

# Floral visitors of *Eucalyptus globulus* subsp. *globulus* in eastern Tasmania

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## Abstract

*Diurnal anthophiles associated with the flowers of Eucalyptus globulus were studied in natural populations in eastern Tasmania. Seven bird and 71 insect species were recorded. Insect species diversity was dominated by native colletid bees, although the introduced honeybee was the dominant species. Geographic variation occurred in the avian species composition, whereas insect communities appeared to vary temporally and according to flowering intensity. However, insects were rarely observed to contact stigmas and showed little evidence of movement between trees. It is argued that birds, particularly anthophilous parrots and wattlebirds, are likely to be the major diurnal contributors to outcrossing in E. globulus.*

## Introduction

The production of seeds in *Eucalyptus* is mainly dependent upon pollen transfer between flowers. This is due to the absence of parthenocarpy in this genus (Griffin *et al.* 1987), as well as the barrier to pollen transfer between anthers and stigma of the same flower (autogamy) which results from protandry (Pryor 1976). The unsuitability of the pollen to transport by wind (Ashton 1975; Pryor 1976; Eldridge *et al.* 1993) necessitates the harnessing of animal vectors to transfer pollen between flowers (allogamous

pollination) (Griffin 1982; Eldridge *et al.* 1993). The eucalypt breeding system favours outbreeding, as a consequence of reduced capsule production, seed yield, and seedling vigour after self pollination compared with cross pollination (Potts and Wiltshire 1997).

The suite of anthophiles (floral visitors) to *Eucalyptus* comprises birds, mammals and a diverse array of insects (Ashton 1975; Armstrong 1979; Ford *et al.* 1979; Griffin 1982). However, their relative abundances on each species are influenced by variation in floral morphology and rewards (Griffin 1982; Savva *et al.* 1988), as well as the weather at the time of flowering (Christensen 1971; Ford *et al.* 1979; Hopper 1981). Ford *et al.* (1979) claimed that eucalypt species with small flowers were predominantly entomophilous (insect pollinated), whereas species with larger flowers were mostly ornithophilous (bird pollinated). Birds may be more important pollinators than insects in southern Australia during winter when it is frequently too cold and wet for insect flight (Christensen 1971; Ford *et al.* 1979; Hopper 1981).

*Eucalyptus globulus* subsp. *globulus* (hereafter *E. globulus*) is a common subdominant, and occasionally dominant, tree of dry and wet sclerophyll forests at altitudes below 400 m in eastern Tasmania (Williams and Potts 1996). Flowering in this species is concentrated between September and December (Williams and Potts 1996), although local flowering intensity may vary enormously between

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years (Brown 1989). The flowers are the largest of any Tasmanian member of this genus (Williams and Potts 1996), the capsule measuring 15–30 mm in diameter (Curtis and Morris 1975). These flowers may be solitary or occasionally arranged in umbels of three (Jordan *et al.* 1993).

*Eucalyptus globulus* is one of the most widely planted eucalypts for pulpwood production in temperate regions of the world (Eldridge *et al.* 1993). Despite considerable research on its population genetic structure (e.g. Hardner *et al.* 1998; Skabo *et al.* 1998) and breeding system (e.g. Hardner and Potts 1995; Hardner *et al.* 1996), there is a paucity of information on the pollination ecology of this species. Such information is fundamental to understanding gene flow and reproductive success, and is now required by tree breeders to optimise the quantity and quality of seed produced in seed orchards of the species.

This study aimed to identify the potential pollinators of *E. globulus* within its natural range. To achieve this, the identities and abundances of diurnal flower visitors were investigated in several localities to determine how these anthophile communities vary in time and space. Observations of foraging behaviour gave some idea of the potential for these floral visitors to pollinate *E. globulus*.

## Methods

The diurnal anthophiles associated with flowers of *E. globulus* were investigated within its natural range in eastern Tasmania during November and December 1997. The study sites were divided into three regional areas:

1. East Coast. This region comprised trees at Swansea (S), Cape Tourville (CT), St Helens (SH) and Binalong Bay (B).
2. Hobart. This region comprised trees at Queens Domain (D) and Cornelian Bay (C).
3. Tinderbox (T).

Insect surveys were restricted to between 0900 h and 1800 h on mild to hot days (17–

35°C). Almost 12 hours were spent counting insects at flowers (Table 3), with another four hours spent observing and catching specimens. Individual trees of *E. globulus* bearing flowers within 3 m of the ground were observed by one of the authors (A.B.H.) for 10 minutes each, with the numbers of individuals from each insect species foraging from the flowers being recorded. Thrips (Thysanoptera) were excluded from the survey due to the impracticality of counting them. The numbers of open flowers within 3 m of the ground were also counted, and the flowering intensity of each tree scored on a scale of 1 (few flowers) to 4 (very heavy flowering).

Bird species and their numbers feeding on flowers of *E. globulus* were noted whenever they were encountered at these sites and other areas near Hobart during the study period. Species nomenclature for birds follows that of Schodde and Tidemann (1990).

Insect species were identified from individuals captured with a sweep net after they had been observed visiting flowers. Taxa other than bees were identified to the level of family using the keys in Borror *et al.* (1981), whereas bees were identified to subgenus using the keys in Michener (1965). Some bees were identified to the level of species using the keys constructed by Walker (1995) for *Lasioglossum* (*Chilalictus*) and those of Houston (1975, 1981) for Hylaeinae. Identifications of other insect species were provided by Dr Peter McQuillan (University of Tasmania, Hobart). Insect species were categorised according to the functional groups defined by Griffin and Ohmart (1986). A voucher collection comprising most insects encountered has been lodged at the Department of Plant Science, University of Tasmania, Hobart.

