Pollination ecology of *Eucalyptus globulus* subsp. *globulus* and *Eucalyptus nitens* (Myrtaceae)

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Submitted in fulfillment of the requirements for the degree of Doctor of Philosophy

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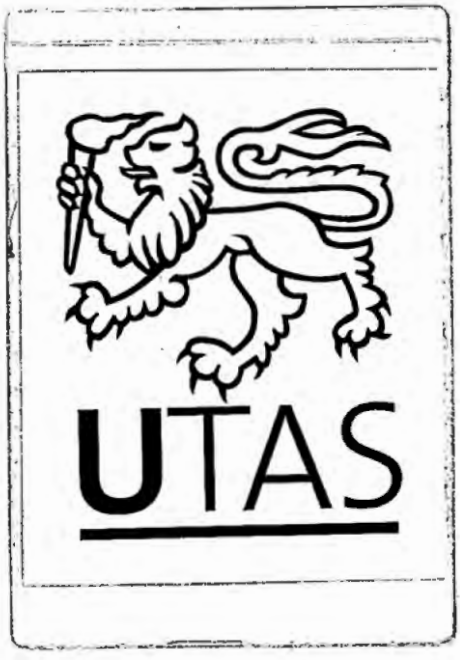


Abstract

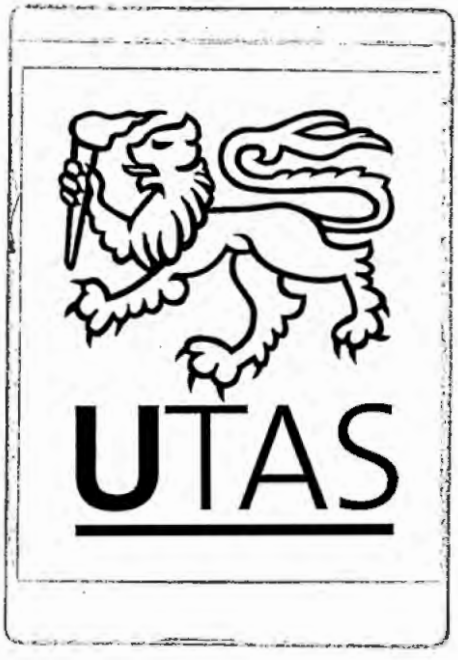
Tasmanian native blue gum *Eucalyptus globulus* subsp. *globulus* and its closely related southeastern Australian mainland congener *E. nitens* are the major trees grown in eucalypt plantations in temperate regions of the world. Plantation stock are mostly grown from seeds, that are increasingly being collected from seed orchards of trees selected for characters desired by the forest industry. Seed production and fitness of the resultant trees are dependent largely upon pollen transfer between flowers on different trees, because of the partial self-incompatibility in these two species. The unsuitability of the pollen to transfer by wind necessitates the harnessing of animals to transfer pollen as they forage at flowers. This research aimed to determine which animals were effective pollinators of these tree species in Tasmania.

These two species have contrasting floral forms, associated with enormous differences in nectar production, that resulted in their flowers being used by different animals as food sources. The small flowers of *E. nitens* produced only 0.3 – 0.6 mg of nectar sugar per day and, accordingly, were visited exclusively by small, mostly native, insects. Introduced honey bees (*Apis mellifera*) and bumble bees (*Bombus terrestris*), being larger, more energy demanding insects, were rarely seen visiting flowers of *E. nitens*, and birds were never seen attempting to feed from these flowers. In contrast, the large flowers of *E. globulus* produced 37 – 56 mg of nectar sugar per day, rendering them attractive to energy demanding birds and exotic bees, as well as the less energy demanding smaller insects.

Single visits to flowers of *E. globulus* by swift parrots (*Lathamus discolor*) resulted in statistically significant increases in seed production above the levels occurring in unvisited flowers. Although other bird species were not sufficiently assessed by this method to determine whether they are also effective pollinators, analyses of their foraging behaviour and pollen loads suggest they are. In contrast, experiments indicated that insects were poor pollinators of *E. globulus*. Single visits to flowers by insects, including honey

bees and bumble bees, did not result in statistically significant increases in seed production above the levels occurring in unvisited flowers. Even prolonged exposure to insects throughout the life of a flower failed to result in the production of as many seeds as that following a single swift parrot visit, despite insects often consuming all of the daily nectar production.

Hence, seed production and the fitness of plantation trees should be enhanced by management practices that benefit populations of native flower-visiting insects in seed orchards of *E. nitens* and birds in orchards of *E. globulus*.



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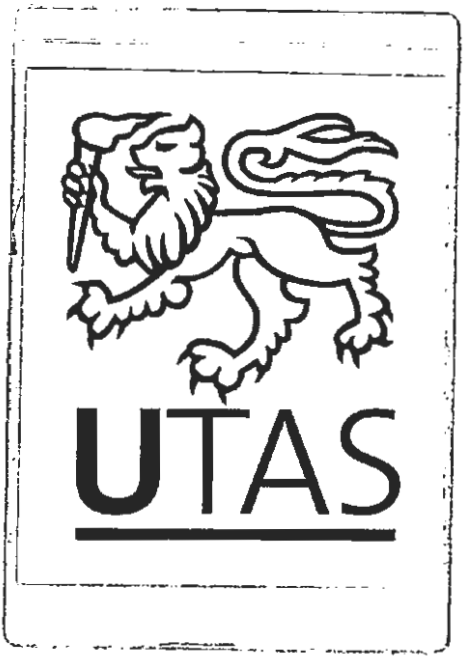

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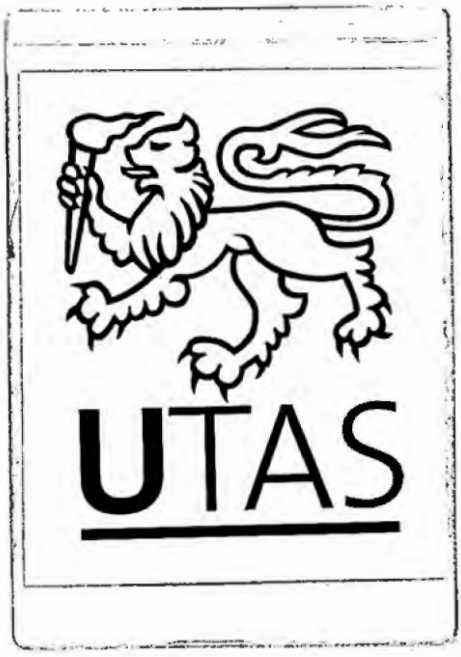


Chapter 1

Eucalypt breeding and pollination

1.1 The *Eucalyptus* species targeted in this study

The two major eucalypts grown in Tasmanian pulpwood plantations are *Eucalyptus globulus* Labill. subsp. *globulus* (hereafter *E. globulus*) and *E. nitens* (Deane & Maiden) Maiden (de Little *et al.* 1992, Orme 1992, Tibbits *et al.* 1997). These species are also grown extensively in plantations in many other temperate regions of the world (Eldridge *et al.* 1993, Tibbits *et al.* 1997). Outside cultivation, *E. globulus* is a common subdominant, and occasionally dominant, tree of dry and wet sclerophyll forests at altitudes below 600 m in eastern Tasmania (Williams and Potts 1996, Tibbits *et al.* 1997). It also occurs on islands in Bass Strait, in coastal Victoria, and in a few small populations on Tasmania's west coast (Jordan *et al.* 1993, Williams and Potts 1996). The natural distribution of *E. nitens* is tall open-forest in montane Victoria and NSW at altitudes between 600 and 1600 m (Boland *et al.* 1984, Tibbits *et al.* 1997), where it is usually distributed in small disjunct populations (Cook and Ladiges 1998).

Plantation stock are grown mostly from seeds that are increasingly being collected from seed orchards of elite trees selected for characters desired by the forest industry (Eldridge *et al.* 1993, Tibbits *et al.* 1997). For this reason, information on the pollination of these species is required by tree breeders to optimise the quantity and quality of seed produced in these orchards.

1.2 Pollination of *Eucalyptus*

The production of seeds in *Eucalyptus* is dependent mainly upon pollen transfer between flowers (allogamy). This is because parthenocarpy is unknown in this genus (Griffin *et al.* 1987), and protandry is a barrier to pollen transfer between anthers and stigma of the same flower (autogamy) (Pryor 1976). However this barrier is not complete, as autonomous pollen sometimes becomes lodged on stigmata of newly opened flowers in some

species and germinates when the stigma becomes receptive (Oddie and McComb 1998).

The tendency for *Eucalyptus* pollen to stick together in lumps makes it unsuitable for transport by wind (Ashton 1975, Pryor 1976, Eldridge *et al.* 1993) and necessitates the harnessing of animal vectors to transfer pollen between flowers (Griffin 1982, Eldridge *et al.* 1993). The open cup-shaped flowers of *Eucalyptus* enable a wide variety of anthophiles (floral visitors), including birds, mammals, and a diverse array of insects, to access nectar and pollen (Ashton 1975, Armstrong 1979, Ford *et al.* 1979, Griffin 1982). The relative abundances of these anthophiles on each species are influenced by variation in floral form 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). Nectar production per flower is related positively to flower size in *Eucalyptus* (Davis 1997), supporting the conclusions of Ford *et al.* (1979) that eucalypt species with small flowers are predominantly entomophilous (insect pollinated), whereas species with larger flowers are mostly ornithophilous (bird pollinated). Birds may also be more important pollinators than insects in southern Australia during winter when it is frequently too cold and wet for insect activity (Christensen 1971, Paton and Ford 1977, Ford *et al.* 1979, Hopper 1981).

In spite of being closely related members of the Subseries Globulinae (Pryor and Johnson 1971), *E. globulus* and *E. nitens* differ markedly in their floral forms and flowering seasons. Flowers of *E. globulus* are the largest of any Tasmanian eucalypt (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). In marked contrast, the capsules of *E. nitens* are only 4 - 7 mm in diameter and arranged in umbels of seven (Boland *et al.* 1984, Tibbits 1989). Flowering in *E. globulus* is concentrated between September and December (Williams and Potts 1996), whereas *E. nitens* usually blooms between January and March in both natural populations (Boland *et al.* 1984) and extra-limital plantings in Tasmania

(Tibbits 1989). These interspecific differences in floral form and flowering season are suggestive of adaptations by *E. globulus* to exploit birds as pollinators and *E. nitens* to exploit insects as pollinators.

1.3 Seed production in *Eucalyptus* and its limiting factors

Seed production in seed orchards of *E. globulus* and *E. nitens* has not been outstanding. Seed yields from orchards of *E. globulus* in Tasmania and Portugal have been regarded as poor, at no more than 6 kg / ha from trees 9 - 10 years old (Eldridge *et al.* 1993, Moncur *et al.* 1995). However, an orchard in northwestern Tasmania which yielded only 1.4 and 3.4 kg / ha at the same age, produced 18.8 kg / ha the following year (de Little *et al.* 1992). *Eucalyptus nitens* produces low quantities of seeds in plantations and natural forests (Eldridge *et al.* 1993, Moncur 1993, Jones *et al.* 2001), a factor that has inhibited its domestication (Moncur and Hasan 1994). However, de Little *et al.* (1992) were satisfied with yields of 1.5 - 12.9 kg / ha in 7 - 10 year old seed orchards in northern Tasmania.

Low seed production can sometimes be attributed to poor flowering, as local flowering intensity often varies enormously between years in both *E. globulus* and *E. nitens* (Brown 1989, Moncur *et al.* 1994, Brereton 1996). The biennial flowering pattern of *E. globulus* (Moncur *et al.* 1994, Brereton 1996) results in good seed crops occurring every two or four years (Moncur 1993). Similarly, up to four years sometimes elapse between good seed crops in *E. nitens* (Moncur 1993). However, this impediment to consistently high seed production in seed orchards has been reduced by application of hormones that promote flowering (Griffin *et al.* 1993, Moncur and Hasan 1994, Moncur *et al.* 1994, Jones *et al.* 2001).

Seed production is sometimes also pollinator limited. For example, the numbers of seeds per capsule following open-pollinations in *E. nitens* (3.8±0.3) were significantly lower than after hand cross-pollinations (7.9±0.4) (Tibbits 1989). In *E. globulus*, however, Hardner and Potts (1995) found no statistically significant differences in the number of seeds per capsule (open =

7.0, cross = 8.4), or the numbers of capsules and seeds produced per flower pollinated by these methods, indicating that natural pollination levels were not a limiting factor for seed production. Moncur and Kleinschmidt (1992) and Moncur *et al.* (1995) proposed that seed set in *Eucalyptus* may be limited by the amount of pollen reaching the stigmata, because the number of seeds set per flower is typically low compared to the number of ovules. Although it is obvious that very low levels of pollen deposition would limit seed production, the argument put forward by Moncur and Kleinschmidt (1992) and Moncur *et al.* (1995) is spurious. Not all eucalypt ovules are penetrated by pollen tubes, even when the number of pollen tubes reaching the base of the style is greater than the number of ovules (Ellis and Sedgley 1992), indicating that the failure of ovules to develop into seeds does not necessarily result from insufficient quantities of pollen being deposited.

Seed set in eucalypts is dependent on the quality, as well as the quantity, of pollen transferred to conspecific stigmata. Seed set per capsule following hand self-pollination is generally 50-75% lower than from open-pollinations (Potts and Cauvin 1988, Hardner and Potts 1995) and hand cross-pollinations (Potts and Cauvin 1988, Tibbits 1989, Hardner and Potts 1995). Hence, both *E. globulus* (Potts and Cauvin 1988, Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995, 1998) and *E. nitens* (Tibbits 1989, Potts *et al.* 1992) produce fewer seeds after self-pollination than after outcrossing. However, the number of capsules per pollinated flower was not significantly lower following selfing versus outcrossing in either *E. globulus* (Potts and Cauvin 1988, Hardner and Potts 1995) or *E. nitens* (Tibbits 1989), in contrast to some other eucalypt species (Griffin *et al.* 1987, Sedgley and Smith 1989, Ellis and Sedgley 1992).

Self pollination, through autogamy or geitonogamy, sometimes also reduces the quality of seeds in self-compatible species (Primack and Silander 1975, Potts and Cauvin 1988). Selfing in *E. nitens* resulted in seeds with lower viability and seedlings with higher rates of abnormalities and mortality compared to outcrossing (Tibbits 1988). In contrast, selfing in *E. globulus*

resulted in lower seed viability (Hardner and Potts 1995), but not lower seedling survival rates, compared to outcrossing (Hardner and Potts 1995, Hardner *et al.* 1998). However, inbreeding depression, in the form of reduced growth rates and increased mortality, became more evident as the *E. globulus* offspring aged in field trials (Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995). Reduced growth rates in progeny from open pollination compared to outcross pollination were also recorded in both species, with this effect being more pronounced in *E. globulus* than in *E. nitens* seed orchards (Hodge *et al.* 1996), suggesting frequent autogamy and/or geitonogamy had occurred.

1.4 The aims of tree breeders

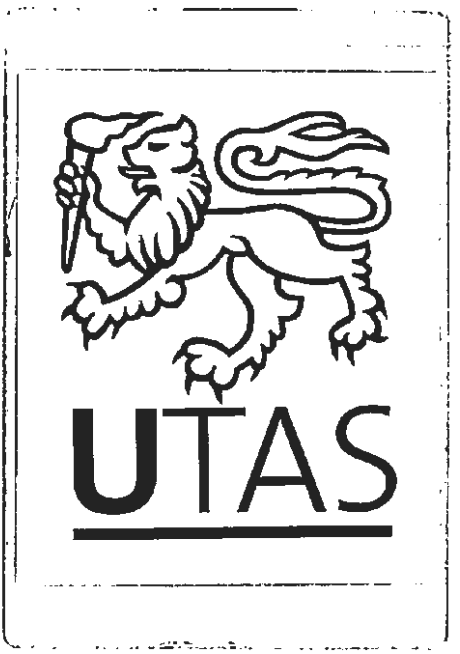
Eucalyptus tree breeders aim to maximise outcrossing rates in seed orchards (Hodgson 1976c, Eldridge *et al.* 1993). This was achieved in a Victorian seed orchard of *E. regnans* where outcrossing was significantly greater than in a nearby natural forest of this species (t = 0.91 v. 0.74) (Moran *et al.* 1989). Those authors attributed their findings to the distribution of trees in blocks within the orchard, with only one tree from each open-pollinated family per block (Moran *et al.* 1989). This reduces the amount of inbreeding resulting from matings between nearest neighbours, which is usually high in natural stands because of local neighbourhoods of related individuals (Moran *et al.* 1989). In a natural stand of *E. globulus* such neighbourhoods are approximately 25 m in diameter (Skabo *et al.* 1998), and matings between trees separated by this distance exhibited inbreeding depression in the form of reduced size after four years (Hardner *et al.* 1998).

Outcrossing rates are also influenced by plant densities. In situations where flowering trees are closer together, xenogamy by insects may be more frequent because the cost of travelling between plants is reduced relative to that between flowers of a single plant (Stucky 1985, House 1997). Indeed, the symptoms of inbreeding depression in *E. globulus* in open-pollinated progeny become progressively less apparent as the density and size of natural stands increase (Borralho and Potts 1996). Isozyme analysis of

progeny from isolated trees and the densest stands demonstrated these differences were related to consistently greater outcrossing rates in the dense stands (Hardner *et al.* 1996).

1.5 Conclusions

The effectiveness of various anthophiles in promoting fruit and seed set in *E. globulus* and *E. nitens*, the viability of the resultant seed, and the vigour of the offspring require investigation (Moncur and Kleinschmidt 1992). An understanding of the factors influencing the abundance and foraging behaviour of the most effective pollinators is also required.



Chapter 2

The effectiveness of flower visitors as pollinators

2.1 Can honey bees be used to pollinate *Eucalyptus* seed orchards?

2.1.1 Propensity for honey bees to visit E. globulus and E. nitens flowers

The most obvious requirement for an animal to be a pollinator of a particular plant species is that the animal must regularly visit this plant's flowers. Both *E. globulus* and *E. nitens* have been documented as nectar and pollen sources for honey bees (*Apis mellifera* L.) in Victoria, where both tree species occur naturally (Goodman 1973), indicating that honey bees forage from flowers of both species. *Eucalyptus globulus* is also an important nectar source for honey bees in California (Wenner and Thorp 1994). Consistent with this, honey bees comprised almost half of the insects seen on flowers of *E. globulus* in eastern Tasmania during late 1997 (Hingston and Potts 1998). However, honey bees were not observed on the flowers of *E. nitens* in an eastern Tasmanian seed orchard during early 1998 in spite of the presence of a hive nearby (A. Hingston pers. obs.). Further doubt regarding the propensity for honey bees to regularly visit *E. nitens* flowers comes from this species not being important to apiculture within its natural distribution in New South Wales (Clemson 1985).

2.1.2 Limitations to the usefulness of honey bees as pollinators

One of the current management practices in seed orchards of *Eucalyptus* involves the introduction of honey bee colonies in hives when flowering commences, in the hope of increasing seed set and outcrossing (Moncur and Kleinschmidt 1992, Moncur *et al.* 1993, 1995). Reliance on honey bees is a widespread practice in many crops requiring pollination because honey bees are easily managed (Westerkamp and Gottsberger 2000). However, Westerkamp and Gottsberger (2000) regarded this reliance on a single species to pollinate all crops as unwise because the uniformity in size of honey bees ,and certain characteristics of their foraging behaviour, often render them ineffective as pollinators (Stephen 1955, Robinson 1979, Parker 1981, Robinson *et al.* 1989, Westerkamp 1991, Bosch and Blas 1994,

Westerkamp and Gottsberger 2000). Moreover, populations of honey bees have been seriously affected by the recent spread of varroa and tracheal mites across many parts of the world (Robinson *et al.* 1989, Kevan *et al.* 1990b, Kevan and Laverty 1990, Wenner and Thorp 1994, Westerkamp and Gottsberger 2000). Collectively, these problems with dependence solely on honey bees for pollination have triggered a resumption of interest in other animals as pollinators (Stephen 1955, Robinson *et al.* 1989, Kevan *et al.* 1990b, Kevan and Laverty 1990, Westerkamp 1991, de Ruijter 1995, Westerkamp and Gottsberger 2000).

There are several reasons why honey bees are sometimes ineffective pollinators. The tendency for individual honey bees to forage for either nectar or pollen, but not both, on any particular trip limits their capacity to transfer pollen from male to female flowers (Doull 1973, DeGrandi-Hoffman and Watkins 2000). As combing unwanted pollen from the body is costly both in time and energy to nectar-gathering honey bees, it has been proposed that such individuals learn to access nectar without contacting anthers and becoming contaminated with pollen (Westerkamp 1991). In addition, pollen groomed from the bodies of honey bees (and bumble bees) is unavailable for pollination because it is either packed tightly in the corbiculae of pollen-gatherers (Macior 1967, Free 1968, Beattie *et al.* 1973, Kendall and Solomon 1973, Green and Bohart 1975, Heinrich 1976, Bernhardt and Weston 1996) or, when foraging for nectar only, discarded (Free 1968, Doull 1973, Heinrich 1976). The viability of pollen packed in corbiculae is also reduced (Mesquida and Renard 1989) because honey bees moisten the grains with nectar, prior to packing, which causes them to hydrate prematurely (Bernhardt and Weston 1996, Westerkamp and Gottsberger 2000). In contrast, pollen transported in the scopal hairs of solitary bees is not moistened, and is therefore more likely to be deposited on stigmata (Kendall and Solomon 1973). Nevertheless, pollen deposited in some regions of a honey bee's (or a bumble bee's) body cannot be reached when combing (particularly around the face, mouthparts, the crevice between the head and thorax, and the bases of the legs) and is therefore likely to be transported between flowers (Macior

1967, Beattie 1971, Green and Bohart 1975). However, pollen may not be deposited in these regions if nectar-gatherers learn to avoid contact with stamens, or pollen-gatherers learn to collect pollen only on the regions of their body from which they can comb pollen into their corbiculae (Westerkamp 1991).

The foraging movements of honey bees may also promote inbreeding (Grant 1950). Individual honey bees often confine their foraging to very small areas for long periods, despite the presence of other conspecific flowers nearby (Butler *et al.* 1943, Hodgson 1976a, Paton 1993, 1997). Indeed, some eucalypts produce so much nectar that a honey bee needs to visit only a single flower to fill its honey stomach (Doull 1973). In addition, Paton (1993, 1997) observed honey bees visiting a total of 4600 flowers of *Callistemon rugulosus* DC (Myrtaceae) 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 honey bee 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, interplant movements averaged 7.3 per hour and one every 400 flowers visited (Paton 1993). As a result, fruit set in flowers visited only by honey bees was comparable to that from bagged flowers that were self-pollinated, and fruit set in open pollinated flowers declined as honey bee activity increased (Paton 1993, 1997). Honey bees were also found to move between trees less frequently than were native insects in a South American dry forest (Aizen and Feinsinger 1994) and a megachilid bee in Spain (Bosch and Blas 1994), and exhibited shorter inter-flower flights than did butterflies and most other bees in Spain (Herrera 1987, 1990). However, the proportion of interflower movements on *Calothamnus quadrifidus* R.Br. (Myrtaceae) in Western Australia that comprised interplant movements was slightly higher for honey bees than honeyeaters (Collins *et al.* 1984).

Nevertheless, the transfer of pollen to female flowers as well as outcrossing rates by honey bees may be greater than expected from their foraging

behaviour. Free and Williams (1972) found pollen in the corbiculae of honey bees from species other than that on which they were foraging, suggesting that pollen may be transferred between individuals while in the hive. This was confirmed by DeGrandi-Hoffman *et al.* (1986) who found that individual honey bees confined to within the hive accumulated sufficient pollen from their forager hivemates within 3 - 4 h to pollinate apples (*Malus domestica* L. Borkh.). However, such transfer is probably only effective if both pollen and nectar are being collected from the same plant species. Honey bees from colonies deployed to pollinate female sunflower (*Helianthus annuus* L.) plants acquired a mean of only 1.1 grains of sunflower pollen via within-hive transfer over a seven hour period, because most pollen-collection was being done from another plant species rather than male sunflowers (DeGrandi-Hoffman and Martin 1995).

Even if honey bees carry large quantities of compatible pollen and move frequently between plants, their effectiveness as pollinators of eucalypts is probably diminished when they avoid female-phase flowers as a result of foraging for pollen rather than nectar. In South Africa, 84% of honeybee visits to flowers of *E. grandis* (Hill) Maiden were in the first two days after anthesis (Hodgson 1976a). However, this pattern was not evident when honey bees foraged on *E. costata* Behr & F. Muell., ex F. Muell. in Victoria as most visits there were to the older flowers that were receptive (Horskins and Turner 1999). As the flowers of *E. globulus* and *E. nitens* are protandrous, with stigmatic receptivity occurring about one week after anthesis (Tibbits 1989, Hardner and Potts 1995), preferential foraging on newly opened flowers by pollen-gathering honey bees in these species would limit pollen deposition on receptive stigmata. Ellis and Sedgley (1992) found that pollen did not adhere well to stigmata of *E. spathulata* Hook., *E. cladocalyx* F. Muell. and *E. leptophylla* F. Muell. ex Miq. prior to stigmatic receptivity. However, some pollen deposited on stigmata of *E. camaldulensis* Dehnh. in the first two days after anthesis remained there until stigmatic receptivity occurred, whereupon they germinated causing seed to form (Oddie and McComb 1998).

2.1.3 Previous assessments of the effectiveness of honey bees as pollinators of eucalypts

It has been claimed that the introduction of honey bee colonies in hives to seed orchards enhances pollination of eucalypts, including *E. globulus* and *E. nitens* (Moncur *et al.* 1993, 1995). Their conclusion was based on comparisons of seed set and outcrossing rates in years with and without the presence of active hives (Moncur *et al.* 1993, 1995). In northwestern Tasmania, addition of active hives was associated with increased seed set per capsule (Moncur *et al.* 1993) but no change in outcrossing rate in *E. globulus*, in contrast to no change in seed set but increased outcrossing in *E. nitens* (Moncur *et al.* 1995). In northern Queensland both seed set and outcrossing rate were greater in natural stands of *E. camaldulensis* when active hives were present (Moncur *et al.* 1995). In contrast, the numbers of seeds per capsule in a Victorian stand of *E. regnans* were unaffected by introduction of honey bee hives (Eldridge 1963).

Unfortunately, all of those studies are fundamentally flawed. In each case, the numbers of capsules produced per flower were not determined, hence, the numbers of seeds produced per flower could not be calculated (Eldridge 1963, Moncur *et al.* 1993, 1995). More importantly, the results were confounded by the 'with hives' and 'without hives' treatments being conducted in different years (Eldridge 1963, Moncur *et al.* 1993, 1995). Because flowering intensity in eucalypts varies enormously between years (Ashton 1975, Brown 1989, Moncur 1993, Moncur *et al.* 1994), and this influences both seed production (Carpenter 1976, Andersson 1988) and outcrossing rates (Beattie 1976, Stephenson 1982, Karron *et al.* 1995), any increase in seed set or outcrossing rate in years when hives were added cannot be attributed solely to pollination by honey bees (Paton 1996). Furthermore, seed production is also affected by the activity levels of other pollinators, environmental conditions and seed predation (Eldridge *et al.* 1993), which also vary between seasons and therefore confounded their results. Because of inadequate experimental design, the results should only be regarded as correlations based on two data points. Even if it were valid to

draw conclusions of cause and effect from correlations based on two data points, such conclusions could not be drawn because no evidence of increases in numbers of honey bees on the flowers after introduction of hives was obtained (Moncur *et al.* 1993, 1995). It cannot be assumed that the introduction of hives by Moncur *et al.* (1993, 1995) increased the numbers of honey bees visiting the flowers (Paton 1996), because feral populations of honey bees are widespread in Australia (Oldroyd *et al.* 1995, Oldroyd 1998) and the number of feral honey bees has been found to increase rapidly following removal of hives (Schaffer *et al.* 1983). Moreover, no evidence of honey bees foraging on any of these species was presented (Moncur *et al.* 1993, 1995).

Another study that examined the effectiveness of honey bees as pollinators of eucalypts is also seriously flawed. In South Africa, honey bees visited emasculated flowers less often than they did intact flowers of *Eucalyptus grandis* (Hill) Maiden (Hodgson 1976a). Because emasculation resulted in a halving in the numbers of seeds set per capsule, it was concluded that honey bees contributed half of the pollination services to this plant (Hodgson 1976a). However, no data were presented on visitation rates to these flowers by other potential pollinators. If other visitors also avoided emasculated flowers, this may have been the reason for the observed decline in seed set. Furthermore, emasculation may alter the frequency with which flower-visiting animals contact stigmata, thereby altering pollination services (Stucky 1985).

A sounder approach to assessing the value of honey bees as pollinators of eucalypts was used by Loneragan (1979). Many more *Eucalyptus diversicolor* F. Muell. seeds were produced per capsule on branches enclosed in cages with a small colony of honey bees (1.98 and 1.15) than on caged branches from which pollinating insects were excluded (1.08 and 0.85), and slightly more than on open-pollinated branches (1.60 and 1.11). However, the numbers of capsules produced per flower were not determined, preventing an analysis of the numbers of seeds produced per flower under the different

treatments. In a related study, the number of seeds per capsule of *E. diversicolor* was much higher within 120 m of an apiary than at 500 - 800 m from the apiary, but the numbers of capsules set per m^2 displayed the opposite trend, resulting in similar numbers of seeds per hectare across the range of distances from the apiary (Loneragan 1979).

Horskins and Turner (1999) found evidence that honey bees were probably also effective pollinators of *E. costata*. Foraging honey bees contacted receptive stigmata on 55.8% of flower visits and carried a mean of 1459 pollen grains per bee, almost all of which were eucalypt pollen (Horskins and Turner 1999).

2.2 The value of other animals as pollinators of *Eucalyptus* seed orchards

2.2.1 Dependence of plants on coevolved pollinators

There is a possibility that seed orchards outside the natural range of the plant species may suffer from poor pollination services because of the absence of coadapted pollinators (Moncur and Kleinschmidt 1992, Westerkamp and Gottsberger 2000, Jones *et al.* 2001). This has been reported for several crops, including vanilla (*Vanilla planifolia* Jacks.), oil palm (*Elaeis guineensis* Jacq.) and red clover (*Trifolium pratense* L.) (Westerkamp and Gottsberger 2000). Similarly, seed set on *Verticordia nitens* (Myrtaceae) in a garden in the absence of its bee pollinator *Euryglossa morrisoni* was only 1% of that in the nearest natural stand where *E. morrisoni* occured (Houston *et al.* 1993). In *Eucalyptus nitens* grown in South Africa, capsule set in open-pollinated flowers was no higher than that from flowers from which all pollinators had been excluded, suggesting that effective pollinators were not present (Jones *et al.* 2001).

Although flowers with exposed nectar and pollen, such as most eucalypts, are typically visited by a wide variety of anthophiles, such apparently allophilic flowers are sometimes quite specialised in their pollinator requirements as a result of differences in the effectiveness of visitors in transferring pollen (Lindsey 1984). These differences are the product of the

relative abundances of particular anthophiles, their pollen carrying capacities, fidelity to the plant in question, capacity to contact receptive stigmata, the frequency with which they move between flowers and plants (Lindsey 1984), and the extent of pollen carryover (Campbell 1985b).

2.2.2 *The effectiveness of native animals as pollinators of E. globulus*

The flowers of *E. globulus* host an enormous array of anthophilous insects, encompassing at least 71 species and 26 families, as well as several bird species (Hingston and Potts 1998). However, those authors proposed that birds are likely to be more effective pollinators than insects because insects were too small to consistently contact stigmata of these large flowers while gathering nectar (Hingston and Potts 1998). After also noting that honey bees did not contact *Grevillea* stigmata, because of the large distances between nectaries and reproductive organs, Taylor and Whelan (1988) suggested that this may be a common phenomenon in Australian native plants adapted to vertebrate pollination (Table 2.1). In addition, nectar-collecting honey bees rarely contacted stigmata of *Banksia* species (Paton and Turner 1985, Vaughton 1992, Hackett and Goldingay 2001), or other *Grevillea* species (Vaughton 1996, Kalinganire *et al.* 2001).

Plant species	% by *Apis*	% by birds	Source
Callistemon rugulosus DC	4.4	> 50	Paton 1993
Calothamnus quadrifidus R.Br.	42	71 - 84	Collins *et al.* 1984
Grevillea mucronulata R.Br.	18.5	98	Richardson *et al.* 2000

TABLE 2.1

Percentages of probes for nectar that resulted in stigmatic contact in Australian native plants visited by both honey bees (*Apis mellifera*) and honeyeater birds.

Ornithophily in *E. globulus* is also promoted by its flowering season. Spring weather in Tasmania is frequently too cold, wet and windy for insect activity (Hingston and Potts 1998). Under such conditions, birds are more reliable pollinators than insects (Christensen 1971, Paton and Ford 1977, Ford *et al.* 1979, Hopper 1981). Even overcast conditions have been found to prevent

Australian native bees from foraging, despite warm air temperatures (Houston *et al.* 1993).

Another tree species in the Myrtaceae with remarkably similar floral structure to *Eucalyptus* is the Hawaiian *Metrosideros collina* (Carpenter 1976). This is also a mass-flowering species visited by birds and insects, which produces vast quantities of seeds enabling it to colonise disturbed areas. Fruit-set from flowers exposed to both birds and insects in this species was greater than that from flowers from which birds were excluded, which in turn was greater than that from which all visitors were excluded and those subjected to manual geitonogamy. Therefore, the breeding system of *M. collina* favoured outcrossing, with both insects and birds contributing to breeding success (Carpenter 1976).

Species	Family	Source
Metrosideros collina	Myrtaceae	Carpenter 1976
Callistemon rugulosus DC	Myrtaceae	Paton 1993, 1997
Calothamnus quadrifidus R.Br.	Myrtaceae	Collins *et al.* 1984
Banksia littoralis R.Br.	Proteaceae	Whelan and Burbidge 1980
Banksia menziesii R.Br.	Proteaceae	Whelan and Burbidge 1980, Ramsey 1988
Banksia spinulosa Smith	Proteaceae	Vaughton 1992
Banksia aemula R.Br.	Proteaceae	Dalgleish 1999
Grevillea barklyana F. Muell. Ex Benth.	Proteaceae	Vaughton 1996
Protea repens L.	Proteaceae	Coetzee and Giliomee 1985
Acacia pycnantha Benth.	Mimosaceae	Vanstone and Paton 1988
Correa reflexa (Labill.) Vent.	Rutaceae	Paton 1993
Delphinium nelsonii Greene	Ranunculaceae	Waser 1978
Ipomopsis aggregata (Pursh) V. Grant	Polemoniaceae	Waser 1978
Fouquieria splendens	Fouquieriaceae	Waser 1979
Penstemon pseudospectabilis	Scrophulariaceae	Reid *et al.* 1988

TABLE 2.2

Plant species exhibiting greater fecundity after their flowers or extrafloral nectaries were visited by both birds and insects, than after being visited by insects only.

The provision of pollination services by birds, additional to those provided by insects, is typical of plants whose flowers or extrafloral nectaries are visited by both birds and insects (Table 2.2). However, exposure of *Banksia attenuata* R.Br., and sometimes *B. spinulosa* Smith and *Protea repens* L., inflorescences to birds did not increase seed set beyond that resulting from

visits by insects (Whelan and Burbidge 1980, Coetzee and Giliomee 1985, Vaughton 1992). The proportion of pollination services provided by insects for flowers visited by both insects and birds is, of course, influenced by the frequency of insect visits (Vaughton 1992, Paton 1993, 1997).

Birds are also likely to be more effective pollinators of *E. globulus* than are insects because of their wider movements which promote outcrossing (Ford *et al.* 1979, Eldridge *et al.* 1993, Paton 1993). In plants that exhibit preferential outcrossing, seed or fruit set resulting from insect pollination is sometimes similar to that from hand self-pollinations, whereas seed or fruit set resulting from insects plus birds is comparable to that from hand cross-pollinations (Paton 1993, 1997). In *Metrosideros collina* fruit set from flowers exposed to both birds and insects was greater when floral density was lower, but flower density had no effect on fruit set in flowers from which birds were excluded (Carpenter 1976). This result was attributed to birds having to travel more frequently between trees while foraging at low floral densities, thereby increasing the ratio of xenogamous to geitonogamous pollinations, whereas insect foraging behaviour may not have been affected by altered densities (Carpenter 1976).

However, Heinrich (1975) speculated that insects may promote outcrossing in mass flowering trees by picking up outcross pollen that had been deposited by birds and spreading it to other flowers in the canopy. Evidence of such secondary pollen transfer has recently been obtained (DeGrandi-Hoffman and Martin 1995, DeGrandi-Hoffman and Watkins 2000). In the USA, native bees transferred sunflower pollen from male-fertile flowers to male-sterile flowers. Honey bees that foraged only on male-sterile flowers appeared to effect pollination by picking up pollen that had been deposited on male-sterile flowers and spreading it to other male-sterile flowers (DeGrandi-Hoffman and Martin 1995, DeGrandi-Hoffman and Watkins 2000).

Outcrossing rates are also influenced by the degree of pollen carryover, where pollen deposited on the pollinator's body at a flower is then transferred to a number of flowers visited subsequently. Although most pollen is sometimes deposited on the first few flowers visited, pollen deposition curves are typically characterised by long tails indicating that pollen is frequently transferred to flowers later in the visitation sequence (Thomson and Plowright 1980, Thomson 1986, Robertson 1992, Morris *et al.* 1994, Cresswell *et al.* 1995). These pollen deposition curves differ between pollinator species (Campbell 1985b). Robertson (1992) regarded the amount of pollen carried by a pollinator as the most important factor influencing the degree of pollen carryover. Pollen carryover should be extensive for large pollinators, such as birds, because the amount of pollen carried is far greater than the amount deposited per visit (Paton and Ford 1977, Paton 1982b, Robertson 1992). In contrast, pollen carryover by bumble bees and honey bees is reduced because of their frequent grooming which prevents pollen from remaining on their bodies (Thomson and Plowright 1980, Thomson 1986).

However, birds do not always facilitate frequent outcrossing. Sampson *et al.* (1989) found low outcrossing rates in a bird pollinated eucalypt, *E. rhodantha* Blakely and Steedman, and an absence of pollen flow between populations separated by only 170 m. Reduced pollen dispersal distances and numbers of flowers receiving pollen have been recorded within a patch of *Justicia secunda* Vahl (Acanthaceae) defended by a territorial hummingbird, as a result of the prevention of other birds from foraging at flowers while the incumbent bird restricted its feeding to the plants within its territory (Linhart and Feinsinger 1980). As many of the Australian Meliphagidae also defend nectar resources (Ford and Paton 1982, Paton 1993), including flowering eucalypts (Ford 1979, Paton 1980, Franklin *et al.* 1989), this is one possible explanation for the low outcrossing rates in *E. rhodantha*. Paton and Ford (1983) found that the territories of both New Holland honeyeaters and red wattlebirds were sometimes restricted to parts of individual trees of *E. leucoxylon* F. Muell. and, hence, outcrossing occurred only when an intruder

entered the territory to feed or a territory holder returned after feeding on flowers from another tree outside its territory. Consequently, the Meliphagidae may be less effective outcrossers of eucalypts than are the non-territorial anthophilous parrots. In cases where the territories of honeyeaters encompass more than one plant, Paton and Ford (1983) proposed that small territorial honeyeaters effect more cross pollination than larger territorial honeyeaters because smaller species visit fewer flowers per visit to each plant and visit individual flowers more frequently than do larger species.

Anthophilous parrots may also be more effective pollinators of eucalypts than are honeyeaters because foraging parrots contact stigmata of eucalypts more often than do honeyeaters. This is because parrots, with shorter bills than honeyeaters, have to bury their heads in flowers to access nectar and pollen (Paton and Ford 1977). Brown (1989) and Gartrell *et al.* (2000) noted that swift parrots foraged in this manner to access nectar of *E. globulus*. For this reason, Hingston and Potts (1998) suggested that swift parrots and musk lorikeets may be the most effective pollinators of *E. globulus* within its native geographic range.

Anthophilous birds also differ in the amounts of pollen they carry. Ford and Pursey (1982) found that eastern spinebills carried fewer *Banksia* pollen grains than did larger honeyeaters such as wattlebirds, white-cheeked and New Holland honeyeaters. Similarly, the amounts of pollen removed from pollen presenters and deposited on stigmata of *Lambertia formosa* (Proteaceae) per visit by four species of honeyeater increased with the body mass of honeyeaters (Paton 1991). In both those studies, the result was attributed to the larger heads of the larger species facilitating greater contact with the reproductive parts of the flower (Ford and Pursey 1982, Paton 1991). Ford and Pursey (1982) also ascribed the smaller *Banksia* pollen loads on eastern spinebills to their longer bills that reduced contact between their heads and pollen presenters. That idea is supported by the results of Hackett and Goldingay (2001), who found that white-cheeked honeyeaters carried fewer *Banksia* pollen grains than did smaller birds with shorter bills.

Most studies have found that honeyeaters carried more pollen than did mammals (Wiens *et al.* 1979, Hopper 1980, Hopper and Burbidge 1982, Wooller *et al.* 1983). However, others found that mammals carried similar quantities of pollen to birds (Hackett and Goldingay 2001) or even more than birds (Goldingay *et al.* 1987). Another study of two *Banksia* species found that birds carried more pollen than did mammals on one species, while the reverse was true for the other species (Carpenter 1978). However, all these results may have been confounded by the different methods used to capture birds and mammals. Pollen samples are taken from birds very soon after capture in mistnets, whereas mammals are sometimes confined in traps for many hours before samples are removed (Wooller *et al.* 1983). As mammals are free to groom pollen from their fur while in traps, but birds are unable to preen while in a mistnet, mammals may remove large amounts of pollen before samples are taken (Wiens *et al.* 1979). As a result, pollen loads on mammals held for long periods in traps are sometimes smaller than those sampled immediately after capture (Goldingay *et al.* 1987, 1991), but in other cases confinement for up to an hour did not significantly reduce pollen loads (Goldingay *et al.* 1987).

2.2.3 The effectiveness of native animals as pollinators of E. nitens

In contrast to *E. globulus*, stigmata of the smaller flowers of *E. nitens* are more likely to be contacted by foraging insects. Indeed, honey bees contacted stigmata of the slightly larger flowers of *E. costata* when receptive on 55.8% of visits (Horskins and Turner 1999).

Entomophily in *E. nitens* is also likely to be promoted by its flowering season, as it blooms during summer in southeastern Australia (Boland *et al.* 1984) when the weather is warmer and drier. A variety of insects were observed feeding on flowers of this species in a seed orchard on 13 January 1998 in southeastern Tasmania, with beetles being particularly abundant. Birds were not observed feeding from flowers although several Meliphagidae species were present in the orchard (A. Hingston pers. obs.).

However, the foraging behaviour of many insects may promote self-pollination rather than outcrossing. Beetles, and a species of syrphid fly, have been observed restricting their foraging to individual bushes of *Thryptomene calycina* (Myrtaceae) for long periods, although large blowflies (Calliphoridae) frequently flew between bushes (Beardsell *et al.* 1993). However, insects often travel long distances between trees in the tropics. Small insects are known to consistently transport pollen between Panamanian tropical rainforest trees separated by several hundred metres (Stacy *et al.* 1996), and large insects frequently fly between trees in subtropical rainforests in NSW (Williams and Adam 1998). Solitary bees have also been recorded travelling up to 1200 m within two hours between conspecific trees in Costa Rican dry forest, although intertree movements were uncommon (Frankie *et al.* 1976).

The effectiveness of various insects as pollinators of *E. nitens* is also influenced by the quantities of pollen they carry on their bodies. Studies in other situations have found that bees usually carry larger pollen loads than do other insects (Beattie *et al.* 1973, Kendall and Solomon 1973, O'Brien 1980). O'Brien (1980) found that Hymenoptera generally carried large pollen loads, with 90% of honey bees carrying over 1000 pollen grains, and the remainder over 100. Approximately 90% of wasps and solitary bees carried over 100 pollen grains, with 34.5% and 46% respectively carrying over 1000 grains. However, flies carried smaller loads. Only 18.2% of specialised flower-feeding flies in the Syrphidae and Bombyliidae carried over 1000 grains, while 39.4% carried less than 100 grains. Unspecialised flies that occasionally visited flowers carried even less, with 82.7% carrying less than 100 grains and none carrying more than 1000. Butterflies carried the smallest pollen loads, with all carrying less than 100 grains (O'Brien 1980). In another study, workers of the bumble bees *Bombus terrestris* and *B. lucorum* carried significantly more apple pollen (mean 16,220 grains) than did the syrphid fly *Eristalis tenax* (mean 2351 grains) (Kendall and Solomon 1973). However, the numbers of pollen grains carried by honey bees (mean 4152 grains) and queens of *B. terrestris* and *B. lucorum* (mean 5093 grains) were not

significantly greater than those carried by *E. tenax*. The amount of pollen carried by solitary bees varied between species, but encompassed a similar range to that carried by bumble bees and honey bees. All of these insects carried far more apple pollen than the European wasp *Vespula vulgaris* (mean 23 grains) and most other insects (Kendall and Solomon 1973). However, Kendall and Solomon (1973) did not include pollen carried on the hind legs of solitary bees in their comparison. A study that did include pollen from all parts of bees' bodies found that North American native bees (mean 29,612 grains) carried more sunflower pollen than did honey bees (mean 1778 grains), and that bumble bee workers (mean 5024 grains) carried less pollen than did females of other native bee species (mean 32,934 grains) (Parker 1981). Another study found that 54% of beetles greater than 9 mm in length collected from flowers of NSW subtropical rainforest trees carried more than 300 pollen grains, while only 18% of wasps and 14% of flies of this length carried this amount (Williams and Adam 1998).

The effectiveness of various insects as pollinators of *E. nitens* may also be influenced by the positioning of pollen on their bodies, a factor that often varies between insect species (Beattie 1971, Beattie *et al.* 1973, Williams and Adam 1998). This was particularly marked for the pollen of *Frasera speciosa* (Gentianaceae) which bees mostly carried on their legs and ventral surfaces, in contrast to flies and butterflies that carried most pollen on their legs and dorsal surfaces (Beattie *et al.* 1973). As it was the ventral surfaces that most frequently contacted stigmata, it was concluded that bees were more efficient pollinators than were flies and butterflies (Beattie *et al.* 1973). A preponderance of pollen deposition on ventral body surfaces was also found in beetles, but not in wasps, collected from flowers of subtropical rainforest trees in NSW (Williams and Adam 1998). In contrast to the primarily dorsal pollen deposition on flies on *F. speciosa* (Beattie *et al.* 1973), pollen was mostly placed on the anteroventral surface of flies collected from NSW rainforests (Williams and Adam 1998).

2.3 The effects of relatively ineffective pollinators on total pollination levels

The presence of flower visitors that are relatively ineffective as pollinators may reduce the total level of pollination if they deter more effective pollinators from visiting the plant in question (Thomson and Thomson 1992). This can occur as a consequence of reduced resource levels (Paton 1993, 1997, Irwin and Brody 1998) or aggressive defence of flowers (Roubik 1982, Gross and Mackay 1998). These effects are influenced by the diurnal activity patterns of the visitors and the patterns of resource presentation by the plant. Anthophiles that feed immediately after resources are presented have an enhanced capacity to impact on, and are also less susceptible to, those feeding later (Paton 1993). However, it has been proposed that resource competition from ineffective visitors may force effective pollinators to visit more flowers to obtain their energy requirements, thereby enhancing pollination (Heinrich and Raven 1972, Maloof 2001). Nevertheless, although nectar theft from *Asclepias curassavica* L. by ants may have increased visitation rates by its legitimate butterfly pollinators, the amount of pollen deposited on stigmata was reduced (Wyatt 1980). That author attributed his findings to butterflies spending less time at each flower after standing nectar crops had been reduced by ants, decreasing the likelihood of pollen deposition during a single visit (Wyatt 1980). Hence, there may be a fine balance between too many and too few ineffective flower visitors to maximise the value of legitimate pollinators. This view is supported by maximal fruit set occurring in trees of *Metrosideros collina* with intermediate nectar secretion rates, as a result of low nectar levels attracting few pollinators and high nectar levels satiating visitors from so few flowers that outcrossing was reduced (Carpenter 1976).

However, plants sometimes readily replenish nectar levels (Pyke 1991), suggesting that the consumption of nectar by ineffective visitors may not greatly influence the foraging behaviour of more effective pollinators. In spite of this, the additional energetic cost to a plant associated with producing additional nectar has been shown to reduce its capacity to

produce seeds (Pyke 1991). Thus, the presence of ineffective visitors is still likely to reduce seed set.

Pollination levels may also be adversely affected by the presence of ineffective visitors when they reduce the amount of pollen that can be transferred by more effective visitors (Pyke 1990, Wilson and Thomson 1991, Paton 1993, Vaughton 1996, Paton 1997, Hackett and Goldingay 2001). This can involve pollen consumption (Wilson and Thomson 1991, Paton 1993, 1997), packing in the corbiculae of honey bees and bumble bees (Free 1968, Green and Bohart 1975, Heinrich 1976, Bernhardt and Weston 1996), transfer to stigmata of other plant species (Campbell and Motten 1985), or transfer to stigmata of the same plant in self-incompatible species (de Jong *et al.* 1993, Klinkhamer and de Jong 1993). The latter two situations not only reduce male fitness through pollen wastage (de Jong *et al.* 1993, Klinkhamer and de Jong 1993), but also lower female fitness by preventing the germination of subsequently deposited compatible pollen (Galen and Gregory 1989, Klinkhamer and de Jong 1993). Moreover, in species with post-zygotic self-incompatibility mechanisms, transfer of self-pollen has been shown to pre-empt available ovules from fertilisation with outcross pollen (Waser and Price 1991, Ramsey *et al.* 1993, Ramsey 1995, Ramsey and Vaughton 2000). However, because not all ovules are penetrated by pollen-tubes in eucalypts, Ellis and Sedgley (1992) concluded that competition for ovules is inconsequential to a eucalypt's fecundity. Ineffective visitors sometimes also reduce seed set by removing pollen from stigmata, as occurs when honey bees visit *Grevillea barklyana* (Proteaceae) (Vaughton 1996) and *Melastoma affine* (Melastomataceae) (Gross and Mackay 1998). These effects are also influenced by diurnal activity patterns of the visitors and patterns of flower opening. The negative impact on seed set by ineffective visitors removing pollen from anthers is greatest when they have first access to flowers (Thomson and Thomson 1992, Paton 1997), but is greatest when removing pollen from stigmata when they are the last visitor (Gross and Mackay 1998).

Chapter 3

Methods previously used to assess the effectiveness of flower visitors as pollinators

3.1 Direct versus indirect methods of assessing pollinator effectiveness

Investigations into pollinator effectiveness may be categorised as direct or indirect methods (Spears 1983). Direct methods involve comparing seed set (the product of the mean numbers of fruits per flower and seeds per fruit), seed viability, and offspring vigour resulting from flower visits by various animals. Indirect methods consist of comparisons of the visitors' pollen loads, foraging constancy, pollen deposition on virgin stigmata, ratios of interfloral movements between conspecific flowers on the same or different plants, and pollen carryover (Spears 1983). Direct methods provide a more accurate measure of plant fitness (Dieringer 1992), and require fewer assumptions than indirect measures (Spears 1983). However, if seed set is limited by resources to the plant rather than by pollen deposition, direct measures would not reveal differences between treatments in pollinator effectiveness.

Lindsey (1984) regarded direct measures as impractical in plants receiving a diverse assemblage of floral visitors, because of the amount of fieldwork involved. Hence, Lindsey proposed a model estimating pollination efficiency in terms of subjective scores for insect size, the frequency with which anthers and stigmata were contacted, and the frequency with which they moved between flowers and plants. From that, pollinator importance was calculated as the product of pollination efficiency, the proportion of the plant's pollen carried by visitors being transported by the visitor species in question, the proportion of all pollen carried by this visitor species which is of this plant species, and the proportional abundance of this visitor species (Lindsey 1984). However, Herrera (1987) found that four congeneric bee species of similar size and foraging behaviour, which would therefore receive similar pollination efficiency scores under this model, varied almost three-fold in the proportion of stigmata to which they transferred pollen. In

addition, Lindsey's model makes no allowance for differential pollen carryover between visitor species, a factor that should alter outcrossing rates (Campbell 1985b, Morris *et al.* 1994).

3.2 Measuring the degree to which seed set is limited by pollination services

Direct measures of pollen limitation involve relatively straightforward procedures. The lack of deposition of compatible pollen as a factor in seed production levels can be tested by comparison of seed set in open-pollinated flowers with those receiving supplemental pollen application to uncaged flowers (Morse and Fritz 1983, Motten 1983, 1986, Dieringer 1992, Gross 1996, Parker 1997, Paton 1997) or hand-pollinated caged flowers (Bertin 1982a, Bawa and Webb 1984). This method is based on the assumption that the hand-pollinated flowers will develop the maximum possible numbers of seeds for flowers on that plant (Thomson 2001). However, this may not be the case if the application of large quantities of pollen to stigmata results in pollen grains or tubes interfering with each other, or attracts pollen thieves that remove the deposited pollen or damage the stigma (Young and Young 1992). It has also been proposed that maximum seed set would not be achieved if hand-pollination damaged the stigma, peak stigmatic receptivity was missed, or insufficient viable pollen was applied (Young and Young 1992). The two techniques of estimating maximum possible seed set also have their own particular problems. Pollen supplementation to open-pollinated flowers does not result in maximum possible seed set if the prior deposition of self pollen by anthophiles results in the pre-emption of ovules by self pollen in species with late-acting self-incompatibility mechanisms (Waser and Price 1991, Ramsey *et al.* 1993, Ramsey 1995, Ramsey and Vaughton 2000). It has been proposed that hand-pollination to caged flowers may not result in maximum possible seed set if caging reduces seed set (Young and Young 1992). In *E. globulus*, maximum seed set does not occur in flowers that are emasculated and bagged because of the mechanical damage to the flowers that this entails (Hardner and Potts 1995).

3.3 Methods used to assess the effectiveness of particular flower visitors as pollinators

3.3.1 Comparisons of plant fecundity levels and variation in anthophile abundance

Visitor profiles to flowers can be manipulated by the introduction or removal of large numbers of particular species to the area. This method is particularly applicable to colonial bees such as honey bees (e.g. Eldridge 1963, Loneragan 1979, Moncur *et al.* 1993, 1995). Indeed, previous direct measures of pollinator effectiveness in *Eucalyptus* have been limited largely to assessing whether the provision of honey bee hives enhances seed set. Those studies involved comparisons of seed set and outcrossing rates in areas between years when commercial hives were absent or present (Eldridge 1963, Moncur *et al.* 1993, 1995). However, as feral populations of honey bees are widespread in Tasmania (Oldroyd *et al.* 1995), and Schaffer *et al.* (1983) found that the number of feral honey bees in a North American site increased rapidly following removal of hives (cf. Patten *et al.* 1993), it cannot be assumed that the introduction or removal of hives would significantly alter the numbers of honey bees in the area (Paton 1996). To overcome this potential experimental flaw, it is necessary to eradicate feral honey bees from the area before colonies are introduced. In a review of techniques used in eradication, Oldroyd (1998) concluded that the remote application of acephate to colonies via foragers was the most cost-effective method.

