979), there are far more megachilid and anthophorid taxa in Victoria than were sampled in this study (Michener, 1965). The Anthophoridae and Megachilidae are considered families of long-tongued bees. Although they may be common throughout the habitats described in this paper, evidence suggests that they forage preferentially on flowers offering pollen and nectar (Armstrong, 1979). In particular, Megachilidae often are associated with zygomorphic flowers, particularly papilionoid legumes (Michener, 1965; Armstrong, 1979). The only anthophorid bees relatively common on *Acacia* were *Exoneura*. These bees were largely confined to the only two arborescent *Acacia* species studied bearing bipinnately compound leaves: *A. mearnsii* and *A. terminalis*. This is probably coincidental, but it would be worthwhile exploring "presumed" foraging preferences that *Exoneura* may express towards sections of *Acacia* s.l.

Climatic conditions may also influence the diversity of bee taxa on *Acacia* with overlapping distributions. During the spectacular drought of 1982 and 1983 no specimens of *Leioproctus* (subgen. *Euryglossidia*) were collected on *Acacia* in the Brisbane Ranges (Bernhardt & Walker, 1984). The Brisbane Ranges had a cool, wet spring in 1984, and in that year *Leioproctus* (subgen. *Euryglossidia*) far outnumbered previously abundant *Leioproctus* (subgen. *Leioproctus*).

Considering the broad polylecticism of the bee taxa on these eight *Acacia* species, one cannot refer to any bee taxon as an "acacia bee" as some entomologists speak of "clover bees," "orchid bees," and "squash and gourd bees" (Michener, 1974, 1979). The very absence of floral and extra-floral nectar in so many Australian *Acacia* species forces bees to forage on other sources. Oligolecty continues to decline as bees exploit co-blooming sources of nectar and additional pollen in competition with *Acacia*.

*Lasioglossum* (Halictidae) and *Leioproctus* (Colletidae) remain the predominant polyad foragers of many *Acacia* species (Bernhardt, 1982; Bernhardt et al., 1984; Bernhardt & Walker, 1984,

1985; Knox et al., 1985). *Lasioglossum* species may be more important pollinators than *Leioproctus* species. *Lasioglossum* were caught on all *Acacia* species studied and were collected in greater numbers than were *Leioproctus*.

*Parsphcodes* and *Chilalictus* were the most commonly collected subgenera on six out of the eight *Acacia* species studied. *Parasphcodes* bees outnumbered *Chilalictus* bees. These allied subgenera may exert preferential foraging patterns when nectarless angiosperms have overlapping flowering periods. From later winter through late spring *Acacia* species and some *Hibbertia* species (Dilleniaceae) have overlapping flowering periods. *Lasioglossum* subgen. *Chilalictus* species forage preferentially on *Hibbertia* (Bernhardt, 1984, 1986), but *Parasphcodes* forage in greater numbers on *Acacia* (Bernhardt & Walker, 1985).

*Polylecticisms and the role of polylectic bees in Acacia cross-pollination.* The Halictidae and Colletidae are both families of short-tongued bees that forage for nectar on flowers with shallow perianths. They are found most commonly on the flowers of Myrtaceae, the largest and most widely distributed family of nectariferous angiosperms in Australia (Costermans, 1983). Most shrubby Myrtaceae flower through the warm spring-summer months when the greatest number of bees (both short- and long-tongued) are active. Out of the four most important nectariferous families that were patronized most frequently by bees in this study, three have flowers with short-tubular or shallow-bowl perianths (Faegri & van der Pijl, 1979): Myrtaceae, Compositae, and Rhamnaceae. The keeled "flag" flowers of the papilionoid legumes are also visited by short-tongued bees probably because the weight of comparatively large-bodied *Leioproctus* and *Lasioglossum* triggers access to the concealed nectaries.

Bees that pollinate nectarless flowers tend to belong to polylectic genera: *Apis* (Michener, 1974), *Bombus* (Buchmann, 1983), *Centris* (Frankie et al., 1983), *Lasioglossum* (Bernhardt, 1984; Bernhardt & Burns-Balogh, 1986). It is not unusual for an individual bee that belongs to a taxon in which foragers are not fed by siblings to visit one to four nectarless but pollen-rich species and six to eight nectariferous species during flowering seasons (Macior, 1968; Bernhardt & Montalvo, 1979; Bernhardt, 1984; Bernhardt & Burns-Balogh, 1986).

*Acacia* species in Australia are, in general, mass-flowering plants that are also highly self-incom-



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