The abundance of each insect species was expressed as a proportion of the total number of insects observed visiting each tree within the 10 minutes, in order that the visitor profiles to each tree could be compared without the confounding effect of varying flower numbers between trees. These profiles were ordinated using semi-strong hybrid

Table 1. Anthophilous bird species and their numbers recorded from the flowers of *Eucalyptus globulus*.

Common name	Scientific name	Family	E. Coast	Hobart	Total	% Total
Swift parrot	<i>Lathamus discolor</i>	Platycercinae	21	17	38	35.19
Musk lorikeet	<i>Glossopsitta concinna</i>	Loriinae	20	1	21	19.44
Brush wattlebird	<i>Anthochaera chrysoptera</i>	Meliphagidae	22	4	26	24.07
Yellow wattlebird	<i>Anthochaera paradoxa</i>	Meliphagidae	7	9	16	14.81
Crescent honeyeater	<i>Phylidonyris pyrrhoptera</i>	Meliphagidae		1	1	0.93
New Holland honeyeater	<i>Phylidonyris novaehollandiae</i>	Meliphagidae	1		1	0.93
Silvereye	<i>Zosterops lateralis</i>	Zosteropidae		5	5	4.63

multidimensional scaling (ssh mds) with the computer program PATN (Belbin 1993). The insect species which were significant ( $P < 0.05$ ) describers of the variation in visitor profiles between trees were fitted to the ordination plot as vectors.

## Results

Seven species of birds were encountered at the flowers of *E. globulus* (Table 1). Anthophilous parrots and wattlebirds dominated the avifauna associated with these flowers, with smaller honeyeaters being occasional visitors. Swift parrots, and to a lesser extent yellow wattlebirds, were common at both Hobart and the east coast. In contrast, musk lorikeets and brush wattlebirds were far more common on the east coast than at Hobart. No birds were observed foraging on flowers of *E. globulus* at Tinderbox (Table 1), although many swift parrots and yellow wattlebirds were present in the area. This absence of foraging by birds can be attributed to observations of these trees being restricted to the middle of warm days, as foraging at flowers by birds was restricted to early morning or during cooler days at other sites throughout the study period.

The flowers of *E. globulus* to the height of 3 m also hosted 71 insect species, although only 10 of these were recorded in all regions (Table 2). Insect diversity and abundance were much greater at Tinderbox than other regions (Table 2), concomitant with the greater average number of flowers surveyed per tree and flowering intensity of trees in this region

(Table 3). Overall, species diversity was dominated by bees of the family Colletidae (Table 2). However, the introduced honeybee, *Apis mellifera* L., was clearly the dominant insect species, constituting almost half of the individual insect observations. The next most abundant functional groups were small Mordellidae, small bees, medium bees, large beetles and soldier beetles. The recently introduced large earth bumblebee, *Bombus terrestris* (L.), was an uncommon visitor to the flowers of *E. globulus* in the two southern regions but was not recorded from the east coast (Table 2).

Comparison of the visitor profile of *E. globulus* with those of other plant species in south-eastern Tasmania recorded by Hingston (1997) revealed that the plant species which shared the most anthophilous bird species with *E. globulus* were *Banksia marginata* and several eucalypts, mainly from the subgenus *Symphyomyrtus* (Table 4). Similar comparisons of the anthophilous insect visitors showed substantial overlap with other eucalypts, other Myrtaceae, and several unrelated plant species (Table 5). While some of these plant species sharing many floral visitors with *E. globulus* may occur in the same communities as *E. globulus*, others occur at higher altitudes. A few of these species display similar flowering phenologies to *E. globulus* but most begin flowering as *E. globulus* is declining in floral abundance in December and January (Tables 4, 5).

A large portion of the variation in insect communities between trees was due to contrasting proportions of beetles, native

Table 2. Anthophilous insects, and the number encountered, on flowers of *Eucalyptus globulus*. Functional groups with approximate body dimensions (mm) are: MBEE = medium bees (11 x 2.5); SBEE = small bees (7 x 1.1); HBEE = honeybees (13.5 x 4); BBEE = bumblebees (17 x 8); SWAS = small wasps (3.5 x 0.9); MWAS = medium wasps (10.5 x 2.1); LWAS = large wasps (14.5 x 4); ICHN = Ichneumonidae (12 x 1.9); SANT = small ants (4 x 1); MANT = medium ants (8 x 2); LANT = large ants (11 x 3); MCAL = medium Calliphoridae (8 x 3); SFLY = small flies (4 x 2); MSYR = medium Syrphidae (8 x 3); LSYP = large Syrphidae (13 x 4.7); LTAB = large Tabanidae (13 x 7); STAC = small Tachinidae (7 x 3); SOLD = soldier beetles (10 x 3); SMOR = small Mordellidae (3.5 x 1.7); SBTL = small beetle (7 x 2.5); LBTL = large beetle (10 x 4).