The previous studies that compared seed set and outcrossing rates in eucalypts between years when honey bee hives were absent or present (Eldridge 1963, Moncur *et al.* 1993, 1995) assumed that any differences in seed set and outcrossing rate could be attributed to altered pollination services. The same assumption has been made in studies of other plants that compared fruit set in different populations of a species, or between seasons in the same population, and related this to the relative proportions of the anthophiles in each case (Bertin 1982a, Schemske and Horvitz 1988). However, such assessments of pollinator effectiveness based on correlation between seed set, or outcrossing rates, and abundances of various flower

visitors are likely to be confounded by other factors. Motten (1983) found that the proportions of lily flowers setting fruit and the numbers of seeds per fruit varied between sites and years even though the amount of pollen deposited on stigmata was never limiting in those studies. Furthermore, seed set following single flower visits by bees varied three-fold between populations of *Agalinis strictifolia* (Dieringer 1992). Indeed, seed production is influenced by many other factors besides pollination, including seasonal conditions, seed predation by insects (Eldridge *et al.* 1993), and the spatial arrangement of flowers (Carpenter 1976, Augspurger 1980, Stephenson 1982, Andersson 1988), all of which vary between seasons and sites. Outcrossing rates are also influenced by the spatial arrangement of flowers (Beattie 1976, Stephenson 1982, Karron *et al.* 1995). These confounding factors can be controlled for by examining the effectiveness of a range of pollinators in one place and time (Augspurger 1980), or by standardising the spatial arrangement of flowers in different places at one time (Steffan-Dewenter and Tscharntke 1999).

The relative contributions of vertebrates and invertebrates to pollen transfer, seed set, and outcrossing can be determined by exclosure experiments. The three standard treatments are: 1) bagging flowers to exclude all visitors; 2) caging flowers in mesh small enough to exclude vertebrates but large enough to allow access to insects; and 3) uncaged flowers which can be accessed by all animals (Carpenter 1976, Waser 1978, 1979, Coetzee and Giliomee 1985, Paton and Turner 1985, Reid *et al.* 1988, Vanstone and Paton 1988, Paton 1993, 1997, Vaughton 1996, Dalgleish 1999, Lange and Scott 1999). The importance of using all three treatments was highlighted in research conducted by Whelan and Burbidge (1980), who employed only treatments 2 and 3. Those authors were unable to differentiate between autonomous self-pollination and pollination by small animals passing through the cage in treatment 2 (Whelan and Burbidge 1980). In contrast, Ramsey (1988) and Keys *et al.* (1995) introduced a fourth treatment which allowed access to small insects but excluded larger insects and vertebrates, allowing the contributions to seed set by small and large insects to be

differentiated. Heard (1994) was also able to compare the pollinator effectiveness of two bee species by enclosing some flowers in a cage that excluded the larger species but allowed the smaller species to pass through freely. Another treatment, exclusion of ants from flowers by encircling stems with Tanglefoot, was conducted by Fritz and Morse (1981). Ramsey (1988) also applied insecticide to treatment 1 to ensure no insect pollination occurred as a result of insects being trapped inside the bag. As insects are sometimes deterred from visiting caged flowers, even when the mesh is large enough for them to pass through (Morse 1981), their visitation rates must be monitored to guard against differences between treatments 2 and 3 (Ramsey 1988, cf. Keys *et al.* 1995). Flowers in treatments 1 and 2 must also be monitored to ensure that they are effective in excluding taxa according to plan (Ramsey 1988).

Visitor profiles to flowers can also be manipulated by growing plants in enclosures containing particular anthophiles (Alcorn *et al.* 1961, Palmer-Jones *et al.* 1966, Loneragan 1979, Heard *et al.* 1990, Kakutani *et al.* 1993). Comparisons of seed set (Alcorn *et al.* 1961, Loneragan 1979, Kakutani *et al.* 1993), and pollen deposition on stigmata (Heard *et al.* 1990), in flowers open while particular anthophiles are present have been used to indicate the pollinator effectiveness of the particular visitors. Such studies can be enhanced by also recording visitation rates to flowers (Heard *et al.* 1990, Kakutani *et al.* 1993) and nectar standing crops (Kakutani *et al.* 1993) in each treatment. Alcorn *et al.* (1961) allowed each species to forage alone in the enclosure for between three and twelve days, with the treatments occurring sequentially. These results were clearly confounded by seasonal changes which were overcome by Kakutani *et al.* (1993) who applied treatments simultaneously to different enclosures containing large numbers of herbaceous plants. However, for trees such as eucalypts it is difficult to have sufficient replicates in each enclosure to overcome the confounding effects of differences between trees. Heard *et al.* (1990) overcame both of these problems by placing different anthophiles in enclosures with individual trees on a rotational basis. Hence, each tree had a period when it was visited by

each anthophile, with the order in which anthophiles foraged on the trees differing between trees (Heard *et al.* 1990).

The relative contributions of diurnal and nocturnal visitors can be determined by only allowing access to particular flowers during one of these time periods. This is very labour intensive, and necessitates the presence of the researcher at dawn and dusk to place and remove the bags or cages (Bertin and Willson 1980, Morse and Fritz 1983, Paton and Turner 1985, Jennersten 1988, Heard *et al.* 1990, Goldingay *et al.* 1991, Jennersten and Morse 1991, Guitan *et al.* 1993, Ghazoul 1997, Groman and Pellmyr 1999, Hackett and Goldingay 2001). When day- and night-length are not equal, this confounding factor can be removed by limiting exposure during the longer period to the same amount of time as the shorter period (Jennersten 1988, Jennersten and Morse 1991). Exposing flowers to anthophiles at different times of day was also used by Herrera (2000) to determine the contributions to pollination by diurnal insects with different activity periods.

3.3.2 Comparisons of plant fecundity following single visits to flowers by different animals

The effectiveness of various insects can be compared by allowing single visits to virgin flowers. This situation can be created by bagging flowers before they open, and then removing the bags when stigmata are receptive and waiting for insects to forage (Motten *et al.* 1981, Parker 1981, Spears 1983, Campbell 1985a, Snow and Roubik 1987, Wilson and Thomson 1991, Dieringer 1992, Bosch and Blas 1994, Keys *et al.* 1995, Vaissiere *et al.* 1996, Olsen 1997, Osorio-Beristain *et al.* 1997, Freitas and Paxton 1998, Gross and Mackay 1998, Miyake and Yahara 1998, Thomson and Goodell 2001). The numbers of pollen grains deposited (Snow and Roubik 1987, Dieringer 1992, Osorio-Beristain *et al.* 1997, Freitas and Paxton 1998, Gross and Mackay 1998, Miyake and Yahara 1998, Thomson and Goodell 2001) or the numbers of fruit or seeds per flower visited (Motten *et al.* 1981, Spears 1983, Campbell 1985a, Dieringer 1992, Bosch and Blas 1994, Keys *et al.* 1995, Vaissiere *et al.* 1996, Olsen 1997, Freitas and Paxton 1998) can be used as measures of

pollinator effectiveness. Flowers that are not exposed to visitors but receiving the same bagging treatment can be used as controls to verify that bagging does prevent pollination (Keys *et al.* 1995, Gross 1996, Gross and Mackay 1998). Vaissiere *et al.* (1996) controlled for the effects of airborne pollen by exposing control flowers for the same period as the visited flowers. From single visits to virgin flowers, Spears (1983), Keys *et al.* (1995) and Freitas and Paxton (1998) calculated pollinator effectiveness as $(P_t - Z)/(U - Z)$, where P_t = the mean number of seeds set per flower receiving a single visit from species I, Z = the mean number of seeds set per flower receiving no visits, and U = the mean number of seeds set per flower receiving unrestrained visitation.

However, pollination levels resulting from single visits may be so low that most visitors have negligible effect when compared to unexposed flowers (Keys *et al.* 1995). Moreover, Olsen (1997) suggested that the pollinator effectiveness of visitors would be underestimated by this technique if single visits result in the deposition of less pollen than the threshold required to initiate fruit set. Techniques to reduce this problem were employed by Motten (1983, 1986) and Stanghellini *et al.* (1998), who compared the pollinator effectiveness of species by allowing flowers to be visited once or more by a single species. Thus, not only could these authors compare seed set resulting from the same numbers of visits from different species over a range of visit numbers, they could also determine the numbers of visits required from each species for pollen saturation to occur (Motten 1983, 1986, Stanghellini *et al.* 1998). However, the experimental use of multiple visits by single species would be almost impossible in the field in a polyphilic genus such as *Eucalyptus*, because individual flowers would probably be visited by a number of different species.

Determining the effectiveness of particular vertebrate taxa by this method is more problematic because of difficulties in observing them from a close enough range to identify which particular flowers are being visited. However, Paton (1991) did manage to observe foraging honeyeaters from a

close enough range to determine which *Lambertia formosa* (Proteaceae) inflorescences they visited and how many probes they made to these tubular flowers within each inflorescence. In another experiment, Paton (1991) was able to observe honeyeaters making single visits to flowers by presenting cut flowers to birds in an aviary. This enabled the quantities of pollen removed from anthers and deposited on stigmata to be determined (Paton 1991). In addition, Arizmendi *et al.* (1996) were able to measure the amount of seeds produced in small plants following a single bird flower visit by enclosing three or four plants in a cage and releasing a bird into the cage. Seed set was investigated on only one of these plants, with the others acting as pollen donors. Each time a bird was released in the cage all but one flower on the recipient plant were bagged with fine mesh. As a result, geitonogamous pollen transfer was precluded. Seed set in flowers receiving single visits from various bird species were compared with each other, and with control flowers receiving either outcross hand pollination or complete exclusion (Arizmendi *et al.* 1996). This technique, however, takes no account of interspecific differences in ratios of geitonogamous to xenogamous movements or pollen carryover. A method which could incorporate this factor into the experimental design is determining the mean number of flowers visited on a tree before the birds flew to another tree, and allowing the captured bird to visit this number of flowers on one tree after being dusted with outcross pollen.

Another technique that has been used to estimate pollinator effectiveness of birds is holding live birds to flowers so that they can feed from them (Collins and Spice 1986). Hopper and Burbidge (1978), Collins *et al.* (1984) and Arizmendi *et al.* (1996) also managed to induce birds to feed from flowers while holding them. A variation on this was used by Ramsey (1988) and Paton (1991) who probed virgin flowers with a dead bird that had been loaded with pollen in a manner mimicking the foraging behaviour of the species. However, it is not possible to accurately repeat the probing behaviour of birds with a stuffed bird in open cup-shaped flowers such as those of *Eucalyptus* (Paton and Ford 1977).

3.3.3 Assessing the contributions made by various animals to self- and cross-pollination

On self-compatible trees, seed set results from deposition of both self and outcross pollen, but in *Eucalyptus* self pollen is less likely to produce seeds than is outcross pollen (Griffin *et al.* 1987, Sedgley and Smith 1989, Tibbits 1989, Ellis and Sedgley 1992, Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995, 1998). Hence, different levels of seed set between eucalypt flowers subjected to different visitors may be a consequence of differences in pollen quantity or quality (Hardner and Potts 1995). As selfing leads to inbreeding depression in *E. globulus* and *E. nitens* (Tibbits 1988, Hardner and Potts 1995, Hardner *et al.* 1995, 1998), it is desirable to differentiate between the effects of pollen quantity and quality.

Charlesworth (1988) proposed that the selfing rate could be determined, from any variable influenced by outcrossing rate, by the equation

$$S = P_x - P_o \,/\, P_x - P_s$$

where P_x is the value of any quantity derived from manual outcrossing, P_o is the value derived from the treatment in question, and P_s is the value derived from manual selfing. Paton (1993) used this method to derive selfing rates from fruit set. However, seed set may be confounded by differences in pollen quantity between manual pollinations and the treatment in question (Hardner and Potts 1995). To overcome this problem, Paton (1993) investigated the treatment at a range of honey bee visitation frequencies, and found that selfing rate in *Callistemon rugulosus* increased with honey bee visitation frequency. This formula could also be used on the degree of inbreeding depression in the progeny. However, as both pre- and post-zygotic incompatibility mechanisms occur in eucalypts (Griffin *et al.* 1987, Sedgley and Smith 1989, Ellis and Sedgley 1992, Hardner and Potts 1995), the frequency of selfing displayed in the seedlings is likely to be less than that of the pollen deposited (Charlesworth 1988).

Another technique for determining proportions of seed derived from selfing stems from the variable degree of self-compatibility in eucalypts between

conspecifics (Hodgson 1976b, Griffin *et al.* 1987, Moran *et al.* 1989, Tibbits 1989, Ellis and Sedgley 1992), with some being completely self-incompatible (Moran *et al.* 1989, Tibbits 1989, Ellis and Sedgley 1992). The average difference in seed set between self-compatible and self-incompatible trees receiving the same treatment should give some idea of the level of self-pollination for that treatment. However, Hodgson (1976b) and Tibbits (1989) found that trees that set no seed after selfing in one year, did set seed after selfing in another year. For this reason, trees should be tested over several seasons to verify full self-incompatibility (Potts and Wiltshire 1997).

3.3.4 Assessing how efficient various animals are as pollinators

It makes little sense to compare the effectiveness of various taxa as pollinators, in terms of seed production or pollen deposition, unless they are removing similar amounts of floral resources. This is because the presence of an inefficient pollinator sometimes reduces the overall level of pollination by displacing more efficient pollinators or reducing the quantity of pollen available for transfer by more efficient pollinators (see Section 2.3). Paton (1990) found that birds consumed 2.7 times as much nectar as did honey bees per floral visit to *Eucalyptus remota* Blakely, but that honey bees removed 9.5 times as much pollen as did birds per visit. Hence, these measures of effectiveness should be standardised in terms of pollen and nectar consumed per reproductive output to determine the efficiency of pollination for various taxa (e.g. Primack and Silander 1975, Morse and Fritz 1983, Wilson and Thomson 1991).

The quantity of pollen consumed per visit can be determined by comparing the amount present after a single visit by a particular anthophile with that in virgin flowers (Paton 1990, Wilson and Thomson 1991, Paton 1993, Freitas and Paxton 1998, Miyake and Yahara 1998). This can be determined by suspending anthers in a known volume of lactophenol, and then counting the number of pollen grains present in subsamples of the solution using a haemacytometer (Paton 1990). The volume of nectar consumed in a single floral visit can be determined by comparing the volume after a visit with a

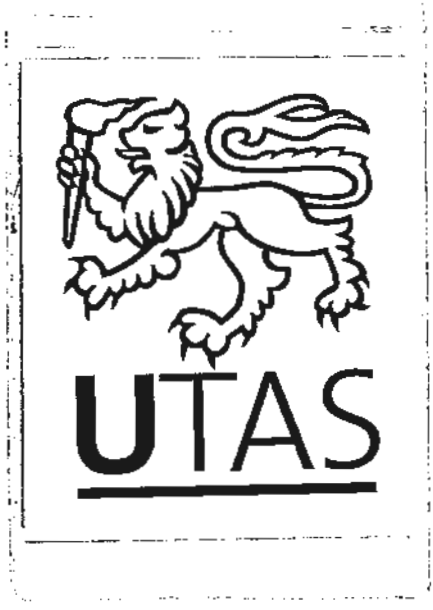
known volume placed in the flower prior to the visit (Paton 1982a), or comparison with mean standing crop in other conspecific flowers at the same time (Paton 1993). Such volumes can be determined by collecting nectar in capillary tubes (Paton 1982a, Paton and Turner 1985, Herrera 1990). If nectar is too viscous to be collected in this way, a known volume of distilled water can be added to reduce the viscosity (Gross 1992, Mallick 2000). The energy content of this nectar can be determined by measuring the sugar concentration with a hand-held refractometer in the field, and adjusting for the densities of the constituent sugars (Paton 1982a, Paton and Turner 1985).

Pollen removal by various size classes of floral visitors can be investigated by enclosing flowers in mesh of different aperture sizes (see Section 3.3.1). The rate of removal by each visitor category can be mapped by collecting all pollen from newly opened flowers, and from other flowers at various ages. By this method, it can be determined whether particular size classes are capable of removing all pollen during the life of the flower, and therefore limit the amount available for transport by other vectors (Ramsey 1988). Similarly, the relative proportions of nectar consumed by various size classes of visitors can be determined by measuring standing crops at intervals throughout the day (Carpenter 1976, Morse and Fritz 1983), or at the end of their daily foraging periods (Fritz and Morse 1981), in different exclosure treatments.

3.4 Assessing the effects of varying abundances of an anthophile on total pollination

The impact of inefficient pollinators on fruit set as part of a community of pollinators can be examined by comparing fruit set from flowers to which they have access with those from which they are excluded, while other visitors have access to both groups of flowers (Fritz and Morse 1981). Such data could be gathered from the exclosures of varying aperture size used to determine the proportions of pollinator service provided by various sized visitors (see Section 3.3.1). Alternatively, fecundity from flowers exposed to different levels of activity of the visitor can be compared (Paton 1993, 1997,

Steffan-Dewenter and Tscharntke 1999). An alternative method is to compare seed set in virgin flowers visited by species A then species B, with those visited by species B then species A (Arizmendi *et al.* 1996). If one of these visitors is removing pollen from anthers and is an inefficient pollinator, seed set will be lower when it is the first visitor (Arizmendi *et al.* 1996). If one of these visitors is removing pollen from stigmata and is an inefficient pollinator, seed set would be lower when it is the last visitor (Gross and Mackay 1998).



Chapter 4

Daily nectar production and consumption patterns in *Eucalyptus globulus* subsp. *globulus* and *E. nitens*

Abstract

The patterns of daily nectar production and consumption were investigated in two closely related southeastern Australian tree species; *Eucalyptus globulus* and *E. nitens*. The flowers of *E. globulus* produced approximately 100 times as much nectar per day as did those of *E. nitens*. *Eucalyptus globulus* secreted nectar overnight and during the day, whereas *E. nitens* secreted nectar only during the warmer parts of the day. Both of these factors suggest that *E. globulus* has evolved to exploit large endothermic pollinators, whereas *E. nitens* is adapted to pollination by small ectotherms. Observations of flower visitors were consistent with this. Insects visited the flowers of both species, but birds were observed feeding only from the flowers of *E. globulus*. There was an absence of surplus nectar in all four *E. nitens*, and three of the five *E. globulus*, trees studied. Consequently, the introduction of large numbers of managed pollinators, such as honey bees, to commercial seed orchards of these species may not increase the rates at which flowers are visited by potential pollinators. Indeed, honey bees appear to be of no value as pollinators of *E. nitens* because they were not attracted to the meagre quantities of nectar. In contrast, on the three *E. globulus* trees where all nectar was consumed, feral honey bees were so numerous that they appeared to displace native nectarivorous birds. If honey bees are less efficient pollinators than birds, such competitive displacement by feral or managed honey bees could reduce seed production. However, if honey bees are more efficient pollinators than birds, or surplus nectar is available and honey bees are effective pollinators, the deployment of honey bee hives in *E. globulus* seed orchards could enhance seed production.

4.1 Introduction

Eucalyptus globulus and *E. nitens* are closely related members of the Subseries Globulinae (Pryor and Johnson 1971), and have very similar leaves, bark, and growth habits (Boland *et al.* 1984). However, the two species have markedly different flowers (Plate 4.1). Flowers of *E. globulus* are by far the largest of any Tasmanian eucalypt (Williams and Potts 1996), the seed capsule measuring 15 - 30 mm in diameter (Curtis and Morris 1975). These flowers may be solitary, or occasionally arranged in umbels of three (Boland *et al.* 1984, Jordan *et al.* 1993). In contrast, the capsules of *E. nitens* are only 4 - 7 mm in diameter and arranged in umbels of seven (Boland *et al.* 1984, Tibbits 1989).

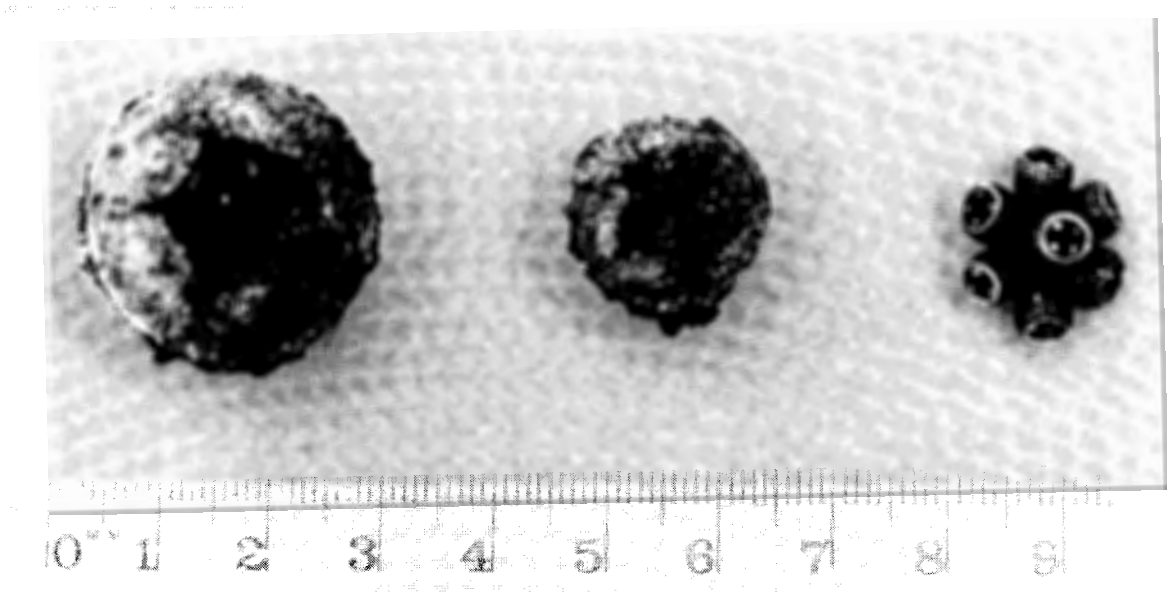


PLATE 4.1

Seed capsules of *E. globulus* (left and centre), showing the variation in size, and an umbel of capsules of *E. nitens* (right). Capsules develop from floral receptacles and are, therefore, indicative of flower size.

The differences in floral form between the two species suggest that they may have evolved to exploit different animals as pollinators. Nectar production per flower is related to flower size in *Eucalyptus* (Davis 1997), supporting the conclusion of Ford *et al.* (1979) that eucalypt species with small flowers are predominantly entomophilous (insect pollinated), whereas species with larger flowers are mostly ornithophilous (bird pollinated). In accordance

with that idea, the flowers of *E. globulus* are visited by a wide variety of birds and insects (Hingston and Potts 1998), whereas the flowers of *E. nitens* are visited by insects but not birds (A. Hingston pers. obs.).

Information on the pollinators of these tree species is required by the forest industry because they are both grown extensively in plantations for wood production in temperate regions of the world (Eldridge *et al.* 1993, Tibbits *et al.* 1997). Plantation stock are grown mostly from seeds, that are increasingly being supplied from seed orchards comprising elite trees with characteristics desired by the forest industry (Eldridge *et al.* 1993, Tibbits *et al.* 1997).

One of the strategies employed by eucalypt seed orchard managers in the hope of increasing seed production is the importation of western honey bee, *Apis mellifera* L., colonies at the time of flowering (Moncur and Kleinschmidt 1992, Moncur *et al.* 1993, 1995). Although this bee has not coevolved with *Eucalyptus*, honey bees might be effective substitutes for native pollinators whose populations have been reduced by land clearance and insecticide use (Moncur and Kleinschmidt 1992). However, if populations of wild pollinators are sufficient to consume all of the floral resources produced by flowers, the deployment of honey bee hives may be unnecessary. Moreover, if all floral resources are consumed in the absence of honey bee hives, the introduction of large numbers of honey bees could be detrimental to the total levels of pollination if it results in displacement of more efficient coevolved pollinators (McDade and Kinsman 1980, Paton 1993, 1997, Irwin and Brody 1998).

This experiment investigated the diurnal patterns of nectar production and consumption in *E. globulus* and *E. nitens* in Tasmania. Comparisons of the quantities of nectar produced, and the timing of nectar secretion, between the two species provides insight into the degree to which they have evolved to exploit different animals as pollinators. The question of whether wild pollinator populations have declined to such low levels that it is necessary to supplement their services by deployment of honey bee hives (Moncur and

Kleinschmidt 1992), was addressed by determining how much of the daily nectar production by both species was consumed. By relating the rates of nectar consumption in *E. globulus* to flower visitor activity, it was also possible to determine which animals consumed most of the nectar from this species.

4.2 Methods

The flowers of *Eucalyptus* are protandrous (Pryor 1976). The annulus of numerous stamens is incurved towards the non-receptive stigma when the woody operculum is first shed (Boland *et al.* 1984). The stamens progressively expand over several days, exposing the nectaries in the hypanthium surrounding the style, as the stigma gradually becomes receptive (Boland *et al.* 1984). All nectar measurements were taken from flowers that were in this latter stage of development, in which neither the stamens nor stigma had begun to senesce. For convenience these flowers will be referred to as 'female-phase' although some had not yet reached peak stigmatic receptivity.

4.2.1 Eucalyptus globulus

The extent and rate of nectar production and consumption in female-phase flowers of *E. globulus* were investigated on heavily-flowering remnant trees growing in pasture in southeastern Tasmania during the springs of 2000 and 2001 (Table 4.1). On trees 1339 and 1338, growing at Nubeena, flowering was concentrated in the lower part of the canopy within a few metres of the ground. The flowers on tree 297 at Tinderbox were also near the ground, because this tree had fallen over a few years earlier so that the entire canopy was less than 5 m in height. In contrast, trees 335 and 341 at Tinderbox were large trees approximately 30 m tall with abundant flowers throughout their spreading canopies.

Nectar production was investigated by taking hourly measurements of nectar standing crops from bagged flowers on heavily-flowering branches within 4 m of the ground. Flowers were bagged to exclude nectarivores by

enclosing 1 - 3 flowers within a small paper bag tied around the peduncle with a piece of string, early on the morning of nectar measurement or late on the previous evening (Table 4.1). Nectar consumption from unbagged flowers was determined by comparing standing crops in unbagged flowers to that in nearby flowers bagged to prevent visitors.

Tree	AGPS	Flowers bagged	Nectar measurements
1339	5621 52286	0630-0830h, 31 Oct. 2000	0930-1830h, 31 Oct. 2000
1338	5621 52286	1900-2000h, 18 Nov. 2000	0630-1630h, 19 Nov. 2000
297	5257 52329	1700-1800h, 10 Sept. 2001	0600-1700h, 11 Sept. 2001
335	5256 52323	1730-1830h, 10 Oct. 2001	0600-1800h, 11 Oct. 2001
341	5259 52325	1830-1930h, 21 Oct. 2001	0600-1700h, 22 Oct. 2001

TABLE 4.1

Locations (AGPS) of trees of *E. globulus* from which nectar measurements were taken, the times when the bags were put in place, and the times when nectar measurements were taken. All times are Eastern Standard Summer Time (ESST), except for those relating to tree 297 which are Eastern Standard Time (EST). To convert EST to ESST, add one hour.

Between five and seven bagged flowers were picked each hour throughout the day (Table 4.1) from the section of the experimental branches where the bags were most numerous. The same number of unbagged flowers of comparable age that were the closest to the selected bagged flowers, were picked at the same time. All selected flowers were placed stigma-up in holes drilled into a block of wood. Nectar was diluted by adding 200 μl of distilled water with a pipette to each hypanthium. This was allowed to stand for approximately 10 minutes before drawing up with a clean 20 μl micropipette. Hand-held refractometers (Atago N1, 0-32% & Atago N2, 28-62%; intra-MARK Catalogue no. 708707, Atago, Tokyo, Japan) were used to measure the sugar concentration (sucrose equivalents) of 40 μl of the extracted solution. The zero-setting for the 0-32% refractometer was checked each hour against samples of distilled water, and concentrations measured with the 28-62% refractometer were adjusted according to the temperature at the time of measurement, as described in the user's manual. Washes and subsequent nectar measurements were conducted twice for each flower on the first four trees studied (Table 4.1), in case some nectar was not removed

during the first wash (Mallick 2000). Because little nectar was extracted with the second washes, and a field assistant was unavailable on the day when tree 341 was studied, flowers from this tree were only washed once. The percentage of sugar measured by the refractometer was converted to μg sugar / μl nectar solution using Table 5.2 in Kearns and Inouye (1993). The amount of sugar present in each wash was then calculated by multiplying the μg sugar / μl nectar solution by the μl of solution. The solution volumes used in these calculations were those extracted from the flower in the first wash, and 200 μl for the second wash.

The mean standing crops of nectar in bagged flowers obtained at hourly intervals throughout the day were compared to determine the diurnal pattern of nectar secretion. By also comparing the mean standing crops of nectar in bagged and unbagged flowers at hourly intervals throughout the day, it was possible to estimate how much of the daily nectar production was consumed and at what time of day it was consumed.

Differences between nectar standing crops in bagged and unbagged flowers during each hour were compared using t-tests. In cases where the raw data did not exhibit normality or equal variances, they were square root transformed. If this transformation did not result in those assumptions of the t-test being met, or some values were less than one, the data were $\log_{10}$ transformed. In cases where this transformation still failed to normalise the distributions, the non-parametric Mann-Whitney Rank Sum Test was employed. Data analyses were conducted using the computer programme SigmaStat (Jandel 1994).

Insect visitation rates were monitored throughout the day on which nectar was measured. This monitoring consisted of one minute spot counts of insects, for the entire section of canopy where the experiment was conducted, every half hour. Insect densities were expressed as the number of insects per number of female-phase flowers at the time, in the section of canopy where the experiment was conducted. Insects could be seen easily on trees 1338,

297, 335 and 341 because the flowers were all 1 - 2.5 m above the ground, allowing insects to be observed from a distance of less than one metre. However some insects, particularly small taxa, were almost certainly overlooked during these counts on tree 1339 because the experimental flowers were 3 - 4 m above the ground and the surveys were conducted from the ground. In spite of this, the technique was deemed adequate to monitor abundances of the larger insects that were most likely to impact on nectar standing crops. It was also noted whether birds fed from the flowers in the experimental section of the canopy during each half hour period. Birds were observed while nectar measurements were taken from the harvested flowers inside a tent approximately 10 m from the experimental branch. Foraging activities of the common insect and bird visitors were then related to nectar consumption to determine which animals removed most nectar from flowers.

4.2.2 Eucalyptus nitens

Similar procedures to those used for *E. globulus* were followed to determine the extent and rate of nectar consumption and production in female-phase flowers of *E. nitens*. Experiments were conducted on two trees of *E. nitens* in each of two seed orchards during January 2001. These orchards were at Bream Creek, in southeastern Tasmania (AGPS 5679 52609), and the Huntsman Valley in the central north (AGPS 4677 53809). Nectar consumption from unbagged flowers was determined by comparing standing crops in unbagged flowers to that in flowers bagged to exclude visitors. The bagged flowers provided information on nectar production.

Visitors were excluded by enclosing at least 10 female-phase flowers within a small paper bag tied around the branch with a piece of string. Bags were put in place just before dusk (between 2000 and 2100 h). Ten bagged flowers, and ten unbagged flowers from nearby on the tree, were picked each hour throughout the following day and placed stigma up in small holes drilled in a block of wood. Nectar was diluted by adding a small quantity of distilled water to each hypanthium with a micropipette and allowing it to stand for

approximately 10 minutes. At Bream Creek 10 μl of water filled the receptacle, whereas 20 μl was needed to cover the larger hypanthia at Huntsman.

It was not possible to remove all the nectar solution with a micropipette because it was situated in a deep and narrow groove between the style base and the rim of the hypanthium. For this reason, the nectar solution was transferred to a hand-held refractometer (Atago N1, 0-32%; intra-MARK Catalogue no. 708707, Atago, Tokyo, Japan) by inverting the flower and tapping it lightly. Ten flowers in a treatment were required to obtain enough solution for a single measurement of the percentage of sugar to be made with the refractometer. The zero-setting for the refractometer was checked every hour against samples of distilled water. The percentage of sugar measured by the refractometer was converted to μg sugar / μl nectar solution using Table 5.2 in Kearns and Inouye (1993). As it was not possible to measure the volume of solution in each flower, it was assumed that the original volume of nectar was negligible. Hence, the amount of sugar present in each flower was calculated by multiplying the μg sugar / μl nectar solution by the assumed 10 or 20 μl of solution.

Observations of flower visitors in the orchards were also made during nectar measurement periods, to determine which animals were consuming the nectar. This was a simple process at Bream Creek where large numbers of cockchafer beetles remained on the flowers throughout the day. However, flowering intensity and numbers of insects on flowers were much lower at the Huntsman orchard. Hence, the composition of the anthophile community at Huntsman was determined by observing flowers throughout the orchard during the periods between measuring nectar.

4.3 Results

4.3.1 Eucalyptus globulus

4.3.1.1 Nectar production in E. globulus

Nectar was produced during both day and night in flowers of *E. globulus* (Figs 4.1-4.3). Higher nectar standing crops in both treatments at dawn than occurred in unbagged flowers late in the afternoon on trees 1338 and 297 (Figs 4.2 and 4.3) indicate, assuming that unbagged flowers were emptied to similar levels on the previous day, that nectar was secreted at night. This assumption is valid because the weather conditions on the days of bagging were similar to those on the corresponding days of nectar measurement, and nectar was not visible in the flowers at the time of bagging. Nectar standing crops in bagged flowers generally increased through the day, although the levels sometimes fluctuated greatly (Figs 4.1-4.3), presumably reflecting variation between flowers in rates of nectar production or nectar dripping from some flowers. On trees 335 and 341, mean standing crops did not increase overnight or through the day because nectar overflowed from many flowers (Figs 4.4 and 4.5).

Large quantities of nectar were produced on all *E. globulus* trees studied. Individual bagged flowers accumulated up to 61 - 74 mg of nectar sugar within one day on the first three trees studied, but sometimes well over 100 mg on trees 335 and 341 (Table 4.2) where nectar may have accumulated over several days because of low numbers of flower visitors (see below). Average standing nectar crops in bagged flowers peaked at between 38 and 59 mg of sugar on the first four trees studied, but over 100 mg of sugar on tree 341 (Table 4.2). Assuming that unbagged flowers had been emptied to similar levels on the previous day on trees 1338, 1339 and 297 (values from Table 4.3), and nectar was not removed from flowers overnight or early in the morning prior to bagging on tree 1339, this equates to average daily nectar production of between 37 and 56 mg of sugar (Table 4.2). As the flowers of tree 1338 were in umbels of three, but all others were solitary, this equates to average daily nectar production per umbel of between 37 and 156 mg of sugar (Table 4.2).

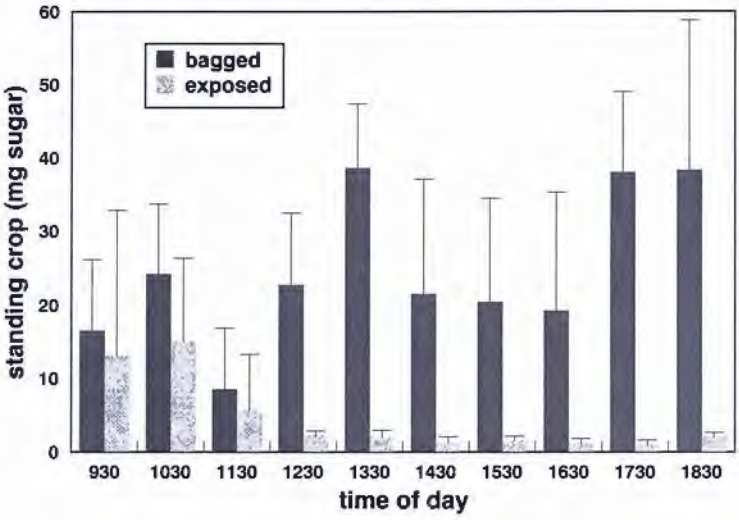


FIGURE 4.1

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. globulus* on tree 1339 during 31 October 2000. Error bars = standard deviations. Statistically significant differences between bagged and exposed flowers occur from 1230 h onwards. Bags were put in place between 0630 h and 0830 h on the same day.

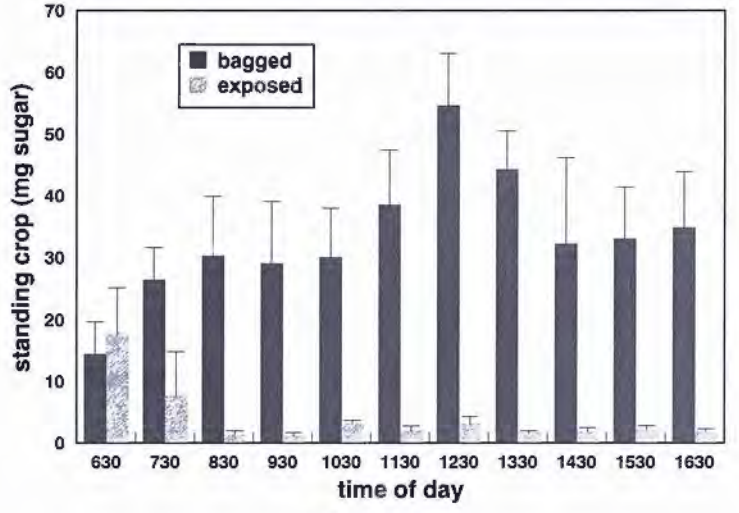


FIGURE 4.2

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. globulus* on tree 1338 during 19 November 2000. Error bars = standard deviations. Statistically significant differences between bagged and exposed flowers occur from 0730 h onwards. Bags were put in place between 1900 h and 2000 h the previous day.

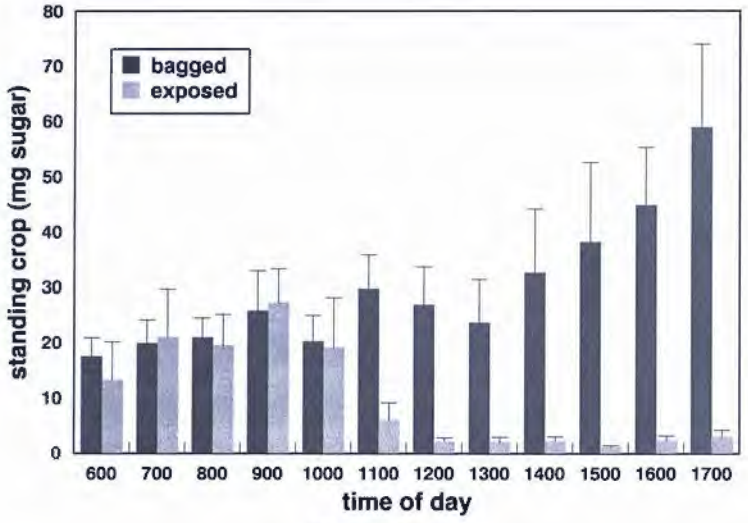


FIGURE 4.3

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. globulus* on tree 297 during 11 September 2001. Error bars = standard deviations. Statistically significant differences between bagged and exposed flowers occur from 1100 h onwards. Bags were put in place between 1700 h and 1800 h the previous day.

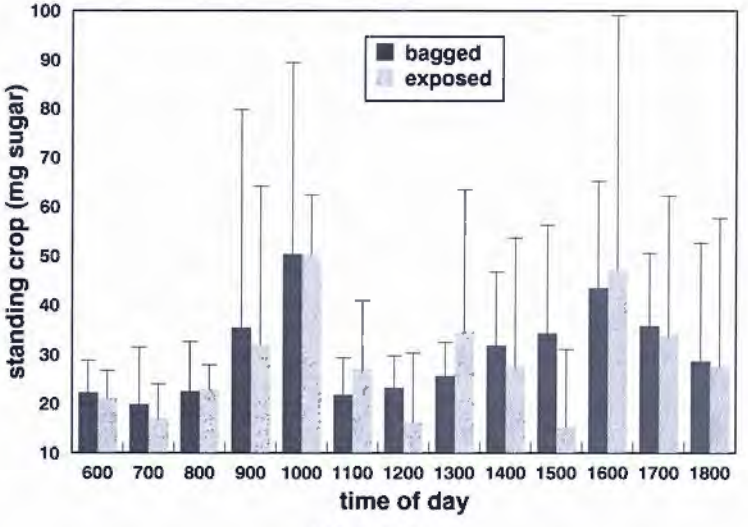


FIGURE 4.4

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. globulus* on tree 335 during 11 October 2001. Error bars = standard deviations. Statistically significant differences between bagged and exposed flowers did not occur at any time of the day. Bags were put in place between 1730 h and 1830 h the previous day.

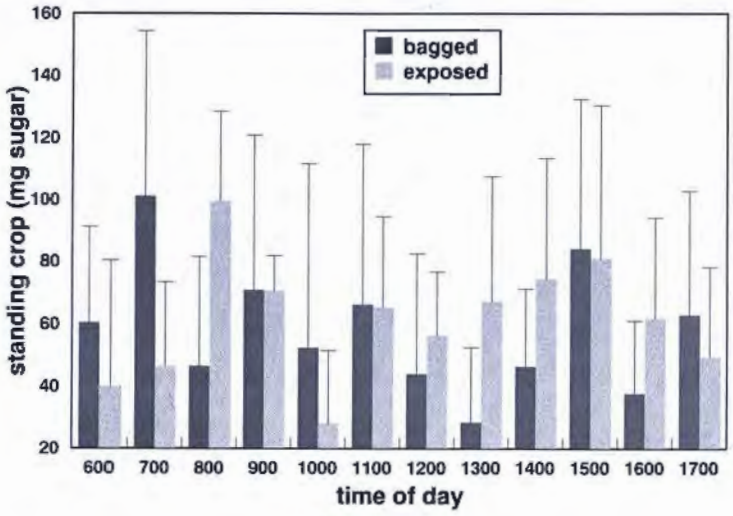


FIGURE 4.5

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. globulus* on tree 341 during 22 October 2001. Error bars = standard deviations. Statistically significant differences between bagged and exposed flowers were found only at 0800 h. Bags were put in place between 1830 h and 1930 h the previous day.

Tree	Maximum mg/flower	Peak mean mg/flower	Daily production mg/flower	Daily production mg/umbel	Concentration wt/wt
1339	61.5	38.6	37.04	37.04	25.9
1338	65.9	54.7	52.06	156.21	21.9
297	73.7	58.9	56.19	56.19	22.4
335	133.9	50.3	?	?	28.0
341	187.2	101.2	?	?	44.5

TABLE 4.2

Characteristics of nectar standing crops from five trees of *E. globulus*. Quantities are given in mg of sugar. Peak mean standing crops were calculated from between five and seven flowers harvested at one time. Daily production was estimated as the difference between peak mean standing crops in bagged flowers and mean standing crops in unbagged flowers in the latter part of the day (Table 4.3). Nectar sugar concentrations were calculated from flowers where at least 300 µl of solution were withdrawn from the first wash.

If it is assumed that all of the solution was extracted in the first wash from bagged flowers where the volume withdrawn was at least 300 µl, the mean concentration of sugar in the nectar from the three trees where the flowers were probably emptied on the previous day was 23.4% (wt/wt) (Table 4.2). However, nectar sugar was more concentrated on the two trees where it had

probably accumulated over several days, suggesting that it had evaporated (Table 4.2).

4.3.1.2 Nectar consumption in E. globulus

Nectar of *E. globulus* was consumed during the day, but not at night. The lack of nocturnal nectar consumption was apparent from the absence of statistically significant differences between standing crops in bagged and unbagged flowers at dawn on all trees that had flowers bagged overnight (Figs 4.2-4.5). However, almost all nectar was consumed during daylight hours from unbagged flowers on three of the five trees studied (Figs 4.1-4.3). On these three trees standing crops of nectar sugar in unbagged flowers declined during the morning to less than 10% of that in bagged flowers, and remained at these levels throughout the afternoon.

Tree	Time (h)	Wash 1 (mg)	Wash 2 (mg)
1339	1230-1830	0.86	0.73
1338	0730-1630	1.31	1.30
297	1100-1700	1.60	1.11

TABLE 4.3

Mean standing crops of nectar sugar measured during successive washes from unbagged flowers on three trees of *E. globulus* during periods when the standing crops exhibited statistically significant differences between unbagged flowers and bagged flowers.

The amount of nectar in unbagged flowers at the time of flower harvesting was probably even lower than that measured, as a result of the flowers continuing to produce nectar from their woody receptacles after being picked. Evidence that picked flowers continued to produce nectar is apparent from almost as much nectar being withdrawn from unbagged flowers from the second wash as from the first wash, at times when statistically significant differences in standing crops occurred between bagged and unbagged flowers (Table 4.3). This contrasts with seven times as much nectar being removed from the first wash as from the second wash in *Eucryphia lucida* (Labill.) Baill. (Mallick 2000). As approximately 20 min elapsed between harvesting and measuring the first wash, and another 20

min passed before measuring the second wash, the flowers on these three trees were probably empty at the time of harvesting.

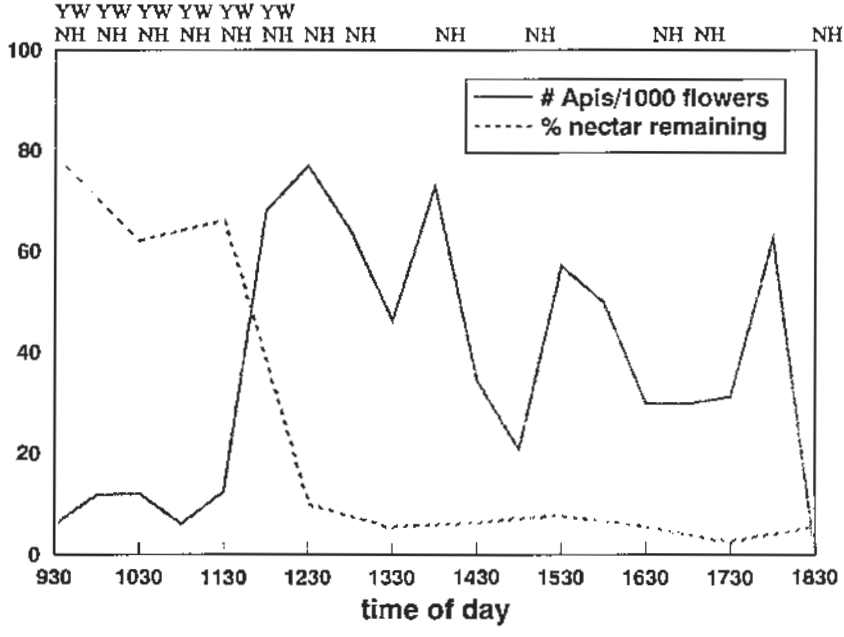


FIGURE 4.6

Mean numbers of honey bees (*Apis mellifera*) seen during spot counts per 1000 female-phase flowers of *E. globulus*, and mean standing crops of nectar (mg sugar) in exposed female-phase flowers divided by the amount in bagged flowers, on tree 1339 during 31 October 2000. The letters YW and NH denote half hour periods during which yellow wattlebirds and New Holland honeyeaters were seen foraging on the flowers in the experimental section of the tree.

The experimental flowers on all three trees exhibiting significantly larger standing crops of nectar sugar in bagged than in unbagged flowers were visited by birds and numerous honey bees *Apis mellifera* L. (Figs 4.6-4.8). In contrast, no birds and far fewer honey bees visited the two trees on which standing crops of nectar sugar were not depleted in unbagged flowers (Figs 4.9 and 4.10). This suggests that birds or honey bees were responsible for most nectar consumption. Honey bees were the major insect visitors on the trees that had most of their daily nectar production removed, despite the apparent absence of managed hives nearby. Honey bees comprised 93.58%, 33.79%, and 87.5% of all insect flower visitors to trees 1339, 1338, and 297,

respectively. Almost all these bees were collecting nectar, rather than pollen, from these flowers. The other insect that visited tree 1338 in large numbers was the soldier beetle, *Chauliognathus lugubris* (Fabricius) (Cantharidae), which comprised 62.88% of insects observed (Fig. 4.7). However, soldier beetles are smaller than honey bees and consume nectar only for their personal energy requirements whereas honey bees gather nectar to feed larvae and store for lean periods. For this reason, a honey bee collects approximately 100 times as much resources as it needs for its own use (Faegri and van der Pijl 1979). Therefore, the total amount of nectar removed by honey bees is likely to have been far greater than that removed by soldier beetles on tree 1338.

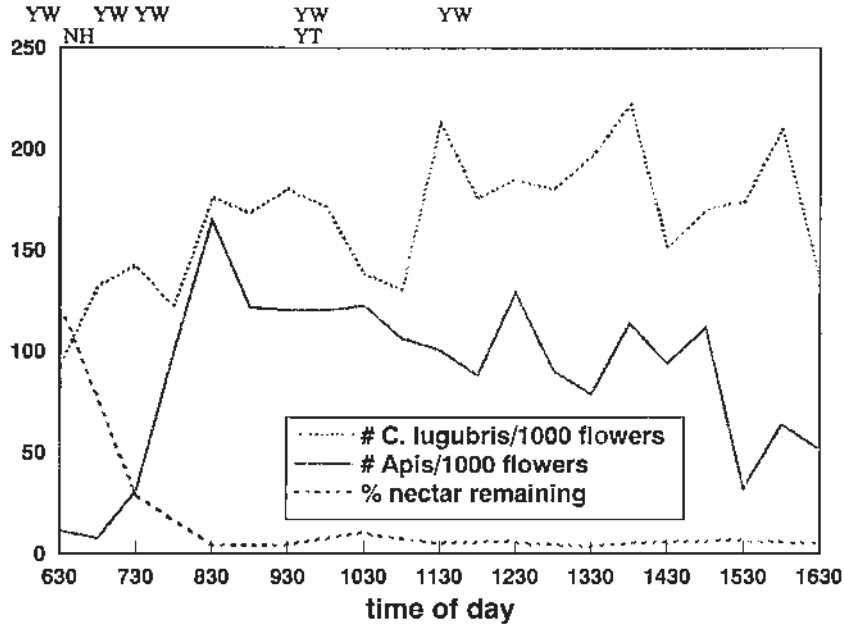


FIGURE 4.7

Mean numbers of soldier beetles (*C. lugubris*) and honey bees (*Apis mellifera*) seen during spot counts per 1000 female-phase flowers of *E. globulus*, and mean standing crops of nectar (mg sugar) in exposed female-phase flowers divided by the amount in bagged flowers, on tree 1338 during 19 November 2000. The letters YW, NH and YT denote half hour periods during which yellow wattlebirds, New Holland honeyeaters and yellow-throated honeyeaters were seen foraging on the flowers in the experimental section of the tree.

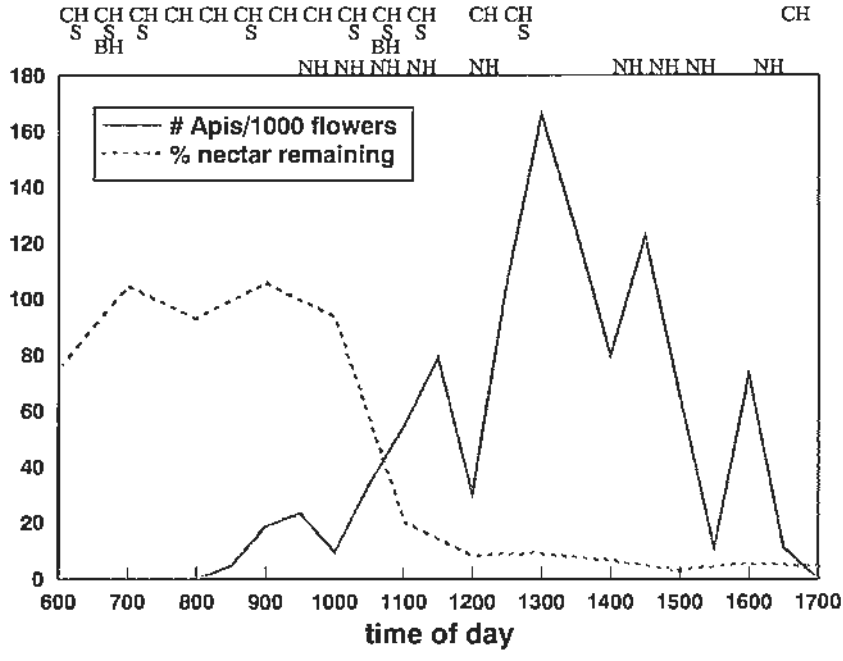


FIGURE 4.8

Mean numbers of honey bees (*Apis mellifera*) seen during spot counts per 1000 female-phase flowers of *E. globulus*, and mean standing crops of nectar (mg sugar) in exposed female-phase flowers divided by the amount in bagged flowers, on tree 297 during 11 September 2001. The letters CH, S, BH and NH denote half hour periods during which crescent honeyeaters, silvereyes, black-headed honeyeaters and New Holland honeyeaters were seen foraging on the flowers in the experimental section of the tree.

The timing of nectar consumption differed greatly between the trees that had most of their nectar removed. On tree 1338, statistically significant differences in standing crops between bagged and unbagged flowers commenced at 0730 h, with flowers being all but empty by 0830 h (Fig. 4.2). Two species of birds, and large numbers of soldier beetles and honey bees foraged at the flowers during the period of declining standing crops of nectar sugar (Fig. 4.7), indicating that at least one of these groups was consuming large quantities of nectar. However, soldier beetles are unlikely to have removed large quantities of nectar because of their low energy requirements. On trees 1339 and 297, differences in nectar standing crops between unbagged and bagged flowers were not statistically significant during the

early morning (Figs 4.1 and 4.3) when birds were regular visitors but insects were not (Figs 4.6 and 4.8), indicating that birds did not consume much nectar. On both of these trees, nectar standing crops in unbagged flowers fell to significantly less than that in bagged flowers during late morning, being all but empty by this time (Figs 4.1 and 4.3). This coincided with rapid increases in honey bee activity (Figs 4.6 and 4.8), suggesting that they were responsible for most nectar removal from flowers on these two trees.

Unbagged flowers remained virtually devoid of nectar for the remainder of the day on all trees that had most nectar removed (Figs 4.1-4.3). Honey bees continued to forage heavily at this time, while bird activity declined after most nectar was removed (Figs 4.6-4.8), suggesting that honey bees were largely responsible for the maintenance of low nectar standing crops.

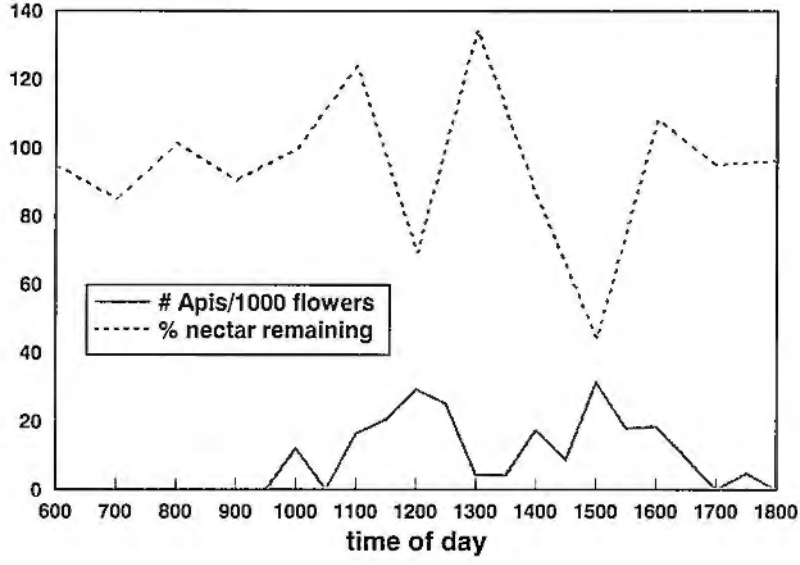


FIGURE 4.9

Mean numbers of honey bees (*Apis mellifera*) seen during spot counts per 1000 female-phase flowers of *E. globulus*, and mean standing crops of nectar (mg sugar) in exposed female-phase flowers divided by the amount in bagged flowers, on tree 335 during 11 October 2001.