Anthophilous species	Group	Code	East Coast	Hobart	T/box	Total	Total (%)	Group total (%)
<i>Callmelitta picta</i>	MBEE	Calpic		1		1	0.04	
<i>Leioproctus (Leioproctus) sp. C6a</i>	MBEE	Lei06a		1	2	3	0.11	
<i>Leioproctus (Leioproctus) sp. C6b</i>	MBEE	Lei06b			1	1	0.04	
<i>Leioproctus (Leioproctus) sp. C6c</i>	MBEE	Lei06c			6	6	0.22	
<i>Leioproctus (Leioproctus) sp. C8</i>	MBEE	Lei08		2	56	58	2.08	
<i>Leioproctus (Leioproctus) sp. C14</i>	MBEE	Lei014	2	3	44	49	1.76	
<i>Leioproctus (Leioproctus) sp. C15b</i>	MBEE	Lei015b	1	10	4	15	0.54	
<i>Euryglossa (Euryglossa) nigrocaerulea</i>	MBEE	Eunigr			1	1	0.04	
<i>Hylaeus (Hylaeorhiza) nubilosus</i>	MBEE	Hynubi		2		2	0.07	
<i>Hylaeus (Euprosopis) honestus</i>	MBEE	Hyhone			6	6	0.22	
<i>Hylaeus (Euprosopoides) sp. Hy1</i>	MBEE	HyEu1		1		1	0.04	
<i>Hyleoides concinna</i>	MBEE	Hyconc		4		4	0.14	
<i>Lasioglossum (Chilalictus) lanarium</i>	MBEE	Chilan			1	1	0.04	
<i>Lasioglossum (Chilalictus) littleri</i>	MBEE	Chilit			5	5	0.18	
<i>Lasioglossum (Chilalictus) orbatum</i>	MBEE	Chiorb		5		5	0.18	
<i>Lasioglossum (Chilalictus) tamburinei</i>	MBEE	Chitam			2	2	0.07	
<i>Exoneura (Exoneura) sp. A1</i>	MBEE	Exon	2	4	8	14	0.50	6.27
<i>Euryglossa (Euhesma) sp. E1</i>	SBEE	Eu1			1	1	0.04	
<i>Hyphesma atromicans</i>	SBEE	Hyphes		1	4	5	0.18	
<i>Hylaeus (Gnathoprosopoides) bituberculatus</i>	SBEE	Hybitu	3		9	12	0.43	
<i>Hylaeus (Prosopisteron) sp. Hy7</i>	SBEE	HyPr	9	47	11	67	2.41	
<i>Hylaeus (Prosopisteron) sp. Hy8</i>	SBEE	HyPr			8	8	0.29	
<i>Hylaeus (Prosopisteron) sp. Hy11</i>	SBEE	HyPr			5	5	0.18	
<i>Hylaeus (Prosopisteron) sp. Hy13</i>	SBEE	HyPr			2	2	0.07	
<i>Hylaeus (Prosopisteron) sp. Hy14</i>	SBEE	HyPr			3	3	0.11	
<i>Hylaeus (Prosopisteron) sp. Hy22</i>	SBEE	HyPr	9	28	11	48	1.72	
<i>Hylaeus (Prosopisteron) sp. unidentified</i>	SBEE	HyPr			16	16	0.57	
<i>Homalictus sp. H4</i>	SBEE	Homali		1	1	2	0.07	
<i>Lasioglossum (Chilalictus) calophyllae</i>	SBEE	Chical	2			2	0.07	
<i>Lasioglossum (Chilalictus) clelandi</i>	SBEE	Chicle			1	1	0.04	
<i>Lasioglossum (Chilalictus) erythrurum</i>	SBEE	Chiery	1		22	23	0.83	
<i>Lasioglossum (Chilalictus) macrops</i>	SBEE	Chimac			1	1	0.04	
<i>Lasioglossum (Chilalictus) mundulum</i>	SBEE	Chimun		9	10	19	0.68	7.73
<i>Apis mellifera</i>	HBEE	Apis	32	33	1314	1379	49.55	49.55
<i>Bombus terrestris</i>	BBEE	Bombus		2	9	11	0.40	0.40
Tenthredinidae sp. 2 <i>Clarissa</i>	SWAS	Tenth2			1	1	0.04	
Pergidae sp. 1 <i>Phylacteophaga</i>	SWAS	Pergid		2		2	0.07	0.11
Sphecidae sp. 3	MWAS	Sphec3		1		1	0.04	
Sphecidae sp. 11	MWAS	Sphec11			1	1	0.04	
Tiphidae sp. 4	MWAS	Tiph			2	2	0.07	0.15
Gasteruptiidae sp. 1	LWAS	Gaster		7	20	27	0.97	
Sphecidae sp. 10	LWAS	Sphec10		1		1	0.04	
Thynnidae <i>Thynnus zonatus</i>	LWAS	Thyn1			1	1	0.04	
Thynnidae <i>Diamma bicolor</i>	LWAS	Thyn2			4	4	0.14	1.19

Table 2. Continued.