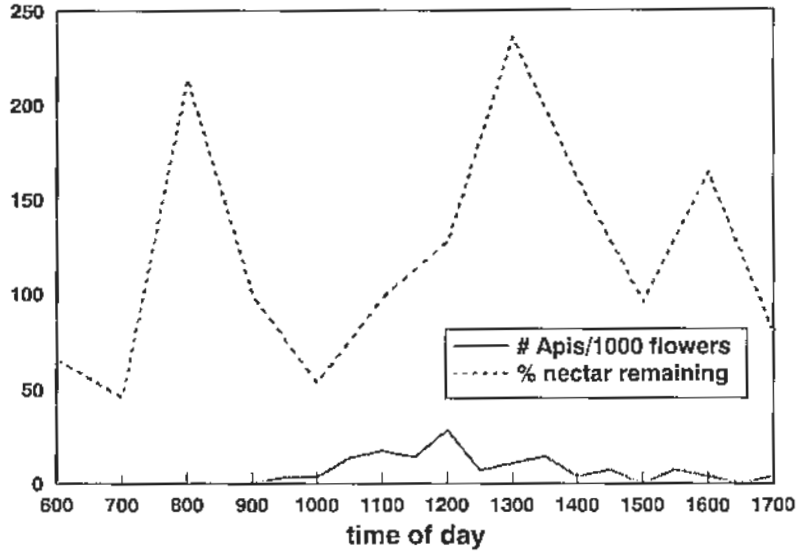


FIGURE 4.10

Mean numbers of honey bees (*Apis mellifera*) seen during spot counts per 1000 female-phase flowers of *E. globulus*, and mean standing crops of nectar (mg sugar) in exposed female-phase flowers divided by the amount in bagged flowers, on tree 341 during 22 October 2001.

4.3.2 *Eucalyptus nitens*

4.3.2.1 Nectar production in E. nitens

In contrast to those of *E. globulus*, flowers of *E. nitens* did not secrete nectar at night. This is apparent from the similar nectar standing crops in both treatments on all trees early in the morning and those that occurred in unbagged flowers late in the afternoon (Figs 4.11-4.14), if it is assumed that unbagged flowers had been emptied to similar levels on the previous day. Dawn standing crops at Huntsman were approximately double those at Bream Creek. This appears to be related to flower size, as twice as much water was needed to wash nectar from flowers at Huntsman than at Bream Creek.

The more rapid accumulation of nectar in bagged flowers at Bream Creek than at Huntsman may have been the result of differing weather conditions at the orchards, because rapid secretion commenced at similar ambient temperatures in the two orchards. At Bream Creek it was sunny throughout the day of nectar measurement, and temperatures rose quickly in the

morning (Fig. 4.15). However, at Huntsman it was overcast all day, resulting in slower warming (Fig. 4.15). On both Bream Creek trees, rapid nectar secretion appeared to commence after 0800 h (Figs 4.11 and 4.12), when the ambient temperature reached 16.9°C (Fig. 4.15). In contrast, matinal nectar secretion was subdued on both trees at Huntsman (Figs 4.13 and 4.14). Rapid secretion did not occur at this site until after 1300 h (Figs 4.13 and 4.14), when the temperature reached 17.4°C (Fig. 4.15).

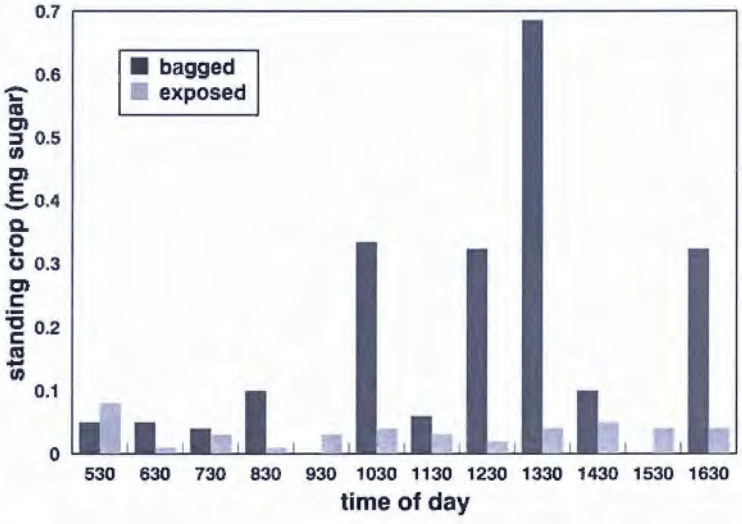


FIGURE 4.11

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. nitens* on tree Bream Creek 2.5 during 1 Jan 2001. Nectar was not sampled from bagged flowers at 0930 h and 1530 h. Bags were put in place between 2000 h and 2100 h on the previous day.

Standing nectar crops in bagged flowers averaged up to 0.686 mg and 0.478 mg of sugar on the two trees at Bream Creek (Figs 4.11 and 4.12) and 0.544 mg and 0.464 mg of sugar at Huntsman (Figs 4.13 and 4.14). Subtracting the standing crops of nectar at dawn from these values gives daily production levels of 0.636 mg and 0.428 mg of sugar at Bream Creek (Figs 4.11 and 4.12) and 0.424 mg and 0.324 mg of sugar at Huntsman (Figs 4.13 and 4.14). Because the flowers usually occur in umbels of seven, this equates to daily nectar production of 4.45 mg and 3.00 mg of sugar per umbel for the two trees at Bream Creek, and 2.97 mg and 2.27 mg of sugar per umbel for the

two trees at Huntsman. It was not possible to determine the nectar concentration in *E. nitens* because the volume of solution withdrawn from washed flowers could not be measured.

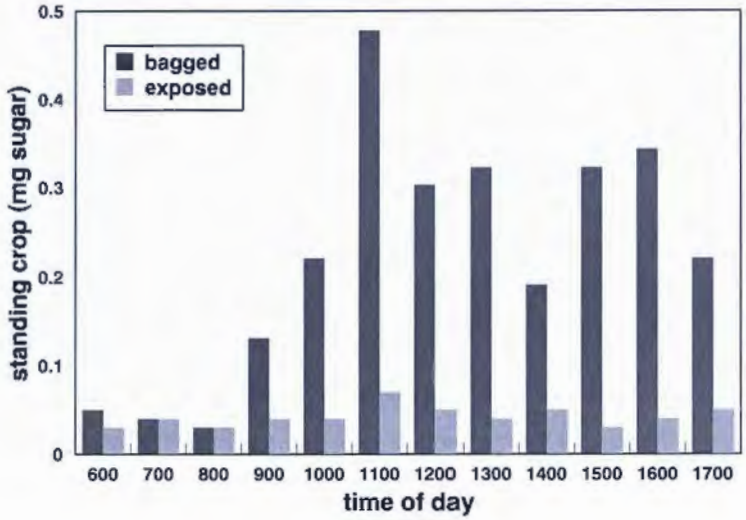


FIGURE 4.12

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. nitens* on tree Bream Creek 2.11 during 1 Jan 2001. Bags were put in place between 2000 h and 2100 h on the previous day.

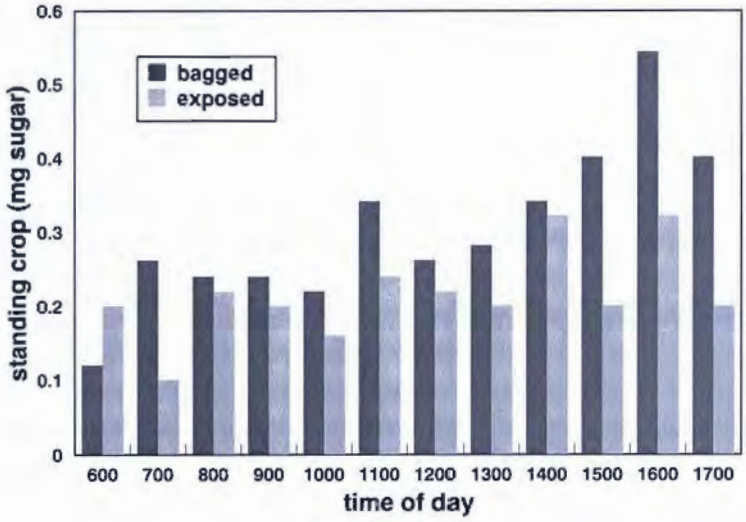


FIGURE 4.13

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. nitens* on tree Huntsman A during 14 Jan 2001. Bags were put in place between 2000 h and 2100 h on the previous day.

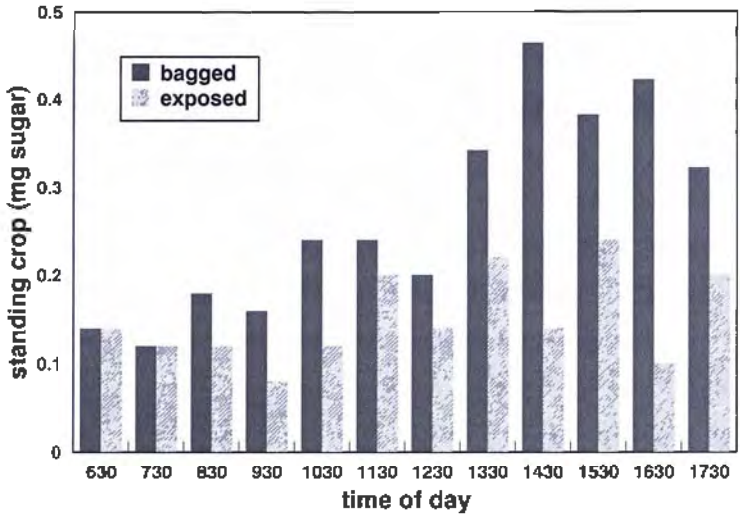


FIGURE 4.14

Mean standing crops of nectar (mg sugar) in bagged and exposed flowers of *E. nitens* on tree Huntsman B during 14 Jan 2001. Bags were put in place between 2000 h and 2100 h on the previous day.

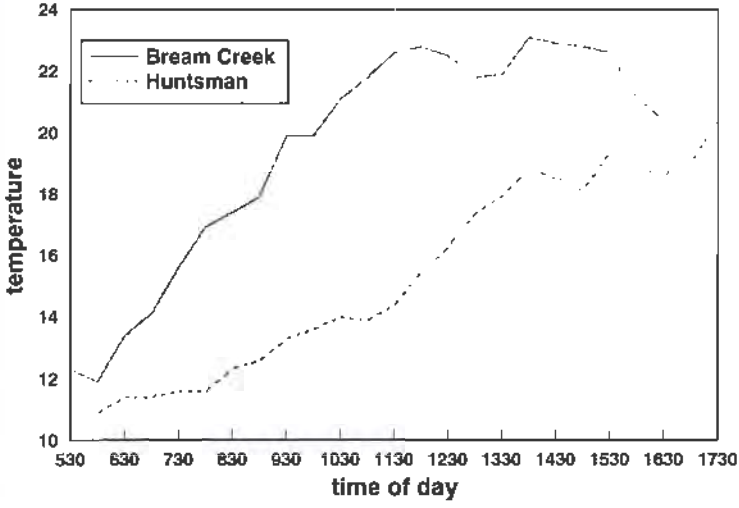


FIGURE 4.15

Air temperature (°C) at two seed orchards of *E. nitens* while nectar was being measured. Bream Creek orchard data are for 1 January 2001. Huntsman orchard data are for 14 January 2001.

4.3.2.2 Nectar consumption in E. nitens

On all four trees nectar was consumed during the day, but not at night. The lack of nocturnal nectar consumption was apparent from the similar standing crops in bagged and unbagged flowers at dawn (Figs 4.11-4.14). Differences in standing crops between bagged and unbagged flowers soon became apparent during the day as standing crops increased in bagged flowers but not in unbagged flowers (Figs 4.11-4.14). This indicates that nectar was consumed from unbagged flowers as quickly as it was produced.

At Bream Creek, nectar appeared to be prevented from accumulating in unbagged flowers largely by the actions of numerous cockchafer beetles, *Phyllotocus macleayi* Fischer (Scarabaeidae), that covered the flowers (Plate 4.2). Lower numbers of insects, but higher species diversity, mostly beetles and flies, were noted at Huntsman than at Bream Creek. Despite the lower overall insect numbers, little nectar accumulated in unbagged flowers at Huntsman. In contrast to *E. globulus*, no honey bees or birds were seen feeding on the flowers of *E. nitens*.

PLATE 4.2

Cockchafer beetles *Phyllotocus macleayi* (Scarabaeidae) feeding on flowers of *E. nitens* at Bream Creek. Note the high density, and the presence of copulating couples.

4.4 Discussion

4.4.1 Nectar production in E. globulus and E. nitens

Daily nectar production levels differed greatly between these two species in a manner suggestive of adaptations to bird pollination in *E. globulus* and insect pollination in *E. nitens*. The quantities of nectar secreted daily by individual flowers of *E. globulus* averaged approximately 100 times that by individual flowers of *E. nitens*. Nectar sugar produced per day by flowers of *E. globulus* exceeded the maximum known for this genus (Ford *et al.* 1979, Ford and Paton 1982, Paton 1986a, b, Nicolson 1994), whereas that by *E. nitens* was near the lower end of the range for eucalypts (Ford *et al.* 1979). The daily nectar production per flower by *E. globulus* was higher than that by several other *Eucalyptus* species that attract nectarivorous birds (Bond and Brown 1979, Ford and Paton 1982, Paton and Ford 1983, Paton 1986a, b, 1990). In contrast, daily nectar production per flower in *E. nitens* was similar to that by several bird-visited congeners (Bond and Brown 1979, Paton 1986a, Horskins and Turner 1999), and *E. muellerana* Howitt which is not attractive to birds (Ireland and Griffin 1984). Therefore, the vast quantities of nectar secreted by *E. globulus* are sufficient to attract birds, whereas the rewards offered by *E. nitens* may not be. Indeed, the flowers of *E. nitens* were not observed being visited by birds or honey bees, suggesting that the nectar standing crops were insufficient to attract birds or these energy-demanding insects.

The daily nectar production per flower of *E. globulus* was far in excess of that which would have resulted from fusion of flowers in an umbel similar to that of *E. nitens*. Average daily nectar production per umbel in *E. globulus* was more than 26 times that in *E. nitens*, indicating that *E. globulus* allocates a far greater amount of photosynthate to pollinator attraction than does *E. nitens*. The allocation of large quantities of photosynthate to attract birds must involve substantial fitness costs to *E. globulus*, and would only be favoured by natural selection if these costs were outweighed by the fitness gains that result from bird pollination (Stiles 1978, Paton 1986b). This implies that birds are more effective pollinators of *E. globulus* than are insects (Bertin 1982a, b).

The high rates of nectar production in *E. globulus* may render insects ineffective as pollen vectors between flowers because they may be able to meet all of their energy needs from single flowers (Heinrich and Raven 1972, Doull 1973, Ford *et al.* 1979, Heinrich 1983). This was a distinct possibility when honey bees began foraging in the morning, and on the trees where surplus nectar occurred. Standing crops of nectar were over 10 mg per flower on all five trees early in the morning, and Mallick (2001) found that honey bees collected an average of 5.7 mg of *Eucryphia lucida* nectar per trip at times when the concentration of nectar in *E. lucida* flowers was similar to that found here in *E. globulus*. However, multiple flower visits would be required for honey bees to fill their honey stomachs later in the day on trees where most nectar was consumed when averages of only 1.6 - 2.7 mg of nectar could be extracted from flowers with two washes. The possibility that much of this extracted nectar was secreted after the flowers were picked suggests that honey bees would have to visit numerous flowers at this time to fill their honey stomachs, thereby increasing the chances of pollen transfer between flowers.

Diurnal nectar secretion patterns also differed between the two species in ways suggestive of adaptations to bird-pollination in *E. globulus* and insect-pollination in *E. nitens*. Flowers of *E. globulus* secreted nectar at night and during the day, whereas secretion by *E. nitens* only occurred during the day. By secreting nectar at night and during the morning, *E. globulus* is adapted to attract endothermic bird pollinators that are active in the early morning (Bond and Brown 1979, Kodric-Brown and Brown 1979, Brown *et al.* 1981, Cruden *et al.* 1983). This is consistent with large quantities of nectar being secreted nocturnally in the bird-visited *E. costata* (Behr. & F. Muell., ex F. Muell.) (syn. *E. incrassata* Labill. var *costata*) (Bond and Brown 1979, Horskins and Turner 1999) and *E. ficifolia* F. Muell. (Nicolson 1994). In contrast, restriction of nectar secretion in *E. nitens* to daylight hours, with rapid secretion occurring only at temperatures over 16°C, is suggestive of adaptation to pollination by ectothermic day-flying insects (Cruden *et al.* 1983). The restriction of nectar secretion to temperatures of over 16°C is

known to also occur in another small-flowered eucalypt, *E. melliodora* Cunn. ex Schauer (Nuñez 1977).

The concentration of sugar in nectar of *E. globulus* is also suggestive of adaptation to bird-pollination. The mean concentration of nectar from the three *E. globulus* trees where nectar did not appear to accumulate over several days (23.4%) was similar to the averages for 47 honeyeater-pollinated (21.6%) and 202 hummingbird-pollinated plant species (23.2%), but much lower than the average nectar concentration in 156 largely bee-pollinated plant species (36.0%) (Pyke and Waser 1981). This is much greater than the 9% sugar for nectar of *E. globulus* reported by Moncur *et al.* (1993).

4.4.2 Nectar consumption in E. globulus and E. nitens

In both *E. globulus* and *E. nitens*, there was no evidence of nectar being consumed at night. Therefore, nocturnal nectar-feeders such as mammals and moths were probably not important pollinators of any of these trees.

There was an absence of surplus nectar in all *E. nitens*, and three of the five *E. globulus*, trees studied. This accords with the removal of virtually all nectar in most other studies of eucalypts (Bond and Brown 1979, Ford 1979, Ford and Paton 1982, Collins and Briffa 1983, Paton 1990, Nicolson 1994), and the continued availability of nectar throughout the day in a few others (Ford 1979, Horskins and Turner 1999). In seed orchards where all nectar is consumed the introduction of large numbers of managed pollinators, such as honey bees, may not increase the rates at which flowers are visited by potential pollinators (Schaffer *et al.* 1983, Paton 1996). Moreover, the eschewal of *E. nitens* flowers in these orchards by honey bees, suggests that the introduction of honey bee hives to orchards of this species is unlikely to increase pollination (cf. Moncur *et al.* 1995).

The possibility that honey bees displace other pollinators of *E. globulus*, through competition for the nectar resource, suggests that the introduction of honey bee hives could even reduce the total level of pollination (McDade and

Kinsman 1980, Paton 1993, 1997, Irwin and Brody 1998). This is a likely scenario because *E. globulus* appears to have evolved to exploit birds as pollinators, indicating that birds are effective pollinators, and birds foraged on the experimental flowers less regularly at times of low nectar standing crops. This situation parallels that in *E. costata* (syn. *E. incrassata*) where honeyeaters foraged in smaller numbers while honey bees were active in large numbers (Bond and Brown 1979). Such displacement can occur because small animals are able to continue foraging at lower resource levels than those needed for larger, more energy demanding, animals to forage economically (Bond and Brown 1979, Ford 1979, Kodric-Brown and Brown 1979, Brown *et al.* 1981, Willmer and Corbet 1981). This phenomenon has been demonstrated experimentally in Arizona, where insects displaced hummingbirds from flowers of two shrub species (Kodric-Brown and Brown 1979, Brown *et al.* 1981). Although reduced bird activity can partly be attributed to declining numbers of flowers on the experimental branches as a result of them being picked as part of the experiment, this is unlikely to have had a major effect because the proportions of flowers removed were small (Fig. 4.16).

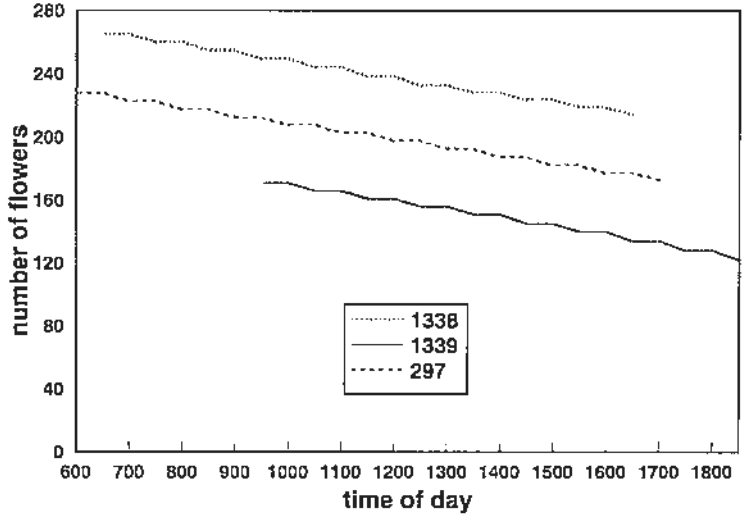


FIGURE 4.16

Numbers of unbagged experimental flowers of *E. globulus* throughout the days when nectar was measured on trees 1338, 1339, and 297.

However, in seed orchards of *E. globulus* where surplus nectar occurs, the introduction of large numbers of managed pollinators is likely to enhance visitation rates to flowers. This is also likely to increase the frequency with which pollinators move between flowers because it would lower standing crops of nectar (Heinrich and Raven 1972). The benefits that this has on seed production depend on how effective the introduced flower-visitors are as pollinators of *E. globulus*.

4.5 Conclusions

The deployment of honey bee hives in seed orchards of *E. nitens* at the time of flowering is unlikely to enhance seed production because nectar is already consumed as quickly as it is produced, and the resultant standing crops are insufficient to attract honey bees. However, the importation of large numbers of honey bees to orchards of *E. globulus* could increase or decrease seed production. The outcome depends largely upon whether all nectar is consumed, and whether the pollination services provided by honey bees are better or worse than those provided by other flower-visitors that could be displaced as a result of competition for the nectar resource.

Chapter 5

The pollinators of *Eucalyptus nitens* in Tasmanian seed orchards

Abstract

The flowers of *Eucalyptus nitens* in Tasmanian seed orchards were observed being visited by a wide variety of insects, but only very rarely by honey bees and never by birds. Most species of insects visiting the flowers of *E. nitens* are likely to be effective pollinators because all regular visitors carried large numbers of eucalypt pollen grains, and the allophilic floral structure facilitates frequent insect contact with stigmata. This contention is supported by the general absence of correlations between the effectiveness of insect communities as pollinators and community composition. Beetles were the most numerous and widespread visitors to the flowers, suggesting that they are important pollinators. Their value as pollinators is likely to be enhanced by the high percentage purity of eucalypt pollen they usually carry. Flies and native bees were also frequent visitors to the flowers, suggesting that they are also important pollinators. Native bees, particularly females of taxa that carry pollen externally, may be particularly effective pollinators because of the particularly large numbers of pollen grains they sometimes carry. However, in spite of the wide variety of insects that are likely to be effective pollinators of *E. nitens*, seed production in Tasmanian seed orchards was consistently limited by the amounts of outcross pollen deposited on stigmata.

5.1 Introduction

Both plantations and natural forests of *E. nitens* produce little seed (Eldridge *et al.* 1993, Moncur 1993, Jones *et al.* 2001), a factor that has inhibited its domestication (Moncur and Hasan 1994). This poor seed set may be the consequence of inadequate pollination services, as an earlier study conducted in Tasmania found the numbers of seeds per capsule following open-pollinations in *E. nitens* to be significantly lower than after hand cross-pollinations (Tibbits 1989).

The floral form, nectar production, and flowering season of *E. nitens* all suggest it is adapted to pollination by insects rather than vertebrates. The flowers are relatively small for the genus, the seed capsules measuring 4 - 7 mm in diameter (Boland *et al.* 1984), which suggests adaptation to insect pollinators (Ford *et al.* 1979, Griffin 1982). Furthermore, nectar production in *E. nitens* flowers is amongst the lowest for the genus (Ford *et al.* 1979), at approximately 0.5 mg of sugar per day, a level that appears insufficient to attract birds (Chapter 4). Nectar secretion is restricted to the warmest parts of the day (Chapter 4), when ectothermic day-flying insects are most active, which is also suggestive of adaptation to these pollinators (Cruden *et al.* 1983). In addition, flowering is concentrated in late summer in both natural populations (Boland *et al.* 1984) and exotic plantings in Tasmania (Tibbits 1989), when anthophilous insects are most abundant in Tasmania (Hingston 1997).

The flowers of *E. nitens* produce nectar and pollen that is exposed to all flower visiting animals. They are actinomorphic, with a single style emerging from a cup-shaped receptacle that is surrounded by an annulus of white stamens, and arranged in umbels of seven (Plates 4.2 and 5.1). Although such apparently allophilic flowers may be visited by a wide variety of anthophiles, those in the Apiaceae are sometimes quite specialised in their pollinator requirements as a result of differences in the effectiveness of visitors in transferring pollen (Lindsey 1984). These differences are the product of the relative abundances of particular anthophiles, their pollen carrying capacities, fidelity to the plant in question, capacity to contact receptive stigmata, the frequency with which they move between flowers and plants (Lindsey 1984), and the extent of pollen carryover (Campbell 1985b).

My study aimed to determine whether production of *E. nitens* capsules and seeds was pollinator limited in Tasmanian seed orchards, and to ascertain which animals were the major pollinators of *E. nitens* in Tasmanian seed orchards.

5.2 Methods

5.2.1 Determination of pollen limitation

This research was conducted in five Tasmanian *E. nitens* seed orchards (Table 5.1, Fig. 5.1) during January and February 1999 and again the following year, except for the Hastings orchard where flower abundance was insufficient for experiments to be conducted during the second year. Experiments involved approximately three or four trees in peak flower per orchard each year, and up to four small branches per tree between 0.8 and 5.0 m above the ground. Each experimental branch carried between 48 and 531 open-pollinated flowers, approximately half of which were open at the time of investigation.

The degree of pollen limitation on each experimental branch was determined by comparing mean capsule and seed set in the open pollinated flowers with that from 7 - 63 nearby flowers receiving supplementary outcross pollen (Gross 1996). Pollen was applied to receptive stigmata late in the day after insect activity had ceased to reduce the chances of this outcross pollen being secondarily transferred to other flowers by geitonogamous pollination (e.g. Heinrich 1975, DeGrandi-Hoffman and Martin 1995, DeGrandi-Hoffman and Watkins 2000). By necessity, flowers on the branches receiving supplementary pollen that were not in female phase at the time were removed. However, such flowers were retained in the open pollinated treatment to maintain any competition between flowers for resources.

During the first year, a pollen mix from 43 trees of *E. nitens* was used for these hand pollinations. This pollen was collected two years earlier from 15 trees in the Bream Creek orchard, and five years earlier from a trial not investigated during this study, and had subsequently been stored in gelatin capsules in jars containing silica gel in a freezer. The viability of the pollen from 12 of these trees was tested prior to mixing by counting the percentage of pollen grains that had germinated after 24 h on an agar plate at room temperature (Potts and Marsden-Smedley 1989) (mean 27.22%, range 11.08% - 59.13%). During the second year, fresh pollen was collected from 19 trees at

the Bream Creek orchard three to five weeks prior to use, and stored in the same manner as that used during the previous year.

Orchard	rainfall (mm/y)	altitude	adjacent vegetation
Bream Ck	600-900	120 m	pasture
Wycombe	900-1200	250 m	*E. nitens* plantation, native forest, pasture
Hastings	1200-1800	20 m	native forest
Kingsclere	1200-1800	320 m	pasture, native forest
Huntsman	1200-1800	500 m	*E. nitens* plantation, native forest

TABLE 5.1

Mean annual rainfall [www.bom.gov.au/cgi-bin/climate.cgi_bin_scripts/annual_rnfall.cgi], altitude, and nature of the adjacent vegetation, for the five *E. nitens* seed orchards studied.

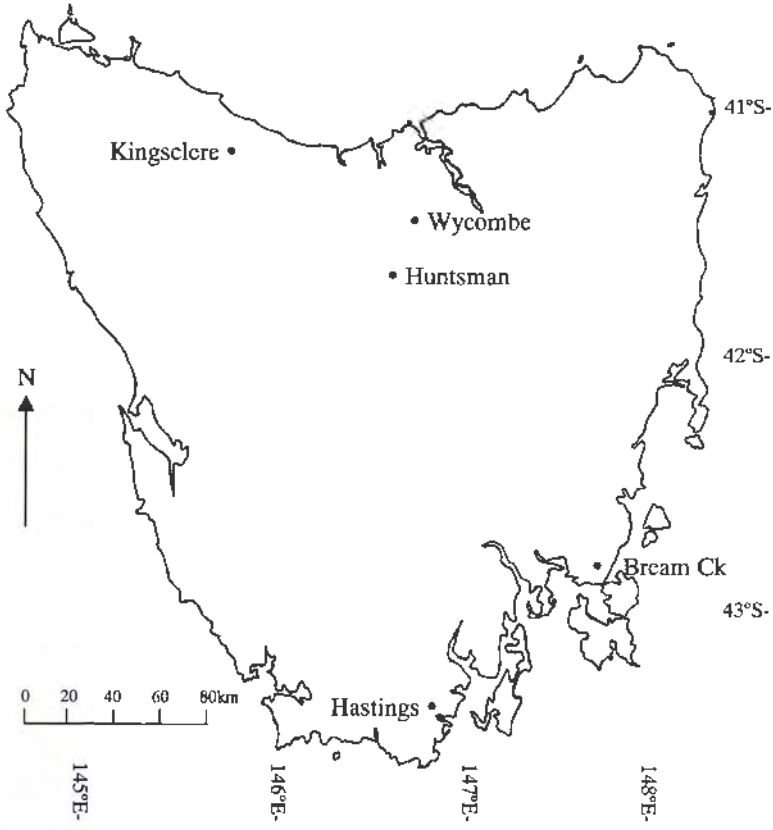


FIGURE 5.1

Tasmania, showing the locations of the *Eucalyptus nitens* seed orchards studied.

Capsules were harvested approximately 10 months after flowering, and placed individually in paper envelopes to dry. After dehiscence, the numbers of fully developed seeds in each capsule were counted. It was assumed that any capsules that had dehisced before harvesting contained the mean number of seeds for capsules that had not dehisced on that branch. Thus, the numbers of capsules per flower, mean seeds per capsule, and mean seeds per flower were determined for each open-pollinated branch and pollen-supplemented branch.

5.2.2 Flower visitor surveys

Insects visiting flowers on experimental branches were identified to the lowest taxonomic level possible while observing them from a distance of less than one metre. Some insects were identified to species, others to genus, and some were classed as a morphospecies of a particular family. Insects less than 3 mm in length were classed as small members of particular orders. Insect visitor communities were identified by counting the numbers of flowers visited by each insect taxon during five minutes on each branch of open pollinated flowers, while I stood on the ground or on an orchard ladder. However, as beetles were sometimes extremely abundant on flowers it was not always possible to count the numbers of flowers visited by each taxon. For this reason the numbers of beetles present on flowers during each census were used as measures of their abundance. As beetles moved slowly between flowers, this only slightly underestimated the numbers of flowers visited during a five minute period.

Insect surveys were conducted over one or two consecutive days in each orchard, whenever the weather was fine and mild to warm between 0730 h and 1830 h. However, insect surveys were not conducted at Huntsman during 1999 because the weather was too cool and overcast to be certain that all insect types were active. Five minute insect censuses were conducted between seven and ten times on each experimental open-pollinated branch. Branches were surveyed in random order on each tree. However, trees were only surveyed in random order if all of the trees studied were separated by a

total of less than 50 metres. When trees were widely spaced they were surveyed in a regular order to minimise the distances carrying the orchard ladder between trees. When trees were surveyed in a regular order, the order was reversed on the second day to prevent particular trees from being surveyed repeatedly earlier or later than others. Visitation rates to flowers per hour were than calculated by dividing the total number of flowers visited by each taxon in all five minute surveys by the product of the number of open flowers and number of surveys, and then multiplying by 12.

Birds were also observed closely whenever they were present in the orchards to ascertain whether they fed on flowers. In addition, each orchard was searched thoroughly for 10 - 20 minutes for birds at sunrise (approximately 0600 h) on the morning of the second day of each visit to the orchard. The taxonomic nomenclature for birds used here is that of Christidis and Boles (1994).

5.2.3 Pollen loads carried by insects

Insects were captured as they foraged at flowers of *E. nitens* in the Bream Creek, Wycombe, Huntsman and Kingsclere seed orchards (Table 5.1, Fig. 5.1) during January 2001. In most cases, insects were placed individually in 6 ml vials containing 3 ml of distilled water. However, copulating pairs of the soldier beetle *Chauliognathus lugubris* (Fabricius) (Cantharidae) were deposited together in the vials. Each vial was shaken for 10 seconds to wash pollen from the insect, after which the insect was released. Most insects appeared unharmed by the process, and flew away within a few seconds of release. However, native bees took several minutes to dry sufficiently to be able to fly, and sometimes did not survive. Native bee survival appeared to be better if they were allowed to dry in the shade rather than in direct sunlight.

Ten subsamples of water from each vial were transferred to a haemacytometer slide in the laboratory. Each vial was shaken for 10 seconds, to suspend the pollen, prior to each subsample being taken. The

numbers of eucalypt and other pollen grains in 338 grid squares 200 μm wide were counted in each subsample under a compound microscope at a magnification of 312.5. From this, the number of pollen grains washed from each insect was estimated. Each pollen grain counted equated to 222 pollen grains in the solution. For pairs of *Chauliognathus lugubris*, the estimated number of grains in the solution was halved to give the number of grains from one insect.

5.2.4 Data analysis

Experimental branches were excluded from the analysis if any part of them died before capsule harvest, or fecundity appeared to be severely limited by physiological factors apparent as less than 10% of flowers receiving supplementary outcross pollen producing capsules.

Fecundity was compared between branches using Two-Way Analysis of Variance, with the five orchards and the two treatments of open-pollination and supplementary outcross pollination as fixed sources of variation. The numbers of capsules per flower, seeds per capsule, and seeds per flower were all analysed in this way. Values were multiplied by 10 or 100 to make them all greater than one, so that they could be square-root transformed if the raw data did not meet the assumptions of normality and equal variance. Whenever statistically significant differences between orchards or treatments occurred, subsequent pairwise multiple comparisons were conducted using Student-Newman-Keuls Method. Data analyses were conducted using the computer programme SigmaStat (Jandel 1994).

The degree to which fecundity was pollen limited on each experimental branch of open-pollinated flowers was calculated by assuming that the maximum possible capsule and seed set for each experimental branch could be achieved by applying supplementary outcross pollen to receptive stigmata of nearby flowers. Hence, the pollinator effectiveness score (pe) for the anthophilous insect community on each branch of open-pollinated flowers was defined as the fecundity of open-pollinated flowers as a

percentage of that resulting on the adjacent flowers that received supplementary outcross pollen. This was calculated using the formula:

$$pe = 100^{*}(F_T/F_S)$$

where F_T = mean fecundity for open-pollinated flowers; and F_S = mean fecundity for flowers receiving supplementary outcross pollen. Pollinator effectiveness scores were calculated for the numbers of capsules per flower, seeds per capsule, and seeds per flower.

Differences between orchards in the effectiveness of pollinator communities were examined by comparing these pollinator effectiveness scores using One-Way Analysis of Variance. If the raw data did not meet the assumptions of normality and equal variance, the data were transformed by taking their square roots. If the transformed data still failed to meet the assumptions of the parametric test, the non-parametric Kruskal-Wallis Test was employed. Data analyses were conducted using the programme SigmaStat (Jandel 1994).

Visitation rates to flowers by each insect functional group (exotic bees, native bees, wasps, ants, flies, beetles and moths) and total insects were also compared between orchards. Because of the non-normality of the data sets, which could not be rectified by square root transformation, the Kruskal-Wallis Test was used for this. Whenever statistically significant differences between orchards occurred, subsequent pairwise multiple comparisons were conducted using Dunn's Test. These data analyses were also conducted using SigmaStat (Jandel 1994).

Pollinator effectiveness was then related to the visitor profile for each open-pollinated branch to determine whether the abundances of any insect taxa were consistently related to the effectiveness of insect communities as pollinators. Branches were ordinated according to the mean visitation rates by insect morphospecies, using semistrong hybrid multidimensional scaling, with the computer programme PATN (Belbin 1993). Those insect morphospecies that were statistically significant ($P < 0.05$) to the variation

between branches, as determined by a Monte Carlo technique, were fitted to the plot as mathematical vectors. The statistical significance of each pollinator effectiveness score for the three fecundity variables (capsules per flower, seeds per capsule, and seeds per flower) to the ordination plot were also determined using a Monte Carlo technique, and fitted to the plot as vectors if significant. Similar ordinations were conducted according to mean visitation rates by insect families, and the insect functional groups.

Relationships between flower visitation rates by various insect taxa and plant fecundity were also explored with regressions using the procedure 'Proc Reg' in the computer programme SAS (SAS Institute 1992). The data were standardised by controlling for the confounding factors (Table 5.2) and regressions were conducted on the residuals. The statistical significance of the residuals of visitation rates by each insect morphospecies, family, functional group, and total insects, to each experimental branch as predictors of the residuals of the pollinator effectiveness scores for the numbers of seeds produced per flower on each experimental branch were investigated using individual regressions. These analyses were restricted to insect taxa that were observed on more than two experimental branches. The *P*-value designated as the level of significance (0.05) was adjusted using the Bonferroni method, to reduce the probability of making any type 1 errors (Sokal and Rohlf 1995).

Confounding Factor
orchard
tree
year of flowering
height of experimental flowers above the ground
aspect of experimental flowers on the tree (° from north)
numbers of open-pollinated flowers on the experimental branch

TABLE 5.2

Confounding factors for which the data were standardized prior to regressions being conducted between flower visitation rates and fecundity.

The effects of height and aspect of the experimental open-pollinated flowers on the tree, and the numbers of open-pollinated flowers on the experimental

branch, on plant fecundity and flower visitation rates by various insect taxa were also explored using regressions with the computer programme SAS (SAS Institute 1992). For the analysis of each factor, the data were standardised by controlling for the other tree-related factors (Table 5.2), and regressions were conducted on the residuals. The statistical significance of the residuals of height, aspect, and numbers of flowers, as predictors of the residuals of the pollinator effectiveness scores for the numbers of seeds produced per flower and visitation rates by insect morphospecies, families, and functional groups, on each experimental branch were investigated using individual regressions. These analyses were restricted to insect taxa that were observed on more than two experimental branches. The *P*-value designated as the level of significance (0.05) was adjusted using the Bonferroni method, to reduce the probability of type 1 errors (Sokal and Rohlf 1995).

Total numbers of pollen grains carried by insects, percentages of pollen grains that were *Eucalyptus*, and the numbers of *Eucalyptus* pollen grains, were compared between insects at three taxonomic levels. These were insect morphospecies, insect family, and the insect functional groups of bees, wasps, flies and beetles. For species of bees where males and females are morphologically distinct, and females carry pollen externally, the sexes were analysed as distinct morphospecies. Comparisons between taxa were restricted to taxa with at least three samples in the data set. Comparisons were made using the non-parametric Kruskal-Wallis One-Way Analysis of Variance, because the distributions of the data could not be normalised by either square-root or $\log_{10}(X + 1)$ transformations, with individual insects used as replicates. Subsequent pairwise tests were made using Dunn's Method against control groups. These data analyses were conducted using the programme SigmaStat (Jandel 1994).

5.3 Results

5.3.1 Capsule and seed production

Fecundity for *E. nitens* differed significantly between orchards in the numbers of capsules per flower, seeds per capsule, and seeds per flower (Table 5.3). The mean number of seeds per flower was significantly higher at Hastings, Kingsclere and Huntsman, than at Bream Creek and Wycombe (Table 5.3). However, the reasons for only producing approximately 40% as many seeds per flower as the other orchards differed between Bream Creek and Wycombe. Low numbers of capsules per flower and seeds per capsule both contributed to the low number of seeds per flower at Bream Creek, whereas the low number of seeds per flower at Wycombe was entirely the result of poor capsule set (Table 5.3).

variables	capsules / 100 flowers	seeds / 10 capsules	seeds / 100 flowers
data type	raw	raw	square root
orchard	$P < 0.0001^{***}$	$P < 0.0001^{***}$	$P < 0.0001^{***}$
Bream Creek	45.2^{b} (4.0)	15.0^{b} (2.2)	72.0^{b} (20.3)
Wycombe	27.8^{c} (4.8)	26.6^{a} (2.7)	73.7^{b} (24.4)
Hastings	63.0^{a} (3.8)	31.0^{a} (2.1)	203.2^{a} (19.2)
Kingsclere	66.7^{a} (3.5)	28.1^{a} (2.0)	194.2^{a} (17.8)
Huntsman	65.3^{a} (3.2)	24.0^{a} (1.8)	169.6^{a} (16.4)
treatment	$P = 0.1337^{NS}$	$P = 0.0008^{***}$	$P = 0.0112^{*}$
open pollination	50.9^{a} (2.5)	21.6^{b} (1.4)	121.4^{b} (12.5)
supplement	56.2^{a} (2.5)	28.3^{a} (1.4)	163.7^{a} (12.6)
interaction	$P = 0.5236^{NS}$	$P = 0.0733^{NS}$	$P = 0.4950^{NS}$

TABLE 5.3

Comparisons of fecundity for branches of flowers of *E. nitens* in five seed orchards subjected to treatments of open-pollination and supplementary outcross pollination using Two-Way Analysis of Variance. Raw mean fecundity for branches in each orchard and treatment across both years, with standard errors in brackets, are given with different superscript letters within each category denoting statistically significant pairwise differences in fecundity between orchards or treatments. Only branches where the pollen supplement treatment produced at least one capsule per 10 flowers were included in the analysis.

The mean numbers of seeds per flower also differed significantly between treatments, with fecundity being significantly enhanced by supplementary outcross pollination (Table 5.3). The limitation of seed production per open pollinated flower to an average of only 74% of that following supplementary

outcross pollination was the result of the numbers of seeds per capsule, but not the numbers of capsules per flower, being significantly pollen limited (Table 5.3).

However, fecundity was not significantly affected by interactions between orchards and treatments (Table 5.3). Hence, low fecundity at Bream Creek and Wycombe reflects limitations in the capacities of these orchards to produce seeds rather than greater pollen limitation. This indicates that the extent of pollen limitation was uniform across orchards. This finding was supported by comparison of the pollinator effectiveness scores for the branches of open-pollinated flowers, which revealed no statistically significant differences between orchards in the degree of pollen limitation affecting the numbers of capsules per flower ($P = 0.188$, $H_4 = 6.15$, Kruskal-Wallis Test), seeds per capsule ($P = 0.0954$, $F_4 = 2.06$, 1-Way ANOVA on raw data), and seeds per flower ($P = 0.207$, $F_4 = 1.52$, 1-Way ANOVA on square-root transformed data) (Table 5.4).

Orchard	# capsules/flower	# seeds/capsule	# seeds/flower
Hastings	92.45 (34.32)	72.97 (43.52)	66.98 (45.82)
Bream Creek	76.54 (43.66)	105.46 (46.45)	75.14 (45.35)
Wycombe	122.91 (76.55)	73.60 (32.97)	87.12 (57.78)
Kingsclere	97.27 (32.96)	113.54 (64.03)	115.28 (83.30)
Huntsman	103.35 (29.68)	93.19 (38.19)	100.40 (59.85)

TABLE 5.4

Mean pe scores (fecundity of open-pollinated flowers as percentages of that in nearby flowers receiving supplementary outcross pollination at peak stigma receptivity) for branches of *E. nitens* flowers in five seed orchards across two years. Standard errors are shown in brackets.

5.3.2 Flower visitors

Birds were never observed feeding from flowers of *E. nitens* in these orchards, or in another seed orchard at Hampshire near Kingsclere. This was in spite of species observed feeding on flowers of *E. globulus* (Chapters 8 and 9) being observed in, or near, all orchards while the trees were flowering (Table 5.5).

Bird species	Orchard					
	Bream Ck	Wycombe	Hastings	Kingsclere	Huntsman	Hampshire
yellow-tailed black cockatoo				*	*	
musk lorikeet	*					
green rosella		*		*	*	
swift parrot	*		*			*
spotted pardalote	*	*		*		
striated pardalote					*	
yellow wattlebird		*	*		*	*
yellow-throated honeyeater	*	*	*	*	*	*
strong-billed honeyeater					*	
black-headed honeyeater			*		*	*
crescent honeyeater			*			
eastern spinebill					*	
silvereye			*	*	*	

TABLE 5.5

Bird species known to feed on flowers of *E. globulus* (see Chapters 8 and 9) that were observed in, or near, *E. nitens* seed orchards while trees were flowering.

Family or Order	Species or morphospecies	Bream Creek	Wycombe	Hastings	Kingsclere	Huntsman
Apidae	*Apis mellifera*	0.000	0.000	0.034	0.000	0.000
	Bombus terrestris	0.000	0.000	0.010	0.000	0.000
Hymenoptera	**Total exotic bees (P = 0.0431)**	**0.000[a]**	**0.000[a]**	**0.044[a]**	**0.000[a]**	**0.000[a]**
Colletidae	*Callomelitta picta*	0.000	0.004	0.142	0.006	0.000
	Leioproctus spp.	0.000	0.000	0.231	0.135	0.000
	Euryglossa (Callohesma) calliopsiformis	0.000	0.000	0.000	0.012	0.010
	Euryglossa (Euryglossa) ephippiata	0.000	0.000	0.000	0.098	0.002
	Euryglossa (Euryglossa) nigrocaerulea	0.000	0.000	0.059	0.000	0.000
	Euryglossa (Euhesma) sp.	0.000	0.000	0.000	0.042	0.000
	*Hylaeus (Euprosopis) honestus**	0.000	0.000	0.005	0.004	0.000
	Hylaeus (Prosopisteron) spp.	0.000	0.000	0.003	0.000	0.000
Halictidae	*Homalictus (Homalictus) sphecodoides*	0.000	0.000	0.000	0.000	0.004
	small *Lasioglossum (Chilalictus)* spp.	0.000	0.006	0.000	0.011	0.000
	large *Lasioglossum (Chilalictus)* spp.	0.000	0.024	0.000	0.003	0.004
	Lasioglossum (Parasphecodes) spp.	0.000	0.000	0.000	0.044	0.000
Hymenoptera	**Total native bees (P < 0.0001)**	**0.000[b]**	**0.034[b]**	**0.440[a,b]**	**0.352[a]**	**0.019[b]**
Evaniidae	sp.1	0.000	0.042	0.000	0.000	0.000
Gasteruptidae	*Gasteruption* spp.	0.000	0.000	0.000	<0.001	0.000
Ichneumonidae	sp.1	0.000	0.084	0.000	0.010	0.000
Hymenoptera	**Total wasps (P = 0.0341)**	**0.000[a]**	**0.126[a]**	**0.000[a]**	**0.010[a]**	**0.000[a]**
Formicidae	unidentified small ants	0.001	0.196	0.000	0.000	0.165
	Myrmecia pilosula	0.000	0.007	0.000	0.000	0.000
Hymenoptera	**Total ants (P < 0.0001)**	**0.001[b]**	**0.203[a]**	**0.000[b]**	**0.000[b]**	**0.165[a]**
Diptera	unidentified small flies	0.004	0.017	0.047	0.026	0.020
Anthomyiidae	sp.1	1.426	0.000	0.000	0.095	0.000
Bombyliidae	sp.3	0.000	0.019	0.000	0.000	0.000
Calliphoridae	*Calliphora stygia*	0.049	0.000	0.026	0.336	0.047

Family or Order	Species or morphospecies	Bream Creek	Wyc ombe	Hast ings	Kings clere	Hunts man
	Calliphora sp.2	0.007	0.000	0.003	0.037	0.000
Muscidae	sp.1	0.000	0.004	0.000	0.000	0.000
Sepsidae	sp.1	0.141	0.002	0.000	0.003	0.000
Stratiomyidae	*Odontomyia* sp.	0.000	0.000	0.000	0.039	0.000
Syrphidae	sp.1	0.000	0.000	0.004	0.015	0.000
	sp.5	0.000	0.003	0.000	0.004	0.000
	sp.8	0.000	0.000	0.000	0.070	0.000
	Psilota sp.	0.000	0.000	0.000	0.002	0.000
	Eristalis tenax	0.000	0.000	0.000	0.020	0.000
Tabanidae	*Scaptia* sp.2	0.000	0.000	0.000	0.010	0.000
Tachinidae	*Senostoma* spp.	0.000	0.011	0.000	0.001	0.000
	Rutilia sp.1	0.000	0.004	0.000	0.000	0.054
Diptera	**Total flies ($P < 0.0001$)**	**1.627^{ab}**	**0.060^{c}**	**0.079^{c}**	**0.657^{a}**	**0.121^{bc}**
Coleoptera	unidentified small beetles	0.000	0.013	0.007	0.002	0.019
Alleculidae	*Atoichus bicolor*	0.000	0.000	0.121	0.000	0.018
Buprestidae	*Castiarina* sp.	0.000	0.000	0.000	0.000	0.014
Cantharidae	*Chauliognathus lugubris*	0.237	0.016	0.245	0.308	0.338
	Chauliognathus nobilitatus	0.004	0.328	0.029	0.001	0.040
	Heteromastix sp.	0.000	0.000	0.005	0.000	0.000
Cerambycidae	sp.2	0.000	0.000	0.019	0.000	0.000
	sp.5	0.000	0.000	0.030	0.000	0.000
	sp.L	0.000	0.003	0.000	0.000	0.000
	Stenocentrus suturalis	0.000	0.002	0.003	0.001	0.003
	Syllitus lineatus	0.012	0.000	0.000	0.000	0.005
Cleridae	*Eleale* sp.	0.000	0.019	0.027	0.001	0.000
Lycidae	*Metriorrhynchus* spp.	0.000	0.027	0.054	0.013	0.034
Mordellidae	*Mordellistena* spp.	0.000	1.269	0.203	0.010	0.560
Oedemeridae	*Ischnomera* sp.	0.000	2.088	0.000	0.014	0.144
Scarabaeidae	*Deuterocaulobius villosus*	0.000	0.000	0.000	0.000	0.005
	Phyllotocus macleayi	3.273	0.259	0.000	0.835	0.000
	Phyllotocus rufipennis	0.002	0.000	0.000	0.033	0.003
Coleoptera	**Total beetles ($P < 0.0001$)**	**3.529^{a}**	**4.024^{ab}**	**0.742^{c}**	**1.219^{bc}**	**1.183^{bc}**
Lepidoptera	unidentified small moths	0.000	0.062	0.000	0.000	0.000
	Total insects ($P < 0.0001$)	**5.156^{a}**	**4.509^{ab}**	**1.305^{b}**	**2.239^{ab}**	**1.488^{b}**

TABLE 5.6

Mean visitation rates (flower visits / flower / hour) by insect taxa to flowers of *E. nitens* in five seed orchards across both years. For each insect functional group, and total insects, the significance of differences between orchards determined by Kruskal-Wallis 1-Way ANOVA is given. Different superscript letters within functional groups denote statistically significant pairwise differences between orchards determined by Dunn's Test. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of eucalypts in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999).

Plants	Bream Ck	Wycombe	Hastings	Kingsclere	Huntsman
Scotch thistle *Onopordum acanthium*	*	*		*	*
creeping thistle *Cirsium arvense*	*				*
blackberry *Rubus fruticosus*	*			*	
cat's ear *Hypochaeris radicata*				*	*
ragwort *Senecio jacobea*					*
manuka *Leptospermum scoparium*			*		
prickly geebung *Persoonia juniperina*		*			

TABLE 5.7

Plants visited by honey bees (*Apis mellifera* L.) in five seed orchards of *E. nitens* over two years.

A wide variety of insects was observed on the flowers of *E. nitens*, encompassing numerous taxa of beetles, flies and bees, as well as a few wasps, ants and small moths (Table 5.6). Beetles were the most common group of flower visitors at all orchards (Table 5.6), and were observed on all trees studied as part of the experiment into pollen limitation on tree fecundity. Beetles were most abundant at Bream Creek and Wycombe, and then Kingsclere and Huntsman, and least common at Hastings (Table 5.6). The numerical dominance of beetles at flowers resulted in similar patterns of total insect visitation rates, with this being highest at Bream Creek, intermediate at Wycombe and Kingsclere, and lowest at Hastings and Huntsman (Table 5.6). Flies were also observed on the flowers of most *E. nitens* trees, although they were most common at Kingsclere, followed by Bream Creek and then Huntsman, and least abundant at Wycombe and Hastings (Table 5.6). Native bees were also frequent flower visitors at Kingsclere and Hastings, occasional at Wycombe and Huntsman, but absent from Bream Creek (Table 5.6). Ants were only common at Wycombe and Huntsman, but were never observed on flowers at Hastings or Kingsclere (Table 5.6). The other insect groups of exotic bees, wasps, and moths were all uncommon visitors to flowers of *E. nitens* (Table 5.6). Only two honey bees *Apis mellifera* L. and one bumble bee *Bombus terrestris* (L.) were observed visiting flowers of *E. nitens*, with these all being on one tree at Hastings. The absence of honey bee visitors to flowers of *E. nitens* was in spite of them being common on other plant species in all orchards (Table 5.7), and ten commercial hives being situated beneath tree B1 at Bream Creek in 1999.

Wasps were recorded occasionally at Wycombe and Kingsclere, but not at other orchards (Table 5.6). Moths were only recorded from one tree at Wycombe (Table 5.6), but were present on this tree during both years.

A great deal of overlap was apparent between the five orchards in insect flower visitor communities on experimental branches. This was the case irrespective of whether the communities were analysed as functional groups (Fig. 5.2), families (Fig. 5.3), or morphospecies (Fig. 5.4). However, several branches at Bream Creek were strongly associated with beetles and flies, some branches at Hastings and Kingsclere were dominated by native bees, and one branch at Huntsman was distinct due to heavy visitation by ants (Fig. 5.2).

At the level of functional groups, abundances of beetles were negatively associated with visitation rates by native bees, while abundances of ants were negatively associated with visitation rates by flies (Fig. 5.2). These patterns reflect the comparisons in abundance of these taxa between orchards, with beetles being common in orchards where native bees were not, and vice versa, and ants being common in orchards where flies were not, and vice versa (Table 5.6). However, at the family and morphospecies levels, beetle taxa produced vectors pointing in most directions of the ordination plots, indicating that most branches carried beetles but the composition of these beetle communities differed between branches (Figs 5.3 and 5.4). Negative associations between ants and flies were also evident at the family level (Fig. 5.3), but not at the morphospecies level (Fig. 5.4).