Anthophilous species	Group	Code	East Coast	Hobart	T/box	Total	Total (%)	Group total (%)
Ichneumonidae sp. 1	ICHN	Ichneu		1	4	5	0.18	0.18
Formicidae small	SANT	Form2	9	2	35	46	1.65	1.65
Formicidae <i>Camponotus consobrinus</i>	MANT	Form1	2		4	6	0.22	0.22
Formicidae <i>Myrmecia pilosula</i>	LANT	FormJ			34	34	1.22	1.22
Calliphoridae <i>Calliphora stygia</i>	MCAL	Cal1	3	4	8	15	0.54	
Calliphoridae sp. 2 <i>Calliphora</i>	MCAL	Cal2			24	24	0.86	
Calliphoridae sp. 6 <i>Calliphora</i>	MCAL	Cal6			12	12	0.43	
Calliphoridae sp. 9 <i>Calliphora</i>	MCAL	Cal9			2	2	0.07	1.90
Muscidae sp. 1	SFLY	Muscid			1	1	0.04	0.04
Syrphidae sp. 1	MSYR	Syrph1	1	3	23	27	0.97	
Syrphidae sp. 3 <i>Psilota</i>	MSYR	Syrph3			3	3	0.11	
Syrphidae sp. 8	MSYR	Syrph8			3	3	0.11	
Syrphidae sp. 10	MSYR	Syrph10			1	1	0.04	1.23
Syrphidae <i>Eristalis pulchella</i>	LSYR	Syrph2			5	5	0.18	0.18
Tabanidae sp. 2 <i>Scaptia</i>	LTAB	Taban2			1	1	0.04	0.04
Tachinidae sp. 2 <i>Senostoma</i>	STAC	Tach2			5	5	0.18	
Tachinidae sp. 10	STAC	Tach10		3		3	0.11	
Tachinidae sp. 11	STAC	Tach11			1	1	0.04	0.33
Cantharidae <i>Chauliognathus lugubris</i>	SOLD	Canth1			129	129	4.64	4.64
Mordellidae sp. 1 <i>Mordellastena</i>	SMOR	Mordel			473	474	17.03	17.03
Alleculidae <i>Atoichus bicolor</i>	SBTL	Allec			17	17	0.61	
Cerambycidae sp. 5	SBTL	Ceram5			1	1	0.04	
Dermestidae sp. 1	SBTL	Derm	1	3	1	5	0.18	0.83
Cleridae sp. 2 <i>Eleale</i>	LBTL	Clerid2		6	35	41	1.47	
Lycidae sp. 1 <i>Metriorrhynchus</i>	LBTL	Lycid1			12	12	0.43	
Cerambycidae <i>Stenocentrus saturalis</i>	LBTL	Ceram1			2	2	0.07	
Scarabaeidae <i>Phyllotocus rufipennis</i>	LBTL	Scarab2		3	85	88	3.16	
Scarabaeidae <i>Phyllotocus macleayi</i>	LBTL	Scarab4			1	1	0.04	5.17

Table 3. Flowering intensity of *E. globulus* trees, survey effort, and insect encounter rates in the three regions surveyed.

Flowering parameter	East Coast	Hobart	Tinderbox
Mean number of flowers below 3 m	c. 80	35.5	c. 340
Mean tree flowering intensity	2.08	1.95	2.55
Number of trees observed	7	6	14
Number of minutes spent counting	110	200	390
Mean number of insects observed/min.	0.7	0.96	6.4

bees, introduced honeybees and other hymenopterans. This is apparent from the significant vectors described by insects on the ordination being largely separated according to higher taxonomic levels (Figure 1). All beetles except the predatory clerid *Eleale* sp. were associated with vectors pointing to the

top left of the plot. These were opposed to the vectors associated with all native bees except *Lasioglossum (Chilalictus) littleri*. The vector associated with *Apis mellifera* was distinct from all others and opposed to those described by small ants and two species of wasps. No flies were significant descriptors

Table 4. Plant species in south-eastern Tasmania studied by Hingston (1997) which share the greatest numbers of species of bird visitors with flowers of *E. globulus*.

Plant species	Flowering phenology	Altitude (m)	No. of bird species shared with <i>E. globulus</i>
<i>Banksia marginata</i>	January–September	0–1000	5
<i>Eucalyptus viminalis</i>	December–May	0–600	5
<i>Eucalyptus obliqua</i>	December–April	0–700	3
<i>Eucalyptus urnigera</i>	March–November	500–1000	3
<i>Eucalyptus johnstonii</i>	December–June	500–900	2
<i>Eucalyptus ovata</i>	June–January	0–700	2

Table 5. Plant species in south-eastern Tasmania studied by Hingston (1997) which share the greatest numbers of species of insect visitors with flowers of *E. globulus*.

Plant species	Flowering phenology	Altitude (m)	No. of insect taxa shared with <i>E. globulus</i>
<i>Leptospermum scoparium</i>	December–April	0–700	28
<i>Leptospermum lanigerum</i>	December–January	0–1200	26
<i>Eucalyptus viminalis</i>	December–May	0–600	23
<i>Bursaria spinosa</i>	December–February	0–400	20
<i>Eucalyptus coccifera</i>	November–February	600–1300	20
<i>Melaleuca squarrosa</i>	October–December	0–300	18
<i>Banksia marginata</i>	January–September	0–1000	17
<i>Eucalyptus amygdalina</i>	September–January	0–600	15
<i>Prostanthera lasianthos</i>	December–January	0–900	15
<i>Leptospermum glaucescens</i>	December–April	0–700	14
<i>Leucopogon collinus</i>	January–December	0–500	13

of the variation between anthophilous insect communities during the surveys (Figure 1).

There was no major geographic separation between the insect communities, with those associated with east coast trees overlapping with those at both of the southern regions (Figure 1). However, there was little overlap on the ordination plot between the two southern regions, with Hobart trees being associated with most native bees and Tinderbox trees with most beetles and the introduced honeybee (Figure 1). While native bees were common in both of these areas, *Hylaeus (Prosopistemon)* spp. Hy7 and Hy22 were more common at Hobart (Table 2). The Hobart trees which fell within the Tinderbox cluster (CBc, DCe and DCf) (Figure 1) all had the majority of their flowers in shade. These trees differed from other trees in the same

region, and in surveys of the same trees when most flowers were in direct sunlight, in carrying greater proportions of beetles but fewer native bees. One tree at Tinderbox (T335) was an outlier from the Tinderbox cluster, due to hosting very few honeybees but many ants, as indicated by its negative and positive associations with these vectors respectively. This tree differed from all others in this region in bearing older flowers.

When the same tree was surveyed repeatedly during one day or on successive days, the anthophilous insect communities were usually similar. Repeated surveys of the same trees at Tinderbox separated by almost three weeks revealed a trend of the later surveys having higher values on the y-axis of Figure 1, indicative of increasing abundances of beetles relative to the numbers of honeybees over this

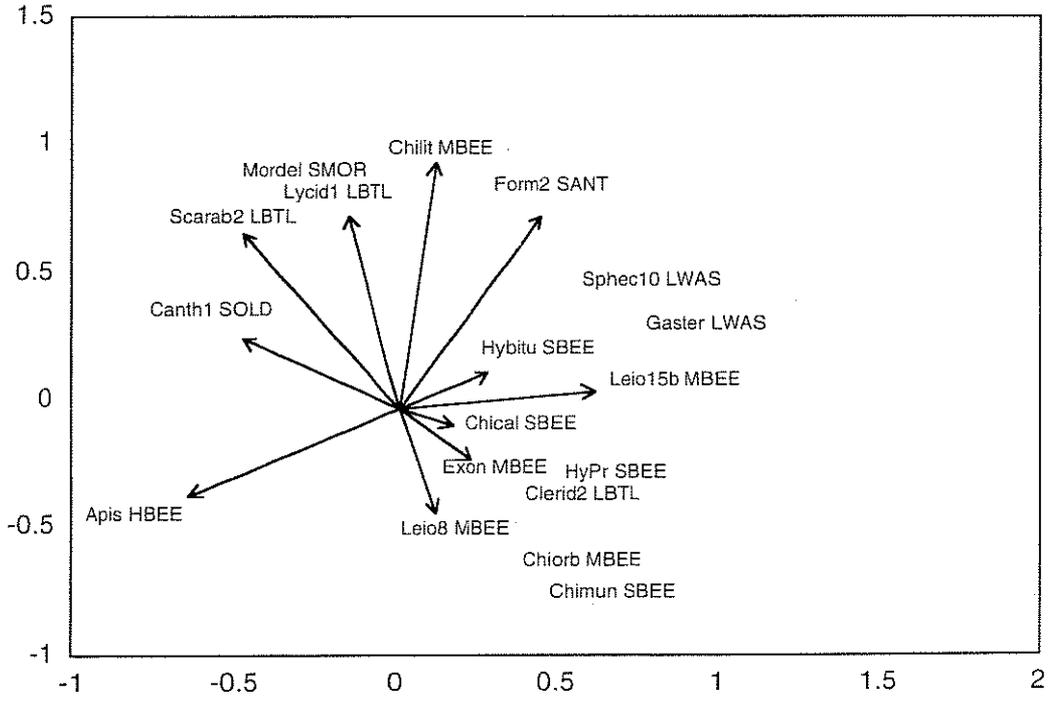
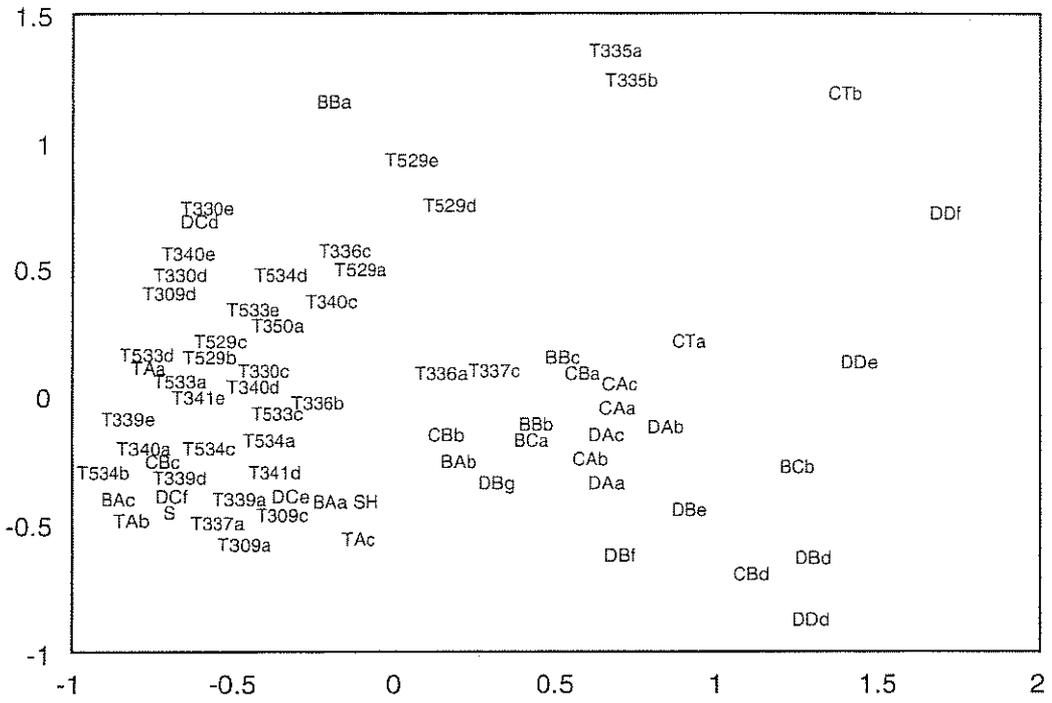