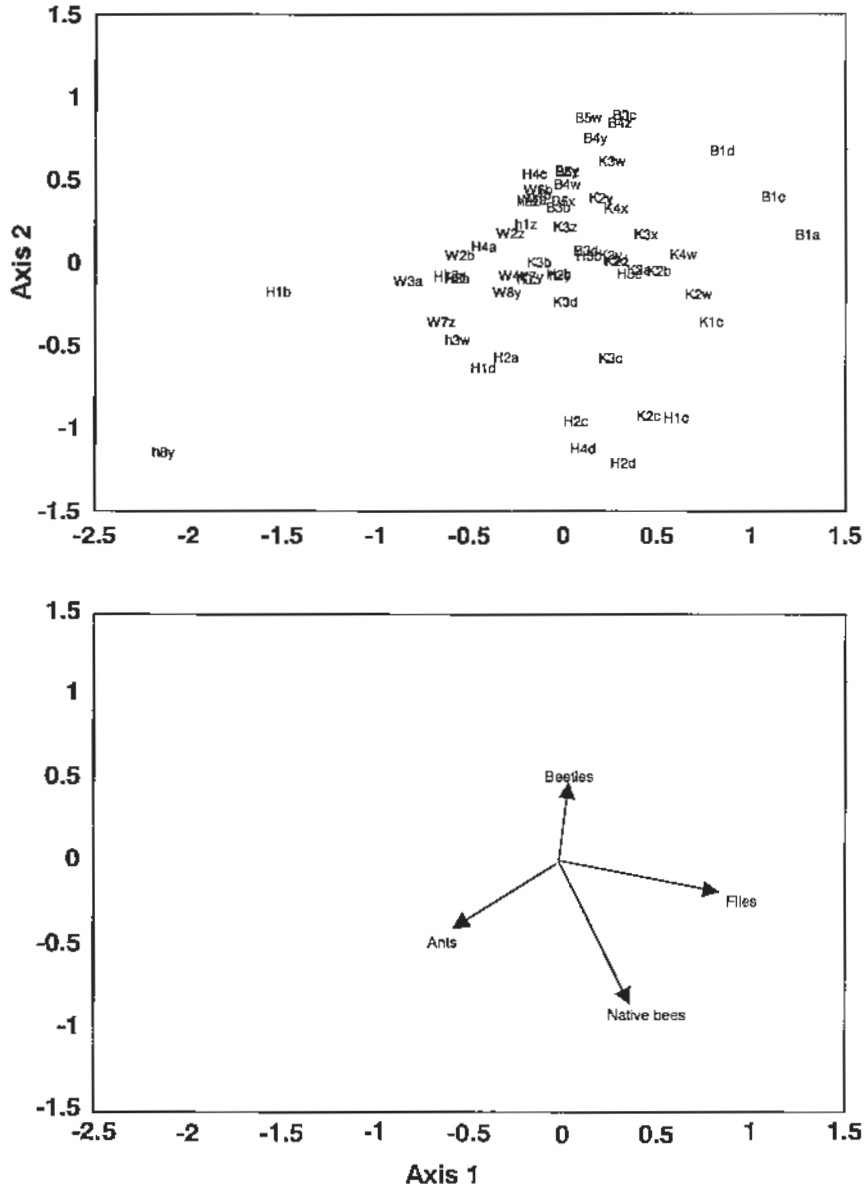


FIGURE 5.2

Ordination of branches according to their flower visitation rates by insect functional groups. Branch codes are as follows. First letter denotes orchard: B = Bream Ck; h = Huntsman; H = Hastings; K = Kingsclere; and W = Wycombe. Number denotes the tree in the orchard. Final letter denotes the branch on the tree: a-d = branches flowering in 1999; w-z = branches flowering in 2000. Significant ($P < 0.05$) insect functional groups have been fitted as vectors, shown in a separate plot for clarity. Stress on 3 axes = 0.112. Only the two axes encompassing the greatest part of the variation between branches are shown.

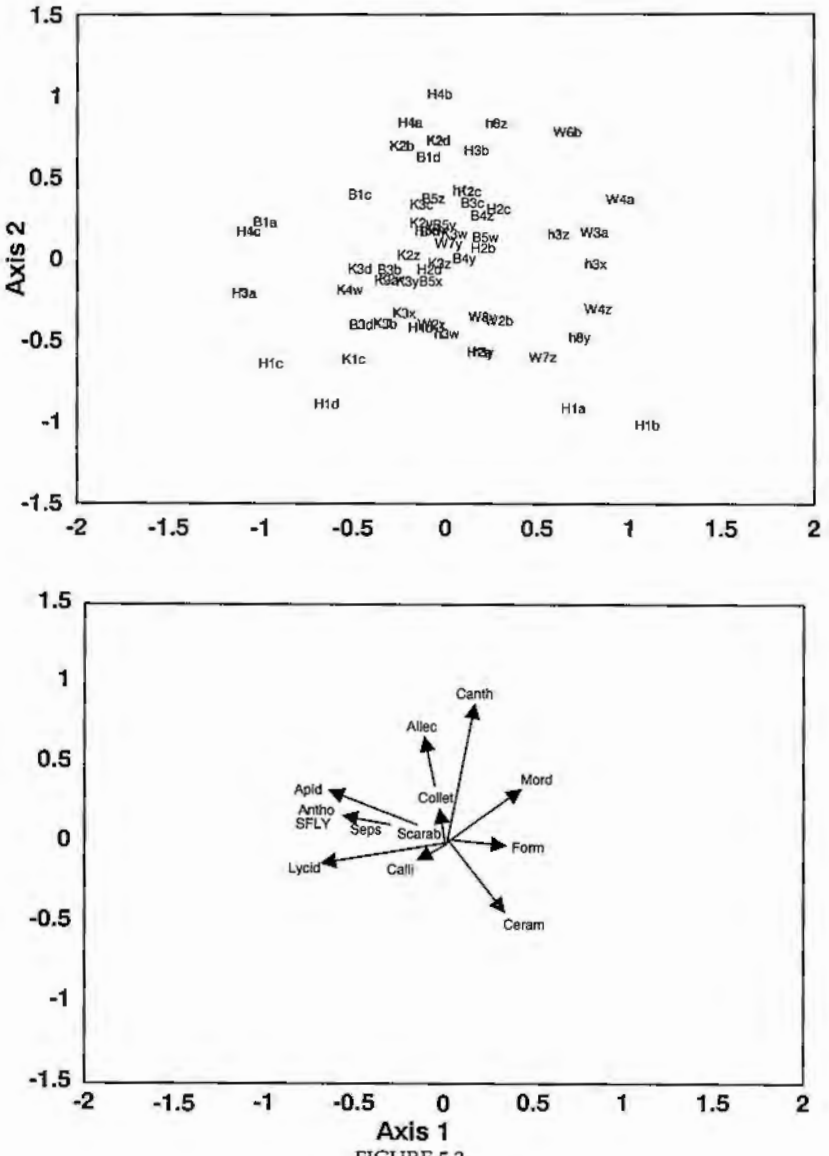


FIGURE 5.3

Ordination of branches according to their flower visitation rates by insect families. Branch codes are detailed in Fig. 5.2. Significant ($P < 0.05$) insect families have been fitted as vectors, shown in a separate plot for clarity. Insect family codes are: Allec = Alleculidae; Antho= Anthomyiidae; Apid = Apidae; Calli = Calliphoridae; Canth = Cantharidae; Ceram = Cerambycidae; Collet = Colletidae; Form = Formicidae; Lycid = Lycidae; Mord = Mordellidae; Scarab = Scarabaeidae; Seps = Sepsidae; SFLY = unidentified small flies. Stress on 4 axes = 0.134. Only the two axes encompassing the greatest part of the variation between branches are shown.

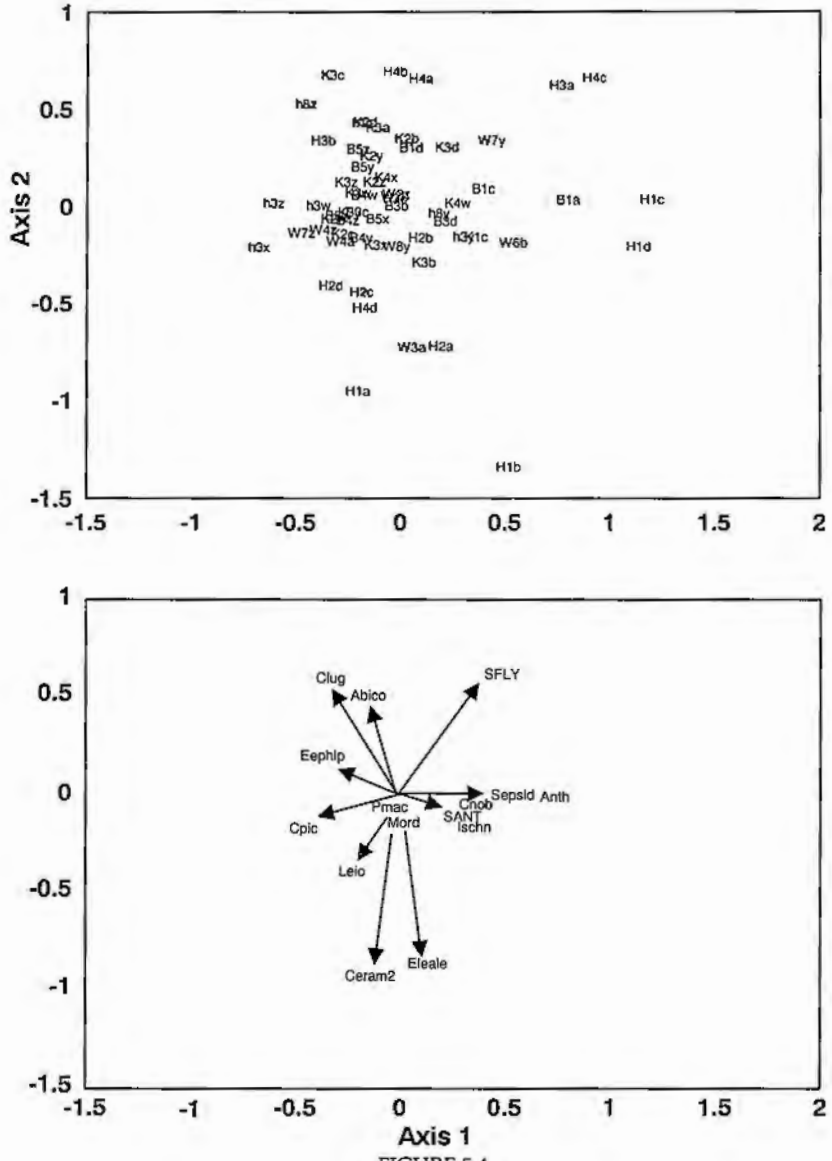


FIGURE 5.4

Ordination of branches according to their flower visitation rates by insect morphospecies. Branch codes are detailed in Fig. 5.2. Significant ($P < 0.05$) insect morphospecies have been fitted as vectors, shown in a separate plot for clarity. Insect morphospecies codes are: Abicn = *Atoichus bicolor;* Anth = Anthomyiidae sp.1; Ceram2 = Cerambycidae sp.2; Clug = *Chauliognathus lugubris;* Cnob = *Chauliognathus nobilitatus;* Cpic = *Callomelitta picta;* Eephip = *Euryglossa ephippiata;* Eleale = *Eleale* sp.; Ischn = *Ischnomera* sp.; Leio = *Leioproctus* spp.; Mord = *Mordellistena* spp.; Pmac = *Phyllotocus macleayi;* SANT = unidentified small ants; Sepsid = Sepsidae sp.1; SFLY = unidentified small flies. Stress on 5 axes = 0.113. Only the two axes encompassing the greatest part of the variation between branches are shown.

5.3.3 Associations between insect flower visitors and pollination

None of the pollinator effectiveness scores (pe) for any of the fecundity variables were statistically significant to the variation between branches in their flower visitor communities, whether analysed at the level of functional groups, families, or morphospecies (Table 5.8). Although pe for capsules per flower and seeds per capsule sometimes approached statistical significance to the ordination plots, the ultimate measure of pollinator effectiveness, pe for seeds per flower, did not approach significance to any of the ordination plots (Table 5.8).

Pollinator effectiveness	Taxonomic groups		
	functional groups	families	morphospecies
Capsules / flower	$P > 0.06$	$P > 0.21$	$P > 0.75$
Seeds / capsule	$P > 0.13$	$P > 0.21$	$P > 0.07$
Seeds / flower	$P > 0.98$	$P > 0.87$	$P > 0.59$

TABLE 5.8

Statistical significance of pollinator effectiveness scores for fecundity variables (fecundity from open-pollinated flowers as percentages of that from flowers receiving supplementary outcross pollen) as vectors fitted to the ordination plots of *E. nitens* branches according to their flower visitation rates by insect functional groups (Fig. 5.2), families (Fig. 5.3) and morphospecies (Fig. 5.4), as determined by a Monte-Carlo technique.

5.3.4 Effects of tree-related factors on insect flower visitors and fecundity

The aspect and height of experimental branches on *E. nitens* trees, and the numbers of flowers on experimental branches had little effect on the visitation rates to flowers by insect taxa or pollinator effectiveness scores for the numbers of seeds per flower (pe s/f) (Table 5.9). The only insect taxon whose abundance was significantly affected by any of these tree-related factors was the cerambycid beetle *Stenocentrus suturalis* (Olivier), which visited flowers more frequently when there were more flowers per branch. None of these tree-related factors had a statistically significant effect on pe s/f (Table 5.9). Hence, no insect taxa were associated with the level of pollinator effectiveness via common responses to variation in any tree-related factors.

Family	Species	Tree-related factors		
		Aspect	Height	# Flowers
Colletidae	*Callomelitta picta*	0.1699	0.7907	0.1442
	Leioproctus spp.	0.0073	0.9609	0.1165
	Euryglossa (Euryglossa) ephippiata	0.9471	0.8953	0.5353
	Euryglossa (Euryglossa) nigrocaerulea	0.6378	0.9265	0.7515
	Euryglossa (Euhesma) sp.	0.1899	0.7218	0.6733
	*Hylaeus (Euprosopis) honestus**	0.1993	0.3739	0.1012
	Total Colletidae	0.0872	0.8445	0.8877
Halictidae	large *Lasioglossum (Chilalictus)* spp.	0.1989	0.3956	0.1970
	Lasioglossum (Parasphecodes) spp.	0.7281	0.1426	0.2665
	Total Halictidae	0.6847	0.2486	0.3713
	Total native bees	0.1010	0.9824	0.7563
Ichneumonidae	sp.1	0.0312	0.3023	0.2153
	Total wasps	0.0312	0.3023	0.2153
Formicidae	unidentified small ants	0.6821	0.5820	0.8835
	Total ants	0.6821	0.5820	0.8835
Diptera	unidentified small flies	0.4923	0.6530	0.0072
Anthomyiidae	sp.1	0.8791	0.0574	0.9496
Calliphoridae	*Calliphora stygia*	0.5954	0.0052	0.6244
	Calliphora sp.2	0.0048	0.7476	0.0031
	Total Calliphoridae	0.9991	0.0053	0.3068
Sepsidae	sp.1	0.0195	0.0059	0.4452
Stratiomyidae	*Odontomyia* sp.	0.0298	0.1469	0.9838
Syrphidae	sp.1	0.0173	0.3338	0.1676
	sp.5	0.0258	0.7946	0.0448
	sp.8	0.0292	0.0043	0.1073
	Eristalis tenax	0.0738	0.3739	0.0387
	Total Syrphidae	0.3599	0.0047	0.2120
Tachinidae	Total Tachinidae	0.2751	0.8007	0.5393
	Total flies	0.8558	0.0114	0.9194
Coleoptera	unidentified small beetles	0.6422	0.3149	0.8209
Alleculidae	*Atoichus bicolor*	0.5916	0.7545	0.1654
Cantharidae	*Chauliognathus lugubris*	0.0694	0.0834	0.5643
	Chauliognathus nobilitatus	0.9479	0.6787	0.2243
	Total Cantharidae	0.0853	0.1148	0.4638
Cerambycidae	sp.2	0.4354	0.6746	0.9951
	Stenocentrus suturalis	0.5961	0.2307	0.0001+
	Syllitus lineatus	0.0447	0.7513	0.1483
	Total Cerambycidae	0.1361	0.6897	0.9951
Cleridae	*Eleale* sp.	0.1202	0.6424	0.5968
Lycidae	*Metriorrhynchus* spp.	0.1675	0.2202	0.5122
Mordellidae	*Mordellistena* spp.	0.7209	0.9415	0.7247
Oedemeridae	*Ischnomera* sp.	0.4822	0.6589	0.0949
Scarabaeidae	*Phyllotocus macleayi*	0.8899	0.4302	0.0505
	Phyllotocus rufipennis	0.0129	0.7425	0.0406
	Total Scarabaeidae	0.7724	0.4437	0.0389
	Total beetles	0.2592	0.7842	0.2257
	Total insects	0.6369	0.0410	0.4918
	pe seeds / flower	0.1104	0.1169	0.2224

TABLE 5.9

The statistical significance of tree-related factors as predictors of visitation rates by each insect taxon to each experimental branch, and pollinator effectiveness scores for the numbers of seeds per flower on each experimental branch, determined using individual regressions after the effects of orchard, tree, year and other tree-related factors (Table 5.2) have been removed. Taxa whose visitation rates were statistically significant predictors of fecundity have the *P*-value in bold, with the direction of the association given as + (positive) or - (negative). The *P*-value designated as the level of significance (0.05) was adjusted for all insect taxa, using the Bonferroni method, to 0.00106. Only insect taxa observed on at least three experimental branches were analysed. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of eucalypts in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999).

5.3.5 Effects of various insect taxa on seed set per flower

Single regressions of visitation rates by insect taxa as predictors of pe s/f found very few statistically significant taxa (Table 5.10). Flower visitation rates by wasps, specifically Ichneumonidae sp.1, were the only statistically significant positive predictors of pe s/f, and no taxa were statistically significant negative predictors (Table 5.10).

Family	Species	*P*
Colletidae	*Callomelitta picta*	0.0960
	Leioproctus spp.	0.0955
	Euryglossa (Euryglossa) ephippiata	0.0742
	Euryglossa (Euryglossa) nigrocaerulea	0.9067
	Euryglossa (Euhesma) sp.	0.0157
	*Hylaeus (Euprosopis) honestus**	0.2963
	Total Colletidae	0.0011
Halictidae	large *Lasioglossum (Chilalictus)* spp.	0.1247
	Lasioglossum (Parasphecodes) spp.	0.7650
	Total Halictidae	0.3200
	Total native bees	0.0021
Ichneumonidae	sp.1	**0.0008+**
	Total wasps	**0.0008+**
Formicidae	unidentified small ants	0.3517
	Total ants	0.3517
Diptera	unidentified small flies	0.4873
Anthomyiidae	sp.1	0.8193
Calliphoridae	*Calliphora stygia*	0.5224
	Calliphora sp.2	0.0405

Family	Species	P
	Total Calliphoridae	0.7990
Sepsidae	sp.1	0.2363
Stratiomyidae	*Odontomyia* sp.	0.9014
Syrphidae	sp.1	0.5402
	sp.5	0.6570
	sp.8	0.2545
	Eristalis tenax	0.0032
	Total Syrphidae	0.3886
Tachinidae	Total Tachinidae	0.3405
	Total flies	0.9630
Coleoptera	unidentified small beetles	0.2783
Alleculidae	*Atoichus bicolor*	0.7861
Cantharidae	*Chauliognathus lugubris*	0.1501
	Chauliognathus nobilitatus	0.4633
	Total Cantharidae	0.2169
Cerambycidae	sp.2	0.5006
	Stenocentrus suturalis	0.2335
	Syllitus lineatus	0.3072
	Total Cerambycidae	0.0687
Cleridae	*Eleale* sp.	0.9552
Lycidae	*Metriorrhynchus* spp.	0.4561
Mordellidae	*Mordellistena* spp.	0.7196
Oedemeridae	*Ischnomera* sp.	0.0119
Scarabaeidae	*Phyllotocus macleayi*	0.6190
	Phyllotocus rufipennis	0.2343
	Total Scarabaeidae	0.6746
	Total beetles	0.8650
	Total insects	0.5336

TABLE 5.10

The statistical significance of visitation rates by each insect taxon to each experimental branch as predictors of the pollinator effectiveness scores for the numbers of seeds produced per flower on each experimental branch determined using individual regressions after the effects of orchard, tree, year, and tree-related factors (Table 5.2) have been removed. Taxa whose visitation rates were statistically significant predictors of fecundity have the *P*-value in bold, with the direction of the association given as + (positive) or - (negative). The *P*-value designated as the level of significance (0.05) was adjusted, using the Bonferroni method, to 0.00106. Only insect taxa observed on at least three experimental branches were analysed. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of eucalypts in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999).

5.3.6 Pollen loads carried by insects

Statistically significant differences occurred between insect taxa in the total numbers of pollen grains, percentages of pollen grains that were *Eucalyptus*, and the numbers of *Eucalyptus* pollen grains, at all three taxonomic levels (Table 5.11).

Taxonomic level	variables	*P*	sig.
morphospecies	total number of pollen grains	<0.0001	***
	% of grains that were eucalypt	0.0014	**
	number of eucalypt pollen grains	<0.0001	***
family	total number of pollen grains	<0.0001	***
	% of grains that were eucalypt	0.0002	***
	number of eucalypt pollen grains	0.0003	***
functional group	total number of pollen grains	0.0006	***
	% of grains that were eucalypt	<0.0001	***
	number of eucalypt pollen grains	0.0199	*

TABLE 5.11

Results of Kruskal-Wallis 1-Way ANOVA tests of differences between insect taxa in pollen carrying while foraging from flowers of *E. nitens*. Functional groups were bees, wasps, flies and beetles. Only insect taxa observed on at least three experimental branches were analysed.

Of the functional groups, bees carried the largest total pollen loads and flies carried the second largest (Table 5.12). Bees carried significantly more pollen grains than did wasps or beetles. Flies also carried significantly more pollen grains than did beetles (Table 5.12).

Small pollen loads on beetles as a group were the result of small beetles carrying low numbers of pollen grains. Halictid bees, and large flies in the Tabanidae and Tachinidae, carried significantly more pollen grains than did the small beetles in the families Oedemeridae, Mordellidae, and Lycidae (Table 5.12). Colletid bees, and large beetles in the Scarabaeidae, also carried significantly more pollen grains than did the Oedemeridae and Mordellidae. The pollen loads carried by large beetles in the Cantharidae also comprised significantly more pollen grains than those carried by the Oedemeridae (Table 5.12).

Morphospecies	Family	Group	n	Median	Mean	Range
[a]*Leioproctus (Leioproctus)*♀	Colletidae	Bees	3	49704	34098	2441-50148
Leioproctus (Leioproctus)♂	Colletidae	Bees	1	666	666	666
Euryglossa nigrocaerulea	Colletidae	Bees	1	222	222	222
*Hyleaus (Euprosopis) honestus**	Colletidae	Bees	2	3328	3328	444-6213
Total	[ab]Colletidae	Bees	7	2441	15691	222-50148
Homalictus niveifrons♀*	Halictidae	Bees	1	59024	59024	59024
Lasioglossum (Chilalictus)♀	Halictidae	Bees	2	7212	7212	0-14423
[a]*Lasioglossum (Parasphecodes)*♀	Halictidae	Bees	3	105178	134394	58580-239423
[abcd]*Lasioglossum (Parasphecodes)*♂	Halictidae	Bees	3	666	592	222-888
Total	[a]Halictidae	Bees	9	14423	53156	0-239423
Total		[a]Bees	16	4327	36765	0-239423
[abcd]Evaniidae sp.1	[abcd]Evaniidae	Wasps	3	444	370	0-666
Ichneumonidae sp.1	Ichneumonidae	Wasps	2	444	444	222-666
Scoliidae sp.	Scoliidae	Wasps	1	444	444	444
Total		[bc]Wasps	6	444	407	0-666
Asilidae sp.1	Asilidae	Flies	1	222	222	222
Bombyliidae sp.4	Bombyliidae	Flies	1	1553	1553	1553
[abcd]*Calliphora stygia*	Calliphoridae	Flies	7	1331	1522	444-3994
[abcd]*Calliphora* sp.2	Calliphoridae	Flies	8	555	693	0-1775
Total	[abcd]Calliphoridae	Flies	15	888	1080	0-3994
Odontomyia sp.	Stratiomyidae	Flies	2	222	222	222
Eristalis tenax	Syrphidae	Flies	1	64793	64793	64793
Syrphidae sp.1	Syrphidae	Flies	1	0	0	0
[abcd]Syrphidae sp.8	Syrphidae	Flies	3	3328	6139	222-14867
Total	[abcd]Syrphidae	Flies	5	3328	16642	0-64793
[a]*Scaptia* spp.	[a]Tabanidae	Flies	5	5325	4704	1331-7322
[a]*Rutilia* sp.1	[a]Tachinidae	Flies	3	3550	3476	2885-3994
Total		[ab]Flies	32	1331	4244	0-64793
Atoichus bicolor	Alleculidae	Beetles	1	888	888	888
Castiarina sp.	Buprestidae	Beetles	1	888	888	888
[ab]*Chauliognathus lugubris*	Cantharidae	Beetles	8	1498	1747	333-3550
[abcd]*Chauliognathus nobilitatus*	Cantharidae	Beetles	9	666	740	0-1775
Total	[abc]Cantharidae	Beetles	17	1109	1214	0-3550
[abcd]*Stenocentrus suturalis*	Cerambycidae	Beetles	3	888	592	0-888
[abcd]Cerambycidae sp.1	Cerambycidae	Beetles	3	888	666	0-1109
Cerambycidae sp.2	Cerambycidae	Beetles	1	4216	4216	4216
Cerambycidae sp.3	Cerambycidae	Beetles	1	3107	3107	3107
Total	[abcd]Cerambycidae	Beetles	8	888	1387	0-4216
[bcd]*Metriorrhynchus* spp.	[bcd]Lycidae	Beetles	9	222	271	0-888
[cd]*Mordellistena* spp.	[cd]Mordellidae	Beetles	11	0	202	0-1553
[d]*Ischnomera* sp.	[d]Oedemeridae	Beetles	11	0	161	0-1109
[abc]*Phyllotocus macleayi*	Scarabaeidae	Beetles	9	1331	1578	0-3550
[abcd]*Phyllotocus rufipennis*	Scarabaeidae	Beetles	9	1331	2860	0-13314
Total	[ab]Scarabaeidae	Beetles	18	1331	2219	0-13314
Total		[c]Beetles	76	666	1051	0-13314

TABLE 5.12

Median, mean, and range of the total number of pollen grains carried by various insect taxa while foraging on flowers of *E. nitens*. Significant differences ($P < 0.05$) between medians for various taxa, as determined by Dunn's Method against control groups following Kruskal-Wallis 1-Way ANOVA, are denoted by different superscript letters. Only insect taxa observed on at least three experimental branches were analysed. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of

eucalypts in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999). The bee identified as *Homalictus niveifrons* may have been *H. megastigmus*.

Morphospecies	Family	Group	n	Median	Mean	Range
[ab]*Leioproctus (Leioproctus)*♀	Colletidae	Bees	3	93.8	84.5	63.6-96.0
Leioproctus (Leioproctus)♂	Colletidae	Bees	1	100	100	100
Euryglossa nigrocaerulea	Colletidae	Bees	1	100	100	100
*Hyleaus (Euprosopis) honestus**	Colletidae	Bees	2	94.6	94.6	89.3-100
Total	[ab]Colletidae	Bees	7	96.0	91.8	63.6-100
Homalictus niveifrons♀*	Halictidae	Bees	1	87.2	87.2	87.2
Lasioglossum (Chilalictus)♀	Halictidae	Bees	1	4.6	4.6	4.6
[ab]*Lasioglossum (Parasphecodes)*♀	Halictidae	Bees	3	62.7	52.0	10.5-82.6
[ab]*Lasioglossum (Parasphecodes)*♂	Halictidae	Bees	3	66.7	55.6	0-100
Total	[b]Halictidae	Bees	8	64.7	51.8	0-100
Total		[b]Bees	15	87.2	70.5	0-100
Evaniidae sp.1	Evaniidae	Wasps	2	100	100	100
Ichneumonidae sp.1	Ichneumonidae	Wasps	2	33.3	33.3	0-66.7
Scoliidae sp.	Scoliidae	Wasps	1	100	100	100
Total		[ab]Wasps	5	100	73.3	0-100
Asilidae sp.1	Asilidae	Flies	1	50	50	50
Bombyliidae sp.4	Bombyliidae	Flies	1	100	100	100
[ab]*Calliphora stygia*	Calliphoridae	Flies	7	75	67.1	0-100
[ab]*Calliphora* sp.2	Calliphoridae	Flies	6	25	41.7	0-100
Total	[ab]Calliphoridae	Flies	13	55.6	55.3	0-100
Odontomyia sp.	Stratiomyidae	Flies	2	50	50	0-100
Eristalis tenax	Syrphidae	Flies	1	0	0	0
[ab]Syrphidae sp.8	Syrphidae	Flies	3	100	66.7	0-100
Total	[ab]Syrphidae	Flies	4	50	50	0-100
[b]*Scaptia* spp.	[b]Tabanidae	Flies	5	0	15.2	0-72.7
[ab]*Rutilia* sp.1	[ab]Tachinidae	Flies	3	68.8	53.7	0-92.3
Total		[b]Flies	29	50	48.5	0-100
Atoichus bicolor	Alleculidae	Beetles	1	100	100	100
Castiarina sp.	Buprestidae	Beetles	1	100	100	100
[a]*Chauliognathus lugubris*	Cantharidae	Beetles	8	100	100	100
[ab]*Chauliognathus nobilitatus*	Cantharidae	Beetles	7	100	86.7	50-100
Total	[a]Cantharidae	Beetles	16	100	94.2	50-100
Stenocentrus suturalis	Cerambycidae	Beetles	2	87.5	87.5	75-100
Cerambycidae sp.1	Cerambycidae	Beetles	2	90	90	80-100
Cerambycidae sp.2	Cerambycidae	Beetles	1	100	100	100
Cerambycidae sp.3	Cerambycidae	Beetles	1	100	100	100
Total	[a]Cerambycidae	Beetles	6	100	92.5	75-100
[ab]*Metriorrhynchus* spp.	[ab]Lycidae	Beetles	5	100	88.3	66.7-100
[ab]*Mordellistena* spp.	[ab]Mordellidae	Beetles	4	100	75	0-100
[a]*Ischnomera* sp.	[a]Oedemeridae	Beetles	3	100	100	100
[a]*Phyllotocus macleayi*	Scarabaeidae	Beetles	8	100	100	100
[a]*Phyllotocus rufipennis*	Scarabaeidae	Beetles	7	100	85.7	0-100
Total	[a]Scarabaeidae	Beetles	15	100	93.3	0-100
Total		[a]Beetles				0-100

TABLE 5.13

Median, mean, and range of the percentage of pollen grains that were eucalypt pollen carried by various insect taxa while foraging on flowers of *E. nitens*. Significant differences ($P < 0.05$) between medians for various taxa, as determined by Dunn's Method against control groups

following Kruskal-Wallis 1-Way ANOVA, are denoted by different superscript letters. Only insect taxa observed on at least three experimental branches, and individual insects carrying some pollen, were analysed. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of eucalypts in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999). The bee identified as *Homalictus niveifrons* may have been *H. megastigmus*.

The morphospecies that carried the most pollen grains were female *Lasioglossum (Parasphecodes)* (Halictidae) and *Leioproctus (Leioproctus)* (Colletidae) bees, and large flies in the genera *Scaptia* (Tabanidae) and *Rutilia* (Tachinidae) (Table 5.12). These four taxa carried significantly more pollen grains than did small beetles in the genera *Ischnomera* (Oedemeridae), *Mordellistena* (Mordellidae) and *Metriorrhynchus* (Lycidae). Large pollen loads were also recorded from the only female *Homalictus niveifrons / megastigmus* (Cockerell) (Halictidae) bee and the single large exotic fly *Eristalis tenax* (L.) (Syrphidae) that were sampled (Table 5.12). One of the largest beetle species, *Chauliognathus lugubris* (Fabricius) (Cantharidae), also carried significantly more pollen grains than did the much smaller *Ischnomera* sp. and *Mordellistena* spp. The pollen loads on *Ischnomera* sp. were also significantly smaller than those on the much larger beetle *Phyllotocus macleayi* Fischer (Scarabaeidae) (Table 5.12).

Of the pollen loads carried by insect functional groups, those carried by beetles contained significantly higher proportions of *Eucalyptus* pollen than did those carried by flies and bees (Table 5.13). This was particularly so for the beetle families Oedemeridae, Cantharidae, Scarabaeidae and Cerambycidae, all of which carried significantly higher percentages of *Eucalyptus* pollen than did flies in the Tabanidae (Table 5.13). Similarly, at the species level, the beetles *Phyllotocus rufipennis* (Boisduval), *P. macleayi* (Scarabaeidae), *Chauliognathus lugubris* (Cantharidae), and *Ischnomera* sp. (Oedemeridae) carried significantly higher proportions of *Eucalyptus* pollen than did the fly *Scaptia* sp. (Tabanidae) (Table 5.13).

Morphospecies	Family	Group	n	Median	Mean	Range
[ab]*Leioproctus (Leioproctus)*♀	Colletidae	Bees	3	46598	32101	1553-48151
Leioproctus (Leioproctus)♂	Colletidae	Bees	1	666	666	666
Euryglossa nigrocaerulea	Colletidae	Bees	1	222	222	222
*Hylaeus (Euprosopis) honestus**	Colletidae	Bees	2	2996	2996	444-5547
Total	[a]Colletidae	Bees	7	1553	14740	222-48151
Homalictus niveifrons♀*	Halictidae	Bees	1	51479	51479	51479
Lasioglossum (Chilalictus)♀	Halictidae	Bees	2	333	333	0-666
[a]*Lasioglossum (Parasphecodes)*♀	Halictidae	Bees	3	48373	69896	11095-150222
[abcde]*Lasioglossum (Parasphecodes)*♂	Halictidae	Bees	3	444	444	0-888
Total	[a]Halictidae	Bees	9	888	29241	0-150222
Total		[a]Bees	16	1220	22897	0-150222
[abcde]Evaniidae sp.1	[ab]Evaniidae	Wasps	3	444	370	0-666
Ichneumonidae sp.1	Ichneumonidae	Wasps	2	222	222	0-444
Scoliidae sp.	Scoliidae	Wasps	1	444	444	444
Total		[ab]Wasps	6	444	333	0-666
Asilidae sp.1	Asilidae	Flies	1	222	222	222
Bombyliidae sp.4	Bombyliidae	Flies	1	1553	1553	1553
[abcde]*Calliphora stygia*	Calliphoridae	Flies	7	666	983	0-2219
[de]*Calliphora* sp.2	Calliphoridae	Flies	8	0	250	0-1109
Total	[b]Calliphoridae	Flies	15	222	592	0-2219
Odontomyia sp.	Stratiomyidae	Flies	2	111	111	0-222
Eristalis tenax	Syrphidae	Flies	1	0	0	0
Syrphidae sp.1	Syrphidae	Flies	1	0	0	0
[abcde]Syrphidae sp.8	Syrphidae	Flies	3	222	5030	0-14867
Total	[ab]Syrphidae	Flies	5	0	3018	0-14867
[bcde]*Scaptia* spp.	[ab]Tabanidae	Flies	5	0	399	0-1775
[abcde]*Rutilia* sp.1	[ab]Tachinidae	Flies	3	2441	1701	0-2663
Total		[b]Flies	32	222	1033	0-14867
Atoichus bicolor	Alleculidae	Beetles	1	888	888	888
Castiarina sp.	Buprestidae	Beetles	1	888	888	888
[abc]*Chauliognathus lugubris*	Cantharidae	Beetles	8	1498	1747	333-3550
[abcde]*Chauliognathus nobilitatus*	Cantharidae	Beetles	9	666	653	0-1775
Total	[a]Cantharidae	Beetles	17	999	1168	0-3550
[abcde]*Stenocentrus suturalis*	Cerambycidae	Beetles	3	666	518	0-888
[abcde]Cerambycidae sp.1	Cerambycidae	Beetles	3	888	592	0-888
Cerambycidae sp.2	Cerambycidae	Beetles	1	4216	4216	4216
Cerambycidae sp.3	Cerambycidae	Beetles	1	3107	3107	3107
Total	[ab]Cerambycidae	Beetles	8	888	1331	0-4216
[cde]*Metriorrhynchus* spp.	[ab]Lycidae	Beetles	9	222	222	0-666
[a]*Mordellistena* spp.	[b]Mordellidae	Beetles	11	0	182	0-1553
[a]*Ischnomera* sp.	[b]Oedemeridae	Beetles	11	0	161	0-1109
[abcd]*Phyllotocus macleayi*	Scarabaeidae	Beetles	9	1331	1578	0-3550
[abcde]*Phyllotocus rufipennis*	Scarabaeidae	Beetles	9	1331	2635	0-13314
Total	[a]Scarabaeidae	Beetles	18	1331	2207	0-13314
Total		[b]Beetles	76	444	1023	0-13314

TABLE 5.14

Median, mean, and range of the number of eucalypt pollen grains carried by various insect taxa while foraging on flowers of *E. nitens*. Significant differences ($P < 0.05$) between medians for various taxa, as determined by Dunn's Method against control groups following Kruskal-Wallis 1-Way ANOVA, are denoted by different superscript letters. Only insect taxa observed on at least three experimental branches were analysed. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of

eucalypts in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999). The bee identified as *Homalictus niveifrons* may have been *H. megastigmus*.

The relatively low quantities of pollen carried by beetles (Table 5.12) and the relatively low proportions of *Eucalyptus* pollen carried by flies (Table 5.13), resulted in these two functional groups carrying significantly smaller numbers of *Eucalyptus* pollen grains than did bees (Table 5.14). Both bee families, Colletidae and Halictidae, carried significantly more pollen of *Eucalyptus* than did the two families of beetles with the smallest species; Mordellidae and Oedemeridae. Of all morphospecies, female *Lasioglossum (Parasphecodes)* bees carried the greatest numbers of *Eucalyptus* pollen grains, with this being significantly more than carried by the beetles *Mordellistena* spp. (Mordellidae), *Ischnomera* sp. (Oedemeridae) and *Metriorrhynchus* spp. (Lycidae), and the flies *Calliphora* sp.2 (Calliphoridae) and *Scaptia* sp. (Tabanidae). Female *Leioproctus* bees also carried significantly more eucalypt pollen grains than did all of these species, with the exception of *Scaptia* sp. (Table 5.14).

However, statistically significant differences in the numbers of eucalypt pollen grains carried were also apparent between beetle and fly taxa (Table 5.14). Two of the families comprising large beetles, Scarabaeidae and Cantharidae, carried significantly more eucalypt pollen grains than did the smaller beetles in the Mordellidae and Oedemeridae. This was also apparent at the species level, with *Chauliognathus lugubris* (Cantharidae) and *Phyllotocus macleayi* (Scarabaeidae) carrying significantly more eucalypt pollen than did *Mordellistena* spp. (Mordellidae) and *Ischnomera* sp. (Oedemeridae). *Chauliognathus lugubris* also carried significantly more eucalypt pollen grains than did the fly *Calliphora* sp.2 (Calliphoridae) (Table 5.14).

5.4 Discussion

5.4.1 Factors limiting seed production

Capsule and seed production in *E. nitens* appeared to be limited by physiological resources to trees. The numbers of capsules and seeds produced per flower were significantly higher in the three seed orchards receiving more than 1200 mm mean annual rainfall than in the two orchards at drier locations. This effect was not significantly influenced by pollination treatment, suggesting that water availability may limit seed production in this species.

Seed production per flower of *E. nitens* also appeared to be limited by pollination services. Supplementary outcross pollination significantly enhanced the numbers of seeds per flower above levels occurring in open-pollinated flowers. This is similar to previous comparisons of fecundity in open-pollinated flowers and those subjected to controlled crosses in this species in Tasmania (Tibbits 1989). In both studies, open-pollinated flowers produced approximately 75% as many seeds as those receiving manual cross-pollinations. As in this study, enhancement of the numbers of seeds per flower by application of outcross pollen in the earlier study was the result of increased numbers of seeds per capsule rather than increased capsule set (Tibbits 1989).

Although seed production from open-pollinated flowers being consistently around 75% of that from flowers receiving manual outcross pollination suggests that pollinator services provided by insects could be improved, this may not necessarily be so. The numbers of seeds produced, from flowers of plants with full or partial self-incompatibility, following manual outcross pollination may be unattainable following visits by animal pollinators that usually carry a mixture of self and outcross pollen (Thomson 2001). In addition, it may not be possible for the numbers of seeds produced from flowers receiving manual outcross pollination to occur from all flowers on a tree because of limited physiological resources. Hence, pollination services

in all orchards investigated here, and the study of Tibbits (1989), may have approximated the best that can be achieved by animal pollinators.

5.4.2 The importance of various flower visitors as pollinators

The suite of potential pollinators comprised a wide variety of insects that varied between orchards and branches of flowers. However, the extent of pollen limitation did not differ significantly between orchards and was not significantly correlated with differences between branches in pollinator assemblages at three taxonomic levels. In addition, the abundances of almost all insect taxa were not significantly correlated with pollinator effectiveness scores for the numbers of seeds per flower. This suggests that the different communities of flower-visiting insects associated with the various orchards and branches were equally effective as pollinators, implying that a wide variety of insects are able to pollinate flowers of *E. nitens*. This view is supported by the finding that all common insect species foraging on flowers of *E. nitens* carried, on average, between hundreds and tens of thousands of eucalypt pollen grains. As stigmata are exserted above the floral receptacle, and the flowers are arranged in umbels of seven, it is likely that most insects will readily deposit pollen on stigmata as they clamber over the umbel in search of nectar and/or pollen (Plates 4.2 and 5.1).

Beetles were the most abundant insects observed on the flowers of *E. nitens*, indicating that they may be particularly important pollinators of this tree species. Their importance as pollinators should be enhanced by the generally high percentages of pollen grains on their bodies that were *Eucalyptus*. In particular, the soldier beetles *Chauliognathus* spp. (Cantharidae) were common and widespread visitors to flowers of *E. nitens* (Plate 5.1). The cockchafer beetle *Phyllotocus macleayi* (Scarabaeidae) was also common in the three orchards near pasture (Plate 4.2), reflecting their larval food requirement of grass roots (Lawrence and Britton 1991). As a result, beetles were most abundant in orchards with pasture nearby. However, many beetles were also found in orchards distant from pasture. In particular, *Ischnomera* sp. (Oedemeridae) and pin-tailed beetles *Mordellistena*

spp. (Mordellidae) were common in the orchards near forest, reflecting the larval food requirements of dead wood in many species in these families (Lawrence and Britton 1991). Although these two smaller species carried small numbers of pollen grains, the densities of pollen on their bodies were probably similar to larger species, making them effective pollinators.

PLATE 5.1

A pair of soldier beetles *Chauliognathus lugubris* (Cantharidae) clambering over flowers of *E. nitens* at Bream Creek.

Flies and native bees were also common visitors to the flowers, suggesting that they are important pollinators. The blowfly *Calliphora stygia* (Fabricius) (Calliphoridae) was widespread, but particularly common at Kingsclere. Flies in the families Anthomyiidae and Sepsidae were particularly common in the orchard surrounded by pasture (Bream Creek). Large numbers of Sepsidae in this orchard can be attributed to them breeding in mammalian dung (Colless and McAlpine 1991). In contrast, native bees were most

common in orchards near native forest and were not observed in the orchard surrounded by pasture. Although generally not as abundant on flowers as beetles were, bees carried more eucalypt pollen grains per insect than did beetles. Observations of bees carrying the largest pollen loads of all insects sampled are consistent with several other studies (Beattie *et al.* 1973, Kendall and Solomon 1973, O'Brien 1980, Mallick 2001). However, very large pollen loads were limited to females of bee genera that transport pollen to their nests by accumulating them in scopal hairs, such as *Leioproctus, Lasioglossum* and *Homalictus*. Male bees, that do not collect pollen for larvae, and females of genera such as *Hylaeus* and *Euryglossa* that transport pollen in their crops, carried similar numbers of pollen grains to most other insects.

The insect species that was the only statistically significant predictor of high numbers of seeds per open-pollinated flower relative to the maximum possible level on that branch, the wasp Ichneumonidae sp.1, was one of the more uncommon visitors. In addition, the two specimens examined for pollen carried relatively small pollen loads comprising relatively small proportions of eucalypt pollen, suggesting that the positive regression result cannot be attributed to this species being an outstanding pollinator of *E. nitens*.

The wide variety of insects foraging on flowers of *E. nitens* is in accordance with observations on numerous other *Eucalyptus* species (Ashton 1975, Ireland and Griffin 1984, Hingston and Potts 1998, Horskins and Turner 1999, Hingston and McQuillan 2000). However, the predominant native anthophilous insects on most other *Eucalyptus* species studied to date were bees and/or flies (Ashton 1975, Ireland and Griffin 1984, Hingston and Potts 1998, Hingston and McQuillan 2000). Only *E. foecunda* Schau., *E. cylindrifolia* Maiden et Blakely (Hawkeswood 1981), and *E. costata* (Behr & F. Muell, ex F. Muell.) (Horskins and Turner 1999) are known to be similar to *E. nitens* in hosting more beetle taxa than other insect groups. Nevertheless, this trend towards cantharophily in *E. nitens* is not as pronounced as in *E. foecunda* and

E. cylindrifolia in southwest Western Australia, both of which were visited almost exclusively by beetles (Hawkeswood 1981).

Eschewal of flowers of *E. nitens* as food sources by honey bees indicates that they play no role in the pollination of this species. Therefore, the greater outcrossing rates recorded by Moncur *et al.* (1995) in a Tasmanian *E. nitens* orchard following a year in which honey bee hives were deployed, than following a year when no hives were present, was almost certainly not the result of beneficial pollination services provided by honey bees (cf. Moncur *et al.* 1995). This may have been the result of different flower densities between years, a common phenomenon in eucalypts (Ashton 1975, Brown 1989, Moncur 1993, Moncur *et al.* 1994), which strongly influences outcrossing rates (Beattie 1976, Stephenson 1982, Karron *et al.* 1995). Alternatively, the different outcrossing rates observed by Moncur *et al.* (1995) may have been the result of varying levels of activity in insect species that did visit the flowers.

The absence of birds and honey bees on the flowers of *E. nitens* is in stark contrast to their frequent use of *E. globulus* (Hingston and Potts 1998, also see Chapters 6, 8 and 9), *E. viminalis* Labill., *E. obliqua* L'Herit., *E. ovata* Labill., *E. johnstonii* Maiden, and *E. urnigera* Hook. f. in Tasmania (Hingston and McQuillan 1998, 2000). However, the absence of birds and low numbers of honey bees feeding on its flowers is consistent with observations on other small-flowered species such as *E. muellerana* Howitt in Victoria (Ireland and Griffin 1984), and members of the *Piperitae* in Tasmania (Hingston 1997). This can be attributed to the very low levels of nectar production per flower in *E. nitens* (Chapter 4), and provides support to the conclusion of Ford *et al.* (1979) that small-flowered eucalypts are predominantly entomophilous.

5.4.3 Management implications

The reliance on wild insect populations to pollinate flowers of *E. nitens* has implications for control measures for herbivorous insects in and near seed orchards. The detrimental impacts of broad spectrum insecticides on insect

pollinators, and subsequent reduced seed set, are well known in other systems (Kevan 1975, Johansen 1977, Thaler and Plowright 1980, Kevan 1986, Kevan *et al.* 1990a, Kevan 1991, 1999). Although this has been little studied in this system, the broad spectrum insecticide commonly used in plantations of *E. nitens* is highly toxic to the soldier beetle *Chauliognathus lugubris* (Greener and Candy 1994). This species was one of the most common visitors to flowers of *E. nitens* in this study. Hence, refraining from using broad spectrum insecticides in the vicinity of flowering seed orchards, in both time and space, is likely to assist in maintaining pollination services to *E. nitens*.

Populations of wild insect pollinators are also susceptible to habitat destruction (Kevan *et al.* 1990a, Kevan 1991, 1999). This may involve loss of alternative food sources during periods when the crop plant is not flowering, and sites necessary for mating, nesting, oviposition, or resting (Kevan *et al.* 1990a, Kevan 1991, 1999). When a pollinator lives longer than the duration of a single species' flowering, other plants with different flowering periods are necessary for the maintenance of the pollinator population in the area (Heinrich and Raven 1972, Faegri and van der Pijl 1979, Augspurger 1980, Williams and Batzli 1982). For this reason, pollinator populations in agricultural crops may be enhanced by growing other food plants in the vicinity (Patten *et al.* 1993). The importance of nesting sites for pollinators became apparent after reduced alfalfa seed production in Manitoba, Canada, during the mid-twentieth century following clearing of native vegetation (Stephen 1955). When small areas of native vegetation were cleared for alfalfa seed crops, yields were typically around 1000 pounds per acre. However, as more land was cleared, seed production fell to around 150 pounds per acre. This was attributed to reduced abundances of the major pollinator of alfalfa, bees in the genus *Megachile*, as a consequence of the removal of dead trees in which they nested in the native forest (Stephen 1955). The importance of the surrounding habitat to certain insect taxa in this study was apparent from some species being restricted to orchards near pasture while others were only found near native forest. However, the capacity for *E. nitens* to be pollinated by a wide variety of insect taxa resulted

in similar pollination services occurring irrespective of the surrounding habitat.

The other major potentially harmful factors to pollinator populations and pollination services are the introduction of exotic predators, anthophilous insects, parasites and pathogens (Kevan 1999). The European wasp *Vespula germanica* (F.) (syn. *Paravespula germanica*) preys upon a wide variety of insects in Tasmania, particularly calliphorids and other large flies (Madden 1981) that are common visitors to flowers of *E. nitens*. This, together with predation from the more recently introduced *V. vulgaris* (L.), appears to dramatically reduce populations of Calliphoridae (Bashford 2001). Populations of insects that visit flowers of *E. nitens* may also be adversely affected by competition from the European bees *Apis mellifera* and *Bombus terrestris* when feeding on plants other than *E. nitens*, as they are both known to displace Australian native bees (Gross and Mackay 1998, Hingston and McQuillan 1999, Gross 2001). However, such displacement of insects from other plant species flowering concurrently with *E. nitens* could enhance seed production in *E. nitens* if it forces more insects to forage on *E. nitens*.

Chapter 6

Which animals are the most effective pollinators of *Eucalyptus globulus* subsp. *globulus*, insects or birds?

Abstract

The effectiveness of birds and insects as pollinators of the southeastern Australian forest tree *Eucalyptus globulus* subsp. *globulus* was investigated by comparing the numbers of capsules and seeds produced from flowers that were visited once by various anthophiles. The swift parrot *Lathamus discolor*, an endangered native bird, was a highly effective pollinator of *E. globulus*. A single *L. discolor* visit to a flower at peak stigmatic receptivity resulted in an average of 76% of the maximum possible seed set. In contrast, no insect species had a statistically significant effect on capsule or seed production. Single visits by either species of exotic social bee, the honey bee *Apis mellifera* or the bumble bee *Bombus terrestris*, resulted in less than 7% of the maximum possible seed set. Single visits by native insects resulted in only occasional capsule set, none of which contained viable seeds. The effectiveness of *L. discolor* as pollinators of *E. globulus* can be partly attributed to them almost always contacting the stigma while they consumed nectar. However, this was not the major reason for differences in pollinator effectiveness between *L. discolor* and insects, because single visits by *L. discolor* that involved stigmatic contact resulted in significantly greater capsule and seed set than single visits by either *A. mellifera* or *B. terrestris* that involved stigmatic contact. Hence, this difference in pollinator effectiveness may be the result of *L. discolor* depositing more outcross pollen than insects did per stigmatic contact in this partially self-incompatible tree species.

6.1 Introduction

Flowers of the southeastern Australian forest tree, *Eucalyptus globulus* Labill. subsp. *globulus* (Myrtaceae) (hereafter *E. globulus*) are visited frequently by both nectarivorous birds and insects (Hingston and Potts 1998, Chapter 4).

In this chapter the effectiveness of birds and insects as pollinators of *E. globulus* is compared within its natural distribution in southeastern Tasmania. I also examine whether differences between anthophile species in pollinator effectiveness are largely the result of the frequency with which various taxa contact stigmata, as previously suggested for *E. globulus* (Hingston and Potts 1998).

Birds should be better pollinators than native insects for the following reason. It is generally believed that bird-pollinated flowers evolved from insect-pollinated flowers (Faegri and van der Pijl 1979, Ford *et al.* 1979, Hopper and Burbidge 1986, Paton 1986b). This involved increased nectar production to meet the energy requirements of birds (Stiles 1978, Ford *et al.* 1979, Bertin 1982b, Paton 1986b). The flowers of *E. globulus* produce approximately 100 times as much nectar per day than those of the closely related *E. nitens* (Deane & Maiden) Maiden (Chapter 4), which is exclusively insect-pollinated (Chapter 5). For such a change to be favoured by natural selection, the fitness gains to the plant from bird-pollination must be great enough to offset the increased costs associated with greater allocation of photosynthate to nectar production (Stiles 1978, Paton 1986b). This implies that the pollination services provided by birds must be much better than those by insects with which the plant has evolved (Bertin 1982a, b).

In addition, the production of sufficient nectar to attract large endothermic animals, such as birds, may satiate small ectothermic insects without them having to move frequently between flowers (Paton 1986a). Consequently, insects would not move as widely as birds, thereby promoting selfing rather than outcrossing (Ford *et al.* 1979, Eldridge *et al.* 1993, Paton 1993). Self-pollination in *E. globulus* results in the production of fewer seeds, lower seed viability, and slower growth rates and higher mortality rates in offspring, than after outcrossing (Hardner and Potts 1995, Hardner *et al.* 1998).

However, the most common insect visitors to flowers of *E. globulus* within its natural distribution in southeastern Tasmania are not species with which it

has evolved. The most frequent visitor is the western honeybee, *Apis mellifera* L. (Hingston and Potts 1998, Chapter 4). The recently introduced European bumblebee, *Bombus terrestris* (L.), also forages regularly on *E. globulus* (Hingston and McQuillan 1998). Because these introduced colonial bees are larger and more energy demanding than most native insects, they may be more effective pollinators. Individual *A. mellifera* collect approximately 100 times as much nectar as they need for their own use (Faegri and van der Pijl 1979). This suggests that they will forage more widely than native insects, thereby enhancing their value as pollinators.

Information on the pollinators of *E. globulus* is of great value to the forest industry. This tree is grown extensively in commercial forestry plantations in many temperate regions of the world (Eldridge *et al.* 1993, Tibbits *et al.* 1997). Plantation stock are grown mostly from seeds, that are being collected increasingly from seed orchards of trees selected for characters desired by the forest industry (Eldridge *et al.* 1993, Tibbits *et al.* 1997). For this reason, knowing which animals are the most effective pollinators of *E. globulus* will assist tree breeders optimise the quantity and quality of seed produced in these seed orchards. Because *A. mellifera* and *B. terrestris* are colonial insects, their populations in seed orchards can be increased easily by importing hives at the time of flowering. Hence, if these bees are effective pollinators of *E. globulus* they may provide a simple means of ensuring high yields of good quality seeds from seed orchards (Moncur and Kleinschmidt 1992).

6.2 Methods

6.2.1 The plant species

The flowers of *E. globulus* exhibit an allophilic syndrome (*sensu* Faegri and van der Pijl 1979), with nectar and pollen exposed to all flower visitors (Plate 6.1). They are actinomorphic, being open dish-shaped with a single robust style emerging from a broad nectar-secreting hypanthium that is surrounded by a dense annulus of long white stamens (Curtis and Morris 1975) (Plate 6.1). These are the largest flowers of the 29 members of this genus in

Tasmania, the floral bud measuring 15 - 30 mm in length and 15 - 20 mm in diameter (Curtis and Morris 1975).

PLATE 6.1

A receptive flower of *Eucalyptus globulus*. Note the separation between anthers and stigma in space (herkogamy) through the straightening of the filaments as the flower ages, and time (dichogamy) through dehiscence of the anthers prior to stigma receptivity. The ant in the lower right is a species of *Camponotus* that feeds on eucalypt nectar.

The flowers of *Eucalyptus* are protandrous (Pryor 1976). Floral development involves initial shedding of the woody operculum, to expose the anthers and non-receptive stigma (Boland *et al.* 1984). In *E. globulus*, peak stigmatic receptivity occurs approximately one week after operculum shed (Hardner and Potts 1995), and flowers senesce when about 15 days old (Brown 1989).

6.2.2 Effects of flower visitors on tree fecundity

The effectiveness of flower visitors as pollinators of *E. globulus* was investigated by comparing the numbers of capsules and seeds produced following single visits to flowers with receptive virgin stigmata in two separate experiments conducted between December 1998 and December

2000. These were also compared to the numbers of capsules and seeds developing from flowers whose stigmata were never exposed and those hand-pollinated with outcross pollen.