Figure 1. Ordination of the proportions of insect species foraging at flowers of each *E. globulus* tree. The insects which were significant contributors to the variation between trees have been fitted as vectors, shown in a separate plot for clarity. Stress on three axes = 16.5%. Codes for trees are given in the appendix, and those for insects are shown in Table 2.

period. This was the result of the cockchafer *Phyllotocus rufipennis* being common at the end of the period but absent at the beginning, as well as increasing abundances of *Metriorrhynchus* sp. over this period. However, this trend towards greater numbers of beetles later in the flowering season was offset to some extent by declining numbers of the soldier beetle *Chauliognathus lugubris*. There was also a shift in the relative abundances of two native bees in the genus *Leioproctus* at this site over this period. This involved declining abundances of *Leioproctus* sp. C8 and increasing abundances of *Leioproctus* sp. C15b. The latter species also became more common at Hobart during this period.

## Discussion

This survey found similarities between the anthophilous communities associated with *E. globulus* and those foraging on related plants. The similarities between the visitor profiles of *E. globulus* and other species in the Myrtaceae is apparent from the prevalence of this family in Tables 4 and 5. The dominance of the introduced honeybee, *Apis mellifera*, in insect communities on eucalypt flowers appears to be a common and widespread occurrence in south-eastern Australia, as both Ashton (1975) and Bond and Brown (1979) also found this to be the case in Victoria. The high diversity of native bees in the family Colletidae noted on the flowers of *E. globulus* concurs with other records of anthophiles associated with the Myrtaceae (e.g. Michener 1965; Armstrong 1979; Hingston 1997). However, the composition of this fauna differed noticeably from that of leatherwoods, *Eucryphia lucida* and *E. milliganii*, which occur in Tasmanian rainforests (Ettershank and Ettershank 1993). The preponderance of species of Hymenoptera, especially Apoidea, on *E. globulus* contrasts with the greater numbers of species of Coleoptera and Diptera collected from leatherwoods (Ettershank and Ettershank 1993). Furthermore, birds were not recorded from flowers of leatherwoods while a few insect orders were collected from leatherwoods but not *E. globulus*.

Nevertheless, numerous anthophile taxa were recorded from both *E. globulus* and *Eucryphia*. For both taxa, honeybees were the most frequent visitor while the cantharid *Chauliognathus lugubris* was also common (Ettershank and Ettershank 1993).

The relationship between *E. globulus* and other plants which share floral visitors may involve competition or mutualism. Competition for the visits of pollinators may occur between co-occurring plants which bloom synchronously (Green and Bohart 1975; Thomson 1978; Rathcke 1988). Reproductive success is sometimes adversely affected in synchronously flowering co-occurring species if pollen is transferred between species as a consequence of a lack of pollinator constancy (Waser 1978). This may involve reduced male fitness through loss of pollen via transfer to stigmas of other plant species (Campbell and Motten 1985) or lower female fitness through the clogging of the stigma with the pollen of other plant species (Stucky 1985; Galen and Gregory 1989). However, the presence of other plant species flowering simultaneously sometimes enhances pollinator visitation rates to individual species by increasing the pool of attraction (Thomson 1978, 1981). As local flowering intensity of *E. globulus* varies enormously between years (Brown 1989), other plant species with similar flowering phenologies may maintain the population sizes of pollinators of *E. globulus* during years when its flowering is poor. For example, swift parrots forage on *E. ovata* during spring when *E. globulus* flowering is poor (Brown 1989). When a pollinator lives longer than the duration of a single species' flowering, other plants with different flowering phenologies are necessary for the maintenance of the pollinator population in the area (Heinrich and Raven 1972; Faegri and van der Pijl 1979). An example of such mutualism between sequentially flowering plants which shared the same pollinator was found by Waser and Real (1979). When drought led to poor flowering of *Delphinium nelsonii*, the population of hummingbirds which pollinated both *D. nelsonii* and *Ipomopsis*

*aggregata* was adversely affected. This in turn resulted in poor seed-set in the latter self-incompatible species.

Insect communities on the flowers of *E. globulus* exhibited clear differences between Hobart and Tinderbox, with beetles comprising a much greater proportion of individuals at the latter site (Figure 1). These differences may be attributed to the much greater flowering intensity at Tinderbox, as House (1997) found that although abundances of individual insects were greatest on the most heavily flowering trees of *E. stellulata* within a population, this trend was stronger for beetles and flies than other taxa. However, an absence of major geographic variation in the insect visitors to flowers of *E. globulus* is indicated by the similarities between community compositions on east coast trees with those at both Hobart and Tinderbox, illustrated in the ordination.

Noticeable changes in the community structure of insects associated with the flowers of *E. globulus* within sites over a three-week period, together with the marked changes in anthophilous insect communities in south-eastern Tasmania during spring and summer observed by Hingston (1997), suggest that the suite of potential insect pollinators of *E. globulus* may change greatly during its flowering phenology. Ireland and Griffin (1984) also found that insect communities associated with flowers of *E. muellerana* in Victoria changed during its flowering period from October to January, with beetles becoming more frequent at the end. Anthophilous insect communities also varied with the amount of sunlight on the flowers, in accordance with numerous other studies (e.g. Butler *et al.* 1943; Kevan and Baker 1983).

Similarities between insect communities at individual trees surveyed repeatedly during a single day, and on successive days, raise the possibility that insects did not move frequently between trees while foraging. If so, they would not contribute greatly to outcrossing (xenogamous pollination). Beetles, and a species of syrphid fly, have also been observed

restricting their foraging to individual bushes of *Thryptomene calycina* for long periods, although large blowflies frequently flew between bushes (Beardsell *et al.* 1993). Any tendency for insects to remain within individual *E. globulus* canopies for long periods may, however, have been accentuated by the wide spacing of trees at all of the study sites. In situations where flowering trees are closer together, xenogamy by insects may be more frequent, as such inter-tree movements are promoted when the cost of travelling between plants is reduced relative to that between flowers of a single plant (Stucky 1985; House 1997). Nevertheless, previous observations of the behaviour of the honeybee, which was the dominant insect species observed on flowers of *E. globulus*, suggest that individuals confine their foraging to very small areas or particular bushes for long periods despite the presence of other conspecific flowers nearby (Butler *et al.* 1943; Paton 1993, 1997). In one of these studies, Paton (1993) observed honeybees visiting a total of 4600 flowers of *Callistemon rugulosus* on plants separated by a minimum of only 3 m for a total of 9.9 hours without recording an individual moving between plants. In fact, each honeybee restricted its foraging to a small section within a particular bush over several days (Paton 1997). In contrast, during a similar amount of time observing New Holland honeyeaters foraging at the same plants, inter-plant movements averaged 7.3 per hour and one every 400 flowers visited (Paton 1993). Consequently, in plants exposed to both of these visitors, outcrossing and fruit production declined as honeybee activity increased (Paton 1997). Hence, birds are likely to be more effective pollinators than insects because of their wider movements (Ford *et al.* 1979; Eldridge *et al.* 1993; Paton 1993).

The effectiveness of insects as major pollinators, xenogamous or otherwise, of *E. globulus* is questionable. Very few insects were observed to contact stigmas, as only those insects greater than or equal to the length of a honeybee could contact the stigma while feeding on nectar. As only seven of the insect species observed were as long or longer

than honeybees, this precluded most species from contacting the stigma while feeding on nectar. Hopper (1981) also found that insects can gather nectar from large flowers of *Eucalyptus* without contacting the stigma. Even honeybees seldom contacted stigmas, as they usually fed on nectar while standing on the hypanthium, with the main axis of their body parallel to its surface. Other nectar-feeding insects also usually adopted this position. Minimal stigma contact by honeybees on these large flowers is consistent with the findings of Moncur *et al.* (1995) where the impact of introducing honeybee hives on both seed production per capsule and outcrossing rate was lower in *E. globulus* than in the smaller flowered congeners *E. nitens* and *E. camaldulensis*. The protandrous nature of the flowers, together with the spreading of the long stamens away from the stigma prior to the latter becoming receptive, also reduced the chance of insects contacting receptive stigmas while gathering pollen. However, beetles have difficulty landing precisely on flowers (Faegri and van der Pijl 1979) and therefore could conceivably contact the stigma in the process of landing.

The effectiveness of insects as pollinators would be further reduced by the flowering phenology of *E. globulus*. The weather during spring in Tasmania is often cold, wet and windy; conditions which are not conducive to insect activity. Houston *et al.* (1993) found that cloud, even on warm days, was sufficient to prevent a colletid bee from foraging. Consequently, birds are more reliable than insects as pollinators during inclement weather (Christensen 1971; Ford *et al.* 1979; Hopper 1981). Hence, we argue that birds are likely to be the major diurnal pollinators of *E. globulus*, in accordance with previous claims of large-flowered eucalypts being mostly ornithophilous (e.g. Ford *et al.* 1979; Hopper 1981).

Paton and Ford (1977) found that foraging parrots contacted stigmas of eucalypts more often than honeyeaters did, due to the longer bills of the latter. Hence, the two species of parrots may be the major pollinators of

*E. globulus* within its native geographic range. Although able to forage in young regrowth, swift parrots require mature forest on nearby dry ridges for roosting and breeding (Brown 1989; Taylor 1991), with the most frequently used areas consisting of at least 100 ha (Brereton 1997). In fact, both of these species are dependent on tree hollows for nesting sites (Schodde and Tidemann 1990; Taylor 1991). This, together with the fact that flowering in *E. globulus* occurs concomitantly with nesting in both of these parrots (Schodde and Tidemann 1990) (see also Brown 1989), suggests that pollinator activity would be enhanced in proximity to mature forest.

Numerous authors have found that anthophilous birds move between habitats as they follow floral resources (e.g. Christensen 1971; Ford 1979; Hopper 1981; Brown 1989). Consequently, Christensen (1971) and Sampson *et al.* (1995) suggested that efforts should be made to maintain year-round floral resources for these birds, otherwise pollination of ornithophilous eucalypts would be adversely affected. In the case of *E. globulus*, this would be achieved primarily by ensuring that abundances of *Banksia marginata* and the diversity of ornithophilous eucalypts are maintained.

The prevalence of wattlebirds, relative to smaller Meliphagidae species, can be attributed to the aggressive defence of concentrated floral resources frequently conducted by this genus (Bond and Brown 1979; Ford 1979; Paton 1986). Such behaviour was frequently observed at Coles Bay where both wattlebirds occurred.