6.2.2.1 Effects of flower visitors on tree fecundity - Experiment 1

A pilot study was conducted on two trees (847 and 848) planted in a garden in Sandford (Fig. 6.1) in December 1998. Flower buds were enclosed in terylene bags (PBS International, UK) to prevent animals from visiting the flowers. As the stigmata appeared to remain receptive for several days if the flowers were not visited, it was possible to obtain large numbers of receptive virgin flowers by this technique. Opportunities for outcrossing existed because flowering conspecifics were present in the vicinity, with the nearest outcross pollen sources being 8 m from tree 848 and 87 m from tree 847.

When numerous stigmata in a bag were receptive, the bag was removed and the flowers watched from a distance of less than one metre until each was visited once by an insect. A visit was defined as contact with the gynoecium, androecium, or hypanthium. Following a visit, the style was immediately covered with a tight-fitting clear plastic tube which had previously had the distal end sealed with heat. The flower was tagged to denote the visitor. After all receptive flowers on that day had been visited, the terylene bag was replaced to ensure that further visits to flowers did not occur.

Control outcrosses of flowers enclosed in other bags were conducted by applying pollen to receptive stigmata with the head of a matchstick. This pollen was a mix collected during the same flowering season from eight trees growing on the Tinderbox Peninsula, 15 - 20 km to the southwest, on the opposite side of the Derwent Estuary (Fig. 6.1). This pollen was stored in gelatin capsules over silica gel in a freezer between collection and use, and in an insulated container with an ice-block when taken into the field. The viability of the pollen was determined by counting the percentage of pollen grains that had germinated after 24 h on an agar plate at room temperature (Potts and Marsden-Smedley 1989). Germination rates ranged from 48.4% to

66.2%, with a mean of 57.3%. Flowers in other terylene bags acted as controls to measure levels of self-pollination within bags.

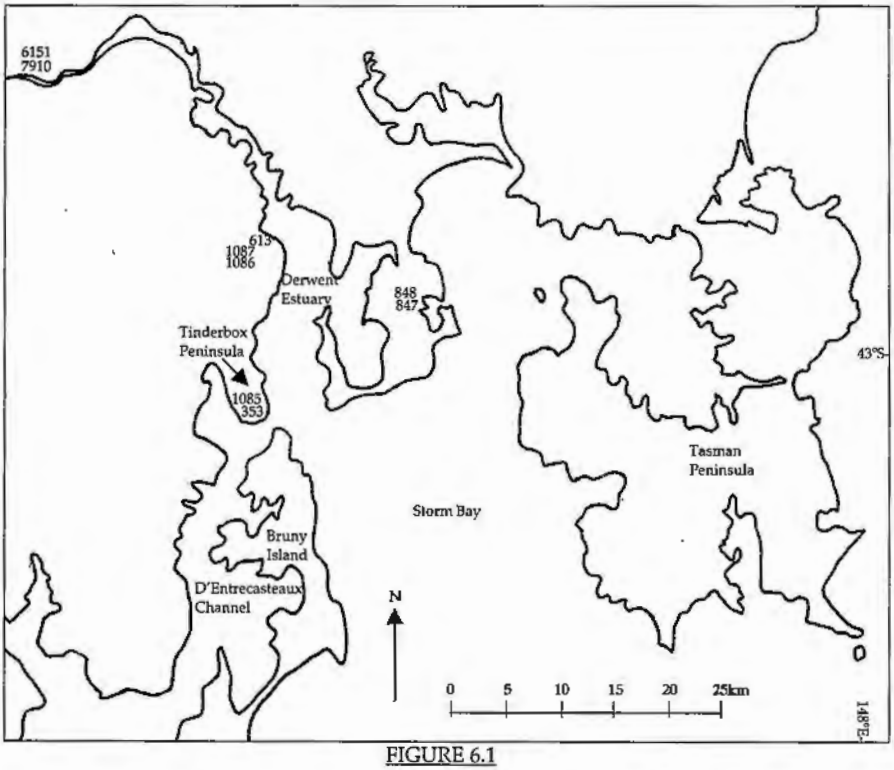


FIGURE 6.1

Southeastern Tasmania, showing the locations of the trees of *E. globulus* used in this study.

For all treatments the bags were removed as soon as flowering ceased. The capsules were harvested approximately 12 months later, and placed individually in paper envelopes to dry. After capsule dehiscence, the numbers of viable seeds were counted. If some capsules had dehisced before harvesting, it was assumed that they contained the mean number of seeds in non-dehisced capsules receiving that pollination treatment on that tree. Only flowers whose tags were recovered at the time of capsule harvest were included in the data set.

6.2.2.2 Effects of flower visitors on tree fecundity - Experiment 2

The behaviour of insects foraging on flowers in Experiment 1 may have been atypical. Because the flowers are protandrous, large quantities of nectar

accumulated in flowers prior to the onset of stigmatic receptivity, and pollen was not removed from anthers during the preceding male phase. For this reason, a technique was devised that allowed nectar and pollen to be removed from flowers prior to peak stigmatic receptivity without stigmata being contacted by flower visitors. This experiment was conducted on another seven trees (Fig. 6.1) between December 1999 and December 2000.

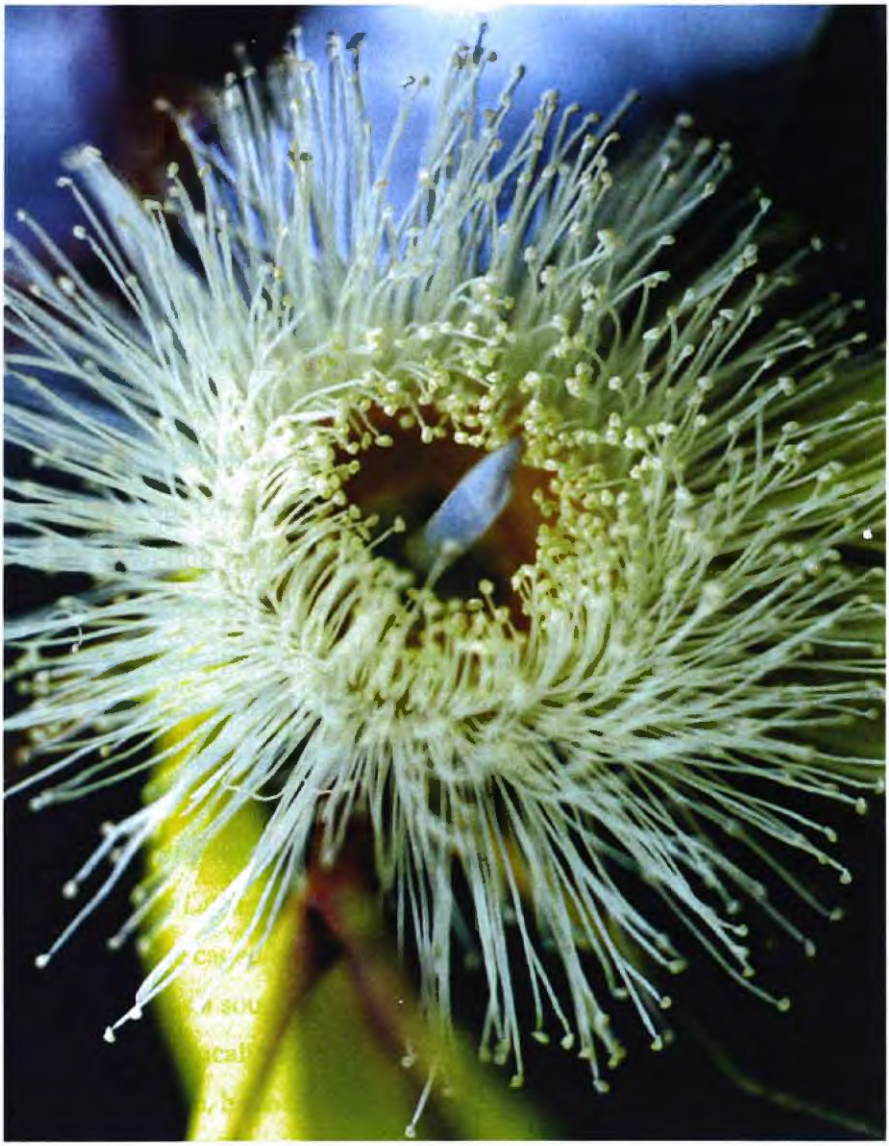


PLATE 6.2

A receptive *E. globulus* flower with a tube over the style.

Stigmatic virginity was maintained until peak receptivity was attained, while flowers remained exposed to anthophiles, as follows. Opercula were removed from flowers as they were beginning to separate from the receptacles. The newly exposed styles were immediately isolated by covering them with a section of tightly fitting plastic tubing which had previously had the distal end heat-sealed (Plate 6.2). This allowed nectar and pollen to be removed as normal, while stigmata could not be contacted.

Tubes were removed from flowers during fine, mild to hot weather between 0900 h and 1800 h, five to eight days later, to expose the receptive virgin stigmata. Each of these female-phase flowers was watched from a distance of less than one metre until a single naturally foraging insect contacted the gynoecium, androecium, or hypanthium. If a nectar feeding bird approached the tree during periods when insects were relatively inactive, I stepped back from the flowers to allow the bird to visit the flowers.

There were ample opportunities for outcrossing during the first season in the form of numerous conspecifics flowering near the experimental trees. However, flowering was scant during the second season, and few trees bloomed concomitantly near experimental trees 613 and 7910. For these two trees, outcrossing opportunities were enhanced by placing branches of flowers collected from Tasman Peninsula (Fig. 6.1) in buckets of water within 5 m of the experimental trees.

Other flowers with virgin stigmata were exposed to single visits by one of two swift parrots *Lathamus discolor* (Shaw) held in a small cage between 1000 h and 1600 h. The caged birds were provided with a few male-phase flowers from other trees as a source of outcross pollen (Paton 1991). *Lathamus discolor* actively consume eucalypt pollen (Gartrell *et al.* 2000, Gartrell and Jones 2001) and, therefore, have the potential to rapidly acquire substantial loads of pollen on the bill and head. During experiments conducted in December 1999 and January 2000, the birds also had outcross pollen brushed onto their heads with a cotton bud prior to the first flower being put through the door

of the cage. The outcross pollen used was a mix made from pollen collected from approximately ten trees at Tinderbox (Fig. 6.1) on 14 September 1999 which had been subsequently stored in gelatin capsules in glass vials with silica gel in a freezer. Pollen was applied at least once every ten flowers visited. However, the paucity of flowers of *E. globulus* during spring 2000 precluded the collection of sufficient pollen to apply pollen to the birds manually during the second season, and pollen loading had to be limited to provision of male-phase flowers.

At the end of the first day in December 1999, pollen swabs were taken from the heads of both birds with four pieces of transparent adhesive tape which were then placed on microscope slides. Pollen samples were taken from the upper, lower, left and right sides of each bird's head. The numbers of eucalypt pollen grains in the first 11 mm from the bill tip (the region that contacted stigmata) were then counted to verify that the birds carried numbers of grains similar to those carried by conspecifics captured in mistnets near flowering *E. globulus* (Table 6.1).

Birds sampled for pollen	n	Distance from bill tip	
		0 - 5.5 mm	5.5 - 11 mm
Birds in this experiment	2	1482	5306
Mist-netted wild birds	20	4808	5748

TABLE 6.1

Mean numbers of eucalypt pollen grains in two 5.5 mm sections from the bill tip of *L. discolor* artificially loaded with pollen in this experiment or mist-netted in the vicinity of flowering trees of *E. globulus*. Details of pollen sampling from mist-netted birds are given in Chapter 7.

Immediately after receiving a single visit from either an insect or bird, styles were recovered with the tube. The flower was then tagged, the identity of the visitor was recorded, along with whether the stigma was contacted, and whether nectar or pollen was consumed. Flowers were subsequently checked to ensure that tubes remained in place until stigmatic senescence.

Other flowers that did not have stigmatic tubes received supplementary outcross pollen when receptive, to estimate the maximum possible capsule

and seed production per flower on each tree (Gross 1996). Pollen was applied to receptive stigmata late in the day after insect activity had ceased to reduce the chances of this outcross pollen being secondarily transferred to other flowers by geitonogamous pollination (e.g. Heinrich 1975, DeGrandi-Hoffman and Martin 1995, DeGrandi-Hoffman and Watkins 2000). During the first season, manually applied pollen was from the same outcross pollen mix used to load *L. discolor*. The pollen used in the second season was collected from numerous trees scattered along the western shore of the D'Entrecasteaux Channel (Fig. 6.1) on 7 September 2000. Pollen was stored in gelatin capsules in glass vials with silica gel in a freezer between collection and use, and in an insulated container with an ice-block while in the field. Other flowers had their styles covered with tubes throughout their lives, to ensure that tubes were effective in preventing pollination.

Capsules were harvested approximately one year after flowering. Harvested capsules were placed in individual paper envelopes to dry, and the number of viable seeds produced per flower was determined as previously described.

6.2.2.3 Data analysis

For each tree in Experiment 1, the proportions of capsules produced per flower visited by insects were compared to those resulting from a) no visits, and b) manual outcross pollinations, using Chi-squared tests. The numbers of seeds per capsule set, and seeds per flower, were also compared between flowers receiving no visits, single visits by insects, and manual outcross pollinations using the Kruskal-Wallis One Way Analysis of Variance because the data were non-normal. Whenever statistically significant differences were found, subsequent pairwise tests were conducted using Dunn's Test.

In Experiment 2, comparisons of the effectiveness of various flower visitors as pollinators were limited to four trees. No data were obtained from tree 1085 because it did not retain any capsules in its canopy, or from tree 7910 which blew over in a storm two weeks after flowering ceased. Tree 613 was also excluded from the data analysis because all 63 capsules abscised soon

after flower wilt while new flowers were still opening, but 12 of the last 34 flowers pollinated produced capsules. The regular abscission of flowers ceased immediately after flowering ended, suggesting that this tree was under environmental stress during flowering. This may have been because nectar production placed stress on the tree, or because of the location of this potted dwarf precocious tree while flowering as it was moved a few metres after flowering ceased.

The only taxa that visited flowers on all of these four trees were captive *L. discolor*, and freely foraging honey bees *Apis mellifera* and bumble bees *Bombus terrestris*. Consequently, the numbers of capsules and seeds produced per flower visited by each of these taxa, and flowers subjected to supplementary cross pollination and permanent stigma coverage were compared across the four trees. Because of the abundance of zeros, the distributions could not be normalised through transformations. For this reason, comparisons were made using Two-Way Analysis of Variance on the ranks of the numbers of capsules and seeds from each flower, with the four trees and five pollination treatments as sources of variation. Whenever statistically significant differences were found, subsequent pairwise tests were conducted using Student-Newman-Keuls Method.

Other tests were conducted to determine whether differences between taxa in pollinator effectiveness were the result of differences in the frequency of stigmatic contact. The numbers of capsules and seeds produced per flower whose stigmata were contacted when visited by *L. discolor*, *A. mellifera* or *B. terrestris*, were compared using Two-Way Analysis of Variance on ranks with the four trees and three taxa as sources of variation. Whenever statistically significant differences were found, subsequent pairwise tests were conducted using Student-Newman-Keuls Method. The numbers of capsules and seeds produced per flower whose stigma was contacted by *A. mellifera* were compared to fecundity from flowers where they removed nectar without contacting stigmata. This also involved using Two-Way Analysis of Variance on rank fecundity, with the four trees and presence or absence of stigmatic

contact as sources of variation. Both of these sets of analyses were limited to flowers on which it was clearly seen whether stigmatic contact was made.

All statistical analyses were conducted using the computer programme SigmaStat (Jandel 1994), except for Chi-squared tests which were done manually.

6.2.3 Pollen deposition

The way in which pollen was applied to stigmata by foraging animals was investigated during October and November 2000 on one tree of the 'Lighthouse' provenance grown at the University of Tasmania in Hobart. Single visits to flowers with virgin stigmata were allowed to occur by using tubes, as in Experiment 2 into the effectiveness of flower visitors in facilitating capsule and seed set (Section 6.2.2.2). After receiving a visit that contacted, or may have contacted, the stigma, the distal 0.5 cm of the style was removed using a clean pair of electrician's wire-cutters, and placed on sticky nail polish on a scanning electron microscope stub. Each stigma was then viewed and photographed using a scanning electron microscope. This also gave some idea of the numbers of grains deposited per visit. By allowing single visits to flowers of varying ages, it was possible to compare pollen deposition on dry and wet stigmata, and to observe the physical changes associated with the development of stigmatic receptivity.

6.3 Results

6.3.1 Effects of flower visitors on tree fecundity - Experiment 1

The two trees differed greatly in their response to total exclusion of pollinators, indicating differences in their degrees of self-compatibility. Tree 847 was partially self-compatible, as flowers enclosed in exclusion bags sometimes set capsules that bore viable seeds (Table 6.2). In contrast, tree 848 showed no evidence of self-compatibility (Table 6.3).

Single visits to flowers by insects did not enhance capsule production in either tree (Tables 6.2 and 6.3). The frequency of capsule set following single

flower visits by insects on the self-compatible (SC) tree was significantly less than following manual cross pollination ($0.01 > P > 0.001$, $\chi^2_1 = 10.43$) or permanent exclusion of pollinators ($P < 0.001$, $\chi^2_1 = 23.54$) (Table 6.2). Only one capsule was produced from the 18 flowers visited by insects on the self-incompatible (SI) tree, a level that was significantly lower than following manual cross pollination ($P < 0.001$, $\chi^2_1 = 14.85$) but not significantly different from after no visitors ($0.20 > P > 0.10$, $\chi^2_1 = 2.49$) (Table 6.3).

Treatment	#flowers	#capsules	#capsules / flower	#seeds	#seeds/ capsule	#seeds/ flower
Hand outcross	58	32	0.552	143.5	4.484[a]	2.474[a]
No visits	100	68	0.680	70	1.030[b]	0.700[ab]
Apis mellifera	15	3	0.200	4	1.333	0.267[b]
Leioproctus spp.	17	5	0.294	4	0.800	0.235[b]
*Hylaeus (Euprosopis) honestus**	2	0	0	0	-	0
Hylaeus (Prosopisteron) spp.	2	0	0	0	-	0
Bombyliidae sp.	1	0	0	0	-	0
Total insects	37	8	0.216	8	1.000[b]	0.216

TABLE 6.2

Fecundity of flowers receiving manual outcross pollination, no visits, or single visits from various insects, on tree 847. Insects, in order, are honey bees, three species of native bees (Colletidae), and one fly. Different supercripts within columns denote statistically significant differences between treatments in fecundity, as determined by Dunn's Tests subsequent to Kruskal-Wallis Tests. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit *E. globulus* flowers in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999).

There were significant differences in the numbers of viable seeds per capsule produced from flowers receiving no visits, single visits by bees, and manual cross pollinations on the SC tree ($P < 0.0001$, $H_2 = 18.9$, Kruskal-Wallis 1-Way ANOVA). Subsequent pairwise tests showed these differences to be statistically significant between manual cross pollinations and bees, as well as between manual cross pollinations and no visits, but not between bees and no visits (Table 6.2). Therefore, the mean numbers of seeds produced per capsule from flowers receiving single visits by either *A. mellifera* or

Leioproctus spp. were comparable to that from flowers receiving no visits, but much lower than that from flowers receiving supplementary pollinations (Table 6.2).

Statistically significant differences in the numbers of seeds produced per flower were apparent between treatments on the SC tree ($P = 0.0030$, $H_3 = 13.9$, Kruskal-Wallis 1-Way ANOVA) and the SI tree ($P < 0.0001$, $H_2 = 26.7$, Kruskal-Wallis 1-Way ANOVA). On the SC tree, seed production per flower visit by *A. mellifera* or *Leioproctus* spp. was significantly lower than following manual cross pollination, but not significantly different to that in the exclusion bags (Table 6.2). No seeds were produced as a result of single flower visits by insects on the SI tree (Table 6.3). As a result, the numbers of seeds produced per flower were significantly lower following insect visits or no visits than after manual cross pollination (Table 6.3).

Treatment	#flowers	#capsules	#capsules / flower	#seeds	#seeds/ capsule	#seeds/ flower
Hand outcross	46	27	0.587	76	2.815	1.652[a]
No visits	44	0	0	0	-	0[b]
Leioproctus spp.	9	1	0.111	0	0	0
Euryglossa nigrocaerulea	4	0	0	0	-	0
Euryglossa (Euhesma) sp.	1	0	0	0	-	0
Homalictus sp.	1	0	0	0	-	0
Chauliognathus lugubris	1	0	0	0	-	0
Phyllotocus rufipennis	2	0	0	0	-	0
Total insects	18	1	0.056	0	0	0[b]

TABLE 6.3

Fecundity of flowers receiving manual hand pollination, no visits, or single visits from various insects, on tree 848. Insects, in order, are four species of native bees, and two species of beetles. Different supercripts within the final column denote statistically significant differences between treatments in the numbers of seeds produced per flower, as determined by Dunn's Tests subsequent to Kruskal-Wallis Tests.

6.3.2 Effects of flower visitors on tree fecundity - Experiment 2

Female-phase flowers of *E. globulus* were visited by captive *L. discolor*, five other species of naturally foraging birds, and 21 taxa of insects (Table 6.4). These visits almost always involved attempts to obtain nectar, although

Family	Pollination treatment or visitor	353	1085	1086	1087	613	6151	7910
	Cross supplement	23	20	27	28	16	30	43
	No visits	7	38	38	35	9	32	51
Psittacidae	*Lathamus discolor**	3	29	28	24	19 (1p)	31	31
Meliphagidae	*Lichenostomus flavicollis*					4		
	Melithreptus affinis					6		1
	Phylidonyris pyrrhoptera					1		
	Phylidonyris novaehollandiae					6		1
Zosteropidae	*Zosterops lateralis*					1		
Apidae	*Apis mellifera*	6	57 (1p)	71	68	4	50	122
	Bombus terrestris	2	7	21	35	14 (2p)	1	15
Anthophoridae	*Exoneura* spp.					2		
Colletidae	*Leioproctus* spp.		2	1	1		8	35 (2w)
	*Hylaeus (Euprosopis) honestus**							2
	Hylaeus (Prosopisteron) spp.				1	11 (1p)	32	64
Halictidae	*Homalictus* spp.						2	
	large *Lasioglossum (Chilalictus)* spp.				2			
Scoliidae	spp.		1					8
Sphecidae	sp.3						1	
Thynnidae	*Thynnus zonatus*							2
Vespidae	*Vespula* spp.			1	5			8
Formicidae	small ant						1	6
	Myrmecia pilosula							4
Calliphoridae	*Calliphora* spp.						16	3
Sepsidae	sp.1					2		
Syrphidae	sp.1						3 (2p)	
Tachinidae	*Rutilia* sp.1							1
Cantharidae	*Chauliognathus* spp.		2 (1p)		1		127 (17w)	3
Cerambycidae	spp.		2 (1p)					
Cleridae	*Eleale* sp.							1
	Blooming period	Dec 99	Dec 99-Jan 2000	Dec 99-Jan 2000	Dec 99-Jan 2000	Oct-Nov 2000	Nov-Dec 2000	Nov-Dec 2000

TABLE 6.4

Numbers of flowers from which tags were recovered after being subjected to supplementary outcross pollination, permanent stigma coverage, or single visits by various animals, on trees of *E. globulus* in Experiment 2. In cases where not all flowers were probed for nectar, the number not probed for nectar is shown in brackets together with the activity of the flower visitor: p = attempting to collect pollen; w = walking over the flower without attempting to feed. Common names for bird species: *L. discolor* = swift parrot; *L. flavicollis* = yellow-throated honeyeater; *M. affinis* = black-headed honeyeater; *P. pyrrhoptera* = crescent honeyeater; *P. novaehollandiae* = New Holland honeyeater; and *Z. lateralis* = silvereye. *all *L. discolor* visits were by captive birds. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of *E. globulus* in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999).

occasionally flowers were visited in the search for pollen, or contacted by insects walking over flowers (Table 6.4). *Apis mellifera* was the most common and widespread insect visiting the flowers. *Bombus terrestris* also visited flowers on all seven trees. All other insects were found on only some of the trees, and were usually uncommon. However, native bees in the genus *Leioproctus* were regular flower visitors on tree 7910, soldier beetles *Chauliognathus lugubris* (Fabricius) were abundant on tree 6151, and *Hylaeus (Prosopisteron)* bees were common on both of these trees. Few experimental flowers were visited by naturally foraging birds while I was nearby, with most of these being on tree 613 (Table 6.4).

Some birds and insects were sufficiently effective as pollinators to cause seeds to be produced after a single visit to a flower. Seeds were produced following supplementary outcross pollination, and single flower visits by *L. discolor*, *A. mellifera* and *B. terrestris* (Table 6.5). Single flower visits by other insect taxa failed to result in seeds being produced (Table 6.5). Although little data were obtained for other bird species, one seed was produced on tree 613 following a single visit by a black-headed honeyeater *Melithreptus affinis* (Lesson).

Significant differences in capsule ($P < 0.0001$, $F_{4,12} = 64.22$, 2-Way ANOVA) and seed set ($P < 0.0001$, $F_{4,12} = 63.04$, 2-Way ANOVA) occurred between flowers visited once by *L. discolor*, *A. mellifera*, or *B. terrestris*, permanent stigma coverage, and open-pollinated flowers receiving supplementary outcross pollen. Single flower visits by *L. discolor* resulted in significantly more capsules and seeds being produced per flower than did single flower visits by *A. mellifera* or *B. terrestris* (Table 6.5). Single visits by *L. discolor* significantly enhanced capsule and seed set above the levels occurring in flowers with permanent stigma coverage, whereas single visits by *A. mellifera* or *B. terrestris* did not (Table 6.5). Across the four trees, capsule and seed set following single visits by *L. discolor* averaged 80% and 76%, respectively, of the maximum possible fecundity estimated by applying outcross pollen to receptive stigmata that were permanently exposed to flower visitors. In

contrast, single flower visits by *A. mellifera* facilitated only 17% and 6.8% of the maximum possible capsule and seed set, and *B. terrestris* only 11% and 6.3% (Table 6.5).

Fecundity Tree	Capsules/flower 353	1085	1086	6151	total	Seeds/flower 353	1085	1086	6151	total
Cross supplement	0.87	0.50	0.93	0.27	0.64[a]	10.70	5.25	11.70	5.10	8.19[a]
No visits	0	0	0	0	0[c]	0	0	0	0	0[c]
Lathamus discolor	1.00	0.14	0.64	0.25	0.51[b]	4.00	1.59	15.05	4.31	6.24[b]
Apis mellifera	0.33	0.05	0.07	0	0.11[c]	1.67	0.11	0.45	0	0.56[c]
Bombus terrestris	0	0.14	0.14	0	0.07[c]	0	1.86	0.21	0	0.52[c]
Leioproctus spp.		0	0	0			0	0	0	
H. (Prosopisteron) spp.				0					0	
Homalictus spp.				0					0	
Scoliidae spp.		0					0			
Sphecidae sp.3				0					0	
Vespula spp.			0					0		
small ant				0					0	
Calliphora spp.				0					0	
Syrphidae sp.1				0					0	
Chauliognathus spp.		0		0.02			0		0	
Cerambycidae spp.		0					0			

TABLE 6.5

Mean numbers of capsules and seeds produced per flower visit by various taxa and control treatments for four trees that set capsules. Different supercripts within total columns denote statistically significant differences between treatments in fecundity, as determined by Student-Newman-Keuls Method subsequent to Two-Way ANOVA on ranks. Taxonomic affinities of visitors are given in Table 6.4.

The effectiveness of *L. discolor* as pollinators of *E. globulus* can be attributed, at least partly, to them almost always contacting stigmata while feeding from female-phase flowers (Table 6.6). This usually involved contact with the bill and tongue as they licked nectar from the hypanthium (Plate 6.3; also see Figs 7.1 and 7.2). In contrast, smaller insects, such as *A. mellifera*, were able to access nectar without contacting stigmata (Table 6.6) because of the gap between the stamens and style (Plate 6.4). Smaller insects only contacted stigmata if they clambered over the style as they moved between the hypanthial pits where nectar pooled, or if they used the stigma as a landing or take-off platform on the flower. As a result, insect contact with stigmata usually involved their legs, mesosoma or metasoma.

Visitor	Tree			
	353	1085	1086	6151
Lathamus discolor	1.00	1.00	0.89	1.00
Apis mellifera	0.50	0.39	0.41	0.79
Bombus terrestris	1.00	1.00	0.71	1.00
Leioproctus spp.		0	0	0.38
H. (Prosopisteron) spp.				0.10
Homalictus spp.				0.50
Scoliidae spp.		0		
Sphecidae sp.3				1.00
Vespula spp.			1.00	
small ant				1.00
Calliphora spp.				0.27
Syrphidae sp.1				0
Chauliognathus spp.		0.50		0.80
Cerambycidae spp.		1.00		

TABLE 6.6

Proportions of visits to female-phase flowers by various taxa that resulted in stigma contact. Taxonomic affinities of visitors, and numbers of flowers visited, are given in Table 6.4.

PLATE 6.3

A nectar-feeding swift parrot *Lathamus discolor* contacting the stigma of *E. globulus*. See Figs 7.1 and 7.2 for more detail of stigma contact.

PLATE 6.4

Apis mellifera collecting nectar from a flower of *E. globulus* without contacting the stigma.

PLATE 6.5

A nectar-gathering *Bombus terrestris* contacting the stigma of *E. globulus*.

The relative ineffectiveness of insects as pollinators of *E. globulus* cannot be attributed exclusively to them being able to remove nectar without contacting stigmata. As a result of their large size, *B. terrestris* contacted stigmata almost as frequently as did *L. discolor* (Table 6.6, Plate 6.5). However, they facilitated significantly lower capsule and seed set per visit than did *L. discolor* (Table 6.5). Moreover, when single visits to flowers that did not result in stigmatic contact were excluded from the analysis, *L. discolor* still facilitated significantly greater capsule and seed set than did either *A. mellifera* or *B. terrestris* (Table 6.7). Indeed, fecundity from flowers whose stigmata were contacted by *A. mellifera* was not significantly greater, for capsule ($P = 0.765$, $F_{1,3} = 0.090$, 2-Way ANOVA) or seed set ($P = 0.943$, $F_{1,3} = 0.005$, 2-Way ANOVA), than those where *A. mellifera* had removed nectar without contacting stigmata (Tables 6.5 and 6.7).

Visitor	Capsules/flower					Seeds/capsule				
	353	1085	1086	6151	total	353	1085	1086	6151	total
Lathamus discolor	1.00	0.14	0.65	0.26	0.51[a]	4.00	1.59	16.02	4.45	6.51[a]
Apis mellifera	0.33	0.09	0.07	0	0.12[b]	0.67	0.14	0.69	0	0.37[b]
Bombus terrestris	0	0.14	0.13	0	0.07[b]	0	1.86	0.30	0	0.54[b]

TABLE 6.7

Mean numbers of capsules and seeds produced per flower visit involving stigmatic contact for four trees that set capsules. Different supercripts within total columns denote statistically significant differences between treatments in fecundity, as determined by Student-Newman-Keuls Method subsequent to Two-Way ANOVA on ranks. Taxonomic affinities of visitors are given in Table 6.4.

6.3.3 Pollen deposition

Dramatic changes occurred in the appearance of stigmata as they became receptive (Plates 6.6 - 6.12). Initially, the surface was covered with a smooth cuticle (Plate 6.6). The surface area increased as the cuticle ruptured via the development of papillae (Plate 6.7) and sometimes splitting of the apex (Plate 6.8). Development of papillae commenced at the apex (Plates 6.7 - 6.10), and gradually extended to cover the entire stigma (Plate 6.11). After papillae had developed over approximately half of the stigma, a stigmatic exudate was

produced (Plate 6.10). Exudate production and papillae extension continued if the stigma was not pollinated (Plate 6.12).

Pollen adhered to both wet and dry stigmata. On wet stigmata, pollen deposited by birds and bees was embedded within the exudate, thereby sticking them to the surface (Plates 6.13 - 6.15). Pollen deposited by birds and bees adhered to dry stigmata without lodging between papillae (Plates 6.16 - 6.20). Pollen grains adhered to very smooth sections of cuticle prior to development of papillae, sometimes attaching by their corners in a manner indicating that friction was not responsible for their attachment (Plates 6.16 and 6.18).

A comparison of the numbers of grains deposited per visit by various taxa was not possible by this method because it was not possible to ascertain whether all pollen grains could be seen. This was because some grains may have been embedded deep in the exudate of wet stigmata, and only one side of the stigma was viewed. However, large numbers of pollen grains were sometimes deposited on a stigma during a single flower visit by *L. discolor* (Table 6.8, Plate 6.21). Pollen was also observed on stigmata following single visits by honeyeaters and bees, although only small quantities were observed following single stigmatic contacts by native bees (Table 6.8).

Visitor	Maximum number of pollen grains deposited
Lathamus discolor	117
Melithreptus affinis	19
Apis mellifera	10
Bombus terrestris	43
Exoneura spp.	1
Homalictus spp.	3
Lasioglossum (Parasphecodes) spp.	7

TABLE 6.8

The maximum numbers of eucalypt pollen grains seen on stigmata of *E. globulus* under SEM following single visits by various taxa. Taxonomic affinities of visitors are given in Table 6.4.

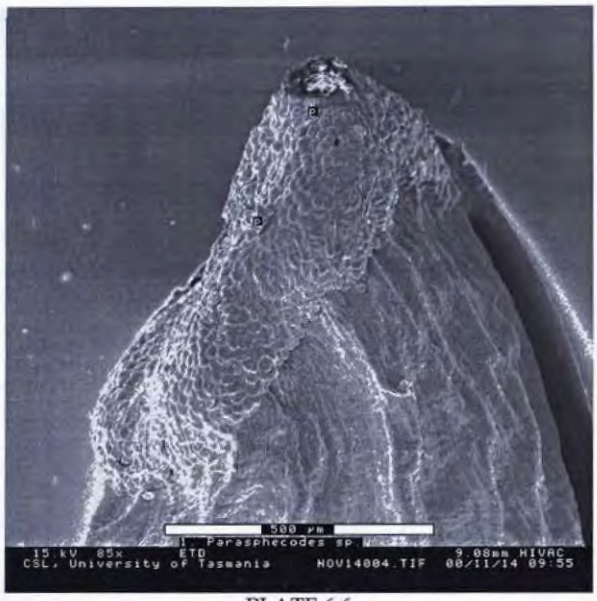


PLATE 6.6

Stigma of *E. globulus* prior to development of papillae and secretion of exudate. The letter 'p' denotes where pollen was observed after the stigma was contacted by the metasternum and rear tarsi of a nectar-collecting *Lasioglossum (Parasphecodes)* sp. (Halictidae) The contrasting shades at the tip are an artefact of the SEM microscopy.

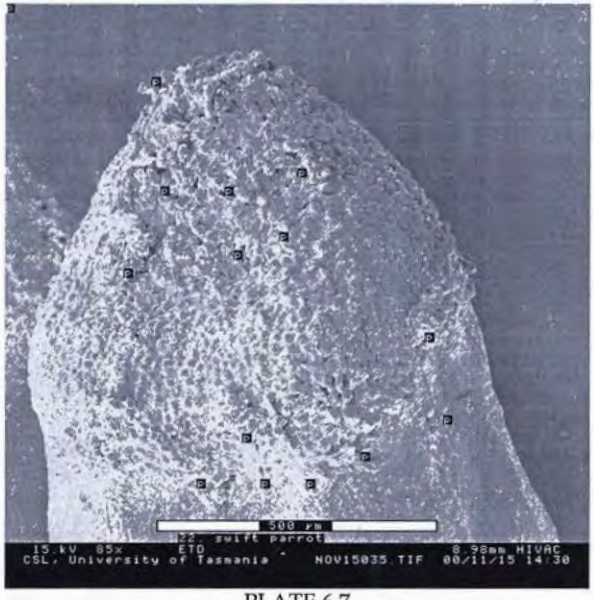


PLATE 6.7

Stigma of *E. globulus* with apical papillae developing. Exudate production has not yet commenced. The letter 'p' denotes where pollen was observed after the flower was visited once by a nectar- and pollen-collecting *Lathamus discolor*.

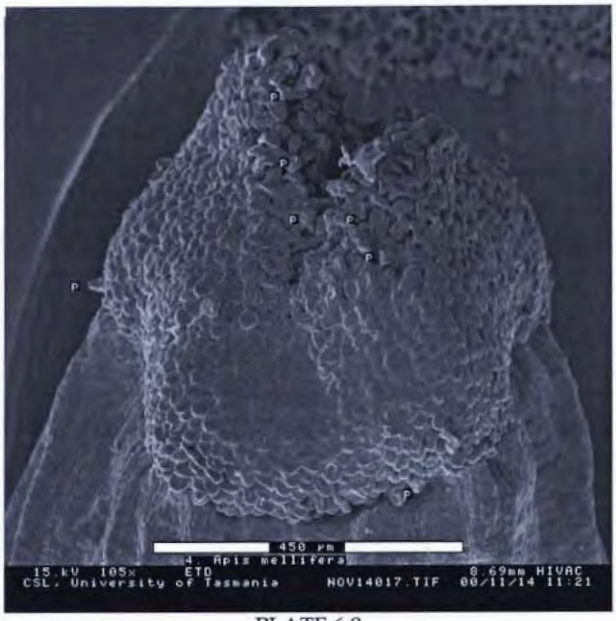


PLATE 6.8

Stigma of *E. globulus* with apical papillae developing and apex splitting. Exudate production has not yet commenced. The letter 'p' denotes where pollen was observed after the stigma was contacted by the metasternum of a nectar-collecting *Apis mellifera*.

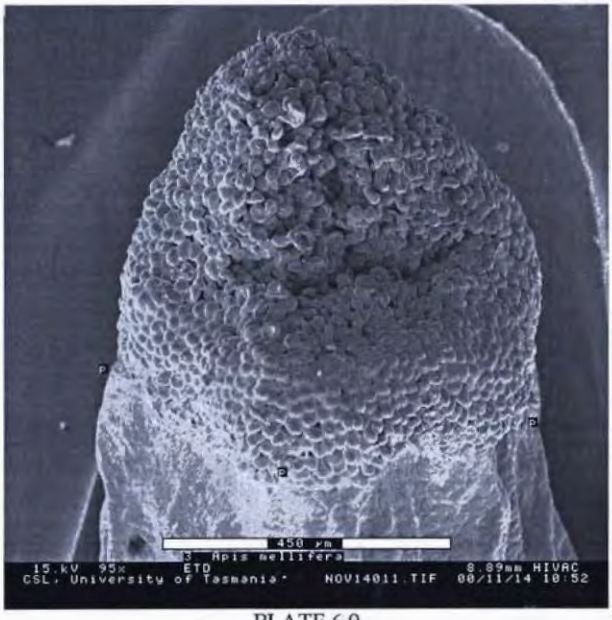


PLATE 6.9

Stigma of *E. globulus* with papillae developed over the apical half. Exudate production has not yet commenced. The letter 'p' denotes where pollen was observed after the stigma was contacted by the metasternum of a nectar-collecting *Apis mellifera*.

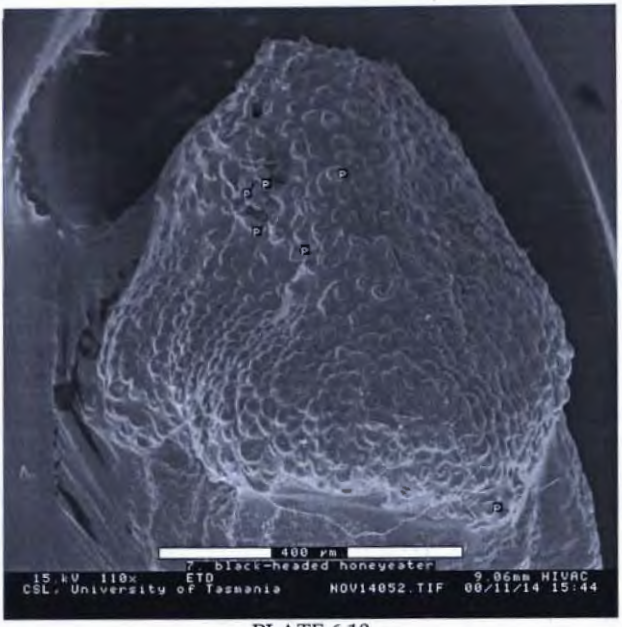


PLATE 6.10

Stigma of *E. globulus* with papillae developed over the apical half. Exudate now covers the stigma, and is starting to run down the style. The letter 'p' denotes where pollen was observed after the flower was visited once by a nectar-feeding *Melithreptus affinis*.

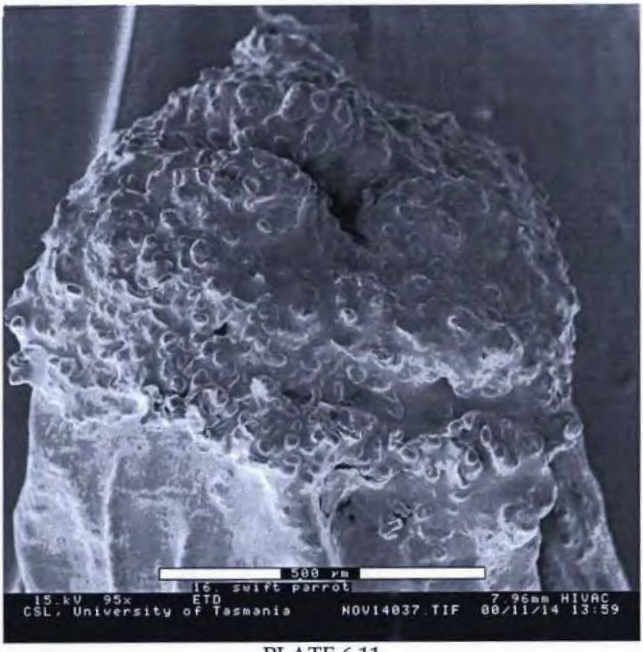


PLATE 6.11

Stigma of *E. globulus* which has produced sufficient exudate to cover the stigma and upper style. Papillae are now developed over the entire stigma.

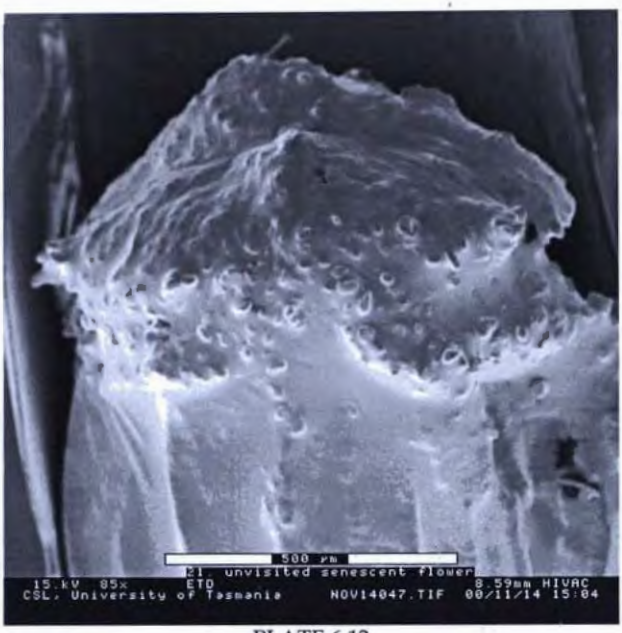


PLATE 6.12

Stigma of *E. globulus* which has been covered with a tube until the stamens have begun to wither. The stigma and upper style are covered in a thick layer of exudate. Clumps of long papillae protrude from half-way down the stigma, giving it a flat-topped appearance.

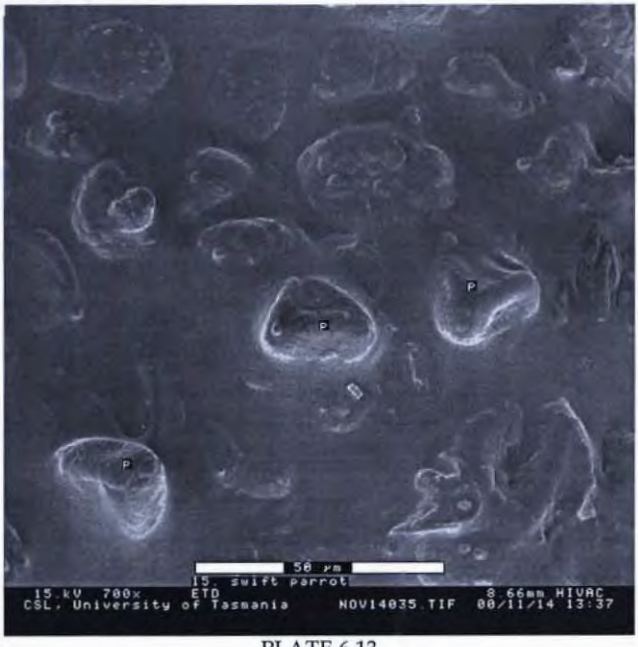


PLATE 6.13

Eucalypt pollen grains embedded in exudate on a stigma of *E. globulus* after being visited once by a nectar-feeding *Lathamus discolor*.

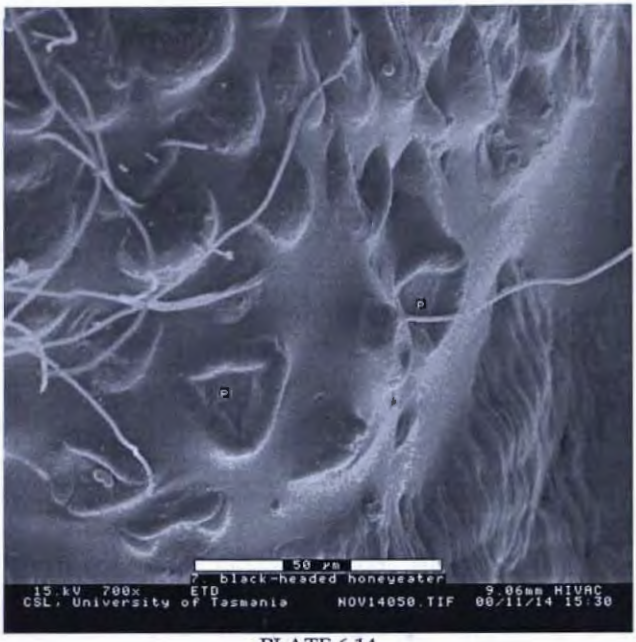


PLATE 6.14

Eucalypt pollen grains embedded in exudate on a stigma of *E. globulus* after being visited once by a nectar-feeding *Melithreptus affinis*.

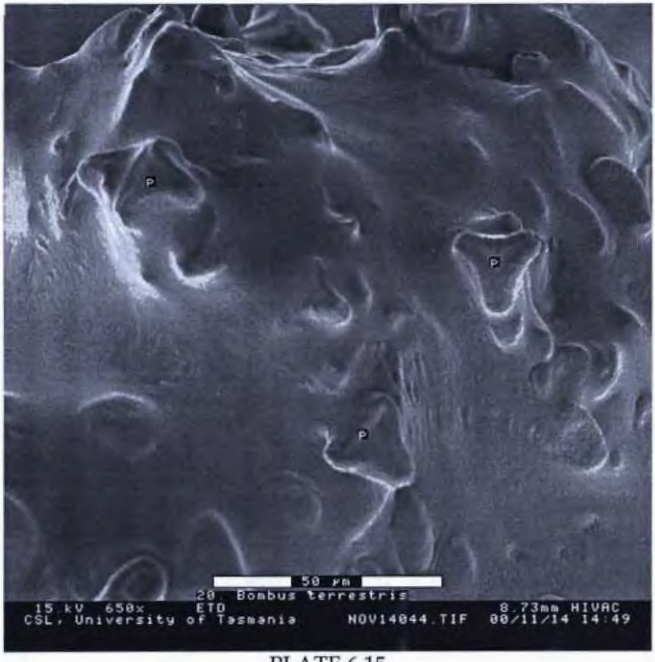


PLATE 6.15

Eucalypt pollen grains embedded in exudate on a stigma of *E. globulus* after being contacted by the sterna of a nectar-collecting *Bombus terrestris* worker.

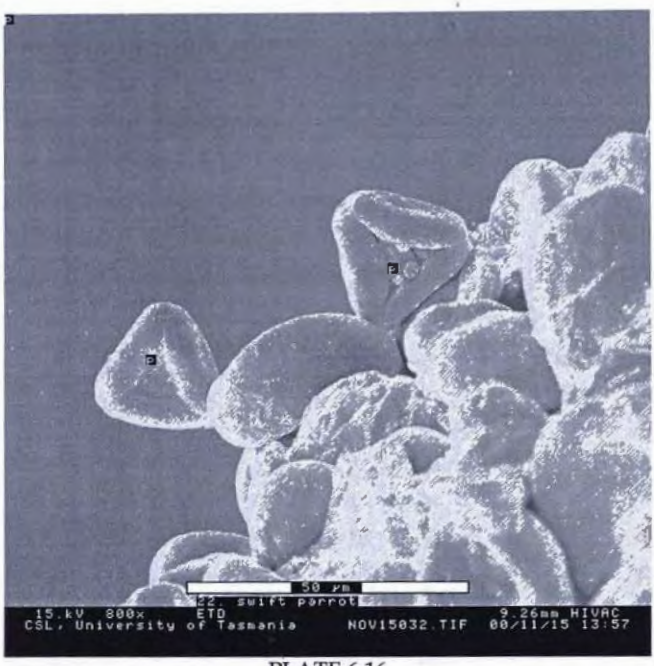


PLATE 6.16

Eucalypt pollen grains on a dry stigma of *E. globulus* after being visited once by a nectar- and pollen-feeding *Lathamus discolor*.

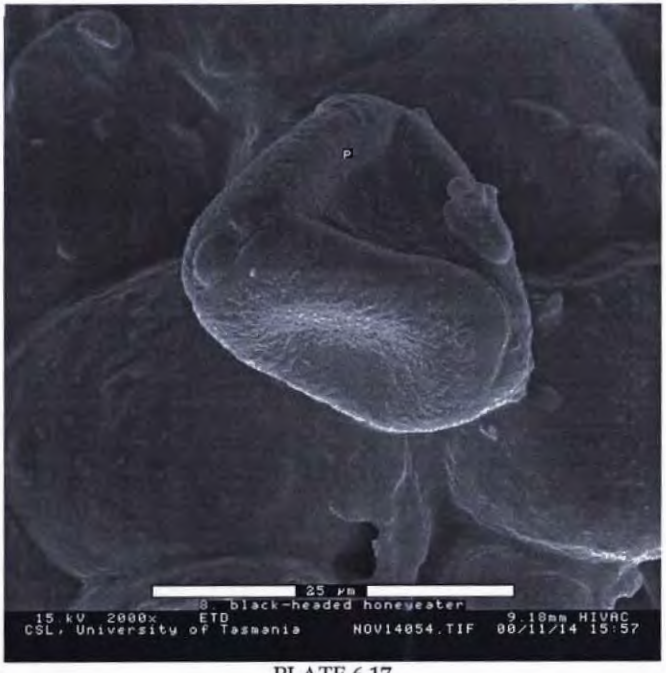


PLATE 6.17

Eucalypt pollen grain on a dry stigma of *E. globulus* after being visited once by a nectar-feeding *Melithreptus affinis*.

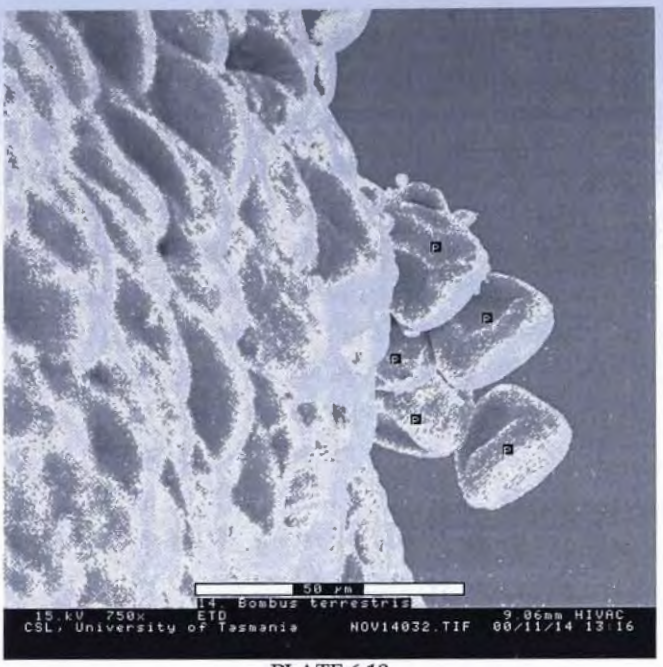


PLATE 6.18

Eucalypt pollen grains on a dry stigma of *E. globulus* after being visited once by a nectar-collecting *Bombus terrestris* worker.

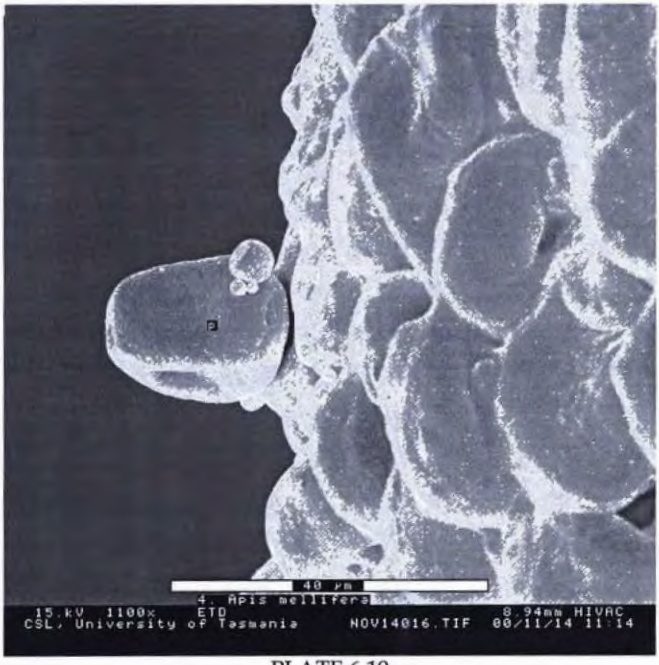


PLATE 6.19

Eucalypt pollen grain on a dry stigma of *E. globulus* after being contacted by the metasternum of a nectar-collecting *Apis mellifera*.

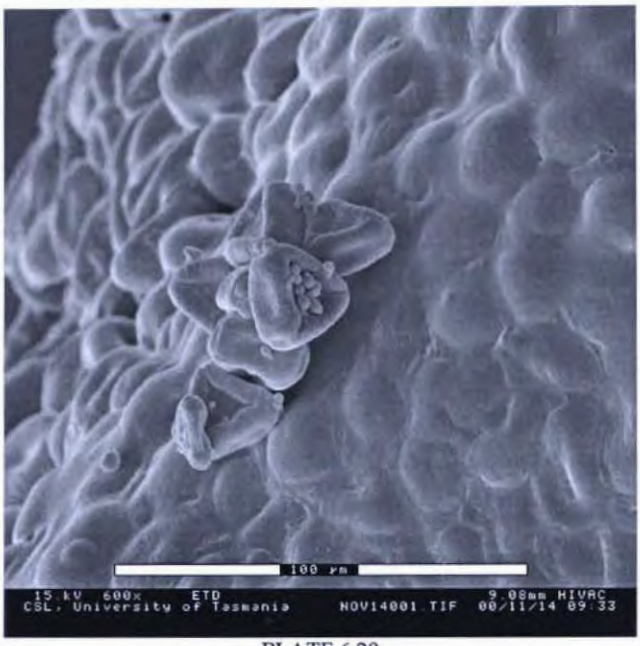


PLATE 6.20

Eucalypt pollen grains on a dry stigma of *E. globulus* after being contacted by the metasternum and rear tarsi of a nectar-collecting *Lasioglossum (Parasphecodes)* sp. (Halictidae).

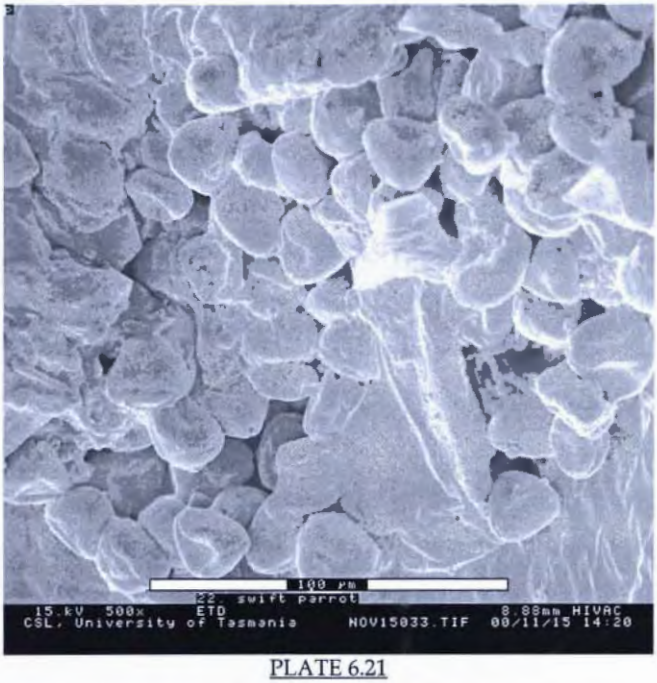


PLATE 6.21

Numerous eucalypt pollen grains on a dry stigma of *E. globulus* after being visited once by a nectar- and pollen-feeding *Lathamus discolor*.

6.4 Discussion

Lathamus discolor was the only flower visitor that facilitated statistically significant levels of seed production in this study. In both experiments, the numbers of seeds produced per flower following visits by insects were not significantly different from that developing in control flowers that received no visitors.

6.4.1 Management implications

The finding that single visits to flowers of *E. globulus* by *L. discolor* resulted in 76% as many seeds as supplementary outcross pollination of open-pollinated flowers, indicates that these birds can provide good pollination services in seed orchards of this tree. This is remarkably high considering that the numbers of seeds produced, from flowers of plants with full or partial self-incompatibility, following manual outcross pollination may be unattainable following visits by animal pollinators that usually carry a mixture of self and outcross pollen (Thomson 2001). Although these birds were loaded with outcross pollen prior to feeding on female-phase flowers, they also consumed pollen from male-phase flowers on the same branch as the experimental female-phase flowers when the branch was introduced to their cage, and therefore would also have accumulated self-pollen. For this reason, the proportional composition of self and outcross pollen carried by *L. discolor* used in this experiment probably approximated that carried by freely foraging conspecifics.

Moreover, the levels of seed production following single flower visits by wild *L. discolor* may have been underestimated by this experiment, because these captive birds carried less than one-third as many pollen grains as did their freely foraging conspecifics on the distal 5.5 mm of the bill after pollen was brushed onto the captive birds' heads. As pollen was applied in this way when the captive birds foraged on only three of the four trees analysed, pollen loads were probably even smaller than this when they foraged at flowers of tree 6151.

Unfortunately, the capacity of *L. discolor* to provide pollination services to seed orchards is limited by its distribution in southeastern Australia and the declining size of its population (Brown 1989, Brereton 1996). The most recent estimate of its wild population is only 940 pairs (Brereton 1996), and it is classified as endangered under Australia's *Environment Protection and Biodiversity Conservation Act 1999*. In spite of this, *L. discolor* still occurs in large numbers on flowering *E. globulus* at some times and places in Tasmania (Brown 1989, Hingston and Potts 1998). Therefore, this bird is likely to be responsible for the production of considerable quantities of seeds in some stands of *E. globulus*, and efforts aimed at the recovery of *L. discolor* (Brereton 1996) are likely to benefit seed production of *E. globulus* in Tasmania.

Several other bird species are also attracted to the flowers of *E. globulus*, particularly other parrots and honeyeaters (Meliphagidae) (Brown 1989, Hingston and Potts 1998, Chapter 4, 8 and 9). These probably also make major contributions to pollination of *E. globulus*, because large differences between bird species as pollinators of individual species of Australian plants have not been found previously (Paton 1991). Although little data were obtained for other bird species in this study, one seed was produced following a single visit by a black-headed honeyeater *Melithreptus affinis*, and this species deposited numerous pollen grains on stigmata, suggesting that this species is able to pollinate *E. globulus*. However, Paton and Ford (1977) found that parrots contacted eucalypt stigmata more frequently than did honeyeaters, because of the shorter bills of the former. For this reason, long-billed honeyeaters may be less effective at pollination of *E. globulus* than parrots such as *L. discolor* (Hingston and Potts 1998).

As both species of social bee were far less effective as pollinators than *L. discolor*, increasing their abundances in seed orchards of *E. globulus* by deployment of hives could reduce seed set. Several studies have found that the presence of ineffective pollinators reduces the frequency with which effective pollinators visit flowers through resource competition, thereby

reducing plant fecundity (Paton 1993, Roubik 1996, Paton 1997, Irwin and Brody 1998).

However, such reductions in seed set in *E. globulus* through competitive displacement of birds by social bees would only occur if a large proportion of the nectar was consumed, and the greater pollinator effectiveness of birds than bees per flower visit was the result of greater pollinator *efficiency* of birds. That is, seed set would be reduced if bees displaced birds through competition for nectar, and bees facilitated less seed production than birds *per unit of* nectar consumed. This is likely to be the case, as *E. globulus* flowers often contain almost no nectar during the middle of fine days (Chapter 4), such as those on which this experiment was conducted. Therefore, in many situations *L. discolor* would not consume much more nectar than bees per flower visit, and the observed differences in pollinator effectiveness probably reflect similar differences in pollinator efficiency. Moreover, single visits to *E. globulus* flowers by *L. discolor* in this study resulted in over 11 times as many seeds as single visits by either species of social bee, but Paton (1990) found that birds removed only 2.7 times as much nectar as *A. mellifera* per flower visit to *Eucalyptus remota* Blakely (Paton 1990), suggesting that these birds were more efficient pollinators of *E. globulus* than were the bees.

Although single visits by insects did not cause statistically significant levels of seed set in *E. globulus*, increasing their abundances in a seed orchard may sometimes enhance seed set. Surplus nectar sometimes occurs in *E. globulus* (Chapter 4) and, as single flower visits by *A. mellifera* and *B. terrestris* appear to facilitate some seed set, the deployment of hives of these bees to consume surplus nectar might increase seed set in commercial seed orchards. However, if too many hives are deployed when surplus nectar occurs, reduced seed set could occur as a result of displacement of birds through competition for the smaller quantities of available nectar. In addition, the introduction of large numbers of ineffective bees under conditions of nectar surplus could still reduce the total levels of pollination if they decrease the

quantity of pollen available for transfer by more effective pollinators (Pyke 1990, Wilson and Thomson 1991, Paton 1993, 1997), or remove pollen from stigmata that has been previously deposited by other pollinators (Gross and Mackay 1998).

6.4.2 Why is Lathamus discolor a better pollinator than insects?

Lathamus discolor may be a better pollinator of *E. globulus* than are insects for several reasons. It has been suggested previously that insects are likely to be less effective pollinators of *E. globulus* than birds, because insects were too small to consistently contact stigmata of these large flowers while gathering nectar (Hingston and Potts 1998). This common phenomenon in Australian native plants adapted to vertebrate pollination (Collins *et al.* 1984, Paton and Turner 1985, Taylor and Whelan 1988, Vaughton 1992, Paton 1993, Vaughton 1996, Richardson *et al.* 2000, Kalinganire *et al.* 2001) was confirmed for most insect species during this study. However, this was not the major factor contributing to insects being relatively ineffective pollinators of *E. globulus*, because single visits by insects that did result in stigmatic contact still produced very few seeds. There was some evidence that *L. discolor* may be able to deposit more pollen grains per stigmatic contact than can insects, although this finding is far from conclusive.

Because *E. globulus* produces fewer seeds after self-pollination than outcrossing (Potts and Cauvin 1988, Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995, 1998), the poor seed set following stigmatic contact by insects may be the result of them mostly depositing self-pollen. Anthophilous insects frequently remain on one plant for long periods (Hodgson 1976a, Beardsell *et al.* 1993, Paton 1993). For example, Paton (1993, 1997) never saw *A. mellifera* fly between *Callistemon rugulosus* DC (Myrtaceae) plants separated by as little as 3 m while they visited a total of 4600 flowers during 9.9 hours, whereas New Holland honeyeaters averaged 7.3 interplant movements per hour and one every 400 flowers visited (Paton 1993). The capacity for *A. mellifera* and bumblebees, such as *B. terrestris*, to transfer pollen between plants is also reduced by their frequent grooming (e.g. Free

1968, Beattie *et al.* 1973, Bernhardt and Weston 1996) that lowers pollen carryover (Thomson and Plowright 1980, Thomson 1986).

Evidence of *A. mellifera* depositing mostly self-pollen comes from stigmatic contact by *A. mellifera* not increasing seed set above levels in flowers that they visited without stigmatic contact. Small numbers of seeds developed after *A. mellifera* visited flowers without contacting stigmata, suggesting that their movements may have caused pollen to fall from the anthers onto the stigma of the same flower. As stigmatic contact did not enhance seed set above this level, in this largely self-incompatible species (Potts and Cauvin 1988, Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995, 1998), most pollen deposited on stigmata as a result of contact by *A. mellifera* may have been self-pollen.

These differences between taxa in pollinator effectiveness do not appear to be the result of differing ways in which pollen was deposited on stigmata. Both birds and bees deposited pollen on wet receptive and dry pre-receptive stigmata. Pollen deposited by both groups was embedded within the exudate on wet stigmata, and adhered to dry stigmata in a manner suggesting forces other than friction were involved. Eucalypt pollen is slightly sticky (Paton and Ford 1977), which may explain the observations of it adhering to dry stigmata. This could also be the consequence of electrostatic forces between negatively charged stigmata and positively charged pollen grains on the bodies of flower visitors (Vaknin *et al.* 2000). It has long been suggested that bees accumulate positive charges while in flight (reviewed in Vaknin *et al.* 2000).

6.4.3 Stigma development and pollination

It is not known if pollen deposited by animals on dry stigmata remains there until the onset of stigmatic receptivity. Pollen deposited on the cuticle may be lost if the cuticle is sloughed as it ruptures, but that deposited on dry papillae could conceivably remain in place until exudate is produced. Pollen can adhere to non-receptive stigmata and germinate later in some other

protandrous plant species (Ramsey 1995, Ramsey and Vaughton 2000), including *Eucalyptus camaldulensis* Dehnh. (Oddie and McComb 1998). Although large quantities of pollen did not adhere to stigmata of *Eucalyptus spathulata* subsp. *spathulata* Hook., *E. cladocalyx* var. *nana* F. Muell. and *E. leptophylla* F. Muell. ex Miq. prior to stigmatic receptivity, this pollen was applied by hand rather than being deposited by foraging animals (Ellis and Sedgley 1992).

The changes to the stigma associated with the onset of receptivity were similar to those documented in *Eucalyptus spathulata, E. cladocalyx* and *E. leptophylla* (Ellis and Sedgley 1992). As in these three other *Symphyomyrtus* species, the stigma was originally covered in a smooth cuticle that ruptured as the papillae developed, after which exudate was produced. However, in contrast to *E. leptophylla* (Ellis and Sedgley 1992), enough exudate was produced to completely cover pollen grains deposited on *E. globulus* stigmata.

6.4.4 Evolutionary implications

These results suggest that *E. globulus* is rather specialised towards ornithophily, in spite of displaying an apparently allophilic syndrome and being visited by numerous insects, which cautions against predicting a plant's pollinators from either floral form or visitor profile. This raises the question of why *E. globulus* has not evolved means of deterring insects from taking nectar. Many other bird-pollinated flowers have evolved characters to maximise the proportion of their nectar production available to birds, by discouraging insects from removing nectar (Faegri and van der Pijl 1979, Paton 1986b). Such characters include tubular corollas (Ford *et al.* 1979, Rebelo *et al.* 1984, Paton 1986b) and long hairs (Ford *et al.* 1979, Paton 1986b) that physically block insect access to nectar, sticky corolla surfaces that capture insects (Rebelo *et al.* 1985), and red colouration to make the flowers less obvious to insects (Faegri and van der Pijl 1979, Ford *et al.* 1979, Paton 1986b). In some other bird-pollinated species of *Eucalyptus* the stamens have evolved to be red (Ford *et al.* 1979), or incurved over the nectaries to block

access by insects to nectar (Bond and Brown 1979, Hopper and Moran 1981, Hopper and Burbidge 1986).

It may be that native insect visitors consumed so little nectar that there was little selective advantage in excluding them. This explanation would be valid if current native insect visitation rates have not been higher in the past, as it is introduced bees that are responsible for most nectar consumption in *E. globulus* (Chapters 4 and 9).

Alternatively, there may be a selective advantage in having some insect visitors in situations where bird-pollinators are scarce. Although single flower visits by native insects did not facilitate any seed set in this experiment, this may have been because they deposited insufficient pollen in one visit to initiate fruit set (Olsen 1997), and multiple insect visits might result in seed set. If so, there may be a selective advantage in having insects visit flowers low in the canopy, as pollination services to the lower parts of *E. globulus* canopies are inferior to those in the upper parts (Patterson *et al.* 2001), and birds seldom visit flowers in the lower parts of canopies (Chapters 8 and 9). This may result in contrasting selective forces acting in different parts of the canopy; selection for exclusion of insects in the upper canopy, and attracting insects in the lower canopy.

Incurved stamens that prevent insects from taking nectar, as occurs in *E. stoatei* C. Gardner (Hopper and Moran 1981, Hopper and Burbidge 1986) and to a lesser extent *E. incrassata* Labill. (Bond and Brown 1979), may not have evolved in *E. globulus* if *L. discolor* or other short-billed birds have historically played a central role in its pollination. Incurved stamens would prevent short-billed birds from taking nectar, limiting the suite of potential pollinators to long-billed honeyeaters (Hopper and Moran 1981). Hence, the loss of some nectar to insects may be an unavoidable cost associated with making nectar available to effective short-billed bird pollinators such as *L. discolor*.

Chapter 7

Pollen loads carried by birds feeding on the flowers of *Eucalyptus globulus* subsp. *globulus* in southeastern Tasmania

Abstract

The numbers of *Eucalyptus* pollen grains carried on the bills and heads of flower-feeding birds, captured in mistnets in the vicinity of flowering trees of *Eucalyptus globulus*, were compared. All four captured species carried hundreds or thousands of pollen grains on regions of the bill and head that were likely to contact stigmata as they fed from flowers of *E. globulus*. However, the nationally endangered swift parrot *Lathamus discolor* carried significantly more eucalypt pollen grains than the three species of Meliphagidae, suggesting that it has the greatest capacity to pollinate the flowers. Analysis of the distribution of pollen across the bills and heads of swift parrots, and observations of the foraging behaviour of captive swift parrots at flowers, indicated that the heaviest concentrations of pollen were on the regions of the bill and head that frequently contacted stigmata. It is argued that the flowers of *E. globulus* are well adapted to pollination by swift parrots, but that other birds are likely to also pollinate the flowers.

7.1 Introduction

The allophilic floral syndrome of *Eucalyptus globulus*, together with the large quantities of nectar and pollen produced, render the flowers attractive to an enormous array of anthophilous insects as well as numerous bird species (Hingston and Potts 1998). However, insects are relatively ineffective pollinators of this species. Single visits by insects to flowers of *E. globulus* during peak stigmatic receptivity did not result in the production of statistically significant numbers of seeds (Chapter 6). In contrast, receptive flowers of *E. globulus* visited once by a swift parrot *Lathamus discolor* (Shaw) produced significantly more seeds than resulted from no visits or single insect visits, indicating that the former are effective pollinators (Chapter 6).

Although historical and anecdotal records suggest that the swift parrot was once common (Brown 1989), the most recent estimate of its population was only 940 pairs (Brereton 1996). Consequently, this species is classified as endangered under Australia's *Environment Protection and Biodiversity Conservation Act 1999*. Swift parrots are largely dependent on the flowers of *E. globulus* as a food source during their breeding season (Brown 1989, Brereton 1996), harvesting large quantities of nectar and pollen from the trees (Brown 1989, Gartrell *et al.* 2000, Gartrell and Jones 2001). The swift parrot has developed alimentary adaptations to nectarivory including a brush tongue, a larger crop than its closest relatives and a modified proventriculus (Gartrell *et al.* 2000).

However, the extent to which the dependence of swift parrots on *E. globulus* is mirrored by the dependence of the tree on the parrot in this plant-pollinator mutualism remains unknown. Numerous other bird species also visit these flowers (Brown 1989, Hingston and Potts 1998, Chapters 4 and 6), but it is not known if they are as effective at pollination as is the swift parrot. Large differences between bird species as pollinators of individual species of Australian plants have not been found in the past (Paton 1991), although *Eucalyptus stoatei* C. Gardner appears to be specialised for pollination by the Meliphagidae rather than by shorter-billed birds (Hopper and Moran 1981).

One of the major factors determining how effective any flower visitor is as a pollinator is the quantity of pollen carried by that animal on regions of its body that are likely to contact receptive stigmata (Lindsey 1984). Differences in the amounts of pollen carried by species of Australian anthophilous birds have been recorded previously (Ford and Pursey 1982, Hackett and Goldingay 2001).

This study investigates the quantities, and distributions, of eucalypt pollen on the bills and heads of wild swift parrots and other birds while they foraged on flowers of *E. globulus*. These factors, together with observations

of captive swift parrots foraging on flowers of *E. globulus*, provide insight into the degree to which *E. globulus* is adapted to pollination by swift parrots.

7.2 Methods

Mistnets were erected in two naturally occurring stands of *E. globulus* near Hobart in southeastern Tasmania during peak flowering in the springs of 1998 and 1999. No other *Eucalyptus* species were observed flowering nearby at the time of mistnetting. Nets were checked for birds every 30 minutes. The pollen loads carried by captured individuals of species observed feeding from flowers of *E. globulus* were determined by pressing transparent sticky tape (Scotch® red plaid) against their bill and head feathers. Separate pieces of tape were used for the four different orientations of the head (forehead, chin, and both lores), with these being transferred subsequently to microscope slides. The tape was applied systematically from the bill tip caudally and in the sequence: forehead; lores; and finally the chin.

The numbers of pollen grains that were indistinguishable from those of *E. globulus* in the first 22 mm from the bill tip were counted in four sections of 5.5 mm on each slide. This was achieved by scanning across the width of the sticky tape and counting all pollen grains within the diameter of one field of view at a magnification of 312.5 (0.6875 mm). This was conducted 32 times, resulting in the entire width of the sticky tape being counted along a length of 22 mm. All pollen grains were counted, unless they were aggregated in dense clumps whereupon the area occupied by 50 grains was determined and the aggregation then counted in blocks of 50 pollen grains.

The total number of pollen grains within 22 mm of the bill tip was compared between the four captured species using One-Way Analysis of Variance, after the distributions were normalized by $\log_{10}$ transformation of the data. Subsequent pairwise comparisons were conducted using Student-Newman-Keuls Method.

The distributions of pollen within 22 mm of the bill tip were investigated on the two most frequently captured bird species, namely swift parrots and New Holland honeyeaters *Phylidonyris novaehollandiae* (Latham). Statistical analysis involved using Two-Way Analysis of Variance, with the orientation (forehead, chin, and lores) and distance from the bill tip (four sections of 5.5 mm) as sources of variation. The values used for lores were the averages of the two lores on each bird. For New Holland honeyeaters, the data were $\log_{10}$ transformed to normalize their distributions. However, the swift parrot data could not be normalized, resulting in the Two-Way ANOVA being conducted on ranks. If orientation or distance were statistically significant to the variation in pollen distribution on the bird species, subsequent pairwise tests were conducted using Student-Newman-Keuls Method.

All statistical analyses were conducted using the computer programme SigmaStat (Jandel 1994).

7.3 Results

Statistically significant differences between flower-feeding bird species in the quantities of eucalypt pollen carried within 22 mm of the bill tip were apparent ($P < 0.0001$, $F_3 = 13.5$, 1-Way ANOVA). Swift parrots carried significantly more eucalypt pollen than each of the Meliphagidae species (Table 7.1). However, there were no statistically significant differences between Meliphagidae species in eucalypt pollen loads (Table 7.1). Most birds carried almost pure *Eucalyptus* pollen loads, with only two swift parrots and one New Holland honeyeater carrying large numbers of foreign pollen grains.

Both orientation and distance from the bill tip were statistically significant to the variation in pollen distribution on swift parrot bills and heads (Table 7.2). The effects of orientation and distance were independent of each other, as no statistically significant interaction occurred between these factors (Table 7.2). In contrast, there were no statistically significant effects of position on the pollen loads carried by New Holland honeyeaters (Table 7.2).

Species	Family	n	Mean # pollen grains
[a]swift parrot	Psittacidae	20	14656.3 ± 2344.4
[b]New Holland honeyeater	Meliphagidae	13	4855.5 ± 2387.3
[b]yellow wattlebird	Meliphagidae	3	3781.3 ± 2191.5
[b]crescent honeyeater	Meliphagidae	1	663.0 ± 0

TABLE 7.1

Mean (± standard error) numbers of eucalypt pollen grains carried on the bill and head within 22 mm of the bill tip on four species of flower-feeding birds. Species with statistically significant differences in pollen loads have different superscripts. Significances determined by Student-Newman-Keuls Method following 1-Way ANOVA of $\log_{10}$ transformed data.

Species	orientation	distance	orientation x distance
swift parrot	$P < 0.0001$	$P < 0.0001$	$P = 0.9946$
New Holland honeyeater	$P = 0.3735$	$P = 0.3089$	$P = 0.5390$

TABLE 7.2

Significance of effects of orientation and distance from the bill tip, and their interaction, on eucalypt pollen loads in the first 22 mm from the bill tip in two flower-feeding bird species determined by 2-Way ANOVA. Analysis of swift parrot pollen loads was conducted on the ranks of the pollen loads in the various sections of the head. Analysis of New Holland honeyeater pollen loads was conducted on $\log_{10}$ transformed data.

	[ab]0 - 5.5 mm	[a]5.5 - 11 mm	[b]11 - 16.5 mm	[c]16.5 - 22 mm
[c]forehead	684.9	886.7	388.9	104.7
[b]lores	971.4	981.2	369.3	179.1
[a]chin	2181.1	2899.2	1828.4	682.9

TABLE 7.3

Matrix of mean numbers of eucalypt pollen grains in different regions of the bills and heads of 20 swift parrots. Distance categories are distances from the bill tip. Statistically significant differences in pollen loads between distance categories or orientation classes are denoted by different superscripts. Significances determined by Student-Newman-Keuls Method following 2-Way ANOVA of rank data.

The statistically significant effect of orientation on pollen loads on swift parrots involved the heaviest loads being on the chin and lightest on the forehead (Table 7.3). Because pollen was always sampled in the order:

forehead; lores; then chin, this difference may have been underestimated. Pollen loads were also highest in the 11 mm nearest the bill tip, declining significantly between 11 mm and 22 mm from the bill tip (Table 7.3).

7.4 Discussion

Swift parrots, New Holland honeyeaters, yellow wattlebirds *Anthochaera paradoxa* (Daudin) and the crescent honeyeater *Phylidonyris pyrrhoptera* (Latham) captured in the vicinity of flowering *E. globulus* all carried large quantities of eucalypt pollen on their bills and head feathers. Paton and Ford (1977) also noted that pollen of *Eucalyptus* adhered to both the bill and feathers of flower-feeding birds. Consequently, contact with stigmata of *E. globulus* by the bills or head feathers of any of these species is likely to result in pollination. The loads recorded from meliphagids in this study are comparable to the quantities of *Banksia* pollen found on New Holland honeyeaters and a red wattlebird *Anthochaera carunculata* (Shaw) in NSW (Ford and Pursey 1982), but larger than *Banksia* pollen loads recorded on eastern spinebills *Acanthorhynchus tenuirostris* (Latham) (Ford and Pursey 1982, Goldingay *et al.* 1987).

The significantly greater pollen loads on swift parrots than on the three Meliphagidae species, on the parts of the body most likely to contact stigmata, suggests that the former has a greater capacity to deposit pollen on stigmata. Differences between these two taxa in the capacity to deposit pollen is enhanced further by the greater likelihood of stigma contact by parrots than honeyeaters, while feeding on eucalypt nectar, because of the shorter bills of the former (Paton and Ford 1977). These two factors suggest that swift parrots are more effective pollinators of *E. globulus* than are the Meliphagidae.

The greater pollen loads on swift parrots than meliphagids can be attributed, at least partly, to the shorter and thicker bills of swift parrots. Heavier pollen loads on bird species with shorter bills than on those with longer bills have also been reported from New South Wales (Ford and Pursey 1982, Hackett

and Goldingay 2001). Pollen sampling from honeyeaters in this study would have been limited largely to their slender bills, as mean bill lengths for New Holland honeyeaters are approximately 20 mm (Ford 1976, Paton and Ford 1977). In contrast, pollen sampling from swift parrots would have included larger areas of the head because of the shorter bills in this species. Hence, the total area sampled per swift parrot would have been greater than the area sampled per meliphagid because the bills of swift parrots are wider and proportionally more head area was sampled on swift parrots than on meliphagids. However, the area of the head and bill sampled represents the likely area of the bird to contact the flowers while feeding, and is therefore considered to accurately assess the pollinating abilities of the birds (B. Gartrell pers. comm.).

The larger pollen loads on swift parrots than on meliphagids, and the differences in distributions of pollen across the bills and heads between these two taxa, can also be attributed to differences in their foraging behaviour at flowers. Swift parrots actively consume eucalypt pollen from anthers as a protein source (Gartrell *et al.* 2000, Gartrell and Jones 2001). While ingesting pollen, swift parrots tend to hold their upper mandible immediately above the anthers while biting them by sweeping the lower mandible up through the anthers. Such actions may account for the concentration of pollen on the bill, particularly the lower mandible, and the feathers on the chin of swift parrots. Although honeyeaters also ingest pollen (Paton 1981, Ford and Pursey 1982), this is only by accident while collecting nectar (Paton 1981). Hence, anther contact by New Holland honeyeaters is only accidental (Paton 1981), explaining the smaller pollen loads and random distribution of pollen across the bill and head of this species.

The distribution of pollen across the bill and head of swift parrots suggests that the flowers of *E. globulus* are adapted to maximise rates of pollen deposition by this species. The heaviest pollen loads were in the distal 11 mm and on the chin, and it is these parts that consistently contact stigmata of *E. globulus*. In addition, swift parrots press anthers against their palates with

their tongues while harvesting pollen of *E. globulus* (Gartrell *et al.* 2000, Gartrell and Jones 2001), suggesting that pollen is also carried on the tongue (Ford *et al.* 1979, Hopper and Burbidge 1979). The tongues, bills and chin feathers of nectar-feeding swift parrots make regular contact with the stigmata, while nectar is licked from the hypanthium (Figs 7.1 and 7.2). When feeding on pollen, swift parrots tend to reach across the flower while biting at anthers and, in the process, rest their chins on the stigma (Fig. 7.3). In contrast, the broad hypanthium of *E. globulus* should reduce the probability of long-billed meliphagids contacting stigmata as they probe for nectar, further suggesting that the flowers are adapted to pollination by short-billed birds such as swift parrots.

In addition, the extreme robustness of the style can be considered an adaptation to swift parrots because they frequently bite the style while consuming both pollen and nectar. This is particularly so when eating pollen from newly opened flowers before the stamens have reflexed to draw the anthers away from the stigma.

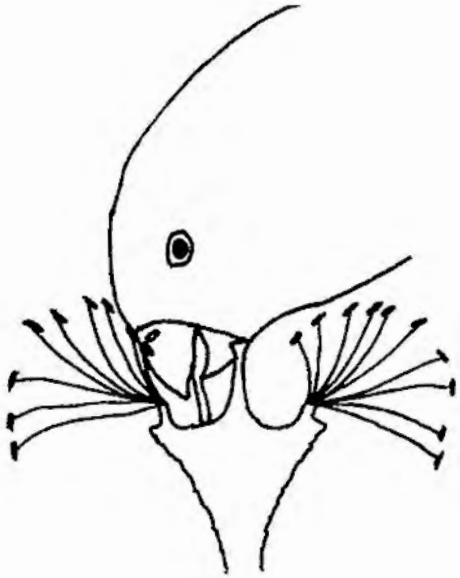


FIGURE 7.1

A swift parrot *Lathamus discolor* licking nectar from the hypanthium of a *Eucalyptus globulus* flower. The stigma of the flower is contacted by the chin and underside of the bill.

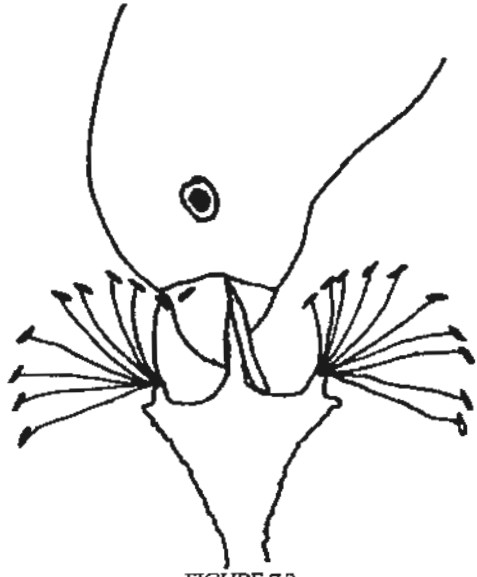


FIGURE 7.2

A swift parrot *Lathamus discolor* licking nectar from the hypanthium of a *Eucalyptus globulus* flower. The stigma of the flower is inside the bird's mouth and is contacted by the upper surface of the tongue.

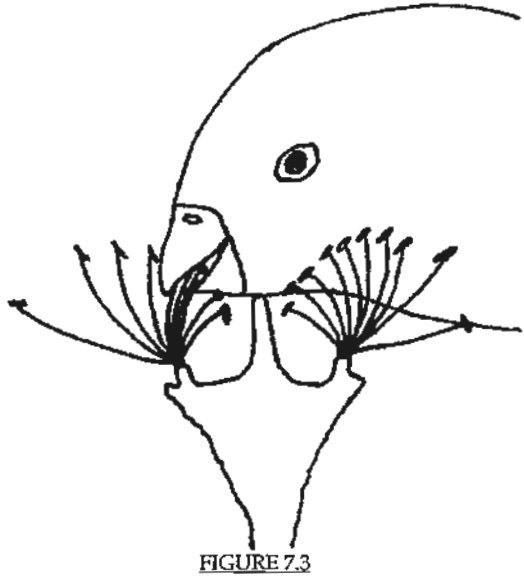
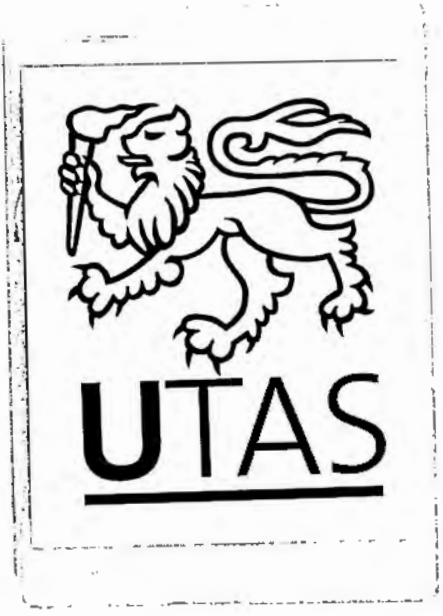


FIGURE 7.3

A swift parrot *Lathamus discolor* eating pollen from the anthers of a *Eucalyptus globulus* flower. The stigma of the flower is contacted by the chin and underside of the bill as the bird reaches across the flower.

Although the flowers of *E. globulus* exhibit some characteristics suggestive of adaptation to exploit swift parrots as pollinators, they are almost certainly also pollinated by other birds. This includes the Meliphagidae species that were found to carry large quantities of pollen during this study. The accidental ingestion of pollen by meliphagids (Paton 1981, Ford and Pursey 1982) is likely to also result in some deposition of pollen on their tongues, which may contact the stigmata while they lick nectar from the hypanthium. In addition, lorikeets (Psittacidae) are likely to carry pollen loads comparable to those of swift parrots because of their short thick bills and active consumption of pollen from eucalypt anthers (Churchill and Christensen 1970, Hopper and Burbidge 1979, Gartrell and Jones 2001). Indeed, it has long been suggested that lorikeets may pollinate flowers of *Eucalyptus* with their tongues (Ford *et al.* 1979, Hopper and Burbidge 1979).



Chapter 8

Movements of anthophilous birds in flowering trees of *Eucalyptus globulus* subsp. *globulus* in southeastern Tasmania

Abstract

Numerous bird species were observed feeding on the flowers of *Eucalyptus globulus* within its natural distribution in southeastern Tasmania. These included species generally regarded as flower-feeding specialists, and species not usually considered to be flower-feeders. Significantly more birds commenced foraging in the upper halves, than in the lower halves, of trees of *E. globulus* with flowers evenly distributed between the two halves. Birds also spent significantly more time foraging in the upper halves, than in the lower halves, of canopies in such trees. These observations are consistent with the published account of greater proportions of outcross seed and more seeds per capsule in the upper, than the lower, sections of *E. globulus* canopies. This suggests that birds are major contributors to the deposition of outcross pollen on stigmata of *E. globulus*, particularly in flowers in the tops of trees. More evidence of birds being effective outcross pollinators comes from the observed brief foraging visits to individual trees, particularly by the Meliphagidae. Inter- and intra-specific aggressive encounters between birds appear to enhance the effectiveness of birds as pollinators of *E. globulus* by reducing the durations of foraging bouts within individual trees.

8.1 Introduction

Eucalyptus globulus appears to be adapted to pollination by birds (Chapter 4). Single visits by insects to flowers of *E. globulus* during peak stigmatic receptivity did not result in the production of statistically significant numbers of seeds (Chapter 6). However, at least one bird species, the swift parrot *Lathamus discolor* (Shaw), is a very effective pollinator of *E. globulus* (Chapter 6). Numerous other species of birds also feed from the flowers of *E. globulus* (Brown 1989, Hingston 1997, Hingston and Potts 1998), but these

may differ in their value as pollinators. These differences are the product of the relative abundances of particular species, their pollen carrying capacities, fidelity to *E. globulus*, capacity to contact receptive stigmata, the frequency with which they move between flowers and plants (Lindsey 1984), and the extent of pollen carryover (Campbell 1985b). Analysis of the pollen loads carried by swift parrots and some Meliphagidae suggests that the former are likely to deposit more pollen on stigmata per flower visit, but that the Meliphagidae are also likely to pollinate the flowers (Chapter 7).

Seed production in *E. globulus* is dependent on the quality, as well as the quantity, of conspecific pollen deposited on stigmata. More seeds are produced following outcross pollination than self-pollination (Potts and Cauvin 1988, Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995, 1998). In addition, selfing reduces seed viability, as well as growth rates and survivorship of offspring, in *E. globulus* (Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995). Recent evidence indicates that the quantity of outcross pollen deposited on stigmata of *E. globulus* probably increases with height in the canopy (Patterson *et al.* 2001). Outcrossing rates were significantly higher at 20 - 25 m above the ground, than at 2 - 5 m above the ground, in self-compatible trees (Patterson *et al.* 2001). Although this difference could be the result of increased deposition of self-pollen on lower flowers as a result of pollen rain (Eldridge 1970), it is more likely to be a consequence of increased outcross pollen deposition in the upper canopy (Patterson *et al.* 2001). This is because the numbers of seeds per capsule were significantly greater at 20 - 25 m than at 2 - 5 m above the ground, in three out of five trees, but never greater from lower than higher in the canopy (Patterson *et al.* 2001).

My study investigated the movements of anthophilous birds while they foraged on flowering trees of *E. globulus* to shed light on the roles of various species in the transfer of pollen within and between canopies. The primary aim was to examine the manner in which anthophilous birds distribute themselves vertically within the canopies of flowering trees of *E. globulus*, to

determine if this was related to published vertical differences in outcrossing rates within canopies of this species (Patterson *et al.* 2001). Interspecific differences in the durations of foraging bouts were also examined, as this should affect the proportions of self- and outcross-pollen transferred by each species. Differences in the compositions of anthophilous bird assemblages between trees were also investigated.

8.2 Methods

8.2.1 Experimental design

Patterns of foraging by anthophilous birds in 23 canopies of *E. globulus* in southeastern Tasmania (Table 8.1, Fig. 8.1) were investigated during August and September 1999. Each tree was observed for at least three hours on between one and three fine days with little wind, but varying levels of cloud cover.

Tree Identities	Locations	Habitat types
AB	Clifton Beach	Suburban park
C	Sandford	Suburban garden
DEF	Hobart Airport	Golf course
G	Sandy Bay	Suburban park
H	Lambert Gully	Suburban bushland reserve
IJKLM	University of Tasmania	University campus
NOPQRSTUV	University Reserve	Urban fringe bushland reserve
W	Mt Nelson	Suburban garden

TABLE 8.1

Locations and habitats of *E. globulus* trees upon which birds were surveyed.

Trees were selected for study on the basis of having flowers distributed evenly over at least two-thirds of the tree height. This allowed canopies to be divided into upper and lower halves, with similar numbers of flowers in each. The amount of time spent by each bird visitor in the upper and lower half of the canopy was recorded. It was also noted whether the bird initially entered the upper or the lower half of the canopy, and if they moved from one half of the canopy to the other while foraging. Only birds that fed among flowers were included in the data. Although most of this foraging involved feeding on flowers, some birds may have collected insects or lerp during this time.

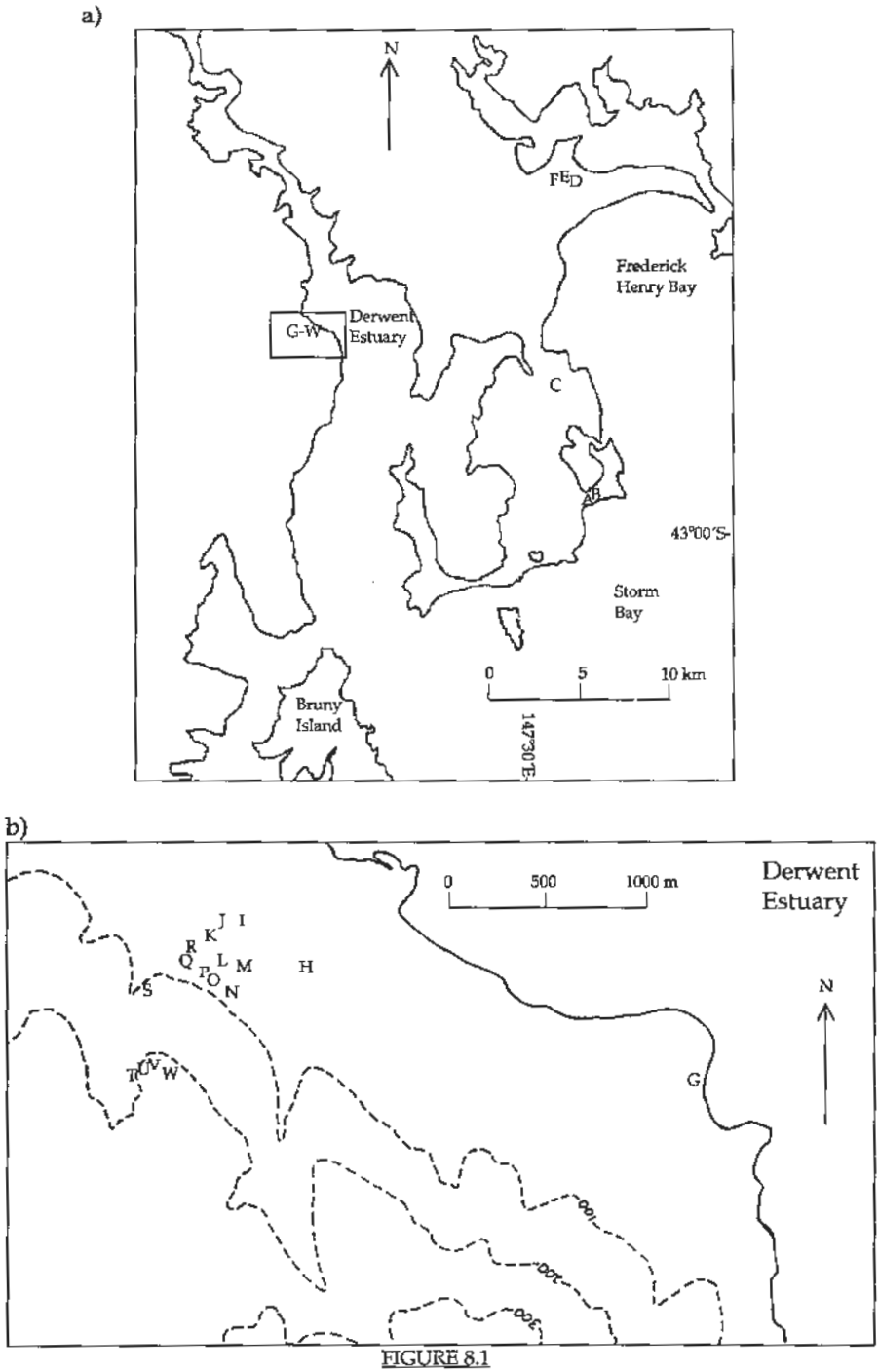


FIGURE 8.1

Locations of *E. globulus* trees upon which birds were surveyed. The box containing trees G-W in a) is shown in detail in b). Contour intervals in b) are in metres.

On two of the larger trees (I and M), it was not possible to record data for all birds. On these trees, data were gathered for all birds during most of the observation period. However, data were not gathered for any individuals entering during the occasional influxes of large numbers of birds that were too numerous to follow.

The taxonomic nomenclature for birds used in this chapter is that of Christidis and Boles (1994).

8.2.2 Data analysis

Differences between the upper and lower halves of canopies in the numbers of individual birds commencing foraging, and the amounts of time spent foraging by all birds, were compared using paired t-tests with trees as replicates. Similar analyses were also conducted for each bird species. These tests were undertaken using the computer programme SigmaStat (Jandel 1994).

The percentages of foraging bouts that began in the upper half of the canopy, and the percentages of time spent foraging in the upper half of the canopy, by each bird species were plotted as functions of $\log_{10}$ average body mass for each species. The significance of linear regressions of these relationships was investigated using SigmaStat (Jandel 1994). The same method was used to investigate the relationships between coefficients of variation for both behavioural characteristics and $\log_{10}$ average body mass for each species. Coefficients of variation were calculated as the standard deviations as percentages of the means (Sokal and Rohlf 1995), for each behavioural characteristic for each bird species on trees that they visited at least five times. Body masses used were the centres of the ranges published in Longmore (1991) and Crome and Shields (1992), with the exception of the yellow-tailed black cockatoo *Calyptorhynchus funereus* (Shaw) where a value near the lower end of this range was used because Tasmanian birds are smaller than those from the Australian mainland (Crome and Shields 1992).

On each tree, the durations of foraging bouts were compared between species that made at least five visits. Because of non-normality of the data, non-parametric tests were used. When only two species were present, the Mann-Whitney Rank Sum Test was employed. When more than two species were present the Kruskal-Wallis Test was used, followed by pairwise tests using Dunn's Method. These analyses were also conducted with SigmaStat (Jandel 1994).

Similarities between trees in their bird visitor profiles were investigated using classification methods. The amounts of time each bird species spent foraging in each tree were converted to proportions of the total time spent by foraging birds in each tree. All 23 trees were classified using UPGMA with the computer programme PATN (Belbin 1993) to produce a dendrogram.

8.3 Results

8.3.1 Flower visiting birds

Fourteen species of birds were observed feeding non-destructively from flowers of *E. globulus* (Table 8.2). These were taxonomically diverse, including seven species of Meliphagidae, four Psittacidae, and one species from each of the Cacatuidae, Pardalotidae, and Zosteropidae. Most of these species were regular visitors, but none were recorded from more than 13 of the 23 trees surveyed (Table 8.2). The most frequently observed species were the musk lorikeet *Glossopsitta concinna* (Shaw), swift parrot *Lathamus discolor* (Shaw), eastern rosella *Platycercus eximius* (Shaw), New Holland honeyeater *Phylidonyris novaehollandiae* (Latham), yellow wattlebird *Anthochaera paradoxa* (Daudin), little wattlebird *A. chrysoptera* (Latham), and noisy miner *Manorina melanocephala* (Latham) (Tables 8.2 and 8.3). Black-headed honeyeaters *Melithreptus affinis* (Lesson), crescent honeyeaters *Phylidonyris pyrrhoptera* (Latham), spotted pardalotes *Pardalotus punctatus* Shaw and silvereyes *Zosterops lateralis* (Latham), were also regular nectar-feeders. However, the yellow-throated honeyeater *Lichenostomus flavicollis* (Vieillot), green rosella *Platycercus caledonicus* (Gmelin) and yellow-tailed black cockatoo *Calyptorhynchus funereus* (Shaw) were irregular visitors (Tables 8.2 and 8.3).

8.3.2 *Foraging height*

Species	Family	# trees	Total duration upper	lower	% upper	*P*
yellow-tailed black cockatoo	Cacatuidae	1	2480	3065	44.7	-
musk lorikeet	Psittacidae	5	34630	11840	74.5	0.017*
green rosella	Psittacidae	2	345	400	46.3	0.806^{NS}
eastern rosella	Psittacidae	7	29635	19750	57.3	0.239^{NS}
swift parrot	Psittacidae	5	44765	19090	70.1	0.038*
spotted pardalote	Pardalotidae	9	4195	875	82.7	0.137^{NS}
yellow wattlebird	Meliphagidae	13	23580	7160	76.7	0.011*
little wattlebird	Meliphagidae	7	38605	7050	84.6	0.054^{NS}
noisy miner	Meliphagidae	7	8450	4205	66.8	0.317^{NS}
yellow-throated honeyeater	Meliphagidae	4	345	20	94.5	0.187^{NS}
black-headed honeyeater	Meliphagidae	10	2395	105	95.8	0.068^{NS}
crescent honeyeater	Meliphagidae	7	2220	95	95.9	0.046*
New Holland honeyeater	Meliphagidae	12	33520	10930	75.4	0.001**
silvereye	Zosteropidae	4	12345	695	94.7	0.181^{NS}
Total		23	237510	85280	73.6	0.0001***

TABLE 8.2

Numbers of trees of *E. globulus* on which each bird species was observed, the total time (seconds) they spent in the upper and lower halves of the canopies, and the percentages of time spent in the upper halves. *P*-values derived from paired t-tests of the amounts of time each species spent in the upper and lower halves of canopies, with trees as replicates.

Species	Code	Entry point (n) upper	lower	% upper	*P*	Movements down	up
yellow-tailed black cockatoo	YBC	3	3	50	-	3	3
musk lorikeet	ML	199	13	93.9	0.008**	32	11
green rosella	GR	3	3	50	1.000^{NS}	0	0
eastern rosella	ER	80	50	61.5	0.165^{NS}	9	14
swift parrot	SP	124	22	84.9	0.011*	16	1
spotted pardalote	SpP	26	6	81.2	0.021*	4	1
yellow wattlebird	YW	225	105	68.2	0.004**	16	28
little wattlebird	LW	258	65	79.9	0.026*	26	28
noisy miner	NM	78	69	53.1	0.716^{NS}	8	13
yellow-throated honeyeater	YTH	7	1	87.5	0.103^{NS}	0	0
black-headed honeyeater	BHH	35	2	94.6	0.013*	0	0
crescent honeyeater	CH	51	3	94.4	0.160^{NS}	0	0
New Holland honeyeater	NHH	511	204	71.5	0.002**	29	36
silvereye	S	69	9	88.5	0.043*	0	2
Total		1669	555	75.0	<0.0001***	143	137

TABLE 8.3

Frequencies with which various anthophilous birds entered the upper and lower halves of flowering canopies of *E. globulus*, the percentages of visits that involved commencing foraging in the upper halves of canopies, and the number of times they moved from the upper half down to the lower half and vice versa. *P*-values derived from paired t-tests of the numbers of times each species commenced foraging in the upper and lower halves of canopies, with trees as replicates.

Across all trees, birds spent significantly more time feeding in the upper than the lower half of the canopy (Table 8.2). The number of individual birds that commenced foraging in the upper half of the canopy was also significantly greater than that in the lower half of the canopy (Table 8.3). This behaviour was exhibited by several of the most common bird species. New Holland honeyeaters, yellow wattlebirds, musk lorikeets and swift parrots all entered the upper halves of canopies, and foraged there, significantly more than they did in the lower halves (Tables 8.2 and 8.3). However, this behaviour was not exhibited by all species. The frequently observed species that did not significantly favour the upper halves of canopies, in at least one of these ways, were noisy miners and eastern rosellas. No species commenced foraging significantly more often, or spent significantly more time foraging, in the lower halves than the upper halves of canopies (Tables 8.2 and 8.3).

The movement patterns of foraging birds within canopies differed between species. Swift parrots and musk lorikeets displayed a tendency towards initially entering the top half of the canopy, and then working downwards into the lower half (Table 8.3). In contrast, noisy miners, yellow wattlebirds, New Holland honeyeaters and eastern rosellas moved upwards slightly more often than downwards (Table 8.3).

Smaller bird species favoured the upper halves of canopies more than larger species did (Figs 8.2 and 8.3). The percentage of times that birds commenced foraging in the upper half of the canopy was negatively associated with $\log_{10}$ body mass ($r^2 = 0.505$; $P = 0.0044$; Fig. 8.2), as was the percentage of foraging time spent in the upper half of the canopy ($r^2 = 0.616$; $P = 0.0009$; Fig. 8.3).

However, there was variation within size classes in the propensity to favour the upper half of the canopy. New Holland honeyeaters were more inclined to commence, and spend time, foraging in the lower half than were other honeyeaters of similar mass. Similarly, noisy miners and both rosellas were more inclined to commence, and spend time, foraging in the lower half than were both wattlebird species (Figs 8.2 and 8.3).

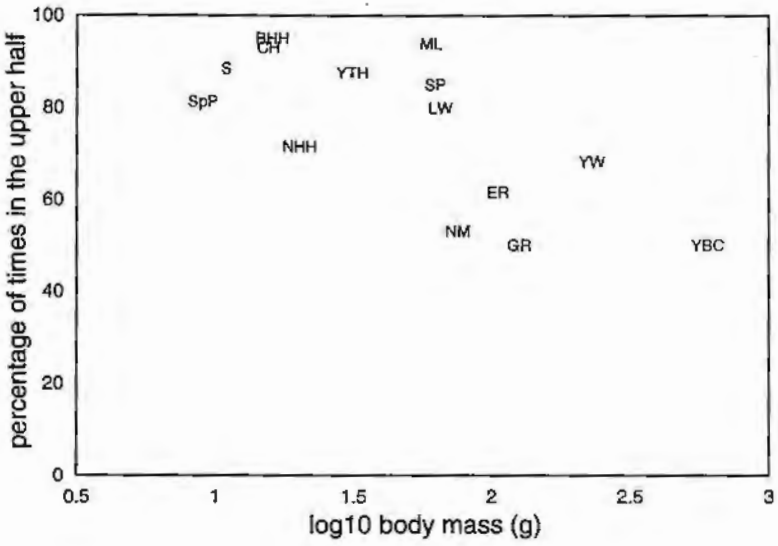


FIGURE 8.2

The percentages of times that species of birds began foraging in the canopies of flowering trees of *E. globulus* in the upper half, as a function of their $\log_{10}$ body mass. Codes for bird species are given in Table 8.3.

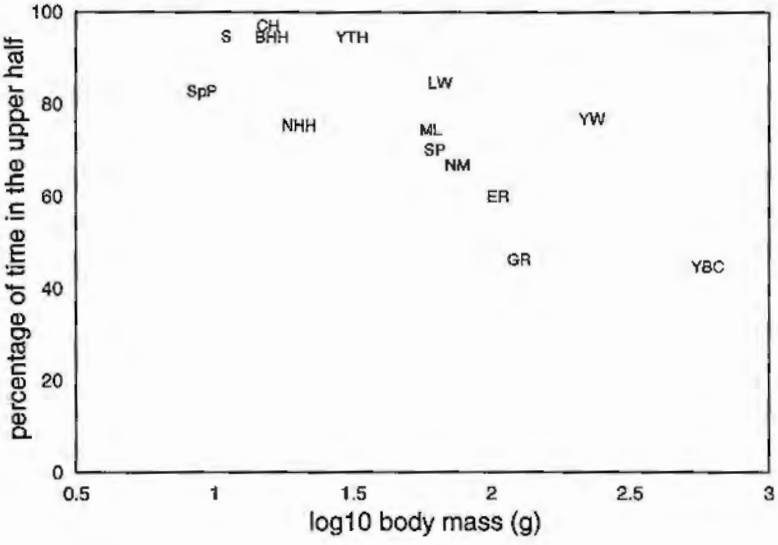


FIGURE 8.3

The percentages of foraging time that species of birds spent in the upper halves of canopies of flowering trees of *E. globulus*, as a function of their $\log_{10}$ body mass. Codes for bird species are given in Table 8.3.

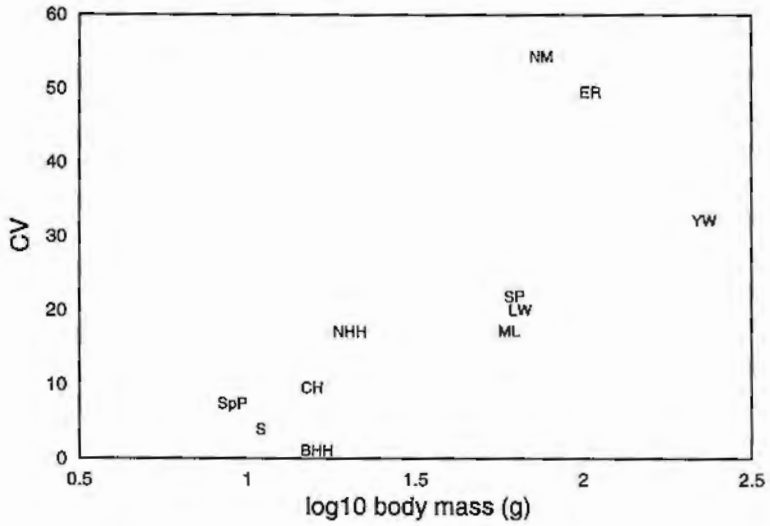


FIGURE 8.4

Coefficient of variation (CV) of the proportions of foraging time that species of birds spent in the upper halves of canopies of flowering *E. globulus* as a function of their $\log_{10}$ body mass. CV = standard deviation as a percentage of the mean. Means and standard deviations calculated for each bird species from trees that they visited at least five times. Codes for bird species are given in Table 8.3.

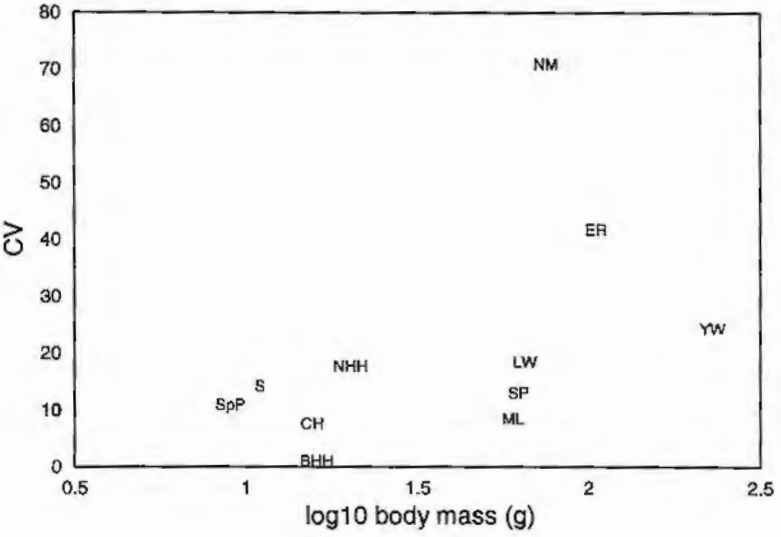


FIGURE 8.5

Coefficient of variation (CV) of the proportions of times that species of birds began foraging in the canopies of flowering trees of *E. globulus* in the upper half as a function of their $\log_{10}$ body mass. CV = standard deviation as a percentage of the mean. Means and standard deviations calculated for each bird species from trees that they visited at least five times. Codes for bird species are given in Table 8.3.