Although insects may not be important xenogamous pollinators of *E. globulus*, their presence may indirectly enhance pollination. Honeyeaters feed on insects around eucalypt flowers (Ireland and Griffin 1984) as a source of protein (Ford and Paton 1976; Ford 1979). Hence, anthophilous insects may help to maintain populations of these birds in areas where *E. globulus* is flowering. Anthophilous insects could also indirectly enhance pollination in *E. globulus* by reducing

standing crops of nectar, thereby forcing birds to visit more flowers across a larger area and hence promote outbreeding (Paton 1986).

## Conclusion

This study found that the flowers of *E. globulus* host a wide variety of insects and birds, with birds more likely to be effective pollinators. However, further research is necessary to determine empirically the effectiveness of these flower visitors as pollinators, including analysis of their contributions to xenogamous and geitonogamous pollinations. More detailed surveys across the full flowering season are needed to fully understand the changes in pollinator communities through time, and across seasons, at the population and individual tree levels. Nocturnal surveys are also required to ascertain whether mammals and moths are significant pollinators of *E. globulus*, while studies from

higher in the canopies of large trees are needed to determine whether anthophile communities there differ from those within 3 m of the ground. The relationships between *E. globulus* and other plants which also host its pollinators require study to determine whether seed-set in *E. globulus* is enhanced or reduced by their presence. Although the nature of these interactions between plants is obviously complex, better understanding of such factors affecting the reproductive success of *E. globulus* is important to maximise the success of seed production areas.

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Appendix. Numbers of insects in each insect group collected from each tree. (Abbreviations of insect groups are given in the caption of Table 2.)

Site	Tree	#flowers	Intensity	Date	Time	Code	MBEE	SBEE	HBEE	BBEE	SWAS	MWAS	LWAS	ICHN	SANT	MANT	LANT	MCAL	SFLY	MSYR	LSYR	LTAB	STAC	SOLD	SMOR	SBTL	LBTL
Swansea		lots	4	8-Nov	1104	S	2	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. Tourville		15	1	8-Nov	1235	CTa	1	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C. Tourville		15	1	8-Nov	1420	CTb	1	1	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0
Binalong	A	41	2	10-Nov	945	BAa	1	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Binalong	B	51	2	10-Nov	1035	BBa	0	0	1	0	0	0	0	0	0	2	0	1	0	1	0	0	0	0	0	0	0
Binalong	C	32	2	10-Nov	1051	BCa	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Binalong	A	41	2	10-Nov	1147	BAb	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Binalong	B	51	2	10-Nov	1353	BBb	0	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Binalong	C	32	2	10-Nov	1407	BCb	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Binalong	A	41	2	10-Nov	1432	BAc	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Binalong	B	51	2	10-Nov	1550	BBc	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
St Helens		74	3	11-Nov	856	SH	0	1	5	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Domain	A	12	2	21-Nov	1103	DAa	1	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornelian	A	68	2	21-Nov	1145	CAa	0	5	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cornelian	B	33	1	21-Nov	1228	CBa	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	2
Cornelian	A	68	2	21-Nov	1310	CAb	2	8	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cornelian	B	33	1	21-Nov	1333	CBb	2	0	3	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Domain	A	12	2	21-Nov	1409	DAb	0	10	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1
Cornelian	A	68	2	21-Nov	1442	CAC	0	4	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cornelian	B	33	1	21-Nov	1501	CBc	0	0	4	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
Domain	A	12	2	21-Nov	1530	DAC	0	6	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T/box	534	lots	4	22-Nov	934	T534a	15	5	89	0	0	0	2	0	0	0	17	3	0	2	0	0	0	4	4	2	1
T/box	A	38	1	22-Nov	1045	TAa	0	2	5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
T/box	335	80	1	22-Nov	1114	T335a	1	1	2	0	0	0	0	0	22	2	2	0	0	0	0	0	0	0	0	0	0
T/box	529	lots	4	22-Nov	1135	T529a	12	9	48	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	50	0	2
T/box	336	250	2	22-Nov	1220	T336a	4	8	17	1	0	0	1	0	0	0	0	3	0	1	0	0	0	0	5	0	3
T/box	350	lots	3	22-Nov	1258	T350a	4	6	54	0	0	0	3	0	0	0	0	1	0	0	0	0	0	24	14	0	1
T/box	339	55	1	22-Nov	1426	T339a	0	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T/box	340	lots	3	22-Nov	1441	T340a	2	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0
T/box	337	180	4	22-Nov	1518	T337a	1	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	1
T/box	533	lots	4	22-Nov	1543	T533a	4	0	60	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	22	0	0
T/box	309	130	4	22-Nov	1607	T309a	1	0	7	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
T/box	529	lots	4	22-Nov	1627	T529b	2	0	110	1	0	0	2	0	0	0	0	4	0	0	0	0	0	0	50	0	6
T/box	336	250	2	22-Nov	1651	T336b	3	2	21	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	5	1	3
T/box	335	80	1	22-Nov	1708	T335b	0	0	1	0	0	0	0	0	13	2	3	0	0	0	0	0	0	0	1	0	2
T/box	A	38	1	22-Nov	1729	TAb	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T/box	534	lots	4	22-Nov	1742	T534b	0	0	88	0	1	0	0	0	0	0	4	0	0	1	0	0	0	5	2	0	0