The variation between trees in the percentages of time bird species spent in the upper half of the canopy was also greater for larger bird species. The coefficient of variation for the percentages of foraging time that species of birds spent in the upper halves of canopies was positively associated with $\log_{10}$ body mass ($r^2 = 0.577$; $P = 0.0067$; Fig. 8.4). However, the coefficient of variation for the percentages of times that species began foraging in the upper halves of canopies was not significantly associated with $\log_{10}$ body mass ($r^2 = 0.254$; $P = 0.1137$; Fig. 8.5).

Tree	Bird species											
	YBC	ML	ER	SP	SpP	YW	LW	NM	BHH	CH	NHH	S
A		100.0	65.4					48.2				
B		64.4						77.7				
C							82.5					
D		78.9	58.4					23.0				
E		92.2	92.8					94.7				
F		75.1						20.6				
G			57.4					72.2				
H												100.0
I			65.2			97.5	96.5		100.0		61.0	
J						85.5						
K							79.9					
L						100.0					80.9	
M			5.8		89.5		72.6				81.4	
N											85.8	
O				67.8		60.5			100.0	100.0	85.7	
P				64.0		49.7			100.0		64.9	
Q				92.2	80.6	90.0	100.0				90.8	92.4
R	44.7					19.7					54.8	
S							55.0			100.0		100.0
T				100.0		66.2					100.0	
U						80.6				84.4	80.2	
V						74.0						
W				100.0		87.1					82.4	100.0

TABLE 8.4

Percentages of time spent foraging in the upper half of the canopy of each flowering tree of *E. globulus* by each bird species. Only species making at least five foraging bouts to particular trees were included. Species codes are given in Table 8.3. Locations of trees are given in Table 8.1 and Fig. 8.1.

Noisy miners and eastern rosellas were far more variable than other species in the percentages of time spent foraging in the upper halves of canopies (Fig. 8.4) and the percentages of times they commenced foraging in the upper halves of canopies (Fig. 8.5). The percentages of time spent foraging in the upper half of the canopy ranged from 20.6% to 94.7% for noisy miners and

5.8% to 92.8 % for eastern rosellas (Table 8.4). The percentages of times they commenced foraging in the upper halves of canopies ranged from 0% to 67.3% for noisy miners and 23.1% to 100% for eastern rosellas (Table 8.5). Eastern rosellas entered the lower half of the canopy more frequently on trees where both species of wattlebirds, New Holland honeyeaters and black-headed honeyeaters occurred (trees I and M) than on those where noisy miners and musk lorikeets occurred (trees A, D, E and G; Table 8.5).

Tree	Bird species											
	YBC	ML	ER	SP	SpP	YW	LW	NM	BHH	CH	NHH	S
A		100.0	100.0					45.2				
B		81.5						67.3				
C							75.6					
D		100.0	63.6					10.0				
E		94.9	83.3					60.0				
F		100.0						0.0				
G			62.5					64.5				
H												100.0
I			50.0			87.5	90.7		100.0		59.7	
J						63.6						
K							65.5					
L						100.0					83.3	
M			23.1		87.5		76.8				75.6	
N											73.8	
O				75.9		50.0			100.0	100.0	77.3	
P				81.2		57.1			100.0		61.2	
Q				100.0	75.0	82.9	100.0				79.2	73.5
R	50.0					42.9					54.9	
S							62.5			100.0		100.0
T				100.0		67.1					100.0	
U						62.7				87.5	87.5	
V						78.4						
W				100.0		77.3					85.0	100.0

TABLE 8.5

Percentages of foraging bouts to each flowering tree of *E. globulus* by each bird species that commenced in the upper half of the canopy. Only species making at least five foraging bouts to particular trees were included. Species codes are given in Table 8.3. Locations of trees are given in Table 8.1 and Fig. 8.1.

There were large differences between trees in the percentage of time foraging birds spent in the upper half of the canopy (Table 8.4), and in the percentages of times birds commenced foraging in the upper half of the canopy (Table 8.5). These differences even occurred between trees growing at the same locality. The percentage of foraging bouts that commenced in the lower half, and the percentage of time spent in the lower half, of tree R was the greatest

of all trees. However when birds visited the nearby tree Q, they all exhibited a very strong preference for the upper half of the canopy (Tables 8.4 and 8.5, Fig. 8.1). A similar situation occurred at Hobart Airport, where the percentage of time birds spent foraging in the upper half of the canopy was far greater in tree E than in trees D and F (Table 8.4, Fig. 8.1).

8.3.3 Durations of foraging bouts

The durations of foraging bouts by different species varied greatly within individual canopies (Table 8.6). There was a strong tendency for Psittaciformes (Psittacidae and Cacatuidae) to have longer foraging bouts than the Meliphagidae. Eastern rosellas had significantly longer foraging bouts than noisy miners on three of the four trees that they both visited (A, D and E), and significantly longer bouts than little wattlebirds and New Holland honeyeaters on tree I (Table 8.6). The duration of foraging bouts by musk lorikeets was also significantly greater than that by noisy miners on tree B. Swift parrots had significantly longer foraging bouts than black-headed honeyeaters on both of the trees that they both visited (O and P), New Holland honeyeaters on four of the five trees they both visited (O, P, Q and T), and yellow wattlebirds on two of the five trees they both visited (P and T). The duration of foraging bouts by yellow-tailed black cockatoos was also significantly greater than that by New Holland honeyeaters on the only tree (R) where the former were observed foraging (Table 8.6).

The median duration of foraging bouts by silvereyes was also sometimes greater than that by the Meliphagidae (Table 8.6). On tree S, this was significantly greater than by crescent honeyeaters and little wattlebirds (Table 8.6). However, no statistically significant differences in foraging bout length occurred between silvereyes and Psittaciformes (Table 8.6).

Statistically significant differences in foraging bout length were uncommon between species of Psittaciformes or species of Meliphagidae (Table 8.6). Of these, eastern rosellas had significantly longer foraging bouts than musk lorikeets on two of the three trees that they both visited (A and D). In the

only case where there were statistically significant differences between two meliphagids, yellow wattlebirds had significantly longer foraging bouts than New Holland honeyeaters (O). However, on the eight other trees where both of these species foraged, no statistically significant differences in foraging bout length were observed (Table 8.6). Hence, the paucity of statistically significant differences between species of Psittaciformes can be attributed to the infrequency with which more than one species foraged on a particular tree. However, this explanation cannot be applied to the Meliphagidae because multiple species frequently foraged on the same tree.

Tree	Bird species											
	YBC	ML	ER	SP	SpP	YW	LW	NM	BHH	CH	NHH	S
A		20^{b}	340^{a}					25^{b}				
B		155^{a}						60^{b}				
C							82.5					
D		90^{b}	340^{a}					62.5^{b}				
E		70^{ab}	135^{a}					20^{b}				
F		185^{a}						122.5^{a}				
G			105^{a}					50^{a}				
H												70
I			487.5^{a}			115^{ab}	117.5^{b}		167.5^{ab}		55^{b}	
J						155						
K							100					
L						45^{a}					20^{a}	
M			140^{a}		177.5^{a}		112.5^{a}				90^{a}	
N											75	
O				140^{a}		45^{ab}			20^{bc}	25^{abc}	22.5^{c}	
P				487.5^{a}		50^{b}			37.5^{b}		20^{b}	
Q				305^{a}	82.5^{ab}	70^{ab}	102.5^{ab}				55^{b}	95^{ab}
R	1050^{a}					135^{ab}					35^{b}	
S							20^{b}			27.5^{b}		50^{a}
T				430^{a}		55^{b}					50^{b}	
U						40^{a}				55^{a}	55^{a}	
V						70						
W				35^{a}		10^{a}					20^{a}	15^{a}

TABLE 8.6

Median durations (seconds) of foraging bouts by bird species making at least five visits to a tree. Different superscripts denote statistically significant differences in median durations between bird species within each tree. Species codes are given in Table 8.3. Locations of trees are given in Table 8.1 and Fig. 8.1.

8.3.4 Bird communities on trees

The assemblages of bird visitors were classified into seven branches on the dendrogram, at a dissimilarity of 0.8 (Fig. 8.6). Five of the six trees surveyed from the eastern side of the Derwent Estuary were classified on Branches 1

and 2, indicating some regional variation in anthophilous bird assemblages (Figs 8.1 and 8.6). However, the Derwent Estuary was not a strict geographic barrier, as tree C from the eastern side was classified on Branch 3, and tree G on the western shore was classified on Branch 1 (Figs 8.1 and 8.6).

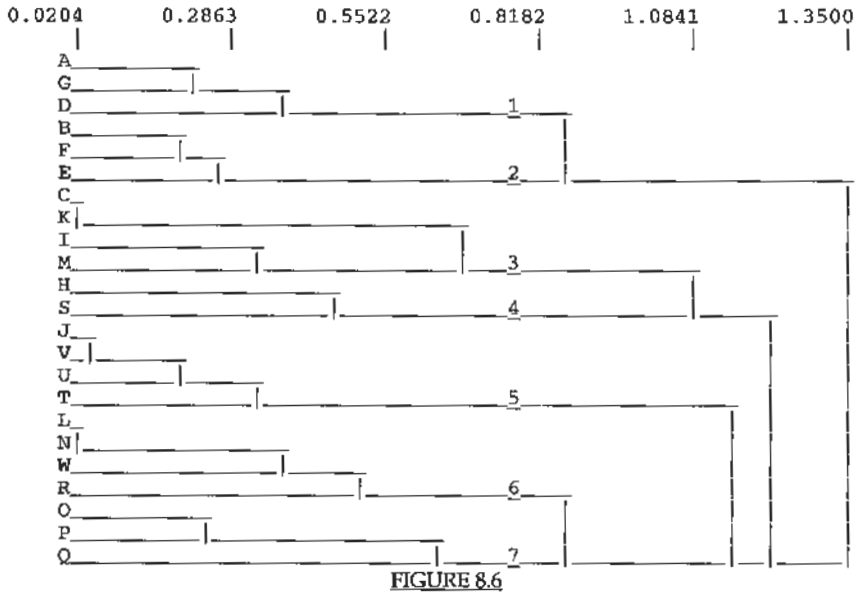


FIGURE 8.6

Dendrogram based on similarities between 23 trees of *E. globulus* in the proportional compositions of their anthophilous bird species, according to the time spent foraging in their canopies. Locations of trees are given in Table 8.1 and Fig. 8.1.

Anthophilous bird communities classified on Branches 1 and 2 of the dendrogram exhibited similarities (Table 8.7). Noisy miners foraged from all trees classified on these two branches. However, trees classified on Branch 1 were dominated by eastern rosellas, whereas those on Branch 2 were dominated by musk lorikeets (Table 8.7). The distinctiveness of the bird assemblages associated with these six trees was apparent from the absence of any other bird species, with the exception of two very brief visits to tree A by little wattlebirds (Table 8.7). Further evidence of the uniqueness of these assemblages comes from the total absence of musk lorikeets and noisy miners from trees classified on other branches. However, eastern rosellas were recorded from two trees (I and M) classified on Branch 3 (Table 8.7).

Branch	Tree	Bird species													
		YBC	ML	GR	ER	SP	SpP	YW	LW	NM	YTH	BHH	CH	NHH	S
1	A	0	0.046	0	0.795	0	0	0	0.001	0.158	0	0	0	0	0
	G	0	0	0	0.621	0	0	0	0	0.379	0	0	0	0	0
	D	0	0.371	0	0.589	0	0	0	0	0.040	0	0	0	0	0
2	B	0	0.747	0	0	0	0	0	0	0.253	0	0	0	0	0
	F	0	0.906	0	0.036	0	0	0	0	0.058	0	0	0	0	0
	E	0	0.705	0	0.279	0	0	0	0	0.016	0	0	0	0	0
3	C	0	0	0	0	0	0.016	0	0.980	0.005	0	0	0	0	0
	K	0	0	0	0	0	0	0	0.980	0	0	0.020	0	0	0
	I	0	0	0	0.407	0	0	0.076	0.327	0	0	0.025	0.001	0.163	0
	M	0	0	0	0.161	0	0.103	0.010	0.486	0	0	0.004	0	0.236	0
4	H	0	0	0	0	0	0	0	0	0	0	0	0	0	1.000
	S	0	0	0	0	0	0.046	0	0.157	0	0	0.039	0.211	0	0.546
5	J	0	0	0	0	0	0	1.000	0	0	0	0	0	0	0
	V	0	0	0	0	0	0	0.958	0	0	0	0	0	0.042	0
	U	0	0	0	0	0	0	0.802	0	0	0	0.003	0.098	0.098	0
	T	0	0	0	0	0.267	0.016	0.681	0	0	0.004	0	0.005	0.027	0
6	L	0	0	0	0	0	0.081	0.100	0	0	0	0	0	0.818	0
	N	0	0	0	0	0	0.061	0.102	0	0	0	0	0	0.838	0
	W	0	0	0.013	0	0.221	0.046	0.102	0	0	0	0.022	0.008	0.511	0.076
	R	0.462	0	0	0	0	0	0.095	0	0	0	0.009	0	0.434	0
7	O	0	0	0	0	0.624	0.003	0.097	0	0	0.006	0.015	0.015	0.240	0
	P	0	0	0	0	0.871	0	0.021	0	0	0.0002	0.007	0.009	0.092	0
	Q	0	0	0.021	0	0.232	0.029	0.195	0.072	0	0.007	0.001	0	0.135	0.309

TABLE 8.7

Proportional species compositions of anthophilous bird assemblages from 23 flowering trees of *E. globulus*, based on time spent foraging. Branches refer to the branches of the dendrogram (Fig. 8.6). Species codes are given in Table 8.3. Tree locations are given in Table 8.1 and Fig. 8.1.

Assemblages of birds classified on Branches 3 and 4 of the dendrogram were less alike than those on Branches 1 and 2 (Fig. 8.6). The little wattlebird was the predominant species on Branch 3 of the dendrogram (Table 8.7), actively defending trees C and K from other species. However, eastern rosellas and New Holland honeyeaters were also common foragers on the other two trees on this Branch (Table 8.7). Bird assemblages on the two trees classified on Branch 4 were dominated by silvereyes, with this being the only species observed on tree H. However, crescent honeyeaters and little wattlebirds also regularly visited tree S, with crescent honeyeaters comprising a far greater proportion of the visits to this tree than to any other (Table 8.7).

Although differences in the bird assemblages between Branches 5, 6 and 7 of the dendrogram (Fig. 8.6) were not clearly defined, trees classified on each branch were dominated by particular species (Table 8.7). Bird assemblages on Branches 5, 6 and 7 were dominated by yellow wattlebirds, New Holland honeyeaters, and swift parrots, respectively (Table 8.7). Yellow wattlebirds were by far the most common species on all of the trees classified on Branch 5, and were the only visitors to tree J. The only species to spend a lot of time foraging in any of the trees dominated by yellow wattlebirds was the swift parrot on tree T (Table 8.7). Of the trees classified on Branch 6, New Holland honeyeaters dominated the bird assemblages on trees L and N, far more than they did on trees W and R. Yellow wattlebirds were also regular visitors to all of these trees, with swift parrots also spending lots of time foraging in tree W, and yellow-tailed black cockatoos in tree R. Of the trees with bird assemblages dominated by swift parrots, New Holland honeyeaters were regular but not abundant visitors to all, and silvereyes and yellow wattlebirds were common on tree Q (Table 8.7).

Only four trees were observed being defended by territorial birds. Trees C and K were defended by little wattlebirds, resulting in few other birds feeding in these trees (Table 8.7). In contrast, tree A was defended by noisy miners but this did not prevent eastern rosellas from foraging regularly. Similarly, New Holland honeyeaters and swift parrots were not prevented from foraging on tree W by the defensive efforts of yellow wattlebirds (Table 8.7). However, on the defended trees, A and W, musk lorikeets and swift parrots exhibited the lowest median durations for foraging bouts of any trees they visited (Table 8.6), and never foraged in the lower halves of the canopies (Table 8.4). In addition, eastern rosellas always entered tree A in the upper half of the canopy whereas they sometimes commenced foraging in the lower halves of the canopies of the other five trees they visited (Table 8.5).

8.4 Discussion

8.4.1 Flower visiting birds

Ten of the 11 bird species previously known to feed on *E. globulus* flowers (Thomas 1980, Brown 1989, Hingston 1997, Hingston and Potts 1998) were observed doing so during this study. Of the 14 species observed here, four have never been recorded feeding on *E. globulus* (Brown 1989, Hingston 1997, Hingston and Potts 1998). These are the first recorded cases of noisy miners, green rosellas, yellow-tailed black cockatoos and spotted pardalotes feeding on flowers of *E. globulus*.

Several of the bird species recorded feeding from the flowers of *E. globulus* during this study are not generally regarded as anthophilous. The two rosellas and the cockatoo are predominantly seed-eaters (Crome and Shields 1992), and the pardalote mostly a leaf-gleaner (Woinarski 1985). However, species of rosellas and pardalotes have been recorded as casual to persistent visitors to flowers, including those of eucalypts (Paton and Ford 1977, Paton 1982b, Brown 1989, Franklin 1999). My study found that eastern rosellas were regular visitors to flowers of *E. globulus*, as did Brown (1989), while the green rosella was a casual visitor. Foraging rosellas are likely to be effective pollinators because they placed their heads into the centre of the flower while licking nectar. This is in contrast to the eucalypt flower-chewing of the crimson rosella *Platycercus elegans* (Gmelin) observed by Paton and Ford (1977). Yellow-tailed black cockatoos also licked nectar but, as their tongues are much larger, their beaks and heads remained distant from the stigmata. However, their tongues probably contacted the stigmata, which may have resulted in pollination. Another member of the Cacatuidae, the little corella *Cacatua sanguinea* Gould, has also been observed taking nectar in the Northern Territory (Franklin 1999).

Such nectar-feeding by bird species not usually regarded as anthophilous has been observed on numerous occasions. Flowers of *Eucalyptus* are sometimes visited by thornbills and shrike-thrushes (Ford *et al.* 1979, Paton 1986b). In New Zealand, starlings, sparrows, mynas and chaffinches take nectar of the

native myrtaceous tree *Metrosideros excelsa* Sol. ex Gaertn. (Schmidt-Adam *et al.* 2000). Pardalotes, thornbills, trillers and ravens consume nectar of *Grevillea petrophiloides* Meisner in Western Australia (Hopper and Burbidge 1986). Franklin (1999) also recorded a wide range of insectivorous, frugivorous, omnivorous and granivorous birds feeding regularly on seasonally abundant nectar in the Northern Territory. Nectarivory by birds unspecialised for this diet, such as warblers, is also common in the Canary Islands (Olesen 1985).

8.4.2 Foraging height

Many anthophilous bird species favoured the upper halves of *E. globulus* canopies as foraging areas, but no species preferred the lower halves, when flowers were evenly distributed between the upper and lower halves. This suggests that pollination services provided by birds, especially smaller species, is greater in the upper than the lower halves. This has previously been documented in the related *Metrosideros collina* in Hawaii, where the contributions by birds to fruit set increased significantly (approximately doubled) with height in the canopy across the range from 1 - 13 m above the ground (Carpenter 1976). Furthermore, the more frequent commencement of foraging by birds in the upper halves suggests that the deposition of outcross pollen would be greater in the upper than the lower canopy. This is particularly so for swift parrots and musk lorikeets, which exhibited strong tendencies towards entering the tree near its crown before working downwards through the canopy. This is consistent with outcrossing rates being higher at 20 - 25 m, than 2 - 5 m, above the ground in self-compatible trees of *E. globulus* (Patterson *et al.* 2001), and suggests that birds play a major role in the deposition of outcross pollen on stigmata of this species.

A possible explanation for the observed vertical distributions is the frequent aggression displayed by the Meliphagidae, which usually involves larger species dominating smaller species (Bond and Brown 1979, Ford 1979, Hopper and Moran 1981, Ford and Paton 1982, Newland and Wooller 1985, McFarland 1986, Rasch and Craig 1988, Franklin *et al.* 1989, Ramsey 1989). It

may be that birds favoured the upper halves of canopies because they were less likely to be attacked from above by another bird, and it was easier for them to see an approaching bird and make a speedy exit from the tree. Such an explanation accords well with the stronger affinity of smaller species, than larger species, with the upper halves of canopies. The tendency for New Holland honeyeaters to show less affinity with the upper halves of canopies than honeyeaters of similar size, and the larger little wattlebird, is also consistent with this hypothesis as New Holland honeyeaters may dominate larger species by attacking them in pairs (McFarland 1986). Similarly, the lower affinity of noisy miners than the two wattlebird species with the upper halves of canopies can be attributed to the renowned aggression of noisy miners towards other birds (Loyn 1985, Brown 1989, Franklin *et al.* 1989). In further support of this hypothesis, several species of Psittacidae exhibited stronger affinities for the upper halves of canopies defended by large Meliphagidae than they did in undefended trees.

An alternative explanation for birds spending more time foraging on flowers in the upper halves of canopies, when flowers were just as abundant in the lower halves, is that more nectar and/or pollen may have been produced per flower higher in the canopy. However, the inverse relationship between bird body mass and propensity to forage in the upper halves of canopies suggests this is unlikely. When floral resources are unevenly distributed, larger bird species tend to monopolise the areas where resources are most abundant; relegating the smaller species to areas where resources are sparse (Ford 1979, Ford and Paton 1982, Pimm and Pimm 1982, Newland and Wooller 1985, McFarland 1986, Rasch and Craig 1988, Ramsey 1989). In this situation, smaller species exhibited stronger propensities to forage in the upper halves than did larger species, suggesting that resources were not more abundant in the upper halves.

Differences in foraging height by anthophilous birds in other tree species were also noted by Ford *et al.* (1986), Rasch and Craig (1988) and Ramsey (1989). In contrast to this study, both Rasch and Craig (1988) and Ramsey

(1989) found that smaller honeyeaters foraged proportionately more in the lower canopies of flowering trees than did larger species. However, the findings of those two studies can be attributed to resource availability rather than inherent size related affinities with different positions in the canopies. Blossoms were less abundant in the lower than the upper canopies in both studies, and the vertical distributions may have reflected the larger birds excluding the smaller ones from the abundant resources in the upper canopy (Rasch and Craig 1988, Ramsey 1989). In the other previous study, where information on the vertical distribution of flowers was not recorded, body mass was not related to foraging height. Little lorikeets *Glossopsitta pusilla* (Shaw) (42 g), red wattlebirds *Anthochaera carunculata* (Shaw) (100 - 130 g) and scarlet honeyeaters *Myzomela sanguinolenta* (Latham) (8 - 9 g) tended to forage on higher flowers than did noisy friarbirds *Philemon corniculatus* (Latham) (92 g) and eastern spinebills *Acanthorhynchus tenuirostris* (Latham) (8 - 13 g) (Ford *et al.* 1986). Even when the different food source preferences were taken into account, there was still no relationship between body mass and foraging height. Little lorikeets (42 g) and red wattlebirds (100 - 130 g) fed higher on eucalypt flowers than did noisy friarbirds (92 g), while scarlet honeyeaters (8 - 9 g) fed higher on mistletoe flowers than did eastern spinebills (8 - 13 g). Aggressive dominance also did not appear to play a role in red wattlebirds foraging higher than noisy friarbirds, because there was no consistent winner from the frequent aggressive encounters between these two species (Ford *et al.* 1986).

Differences between trees in the propensity for birds, particularly large species, to favour the upper half of the canopy may account for differences between trees of *E. globulus* in the relative numbers of seeds per capsule in the upper and lower canopy (Patterson *et al.* 2001). However, such variations in fecundity between trees could also be the result of the observed differences in bird assemblages between trees (Patterson *et al.* 2001).

8.4.3 Durations of foraging bouts

Shorter foraging bouts within canopies by the Meliphagidae than by Psittaciformes suggest that the former may be more effective outcrossers, assuming that the two taxa have broadly similar flower-visiting rates. This is consistent with observations of the purple-crowned lorikeet *Glossopsitta porphyrocephala* Dietrichsen foraging methodically over each branch of a flowering eucalypt (Christensen 1971), which that author suggested would lead to extensive self-pollination (Christensen 1971). However, the effect of foraging bout length on outcrossing rates will be modified by pollen carryover. Pollen carryover is likely to be extensive in birds because the quantities of pollen carried are much greater than the amounts deposited on stigmata (Paton 1982b, Robertson 1992). As swift parrots carry larger pollen loads than the Meliphagidae (Chapter 7), Psittaciformes may have greater pollen carryover than meliphagids, thereby negating the difference in foraging bout length between the two taxa. However, Psittaciformes contact stigmata of eucalypts more frequently than do meliphagids (Paton and Ford 1977), which should cause outcross pollen loads to be lost to stigmata more quickly from Psittaciformes than from meliphagids thereby reducing differences in pollen carryover between the two taxa (Thomson and Plowright 1980).

Outcrossing rates facilitated by birds are likely to be modified by the presence of other individuals, both conspecifics and heterospecifics. Maximum pollen transfer between plants occurs when pollinators move between plants frequently (de Jong *et al.* 1993, Klinkhamer and de Jong 1993), such that foraging bouts are frequent but the number of flowers visited per bout is small (Paton and Ford 1983). However, the factors that make a plant attractive to pollinators, large numbers of flowers that each secrete large quantities of nectar, promote pollinator behaviour that both enhances and reduces outcrossing rates. By attracting numerous pollinators to a plant, these factors promote the importation of outcross pollen. However, these same factors encourage pollinators to remain foraging on that plant for long periods, decreasing the proportion of outcross pollen transferred to stigmata

as outcross pollen on the pollinator is replaced by self pollen (de Jong *et al.* 1993, Klinkhamer and de Jong 1993). For this reason, aggressive interactions between birds that encourage individuals to shorten the duration of their foraging bouts will promote outcrossing, provided that the displaced birds move to conspecific trees. This was apparent in this study, with territorial aggression by Meliphagidae appearing to facilitate shorter foraging bouts by Psittacidae. Hence, meliphagids may increase the pollinator effectiveness of psittacids, such as the swift parrot which is known to be an effective pollinator of this tree (Chapters 6 and 7), in addition to pollinating the flowers themselves.

8.4.4 Bird communities on trees

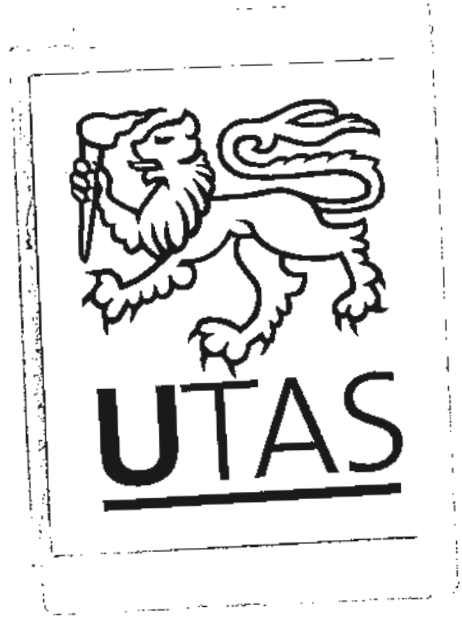
The geographic variation in assemblages of birds feeding on *E. globulus* flowers was mostly longitudinal, with musk lorikeets, little wattlebirds, noisy miners and eastern rosellas being the only species observed along the eastern side of the Derwent Estuary. Hingston and Potts (1998) also found longitudinal variation in bird visitors to the flowers of *E. globulus*, with musk lorikeets and little wattlebirds being more common on the east coast of Tasmania than at Hobart. However, swift parrots and yellow wattlebirds were also common on Tasmania's east coast (Hingston and Potts 1998), indicating that this geographic variation is not a simple case of replacement of a western assemblage with an eastern assemblage.

This geographic variation in anthophilous bird communities may serve to limit long distance pollen dispersal. As a result, birds may not import contaminant *E. globulus* pollen into seed orchards separated by a few kilometres from conspecifics.

8.5 Conclusions

Numerous bird species visit the flowers of *E. globulus* and almost certainly pollinate the flowers, particularly those higher in the trees. As swift parrots are known to be effective pollinators of *E. globulus* (Chapters 6 and 7), observations of swift parrots entering, and spending time in, the top halves

of trees more than the lower halves could explain the greater outcrossing rates and numbers of seeds per capsule in the upper parts of the canopy (Patterson *et al.* 2001). However, the same foraging patterns were exhibited by other bird species, indicating that other species may also be effective pollinators. This is supported by the Meliphagidae carrying large quantities of eucalypt pollen on their heads and bills, albeit smaller loads than those carried by swift parrots (Chapter 7). The maintenance of a diverse avifauna may be important to pollination of *E. globulus* as the profile of flower visitors differ greatly geographically. Furthermore, interspecific interactions promote more frequent intertree movements by birds, thereby promoting outcrossing.



Chapter 9

Pollination services provided by various size classes of flower visitors to *Eucalyptus globulus* subsp. *globulus* in southeastern Tasmania

Abstract

The flowers of *Eucalyptus globulus* subsp. *globulus* were visited by a wide variety, and large numbers, of insects and birds within its natural distribution in southeastern Tasmania. Both insects and birds were able to pollinate the flowers. In spite of this, seed set from flowers within 5 m of the ground was significantly limited by the amounts of outcross pollen deposited on stigmata. Hence, sufficient numbers of effective pollinators did not visit the flowers within 5 m of the ground. This degree of pollen limitation was comparable to that in an extralimital Chilean population of *E. globulus*, suggesting pollination services to these flowers were inferior to those to which *E. globulus* has evolved. Pollination services to *E. globulus* flowers near the ground are known to be inferior to those in the tops of trees. Therefore, *E. globulus* may be adapted to these better pollination services in their upper canopies. However, the consistently poor seed set in these flowers may also reflect a recent decline in the quality of pollination services. The most abundant visitor to these flowers, and major nectar consumer, was the western honey bee *Apis mellifera*. Exposure to hundreds of honey bee visits during the lifetime of a flower still resulted in lower seed set than a single visit by a swift parrot *Lathamus discolor*. Therefore, honey bees are inefficient pollinators of *E. globulus* and their introduction may have caused a decline in pollination services to *E. globulus* by displacing more efficient pollinators such as the swift parrot, or reducing the quantity of pollen available for transfer by birds. Because effective bird pollinators spend far more time foraging in the upper halves of *E. globulus* canopies than the lower halves, these two explanations for the current poor standard of pollination services to flowers within 5 m of the ground are not mutually exclusive.

That is, pollen limitation to flowers near the ground may be the result of effective bird pollinators being displaced from these flowers by competing honey bees. The inefficiency of honey bees as pollinators of *E. globulus*, together with the likelihood that they often displace more efficient bird pollinators and reduce the quantity of pollen available for transfer by birds, means that in most situations the deployment of honey bee hives in seed orchards is unlikely to enhance seed production in *E. globulus*.

9.1 Introduction

The Tasmanian native tree *Eucalyptus globulus* Labill. subsp. *globulus* (hereafter *E. globulus*) is grown extensively in commercial forestry plantations in temperate regions of the world (Eldridge *et al.* 1993, Tibbits *et al.* 1997). Plantation stock are grown mostly from seeds, that are increasingly being collected from seed orchards of trees selected for characters desired by the forest industry (Eldridge *et al.* 1993, Tibbits *et al.* 1997). However, seed yields from orchards of *E. globulus* in Tasmania and Portugal have been regarded as poor, yielding no more than 6 kg / ha at 9 - 10 years of age (Eldridge *et al.* 1993, Moncur *et al.* 1995).

The production of seeds in *Eucalyptus* is dependent mainly upon pollen transfer between flowers (allogamy). This is because of the absence of parthenocarpy in this genus (Griffin *et al.* 1987), as well as the partial barrier to pollen transfer between anthers and stigma of the same flower (autogamy) that results from protandry (Pryor 1976). Therefore, poor seed yields in *E. globulus* may be the consequence of inadequate pollination services. A recent study in Chile found that the numbers of seeds produced per open-pollinated flower could be significantly increased by supplementary manual outcross pollinations (Harbard *et al.* 1999). However, an earlier Tasmanian study found that the numbers of seeds produced from open-pollinated flowers of *E. globulus* were not significantly different from bagged flowers that were hand cross-pollinated after emasculation (Hardner and Potts 1995).

At least one Tasmanian species of bird, the swift parrot *Lathamus discolor* (Shaw), is an effective pollinator of *E. globulus* (Chapter 6). The large quantities of pollen carried on the bills and heads of several bird species (Chapter 7), together with outcrossing rates and numbers of seeds per capsule being higher in parts of canopies of *E. globulus* where anthophilous birds are most abundant (Patterson *et al.* 2001, Chapter 8), suggests that many Tasmanian bird species are effective pollinators. However, the tendency for birds to mainly forage in the upper sections of canopies (Chapter 8) means that birds may not contribute greatly to pollination of *E. globulus* flowers near the ground.

The animals that do forage heavily on flowers of *E. globulus* near the ground, and consume most of the nectar in this part of the canopy, are introduced honey bees *Apis mellifera* L. (Chapter 4). However, honey bees and other insects are far less effective than swift parrots as pollinators of *E. globulus*. In contrast to single visits by swift parrots to flowers with receptive stigmata, single visits by insects did not significantly enhance seed set (Chapter 6). But, as single visits by insects can facilitate some seed production (Chapter 6), there is a possibility that insects could cause full seed set to occur through multiple flower visits (Keys *et al.* 1995, Olsen 1997). Each flower usually lasts for about two weeks (Brown 1989), and the heavy insect visitation rates to flowers (Hingston and Potts 1998, Chapters 4 and 6) would result in them being visited numerous times by insects.

This study investigated the relative contributions of different size classes of animals to pollination of *E. globulus* within 5 m of the ground in southeastern Tasmania. In particular, it examined whether exposure to insects throughout the lives of flowers leads to full seed set, and if birds make major contributions to pollination of flowers of *E. globulus* within 5 m of the ground. By relating seed production to the amounts of nectar consumed by different size classes, their respective pollinator efficiencies were calculated. The contributions of various taxa within size classes as pollinators were also explored, as were the factors influencing their abundances on flowers.

9.2 Methods

9.2.1 Experiment 1

9.2.1.1 Study sites

The first experiment into the relationships between floral visitors and seed production was conducted on both sides of the Derwent Estuary in southeastern Tasmania between October 1998 and January 1999 (Fig. 9.1, Table 9.1). Trees studied on the eastern side of the estuary were all planted as ornamentals, whereas those on the western side consisted of ornamentals at Waldies Rd and remnant trees in pasture at Tinderbox. Studies into nectar production and consumption were conducted during October 2000 on remnant trees in pasture at Premaydena and the Nubeena Back Rd on the Tasman Peninsula 22 - 45 km east to southeast of the other sites (Table 9.1).

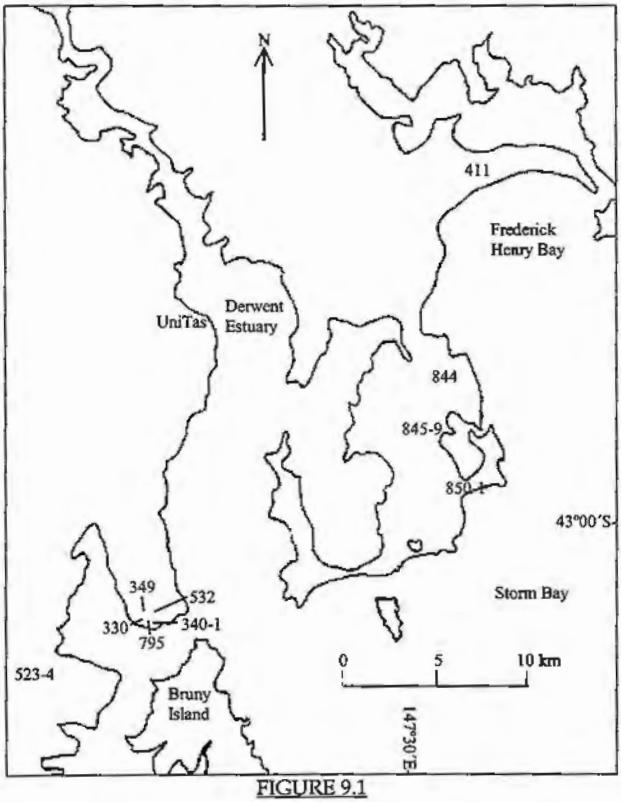


FIGURE 9.1

Locations of trees of *E. globulus* upon which various exclosures were placed around flowers. Numbers denote trees used in Experiment 1. Trees in Experiment 2 were at the University of Tasmania (UniTas).

Site	Tree identities	Altitude (m)	Mean rainfall (mm/y)
Hobart Airport	411	0 - 10	400 - 600
Forest Hill Rd	844	0 - 10	400 - 600
School Rd	845, 846, 849	20 - 30	400 - 600
Clifton Beach	850, 851	0 - 10	400 - 600
Tinderbox	330, 340, 341, 349, 532, 795	50 - 100	600 - 900
Waldies Rd	523, 524	100 - 110	900 - 1200
Premaydena	422	10	600 - 900
Nubeena Back Rd	1337	170	600 - 900

TABLE 9.1

Locations of trees of *E. globulus* upon which various exclosures were placed around flowers (see Fig. 9.1), and the altitude and mean annual rainfall [www.bom.gov.au/cgi-bin/climate.cgi_bin_scripts/annual_rnfall.cgi] at these locations.

9.2.1.2 Experimental design

The effectiveness of flower visitors as pollinators was investigated by excluding various size classes of animals from groups of flowers. Small branches in close proximity were allocated randomly to the following treatments: 1) complete exclusion in terylene bags (PBS International, UK); 2) fibreglass fly-wire mesh with 1 mm apertures; 3) woven nylon fishing net with 5 mm apertures; 4) steel bird-wire with 12 mm apertures; 5) steel chicken-wire with 25 mm apertures; and 6) open pollination (Plate 9.1). Between one and three replicates of these treatments were placed on each tree, depending on the numbers of flowers available.

The intention behind using a wide range of aperture sizes was to create as much variation in visitor profiles between treatments as possible, particularly for the most common insect visitor; the western honey bee *Apis mellifera* (Hingston and Potts 1998, Chapter 4). Honey bees foraged on inflorescences of *Banksia menziesii* R.Br. inside cages with 10 mm apertures (Ramsey 1988) and just managed to pass through 6 mm openings to enter their hives (Boylan-Pett *et al.* 1991). However, they were deterred from foraging on *Penstemon pseudospectabilis* by cages with 20 mm apertures (Lange and Scott 1999). Hence, it was decided to use this range of aperture sizes in the hope that they would pass through the larger apertures but not the smaller.

PLATE 9.1

Caging treatments on *E. globulus* tree 524.

Between five and 70 flowers were allocated to each of the six treatments, which were confined to branches within 5 m of the ground that could be accessed while standing on an orchard ladder (Plate 9.2). Any flowers that had already shed their opercula prior to caging were removed, as were any old capsules. Leaves were also removed from around buds to prevent moisture build-up in the terylene bags and so that they did not inhibit insect access to flowers within the cages or obscure the view of the researcher in all treatments. Small branchlets within each of the six treatments were tied together to keep flowers near the centre of the exclosure so that large visitors that could not pass through the mesh were unable to reach flowers by probing through the mesh. Any flowers that may have been reached from outside the exclosures were marked prior to exclosure removal. These flowers and the exclosures were removed immediately after flowering had ceased. Opercula from within the terylene bags, fly-wire, and fishing net were collected and their external diameters measured to determine mean flower size on each tree.

PLATE 9.2

Eucalyptus globulus tree 524, showing the position of the caging treatments at the base of the canopy.

9.2.1.3 Flower visitors

Insect surveys were restricted to fine mild, warm, or hot weather between 0900 h and 1730 h. This involved 5 min counts on each treatment, in random order, except the total exclusion. The total numbers of flowers visited by each taxon during 5 min were recorded. However, when beetles occurred in large numbers, a single spot count of the number present on the experimental flowers was conducted because it was not possible to keep track of each individual's movements over a five minute period. This value would generally have been only slightly lower than the count of numbers of flowers visited because beetles usually moved between flowers infrequently. By also counting the number of flowers open in each treatment, it was possible to calculate visitation rates for insect taxa as flower visits per open flower per 5 min.

Birds were monitored between 0700 h and 1800 h on fine days, with most surveys being conducted before 1000 h when birds were most active. The order in which trees at any site were surveyed was randomised. The total time spent within the canopy of each tree by each anthophilous bird species during a 30 min period was determined by watching the canopy from a distance of 20 - 30 m. Pardalotes, which fed occasionally from flowers, were excluded from the analysis because they were too small to monitor accurately in the larger trees and usually fed by leaf gleaning. Because the number of flowers on a tree could not be counted, bird visitor profiles were expressed as proportions of the total time spent by anthophilous birds in the canopy of each tree while flowers in the open pollinated treatment bloomed. The proportions for each species on each day were multiplied by the percentage of flowers that were blooming in the open pollinated treatment on that day. These were then totalled, and the proportions calculated for each species. The avian taxonomic nomenclature used is that of Christidis and Boles (1994).

Nocturnal insects and mammals were not surveyed because casual observations with the aid of a torch, and three hours of video footage taken

early on one night during peak flowering at Tinderbox, did not reveal any nocturnal flower visitors to *E. globulus*. In addition, nectar standing crops were not diminished overnight in exposed flowers, in comparison to bagged flowers (Chapter 4). For these reasons, nocturnal visitors were assumed to be negligible.

9.2.1.4 Fecundity measurement

The numbers of capsules developing in each treatment were counted during April 1999. Capsules were collected the following November, and the numbers of viable seeds in each capsule were counted. The numbers of capsules present in each treatment at the time of harvest were used in the data analysis, except in cases where branches had died since April, in which case the April counts were used. This was deemed adequate because only 52 of the 922 capsules present in April, on branches that were still alive in November, had disappeared by November. For branches where some capsules had dehisced before harvesting, the average number of seeds per capsule in non-dehisced capsules on that branch was multiplied by the total number of capsules to determine the number of seeds produced per flower.

Between 10 and 20 other open pollinated flowers near the treatments had supplementary outcross pollen from numerous trees applied to receptive stigmata to determine the maximum possible seed set for flowers in the vicinity (Gross 1996). These pollinations were conducted at the end of the day after insect activity had ceased, to reduce the chances of this outcross pollen being secondarily transferred to other flowers by insects (Heinrich 1975, DeGrandi-Hoffman and Martin 1995, DeGrandi-Hoffman and Watkins 2000). All pollen was stored in gelatin capsules over silica gel in a refrigerator between collection and use, and in an insulated container with an ice-block when taken into the field.

Initial pollen supplementations were done using an old mix of pollen from 13 trees not used as females in this experiment (DW1), which had been stored in gelatin capsules over silica gel in a refrigerator for two years. However

the viability of this pollen, determined by counting the percentage of pollen grains that had germinated after 24 h on an agar plate at room temperature (Potts and Marsden-Smedley 1989), was found to be very low (Table 9.2). For this reason, a fresh pollen mix was collected from eight trees not used as females in this experiment (AH1). The viability of this pollen was much higher (Table 9.2).

Pollen mix	# gelatin capsules tested	mean % germination	max. % germination	min. % germination
DW1	4	1.6	2.8	0.9
AH1	2	57.3	66.2	48.4

TABLE 9.2

Viability of pollen of *E. globulus* used in supplementary pollinations as percentages of grains germinated after 24 h on agar at room temperature.

Because of the difference in germination rates between the two pollen mixes (Table 9.2), their viabilities were also compared by conducting paired t-tests on the numbers of capsules set per flower, seeds per capsule, and seeds per flower resulting from supplementary pollinations on trees where both mixes were used (Table 9.3). Although the pollen mixes resulted in no statistically significant differences in the numbers of capsules set per flower pollinated, or in the numbers of viable seeds per capsule set, use of the older DW1 mix resulted in significantly fewer seeds per flower pollinated than did the use of the AH1 mix (Table 9.3). Consequently, it was decided to only use the data from flowers pollinated with the AH1 mix as a measure of the maximum possible fecundity for flowers on each tree. Between 8 and 17 flowers per replicate received supplementary pollen from the AH1 pollen mix.

Fecundity variable	mean DW1	mean AH1	*P*
capsules/flower	0.594 (0.271)	0.651 (0.315)	0.3223^{NS}
seeds/capsule	9.24 (5.83)	12.94 (12.46)	0.1216^{NS}
seeds/flower	5.70 (5.16)	9.15 (9.05)	0.0270^{*}

TABLE 9.3

Mean fecundity of flowers of *E. globulus* receiving supplementary hand pollinations with outcross pollen mixes DW1 and AH1, with standard deviations shown in brackets. *P*-values were derived from paired t-tests using 12 trees as replicates.

9.2.1.5 Resource consumption

It was not possible to measure standing crops of nectar within the cages to determine the proportion of nectar consumed by each size class of visitor. As a result, this was estimated in a separate experiment on 11 - 12 October 2000. Because trees did not bloom during spring 2000 at any of the experimental sites that had been used in spring 1998, it was necessary to conduct this experiment on the Tasman Peninsula. This was the closest location to the original sites with sufficient flowers. Between four and twelve flowers were enclosed in terylene bags and each of the experimental cages, of aperture diameters 1 mm, 5 mm, 12 mm and 25 mm, or left uncaged. As for the experiment into the effects of caging on seed production, leaves were removed from around the flowers, branchlets were tied together, and any flowers that may have been reached from outside the cage were discarded (see Section 9.2.1.2). All exclosures were set-up and removed late in the afternoon (Table 9.4), after insect activity had declined to negligible levels.

Tree	Site	cage set-up	flower removal	nectar measurements
1337	Nubeena Back Rd	1500-1630h	1700-1730h	1900-2200h
422	Premaydena	1700-1830h	1800-1830h	2200-0100h

TABLE 9.4

Trees of *E. globulus* on which nectar consumption in exclosures was examined, the times when the exclosures were set up on 11 October 2000 and removed on 12 October 2000, and the times when nectar was measured on 12 - 13 October.

Nectarivorous bird visitors to each tree were monitored by recording the amounts of time each species spent foraging in the canopy during five 30 minute observation periods scattered throughout the day while the cages were in place. Insect monitoring on each tree consisted of seven one minute spot counts throughout the day for the entire section of canopy where the experiment was conducted. This ensured that the observer spent very little time near the flowers to prevent birds from being deterred from visiting experimental flowers.

At the end of this period, female-phase flowers were picked and placed stigma up in an egg carton. Nectar was diluted by adding 100 µl of distilled water to each hypanthium with a micropipette. This was allowed to stand for approximately 10 minutes before drawing up with a clean 20 µl micropipette (Mallick 2000). A hand-held refractometer (Atago N1, 0-32%; intra-MARK Catalogue no. 708707, Atago, Tokyo, Japan) was used to measure the concentration of 40 µl of the extracted solution. The zero-setting for the refractometer was checked every 30 minutes against samples of distilled water. Washes and subsequent nectar measurements were conducted twice for each flower, in case some nectar was not removed during the first wash (Mallick 2000). The percentage of sugar measured by the refractometer was converted to µg sugar / µl nectar solution using Table 5.2 in Kearns and Inouye (1993). The amount of sugar present in each wash was then calculated by multiplying the µg sugar / µl nectar solution by the µl of solution. The solution volumes used in these calculations were those extracted from the flower except if less than 100 µl could be extracted after the second wash, in which case the volume was assumed to be 100 µl.

9.2.1.6 Data analysis

Fecundity was compared between treatments, and against supplementary cross-pollinations. To standardise fecundity across trees and replicates, pollinator effectiveness (pe) for the suite of animals visiting flowers in each treatment was calculated as the percentage of the maximum possible fecundity on that replicate or tree. This was calculated using the formula:

$$pe = 100*(F_T/F_S)$$

where F_T = mean fecundity for flowers in the treatment; and F_S = mean fecundity for flowers receiving supplementary hand pollinations with the outcross mix AH1.

Three trees were excluded from the fecundity analysis because of poor capsule set. Tree 844 was excluded because it failed to set any capsules in its canopy, and tree 851 was excluded because the entire experimental section of the tree died. Tree 795 was excluded because none of its flowers receiving

supplementary outcross pollen from the AH1 mix produced capsules, making it impossible to calculate pe scores for the other treatments.

The pe scores for the numbers of viable seeds per flower on the remaining 12 trees were compared using Two-Way Analysis of Variance with the various treatments and trees as fixed sources of variation, using the SigmaStat programme (Jandel 1994). Whenever the treatments were replicated on one tree, the data from all replicates on that tree were pooled to ensure independence of the replicates in the statistical analysis. In all cases the distributions of the data were normalised by square root transformation of the pe scores. These analyses were conducted across all 12 trees, the four partially self-compatible (SC) trees only (those that produced seeds within exclusion bags) and the eight fully self-incompatible (SI) trees only (those that did not produce seeds within exclusion bags). Whenever trees or treatments were statistically significant sources of variation, subsequent pairwise multiple comparisons were conducted using Student-Newman-Keuls Method.

The effects of the various exclosures on insect visitation to flowers were investigated on the 12 trees used in the analysis of the effects of exclosures on fecundity. The visitation rate by all insects was the dependent variable in a Two-Way Analysis of Variance where the various treatments (apart from the exclusion bags) and trees were fixed sources of variation, using SigmaStat (Jandel 1994). Similar analyses were conducted using the pooled classes corresponding to exotic bees, native bees, wasps, ants, flies and beetles as dependent variables. In cases where the raw data did not follow a normal distribution the visitation rates were converted to flower visits per 80 h, to make them all greater than one, and then transformed by taking their square roots. If the data were still non-normal after square root transformation, the Two-Way Analysis of Variance was conducted on the ranks in the raw data set. Whenever trees or treatments were statistically significant sources of variation, subsequent pairwise multiple comparisons were conducted using Student-Newman-Keuls Method.

The effects of tree and caging treatment on nectar standing crops from harvested flowers were also investigated using Two-Way Analysis of Variance. The distributions of these data were normalized using $\log_{10}$ transformations. Subsequent pairwise tests between treatments were conducted using Student-Newman-Keuls Method with SigmaStat (Jandel 1994).

Standing crops of nectar in each treatment were expressed as percentages of those in the terylene bags on that tree, to determine the percentage of nectar consumed in each treatment. Pollinator efficiency in each treatment was then calculated by dividing the mean pollinator effectiveness by the mean percentage of final nectar standing crop in exclusion bags that was consumed in that treatment. Pollinator efficiency scores were calculated for the four SC trees, eight SI trees, and all 12 trees.

Pollinator effectiveness scores were then related to the insect visitor profile for each experimental branch of flowers, where flower visiting insects were common, on the 12 trees that produced capsules from supplementary outcross pollinations. Differences in the effectiveness of various insect assemblages were investigated by relating their compositions to fecundity in each 5 mm, 12 mm and 25 mm exclusion cage, and in open-pollinated flowers. Partially SC and fully SI trees were analysed separately. These experimental branches were ordinated according to the mean visitation rates by insect species, using semistrong hybrid multidimensional scaling, with the computer programme PATN (Belbin 1993). Those insect species that were significant ($P < 0.05$) to the compositional variation between experimental branches in all replicates, as determined by a Monte Carlo technique, were fitted to the plot as vectors. The associations of the pollinator effectiveness scores, calculated within each replicate for the numbers of capsules per flower, seeds per capsule, and seeds per flower, to the compositional variation in the ordination plot were also determined using a Monte Carlo technique and these vectors fitted to the plot if statistically significant.

Using the same ordination technique, the effectiveness of various bird assemblages was investigated by relating their proportional compositions to fecundity in branches of open-pollinated flowers on the 12 trees. This was restricted to two data sets; all trees and SI trees. Partially SC trees were not investigated separately as there were only three replicates in this data set, as a consequence of excluding tree 849 because no birds were seen visiting flowers on this tree. Although a crescent honeyeater was observed inside one 25 mm mesh cage, this treatment was not included in the analysis of bird pollinators because it was not known which other species were small enough to pass through this aperture size.

Relationships between flower visitation rates by various insect taxa and plant fecundity were also explored with regressions using the procedure 'Proc Reg' in the computer programme SAS (SAS Institute 1992). The data were standardised by controlling for the confounding factors (Table 9.5), and regressions were conducted on the residuals. The statistical significance of the residuals of visitation rates by each insect taxon to each experimental branch as predictors of the residuals of the pollinator effectiveness scores for the numbers of seeds produced per flower on each experimental branch were investigated using individual regressions. The *P*-value designated as the level of significance (0.05) was adjusted using the Bonferroni method, to reduce the probability of making any type 1 errors (Sokal and Rohlf 1995). These regressions were conducted on all trees, SC trees only, and SI trees only, and restricted to insects observed on more than two experimental branches.

The effects of the tree-related factors on visitation rates by various insect taxa and on plant fecundity were also explored with regressions using the above SAS procedure. For the analysis of each tree-related factor, the data were standardised by controlling for the other tree-related factors (Table 9.5), and regressions were conducted on the residuals. Hence, the statistical significance of the residuals of each tree-related factor as predictors of the residuals of the pollinator effectiveness scores for the numbers of seeds

produced per flower on each experimental branch were investigated using individual regressions. Similarly, a separate set of individual regressions was conducted between the residuals of tree-related factors and flower visitation rates by various insect taxa. The *P*-value designated as the level of significance (0.05) was adjusted using the Bonferroni method within each set of regressions, to reduce the probability of making any type 1 errors (Sokal and Rohlf 1995). These regressions were conducted on all trees, SC trees only, and SI trees only, and restricted to insects observed on more than two experimental branches. These two sets of regressions were then compared to determine whether visitation rates by any insect taxa were consistently related to increased fecundity, via common responses to tree-related factors.

Confounding Factors	Codes
site where the tree grew	
identity of the tree	
distance of the tree from the nearest flowering conspecific	Distance
height of the experimental branch above the ground	Height
aspect of the experimental branch on the tree	Aspect
numbers of flowers on the experimental branch	#Flowers
mean operculum diameter for the tree	Diameter
caging treatment	
intensity of flowering on the tree when peak flowering occurred on the experimental branch	Peakint
date of peak flowering on the experimental branch	Peakdate

TABLE 9.5

Confounding factors for which the data were standardised prior to regressions being conducted between flower visitation rates and fecundity. The codes are used in Tables 9.19, 9.20 and 9.21.

9.2.2 *Experiment 2*

9.2.2.1 Experimental design

Trees between 1.5 and 3 m in height of the dwarf precocious variety of *E. globulus* 'Lighthouse provenance' were grown in 75 litre woven carry bags. Between 23 September and 6 December 1999, flowers on each tree were allocated in approximately equal proportions to three different treatments: 1) exposure to insect visitors but not birds; 2) exposure to insects and birds, or only to birds; and 3) receiving supplementary outcross pollen. Flowers were tagged individually with coloured electrician's wire to denote the particular

treatment, and the numbers of flowers subjected to each treatment were counted.

Treatments 1 and 2 were applied sequentially to each tree so that the contributions of insects to pollination could be assessed in the absence of birds foraging concurrently in other parts of the canopy. This was done because it has been proposed that outcross pollen imported into the tree canopy by widely-foraging birds could be picked up subsequently by insects that did not move between trees, thereby increasing the insects' contributions to outcrossing (Heinrich 1975). Such secondary outcross pollination has recently been demonstrated (DeGrandi-Hoffman and Martin 1995, DeGrandi-Hoffman and Watkins 2000). Treatment 2 was usually applied first because flowers appeared to remain receptive longer when only exposed to insects. Hence, if the first flowers to open were allocated to Treatment 1, a large proportion of them were still receptive when the last flowers opened resulting in fewer flowers being able to be allocated to one treatment only.

Flowers on all 12 trees were exposed to insect visitors but not birds by enclosing them in 12 mm wire mesh for the entire time that they were open. Four trees also had approximately one-third of their flowers exposed to both birds and insects. The trees were placed in a clump near the greenhouse complex at the School of Plant Science, University of Tasmania, in Hobart while subjected to both of these treatments (Fig. 9.1). Throughout the experiment, naturally occurring *E. globulus* were flowering within 100 m of the experimental trees.

The eight trees not exposed to vertebrates at this site were taken to aviaries at the School of Zoology, University of Tasmania, in Hobart. Six of these trees were placed individually in aviaries containing either five or six swift parrots *Lathamus discolor* (Shaw), while two trees were placed singly with two or three musk lorikeets *Glossopsitta concinna* (Shaw). This was done to assess the contributions to pollination by birds in the absence of insects because

insects can reduce the pollinator effectiveness of birds by displacing them from flowers via resource competition, or reducing the amounts of pollen that birds can transfer to stigmata (Paton 1993, 1997). Throughout the period when trees were placed in aviaries, small branches of *E. globulus* bearing male-phase flowers were collected from trees growing within 800 m of the greenhouse complex as a source of outcross pollen. Approximately 20 fresh flowers were placed in vials of water every Monday, Wednesday and Friday, with flowers being picked from different trees each day. All leaves were removed from these branches as soon as they were picked, to maximise the longevity of the branches. Consequently, flower buds continued to open for approximately one week after being placed in the aviaries, resulting in open flowers from at least three different trees being present at any given time.

Supplementary outcross pollinations were applied to all flowers that were open while the tree was exposed to both Treatments 1 and 2, and also to flowers within cages that may have been reached by birds probing through the wire mesh. These pollinations were conducted at the end of the day after insect activity had ceased, to reduce the chances of this outcross pollen being secondarily transferred to other flowers by geitonogamous pollination (Heinrich 1975, DeGrandi-Hoffman and Martin 1995, DeGrandi-Hoffman and Watkins 2000). Pollen was applied to stigmata with the head of a matchstick when they appeared receptive. The pollen used was a mix collected on the 14 September 1999 from approximately 10 trees growing at Tinderbox, 15 km south of the University. This was stored subsequently in gelatin capsules in glass vials containing silica gel in a freezer.

9.2.2.2 Flower visitors

Insect visitors to flowers on trees near the greenhouse complex were monitored during sunny weather between 0900 h and 1500 h when the ambient temperature was above 15°C. Trees were monitored in random order, with the numbers of flowers visited by various taxa during 5 min periods being recorded. This was then converted to a flower visitation rate

by dividing the number of flowers visited by the number of flowers open on the tree on that day.

9.2.2.3 Fecundity measurement

Capsules were harvested on 1 November 2000, and placed in individual labelled paper envelopes to dry. After capsule dehiscence, the numbers of viable seeds in each capsule were counted.

9.2.2.4 Data analysis

The numbers of capsules produced per flower, seeds per capsule, and seeds per flower were compared between treatments. For the four trees exposed to insects and birds near the glasshouse complex, each of these fecundity variables was compared between the caged, uncaged, and supplementary pollination treatments using Two-Way Analysis of Variance with the means from each tree used as replicates. Visitation rates by each insect species, functional group, and total insects, to caged and uncaged flowers on the four trees were compared using paired t-tests, with trees as replicates, to check for differences that could have confounded the comparisons of pollinator effectiveness. If the data were non-normally distributed, Wilcoxon Signed Rank Tests were used. All of these statistical analyses were conducted with the programme SigmaStat (Jandel 1994).

Of the eight trees transported to the aviaries, only two produced seeds from flowers receiving supplementary outcross pollen, three after exposure to insects only, and two after exposure to birds only. As a consequence only one tree produced seeds after all three treatments, precluding any comparison being made between the three treatments. For this reason, the data from the two trees that produced seeds after supplementary outcross pollination (1018 and 1021) were combined with that from the four trees that were not transported to the aviaries. This allowed comparisons of the numbers of capsules per flower, seeds per capsule and seeds per flower, to be made between flowers exposed to insects only and those receiving

supplementary outcross pollen using paired t-tests with the six trees as replicates. This analysis was also conducted using SigmaStat (Jandel 1994).

Relationships between flower visitation rates by various insect taxa and plant fecundity on the six trees that produced seeds after supplementary outcross pollination were also explored with regressions. The mean numbers of seeds produced per flower within cages on each tree were converted to pollinator effectiveness scores that were percentages of the mean number of seeds produced per flower receiving supplementary outcross pollinations on that tree (see formula in Section 9.2.1.6). The data were standardised by controlling for the confounding factors of numbers of flowers on the tree and the date of peak flowering on the caged treatment, and regressions were conducted on the residuals using the procedure 'Proc Reg' in the computer programme SAS (SAS Institute 1992). The statistical significance of the residuals of visitation rates by each insect morphospecies, functional group, and all insects, to each experimental branch as predictors of the residuals of the pollinator effectiveness scores for the numbers of seeds produced per flower on each experimental branch were investigated using individual regressions. This was limited to insect taxa recorded from at least two trees. The *P*-value designated as the level of significance (0.05) was adjusted using the Bonferroni method, to reduce the probability of type 1 errors (Sokal and Rohlf 1995).

9.3 Results

9.3.1 Experiment 1

9.3.1.1 Tree details

The trees studied varied greatly in self-compatibility, size, flowering intensity and phenology, degree of isolation from sources of outcross pollen, and flower size (Table 9.6). All four trees that exhibited some self-compatibility still displayed preferential outcrossing in the form of far more seeds developing following supplementary outcross pollination than following constant enclosure in bags (Table 9.6). Flowering seasons differed between individuals at both Tinderbox and School Rd. Flowers were

generally smaller at School Rd and Clifton Beach than at other sites (Table 9.6).

site	tree	SI score	# reps	size	peak flowering intensity	peak flowering date	nearest tree (m)	operculum dia. (mm)
Tinderbox	330	100	1	3	2	14-Nov	0	14.89
Tinderbox	340	82.5	1	3	3	20-Nov	0	16.69
Tinderbox	341	100	1	3	4	9-Dec	0	16.66
Tinderbox	795	-	1	4	2	30-Nov	28	15.98
Tinderbox	349	100	3	3	4	1-Jan	7	14.82
Tinderbox	532	100	2	3	3	20-Dec	12	15.99
Waldies Rd	523	100	1	1	3	28-Nov	26	17.97
Waldies Rd	524	100	2	3	4	28-Nov	0	15.06
Airport	411	100	2	3	3	24-Nov	0	17.24
Forest Hill Rd	844	-	2	2	3	16-Nov	1000	19.37
School Rd	845	82.7	1	1	2	10-Nov	1	13.54
School Rd	846	78.7	1	1	3	10-Nov	1	13.26
School Rd	849	74.4	1	1	3	18-Dec	2	11.86
Clifton Beach	850	100	2	2	3	18-Nov	10	13.78
Clifton Beach	851	-	1	2	1	18-Nov	60	14.12

TABLE 9.6

Locations of trees studied, their self-incompatibility scores, the number of caging replicates per tree, tree size class, peak intensity of flowering, date of flowering peak, distance from the canopy of the nearest flowering conpecific, and mean operculum diameter. Self-incompatibility scores were determined by the formula (C-S)/C, where C = the mean numbers of seeds per flower following supplementary outcross pollination, and S = the mean numbers of seeds per flower in exclusion bags. Tree size classes range from 1 (small) to 4 (large). Flowering intensity scores are: 1 = less than 10% of maximum possible; 2 = 10-25%; 3 = 25-50%; 4 = more than 50%.

9.3.1.2 Avian flower visitors

Large numbers of birds were observed feeding on the flowers of *E. globulus* (Table 9.7). The 16 species comprised nine species of Meliphagidae (honeyeaters), four of Psittacidae (parrots), the silvereye (Table 9.7), as well as the spotted and striated pardalotes [*Pardalotus punctatus* Shaw and *P. striatus* (Gmelin)]. Most bird species fed almost constantly from flowers while in the trees. However, noisy miners *Manorina melanocephala* (Latham) and both pardalotes fed from flowers only occasionally in between other forms of foraging.

Species	Family	Tree number															Mean
		330	340	341	795	349	532	523	524	411	844	845	846	849	850	851	
yellow-tailed black cockatoo	Cacatuidae	0	0	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0.16
musk lorikeet	Psittacidae	0	0	0	0	0	0	0	0	99.6	7.1	0	38.6	0	96.4	48.5	19.3
green rosella	Psittacidae	0	0	0	0	0.07	0.76	0	0	0	0	0	0	0	0	0	0.06
swift parrot	Psittacidae	0	0	0	0	0.5	0	0	33.5	0	0	0	0	0	0	0	2.3
yellow wattlebird	Meliphagidae	0.7	55.4	58.1	29.4	0.6	1.8	0	0	0	0	0	0	0	0	0	9.7
little wattlebird	Meliphagidae	0	0	0	0	0	0	0	12.8	0	85.6	64.1	57.3	0	0	0.4	14.7
noisy miner	Meliphagidae	0	0	0	0	0	0	0	0	0.4	7.3	35.9	4.1	0	3.6	51.1	6.8
yellow-throated honeyeater	Meliphagidae	15.2	3.7	8.0	6.8	5.2	10.7	94.4	25.9	0	0	0	0	0	0	0	11.3
strong-billed honeyeater	Meliphagidae	0	0	0	0	0	0	0	3.8	0	0	0	0	0	0	0	0.25
black-headed honeyeater	Meliphagidae	1.8	1.6	1.8	3.7	5.9	13.5	0	1.0	0	0	0	0	0	0	0	2.0
crescent honeyeater	Meliphagidae	0	0	0	0	0	0	5.6	9.1	0	0	0	0	0	0	0	1.0
New Holland honeyeater	Meliphagidae	82.2	39.2	32.2	60.1	87.6	73.2	0	10.7	0	0	0	0	0	0	0	25.7
eastern spinebill	Meliphagidae	0	0	0	0	0	0	0	0.02	0	0	0	0	0	0	0	0.00
silvereye	Zosteropidae	0	0	0	0	0	0	0	0.7	0	0	0	0	0	0	0	0.05
time spent observing (h)		5	6.5	6.5	7	8	11	7.5	11.5	7	12	8.5	8.5	5.5	8.5	7.5	
total time spent by birds (h)		19.3	9.1	12.0	15.1	79.3	65.4	1.2	7.1	17.5	3.6	0.1	1.0	0	11.1	2.5	
side of Derwent Estuary		west	west	west	west	west	west	west	west	east	east	east	east	east	east	east	

TABLE 9.7

Percentages of time spent by each species out of the total time spent by anthophilous birds in the canopy of each tree, the time spent observing birds in each tree, and the total time birds spent foraging in the canopies during observation periods.

Strong geographic variation in bird visitor assemblages was apparent, with the major difference corresponding to the two sides of the Derwent Estuary (Table 9.7, Figs 9.2 and 9.3). Only one species, the little wattlebird *Anthochaera chrysoptera* (Latham), was observed visiting flowers of *E. globulus* on both sides of the estuary. Species richness was generally lower on the eastern than the western side of the estuary (Table 9.7).

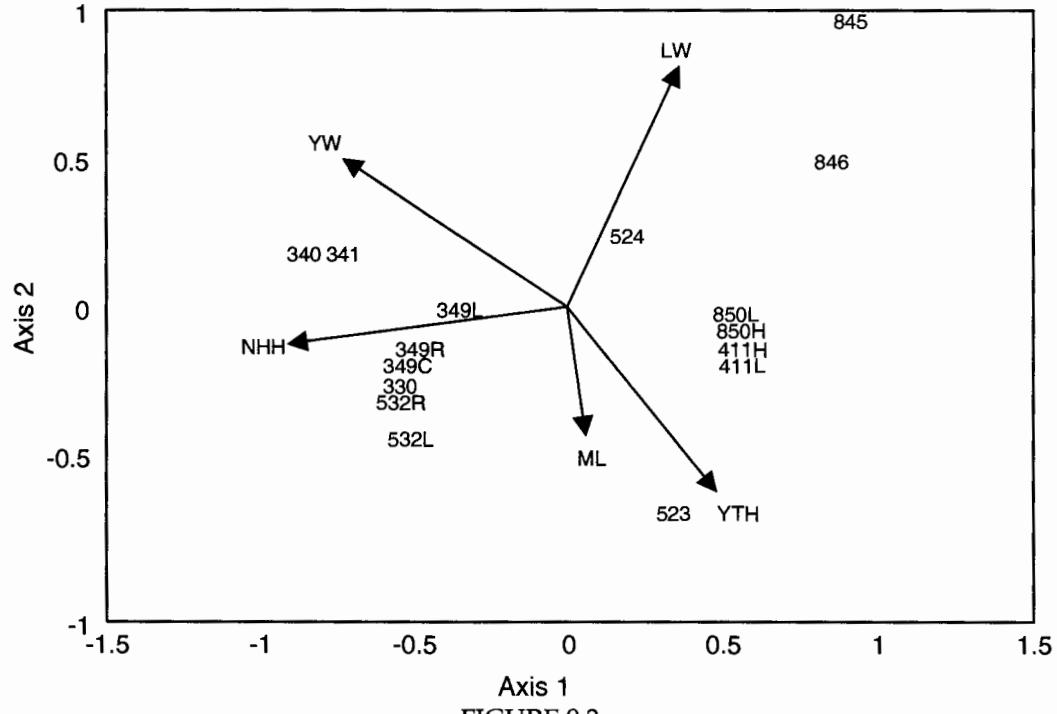


FIGURE 9.2

Ordination of open-pollinated (OP) branches on all trees (excluding 849) according to the proportional bird visitor composition on the entire canopy at the time of flowering on the OP. Branch codes comprise the number of the tree, and a letter if there was more than one branch on that tree. Locations of trees are given in Fig. 9.1 and Table 9.1. Bird species that contribute significantly to the variation in avian community composition between samples are fitted as vectors in the plot. Codes for bird species are: LW = little wattlebird; ML = musk lorikeet; NHH = New Holland honeyeater; YTH = yellow-throated honeyeater; and YW = yellow wattlebird. Stress on 3 axes = 0.039. Only the two axes encompassing the greatest part of the variation between samples are shown.

Musk lorikeets, little wattlebirds and noisy miners were the only birds observed feeding on flowers on trees on the eastern side of the estuary (Table 9.7). However, their relative proportions varied greatly between sites and, to a lesser extent, trees at each site. Most of this variation reflected contrasting abundances of musk lorikeets and little wattlebirds, with the former being

the major flower visitors at Hobart Airport and Clifton Beach where little wattlebirds were virtually absent. At School Road and Forest Hill Road, where little wattlebirds were common, musk lorikeets generally made up low proportions of flower visitors (Table 9.7, Fig. 9.2). This can be attributed, at least partly, to interspecific aggression from little wattlebirds. Tree 844 was defended from musk lorikeets by little wattlebirds throughout its flowering period, with the territory holders frequently flying out from the tree to meet approaching lorikeets before they could enter the tree. Noisy miners also deterred musk lorikeets from tree 851 at Clifton Beach through territorial defence. Hence, musk lorikeets comprised a far greater proportion of the visitors to tree 850 than to tree 851 (Table 9.7). This difference may also have been because of the greater flowering intensity of tree 850 than tree 851 (Table 9.6) rendering the latter less attractive to musk lorikeets. At School Rd, little wattlebirds made up similar proportions of the visitors to trees 845 and 846. However, these two trees, which flowered concomitantly and had their canopies separated by only one metre (Table 9.6), had very different proportions of musk lorikeets and noisy miners (Table 9.7). Musk lorikeets may have visited tree 846 but not tree 845 because the former carried more flowers (Table 9.6). However, differences between these two trees were small when compared to tree 849 which bloomed at the same site one month later (Table 9.6). No birds entered this tree during 5.5 hours of observations (Table 9.7), despite musk lorikeets being common in nearby flowering conspecifics. This was probably because most flowers on tree 849 were full of nectar-feeding cockchafer beetles *Phyllotocus macleayi* Fischer.

Honeyeaters dominated bird assemblages on the western side of the estuary (Table 9.7). The yellow-throated honeyeater *Lichenostomus flavicollis* (Vieillot) was recorded from all western trees, and New Holland honeyeaters *Phylidonyris novaehollandiae* (Latham) and black-headed honeyeaters *Melithreptus affinis* (Lesson) were observed on all western trees except 523 (Table 9.7). Bird assemblages on trees at Tinderbox differed from those at Waldies Rd because of the preponderance of yellow wattlebirds *Anthochaera*

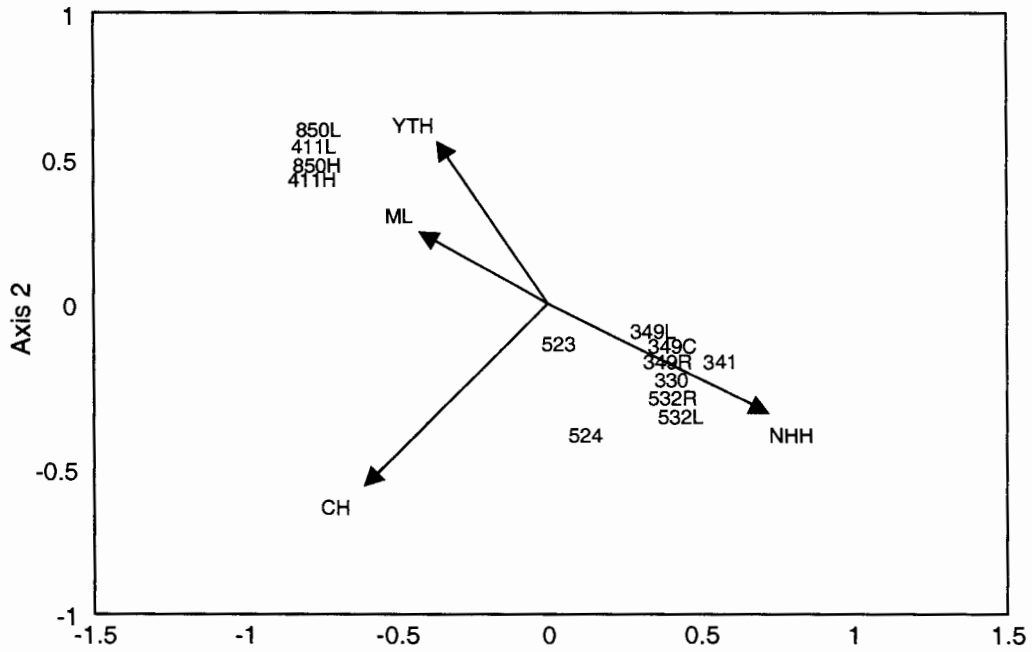


FIGURE 9.3

Ordination of open-pollinated (OP) branches on SI trees according to the proportional bird visitor composition on the entire canopy at the time of flowering on the OP. Branch codes comprise the number of the tree, and a letter if there was more than one branch on that tree. Locations of trees are given in Fig. 9.1 and Table 9.1. Bird species that contribute significantly to the variation in avian community composition between samples are fitted as vectors in the plot. Codes for bird species are: CH = crescent honeyeater; ML = musk lorikeet; NHH = New Holland honeyeater; and YTH = yellow-throated honeyeater. Stress on 3 axes = 0.015. Only the two axes encompassing the greatest part of the variation between samples are shown.

paradoxa (Daudin) and New Holland honeyeaters and the greater proportional abundance of black-headed honeyeaters at the former. In addition, crescent honeyeaters *Phylidonyris pyrrhoptera* (Latham) occurred at Waldies Rd but not Tinderbox, and yellow-throated honeyeaters comprised greater proportions of the bird communities at Waldies Rd than at Tinderbox (Table 9.7, Fig. 9.2). Variation between trees at Tinderbox was largely because of the relative proportions of yellow wattlebirds and New Holland honeyeaters, which both defended particular trees. Yellow wattlebirds defended the adjacent trees 340 and 341 whereas New Holland honeyeaters defended tree 330 throughout their overlapping flowering periods (Table 9.6, Fig. 9.2). However, the boundary between these territories was not static as tree 795, which grew between 340/341 and 330 and bloomed at a similar time

(Fig. 9.1, Table 9.6), was sometimes defended by yellow wattlebirds and sometimes by New Holland honeyeaters. New Holland honeyeaters predominated on the later flowering trees 349 and 532 (Tables 9.6 and 9.7, Fig. 9.2) after yellow wattlebirds became less common at this site. The two trees at Waldies Rd appeared to differ in visitor profile because of size differences, with many more species observed on the larger tree 524 than on the small tree 523. The most abundant species on tree 524 was the swift parrot (Table 9.7).

9.3.1.3 Insect flower visitors

The flowers of *E. globulus* were also visited by a wide variety of insects (Table 9.8). This encompassed two species of exotic bees, 10 morphospecies of native bees, four of wasps, two of ants, nine of flies, 15 of beetles, occasional moths, and one bug (Table 9.8). The most abundant individual taxa were spread across all of these functional groups, except moths and bugs (Tables 9.8 and 9.9). Overall, the introduced honey bee *Apis mellifera* was the most abundant insect, being common on all but two trees (Table 9.9). Honey bees were probably deterred from visiting flowers on these two trees because of the presence of large numbers of small ants (tree 851) or cockchafer beetles *Phyllotocus macleayi* (tree 849; Table 9.9). The common native colletid bees, *Hylaeus (Prosopisteron)* spp. and *Leioproctus* spp., were also recorded from most trees and all sites, although often in small numbers (Table 9.9). In contrast, the common native halictid bees, *Homalictus* spp. and large *Lasioglossum (Chilalictus)* spp., were regular flower visitors at sites on the eastern side of the Derwent Estuary and at Waldies Rd, but were uncommon at Tinderbox (Table 9.9). Geographic restriction was more apparent in the flower wasp *Thynnus zonatus* Guerin-Meneville and small ants, both of which were restricted to sites on the eastern side of the Derwent Estuary (Table 9.9). The common flies, Calliphoridae sp.2 and Syrphidae sp.1, were recorded from most trees, but were not particularly common on any tree (Table 9.9). In contrast, the most abundant beetles, the soldier beetle *Chauliognathus lugubris* (Fabricius) and cockchafer beetles *Phyllotocus macleayi* and *P.*

rufipennis (Boisduval), were not widespread but were sometimes present in very large numbers on particular trees (Table 9.9).

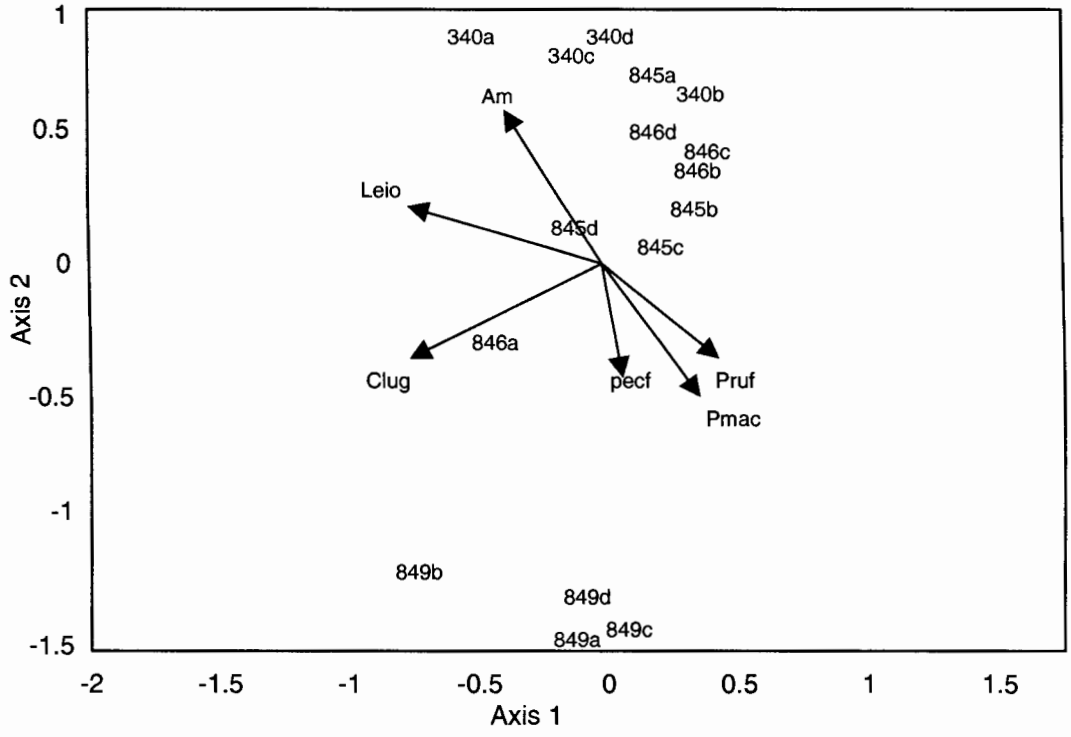


FIGURE 9.4

Ordination of 5 mm (a), 12 mm (b), 25 mm (c) and OP (d) treatments, on SC trees that set seeds, according to their insect visitation rates. Locations of trees are given in Fig. 9.1 and Table 9.1. Insect species that contribute significantly to the variation in insect community composition between samples are fitted as vectors in the plot. Codes for insect species are: Am = *Apis mellifera* (Apidae); Leio = *Leioproctus* spp. (Colletidae); Clug = *Chauliognathus lugubris* (Cantharidae); Pmac = *Phyllotocus macleayi* (Scarabaeidae); and Pruf = *P. rufipennis.* The only significant fecundity measure (pecf = pollinator effectiveness score for the numbers of capsules per flower; Table 9.18) is also fitted as a vector. Stress on 3 axes = 0.041. Only the two axes encompassing the greatest part of the variation between samples are shown.

In contrast to bird assemblages (Table 9.7, Figs 9.2 and 9.3), clear regional variation between insect assemblages on flowers of *E. globulus* was not apparent (Figs 9.4 and 9.5). Trees from different sites, or even sides of the estuary, often supported similar suites of insects. For example, insect assemblages on trees 845 and 846 at School Rd were more similar to those on tree 340 at Tinderbox than those on tree 849 at School Rd (Fig. 9.4).

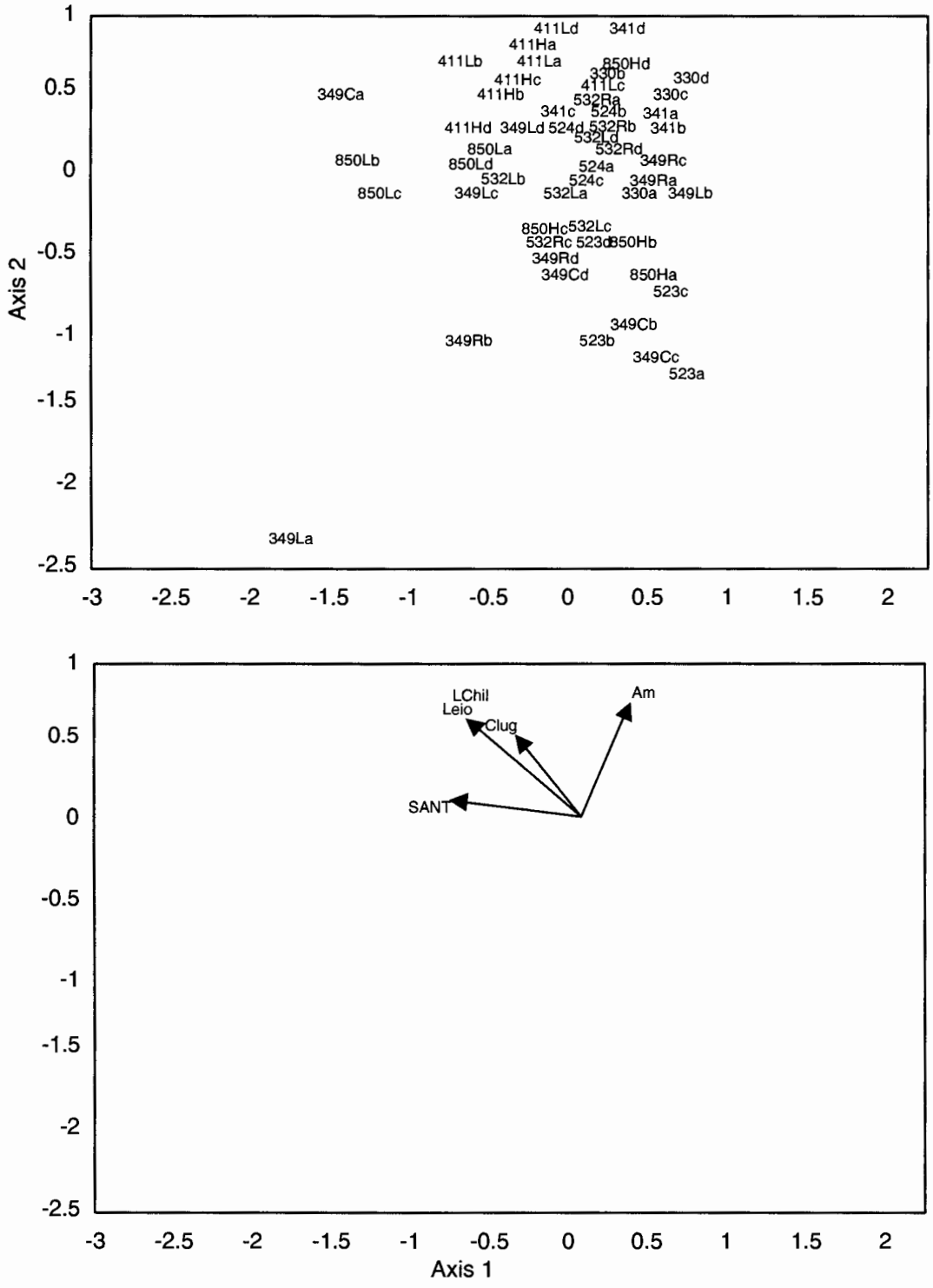


FIGURE 9.5

Ordination of 5 mm (a), 12 mm (b), 25 mm (c) and OP (d) treatments, on SI trees that set seeds, according to their insect visitation rates. Locations of trees are given in Fig. 9.1 and Table 9.1. Insect species that contribute significantly to the variation in insect community composition between samples are fitted as vectors in the plot. Codes for insect species are: Am = *Apis mellifera* (Apidae); Leio = *Leioproctus* spp. (Colletidae); LChil = large *Lasioglossum (Chilalictus)* spp. (Halictidae); Clug = *Chauliognathus lugubris* (Cantharidae); and SANT = unidentified small ants (Formicidae). Stress on 3 axes = 0.147. Only the two axes encompassing the greatest part of the variation between samples are shown.

Family	Insect visitors Species	Caging treatment 1 mm	5 mm	12 mm	25 mm	OP
Apidae	*Apis mellifera*	0	0.3548	0.2982	0.3682	0.5370
	Bombus terrestris	0	0	0.0033	0.0015	0.0064
	Total exotic bees	**0^{c}**	**0.3548^{ab}**	**0.3015^{b}**	**0.3696^{ab}**	**0.5434^{a}**
Anthophoridae	*Exoneura* spp.	0	0.0004	0.0022	0.0009	0.0004
Colletidae	*Leioproctus* spp.	0	0.1035	0.0566	0.0550	0.1023
	Euryglossa (Euhesma) sp.	0.0004	0	0	0	0
	*Hylaeus (Euprosopis) honestus**	0	0.0009	0	0.0003	0.0032
	H. (Gnathoprosopoides) bituberculatus	0	0	0	0	0.0046
	Hylaeus (Prosopisteron) spp.	0.0219	0.0025	0.0184	0.0055	0.0434
Halictidae	*Homalictus* spp.	0.0044	0.0096	0.0134	0.0120	0.0133
	small *Lasioglossum (Chilalictus)* spp.	0.0044	0.0030	0.0022	0.0024	0.0055
	large *L. (Chilalictus)* spp.	0.0006	0.0054	0.0058	0.0023	0.0071
	Lasioglossum (Parasphecodes) spp.	0	0.0031	0.0019	0.0004	0.0010
	Total native bees	**0.0317^{c}**	**0.1284^{bc}**	**0.1006^{cb}**	**0.0788^{bc}**	**0.1808^{a}**
Hymenoptera	unidentified small wasps	0	0.0015	0	0	0
Gasteruptiidae	*Gasteruption* spp.	0	0.0002	0	0	0.0007
Pergidae	*Clarissa* sp.	0	0.0006	0	0	0
Thynnidae	*Thynnus zonatus*	0	0.0005	0.0088	0.0193	0.0126
	Total wasps	**0**	**0.0028**	**0.0088**	**0.0193**	**0.0133**
Formicidae	unidentified small ants	0.0511	0.0110	0.0217	0.0245	0.0080
	Myrmecia pilosula	0	0	0.0006	0	0.0005
	Total ants	**0.0511**	**0.0110**	**0.0223**	**0.0245**	**0.0085**
Anthomyiidae	sp.1	0	0.0024	0.0036	0.0006	0.0044
Calliphoridae	*Calliphora stygia*	0	0	0.0056	0.0165	0.0070
	Calliphora sp.2	0	0.0002	0.0055	0.0114	0.0276
Sepsidae	sp.1	0	0	0.0003	0	0.0021
Stratiomyidae	*Odontomyia* sp.	0	0.0005	0	0	0
Syrphidae	sp.1	0	0.0023	0.0076	0.0155	0.0326
	sp.5	0	0	0	0	0.0006
	Psilota spp.	0	0	0	0.0027	0.0016
Tachinidae	*Senostoma* spp.	0	0	0	0	0.0015
	Total flies	**0^{c}**	**0.0054^{c}**	**0.0225^{bc}**	**0.0467^{b}**	**0.0773^{a}**
Coleoptera	unidentified small beetles	0.0016	0	0	0	0.0003
Alleculidae	*Atoichus bicolor*	0	0	0	0.0002	0
Cantharidae	*Chauliognathus lugubris*	0	0.1157	0.2654	0.1581	0.1172
	Chauliognathus nobilitatus	0	0	0	0.0050	0.0012
Cerambycidae	unidentified spp.	0	0.0006	0.0006	0	0.0012
	Syllitus lineatus	0	0	0.0024	0	0
Cleridae	*Eleale* sp.	0	0.0009	0.0007	0.0010	0.0072
	Lemidia sp.	0	0	0	0	0.0004
Curculionidae	sp.1	0	0	0	0.0007	0
Elateridae	sp.1	0	0.0021	0	0.0009	0
Lycidae	*Metriorrhynchus* spp.	0	0	0.0007	0	0
Mordellidae	*Mordellistena* spp.	0	0.0007	0	0.0022	0.0006
Scarabaeidae	*Deuterocauliobius villosus*	0	0	0	0	0.0004
	Phyllotocus macleayi	0.0016	0.2598	0.1417	0.5392	0.4329
	Phyllotocus rufipennis	0	0.0071	0.0070	0.0124	0.0300
	Total beetles	**0.0031^{c}**	**0.3870^{b}**	**0.4176^{b}**	**0.7196^{ab}**	**0.5914^{a}**
Lepidoptera	unidentified small moths	0	0	0	0.0003	0.0001
Hemiptera	*Amorbus* sp.	0	0.0003	0	0	0
	Total insects	**0.0859^{c}**	**0.8897^{b}**	**0.8733^{b}**	**1.2589^{ab}**	**1.4149^{a}**

TABLE 9.8

Mean visitation rates by insects (flowers visited / open flower / 5 min) to flowers of *E. globulus* in different caging treatments on 12 trees. Significant differences between treatments in visitation rates by functional groups, as determined by pairwise multiple comparisons using Student-Newman-Keuls Method following 2-Way ANOVA, are denoted by different superscript letters. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of *E. globulus* in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999).

9.3.1.4 Effects of exclosures on flower visitors

In spite of the large numbers of birds foraging in most trees (Table 9.7), birds were seldom seen foraging on the experimental branches. This was because most birds spent most of their time in the upper portions of the canopy (also see Chapter 8), while the experimental branches were near the ground. In over 100 hours of quantifying bird visitation to the trees (Table 9.7) and other times spent around the trees, birds were only seen feeding from experimental flowers on tree 523. On this tree, a yellow-throated honeyeater was seen feeding on the experimental uncaged flowers, and a crescent honeyeater entered the 25 mm mesh cage to feed on flowers.

Two-Way Analysis of Variance revealed that the total insect visitation rate to flowers differed significantly between trees and the exclosure treatments that allowed access to flowers (Table 9.10). This pattern was also apparent for visitation rates to flowers by exotic bees, native bees, flies, and beetles. However, visitation rates by wasps and ants were not significantly different between treatments, but did differ significantly between trees (Table 9.10).

Replicate	330	340	341	795	349L	349M	349R	532L	532R	523	524i	524o	mean
Side of Derwent Estuary	west	west	west	west	west	west	west	west	west	west	west	west	west
Apis mellifera	0.914	0.787	1.533	0.446	0.406	0.070	0.121	0.383	0.451	0.067	0.209	0.356	0.479
Leioproctus (Leioproctus)	0	0.003	0.100	0.015	0.312	0.042	0.060	0.075	0.031	0.013	0.051	0.093	0.066
Hylaeus (Prosopisteron)	0.293	0.017	0.017	0.077	0	0.014	0	0.019	0.062	0	0.003	0.053	0.046
Homalictus (Homalictus)	0.017	0.006	0	0	0	0	0	0	0.005	0	0.024	0	0.004
large *Lasioglossum (Chilalictus)*	0	0	0	0	0	0	0	0	0.010	0	0.010	0.006	0.002
Thynnus zonatus	0	0	0	0	0	0	0	0	0	0	0	0	0
unidentified small ants	0	0	0	0	0	0	0	0	0	0	0	0	0
Calliphora sp.2	0.121	0	0.017	0	0	0	0.015	0.019	0.072	0	0	0.004	0.021
Syrphidae sp.1	0.017	0	0.133	0.015	0	0	0.030	0	0.010	0.080	0.034	0.025	0.029
Chauliognathus lugubris	0	0	0.017	0	0	0	0	0.047	0.092	0	0	0	0.013
Phyllotocus macleayi	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllotocus rufipennis	0	0	0	0	0	0	0	0.009	0	0	0	0	0.001

Replicate	411L	411H	844L	844H	845	846	849	850L	850H	851	mean	mean
Side of Derwent Estuary	east	east	east	east	east	east	east	east	east	east	east	both
Apis mellifera	0.707	0.220	0.442	0.326	0.615	0.638	0.012	0.225	0.592	0	0.378	0.433
Leioproctus (Leioproctus)	0.612	0.817	0.062	0.015	0.047	0	0.065	0.127	0.054	0.029	0.183	0.119
Hylaeus (Prosopisteron)	0.017	0.005	0.256	0.322	0.006	0.005	0.016	0	0.090	0	0.072	0.058
Homalictus (Homalictus)	0	0.005	0.008	0	0.059	0.020	0.012	0	0.040	0.063	0.021	0.012
large *Lasioglossum (Chilalictus)*	0.009	0.032	0.045	0.011	0.030	0.005	0	0.028	0.013	0.029	0.020	0.010
Thynnus zonatus	0.147	0	0	0	0.030	0.041	0	0	0	0	0.022	0.010
unidentified small ants	0	0	0	0	0	0	0.004	0.380	0	0.823	0.121	0.055
Calliphora sp.2	0.030	0.102	0.062	0.031	0.012	0.046	0.012	0	0	0.017	0.031	0.025
Syrphidae sp.1	0.086	0.038	0.025	0.011	0	0.025	0	0	0.031	0.006	0.022	0.026
Chauliognathus lugubris	0.047	0.624	0	0	0.361	0.082	0.567	0	0	0	0.168	0.083
Phyllotocus macleayi	0	0	0	0	0	0	5.194	0	0	0	0.519	0.236
Phyllotocus rufipennis	0.017	0.016	0	0	0	0	0.340	0	0	0	0.037	0.017

TABLE 9.9

Summary of flower visit rates (flowers visited per open flower per 5 min) to uncaged branches of *E. globulus* by the most abundant insect morphospecies.

Visitor group	Data type used	Tree (n = 12)	Treatment (n = 5)
exotic bees	raw	0.0001***	<0.0001***
native bees	rank	<0.0001***	0.0003***
wasps	rank	0.0033**	0.1794^{NS}
ants	rank	<0.0001***	0.3947^{NS}
flies	raw	0.0017**	<0.0001***
beetles	rank	<0.0001***	<0.0001***
insects	rank	<0.0001***	<0.0001***

TABLE 9.10

Summary of 2-Way Analyses of Variance on the significance of trees and treatments to insect visitation rates across 12 trees. The treatments did not include complete exclosure.

Multiple pairwise comparisons of the effects of exclosure treatments on insect visitation rates to flowers indicated that the 1 mm mesh deterred insects to a far greater extent than did the larger aperture cages. The only insects that were able to access these flowers were a few small species of native bees, ants and beetles (Table 9.8). One individual of *Phyllotocus macleayi* also found its way through a small tear in the mesh (Table 9.8). Visitation rates by all insects to flowers within the 1 mm mesh were significantly lower than those to all other treatments (Table 9.8). The effectiveness of this exclosure in preventing insect access to flowers was apparent for exotic bees, beetles, flies and, to a lesser extent, native bees (Table 9.8). As a result, nectar regularly accumulated in the flowers enclosed in the 1 mm mesh to the point where it overflowed from the receptacle (Plate 9.3), whereas visible pools of nectar were rarely observed in flowers in the other treatments.

There were almost no statistically significant differences in insect visitation rates to flowers enclosed within the 5 mm, 12 mm, and 25 mm meshes. These three treatments did not differ significantly in their effects on visitation rates by all insects, exotic bees, native bees, wasps, ants, or beetles (Table 9.8). However, the 5 mm mesh deterred flies from visiting flowers significantly more than did the 25 mm mesh (Table 9.8). In particular, the Calliphoridae and Syrphidae were deterred by the 5 mm mesh (Table 9.8).

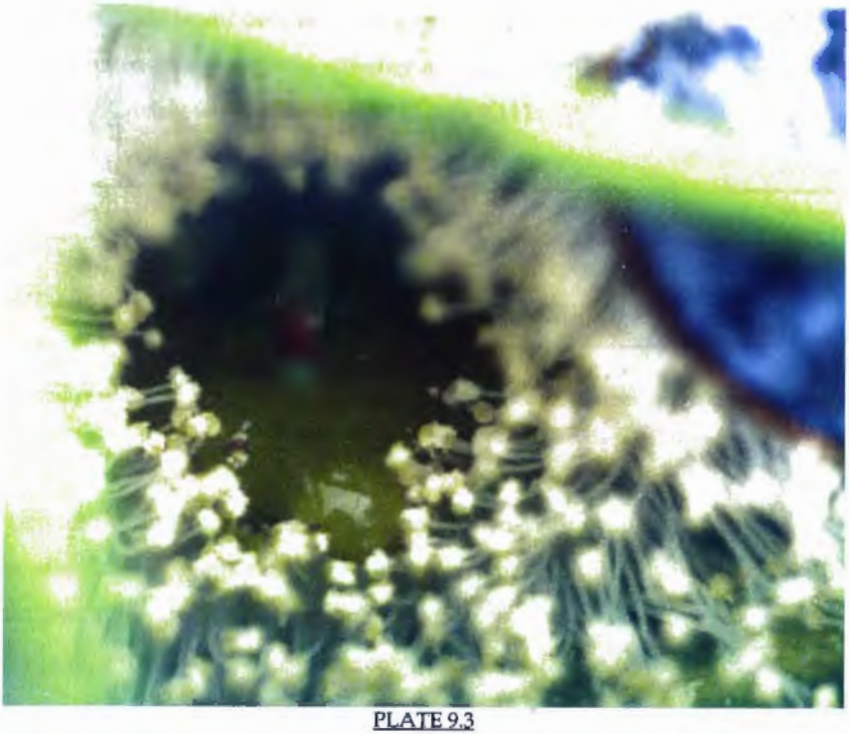


PLATE 9.3

Nectar overflowing from a flower of *E. globulus* with a receptive stigma inside a cage with 1 mm apertures.

The 5 mm, 12 mm, and 25 mm meshes had some effect on insect visitation rates to flowers, when compared to uncaged flowers. Visitation rates by all insects to flowers in the 5 mm and 12 mm meshes were significantly lower than those to uncaged flowers (Table 9.8). The taxonomic group most deterred by these cages was flies. Visitation rates by flies to uncaged flowers were significantly greater than to flowers in all of these cages. In particular, *Calliphora* sp.2 and Syrphidae sp.1 were deterred by cages (Table 9.8). Exotic bees visited flowers in the 12 mm mesh less frequently than uncaged flowers. In contrast, native bee visitation rates were significantly lower to flowers enclosed in 5 mm and 25 mm mesh than to uncaged flowers, while enclosure within 5 mm or 12 mm mesh significantly deterred beetles (Table 9.8).

9.3.1.5 Effects of exclosures on pollination

The numbers of seeds produced per flower, as proportions of those developing after supplementary outcross pollinations (pe score), were

significantly different between exclosure treatments and trees (Table 9.11). This occurred irrespective of whether all trees, or only fully SI, or only partially SC trees were investigated (Table 9.11).

Trees used	Data type used	Tree	Treatment (n = 7)
all	square root	<0.0001*** (n=12)	<0.0001***
SI	square root	0.0198* (n=8)	<0.0001***
SC	square root	0.0115* (n=4)	0.0008***

TABLE 9.11

Summary of 2-Way Analyses of Variance on the significance of trees and caging treatments to pollinator effectiveness for the number of seeds per flower.

Pairwise multiple comparisons following Two-Way Analysis of Variance showed that supplementary outcross pollination significantly enhanced the numbers of seeds produced per flower (Fig. 9.6), above the levels occurring in all other treatments across all trees. On average, the numbers of seeds produced per open-pollinated flower was only 37.5% of the maximum possible (Fig. 9.6). This pollen limitation was more apparent in SI, than in SC, trees. In SI trees, supplementary outcross pollination significantly increased the numbers of seeds per flower (Fig. 9.7) above the levels occurring in all other treatments. On average, the numbers of seeds produced per open-pollinated flower on SI trees was 25.3% of the maximum possible (Fig. 9.7). However, supplementary outcross pollination on SC trees did not significantly enhance the numbers of seeds per flower (Fig. 9.8) above that in open-pollinated flowers. Nevertheless, the numbers of seeds produced per open-pollinated flower on SC trees was still only 69.1% of the maximum possible (Fig. 9.8). Supplementary outcross pollination on SC trees only significantly enhanced the numbers of seeds per flower above those in the exclusion bags, 1 mm, and 5 mm meshes (Fig. 9.8).

The few small insects able to pass through the 1 mm mesh made little contribution to pollination of *E. globulus*. Fecundity in the 1 mm mesh was never significantly greater than that in the exclusion bags, irrespective of the degree of self-compatibility of the trees (Figs 9.6 - 9.8). These insects,

together with pollen rain (pollen falling from flowers higher in the tree; Eldridge 1970) and autonomous pollen deposition, facilitated 13.4% of the maximum possible seed production per flower on SC trees (Fig. 9.8). This was slightly lower than occurred from pollen transfer within exclusion bags (Fig. 9.8). Dehisced pollen was retained within the bags, and was presumably transferred to stigmata when the bags were shaken by wind (see Carpenter 1976). However, these insects may have been responsible for occasional deposition of outcross pollen, as this treatment resulted in 0.004% of the maximum possible seed production per flower being produced on SI trees (Fig. 9.7).

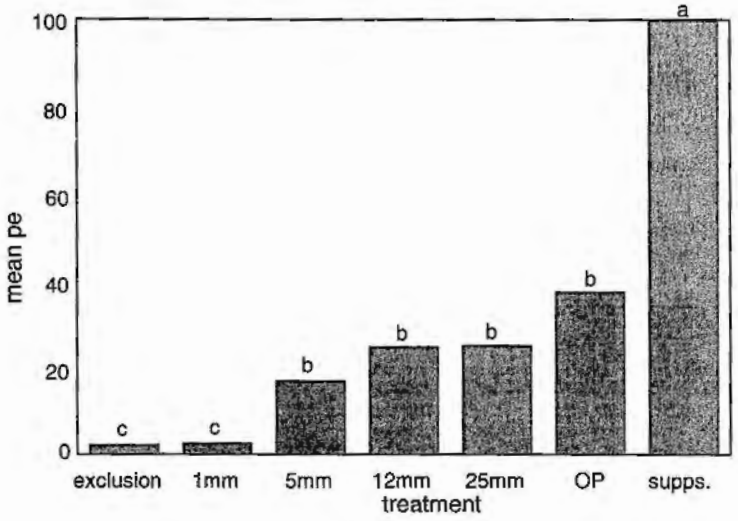


FIGURE 9.6

Backtransformed least square mean pollinator effectiveness for seed set per flower in various treatments on all 12 trees of *E. globulus*. Pollinator effectiveness for seed set per flower in each treatment was calculated as a percentage of seed set from flowers receiving supplementary outcross pollen on that tree. The treatments are as follows: exclusion = enclosing flowers in bags to prevent animals from accessing flowers; 1mm, 5mm, 12mm and 25 mm = enclosing flowers in cages of these aperture sizes; OP = open-pollinated flowers accessible to all flower visitors; and supps = open-pollinated flowers receiving supplementary outcross pollination at peak receptivity with the pollen mix AH1. Different letters denote statistically significant differences between treatments as determined by Student-Newman-Keuls Method following 2-Way ANOVA on square root transformed data.

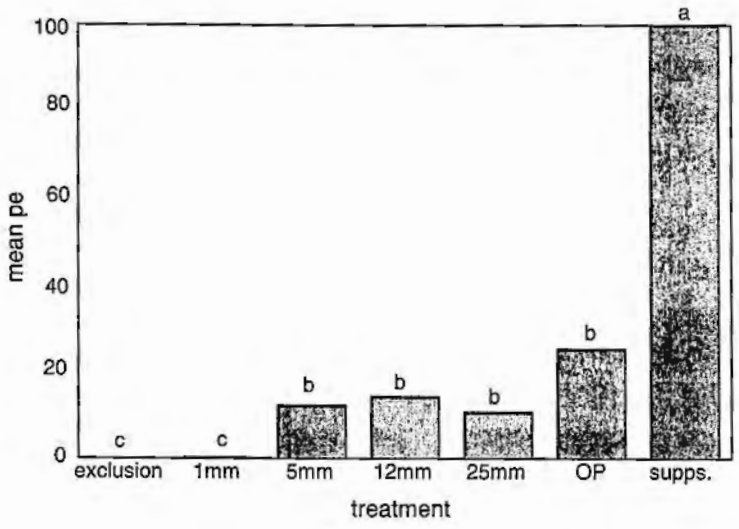


FIGURE 9.7

Backtransformed least square mean pollinator effectiveness for seed set per flower in various treatments on eight self-incompatible trees of *E. globulus*. Pollinator effectiveness for seed set per flower in each treatment was calculated as a percentage of seed set from flowers receiving supplementary outcross pollen on that tree. The treatments are as follows: exclusion = enclosing flowers in bags to prevent animals from accessing flowers; 1mm, 5mm, 12mm and 25 mm = enclosing flowers in cages of these aperture sizes; OP = open-pollinated flowers accessible to all flower visitors; and supps = open-pollinated flowers receiving supplementary outcross pollination at peak receptivity with the pollen mix AH1. Different letters denote statistically significant differences between treatments as determined by Student-Newman-Keuls Method following 2-Way ANOVA on square root transformed data.

Exposure to the numerous larger insects (5 mm and 12 mm meshes) significantly enhanced the numbers of seeds produced per flower above levels occurring after exposure to small insects or no insects on all trees (Fig. 9.6) and SI trees (Fig. 9.7). However, in spite of their abundance, insects that passed through the 5 mm mesh but were excluded by the 1 mm mesh facilitated only 12.3% of the maximum possible seed production on SI trees, and those passing through the 12 mm mesh but not the 5 mm mesh a mere 1.8% (Fig. 9.7). The contributions made by larger insects to pollination of SC trees were only marginally significant (Fig. 9.8). On SC trees, the numbers of seeds per flower in the 5 mm mesh were not significantly greater than in the exclusion bags or the 1 mm mesh. The numbers of seeds per flower in the 12 mm mesh were also not significantly greater than in the exclusion bags, but

were significantly greater than in the 1 mm mesh (Fig. 9.8). The insects that passed through the 5 mm mesh but were excluded by the 1 mm mesh facilitated only 15.2% of the maximum possible seed production, and those passing through the 12 mm mesh but not the 5 mm mesh a further 25.6% (Fig. 9.8).

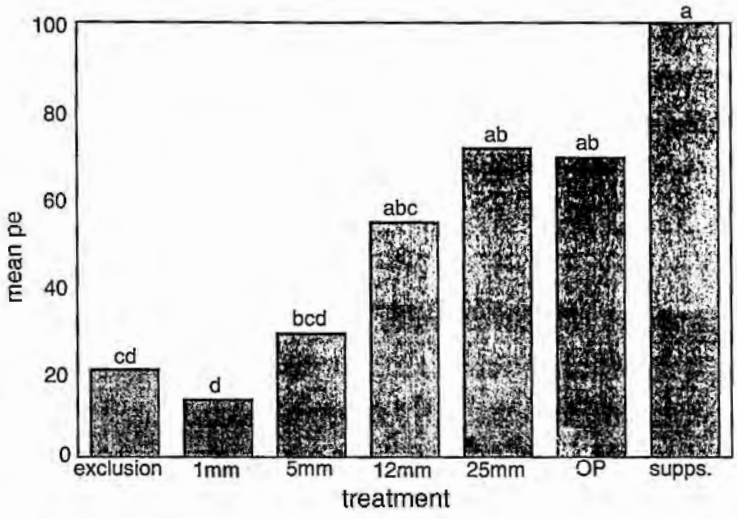


FIGURE 9.8

Backtransformed least square mean pollinator effectiveness for seed set per flower in various treatments on four self-compatible trees of *E. globulus*. Pollinator effectiveness for seed set per flower in each treatment was calculated as a percentage of seed set from flowers receiving supplementary outcross pollen on that tree. The treatments are as follows: exclusion = enclosing flowers in bags to prevent animals from accessing flowers; 1mm, 5mm, 12mm and 25 mm = enclosing flowers in cages of these aperture sizes; OP = open-pollinated flowers accessible to all flower visitors; and supps = open-pollinated flowers receiving supplementary outcross pollination at peak receptivity with the pollen mix AH1. Different letters denote statistically significant differences between treatments as determined by Student-Newman-Keuls Method following 2-Way ANOVA on square root transformed data.

In accordance with the low visitation rates by birds to experimental flowers, exposure to birds did not significantly enhance the numbers of seeds per flower above levels resulting from exposure to larger insects on all trees (Fig. 9.6), SI trees (Fig. 9.7), or SC trees (Fig. 9.8). The insects and birds that passed through the 25 mm mesh but not the 12 mm mesh did not increase seed production on SI trees (Fig. 9.7). However, the insects and birds that were

excluded by cages facilitated at least another 11.2% of the maximum possible seed production (Fig. 9.7). On SC trees the birds and insects that passed through the 25 mm mesh but not the 12 mm mesh facilitated 17% of the maximum possible seed set, but insects and birds that were excluded by the 25 mm mesh made no additional contribution to seed production (Fig. 9.8).

9.3.1.6 Resource consumption

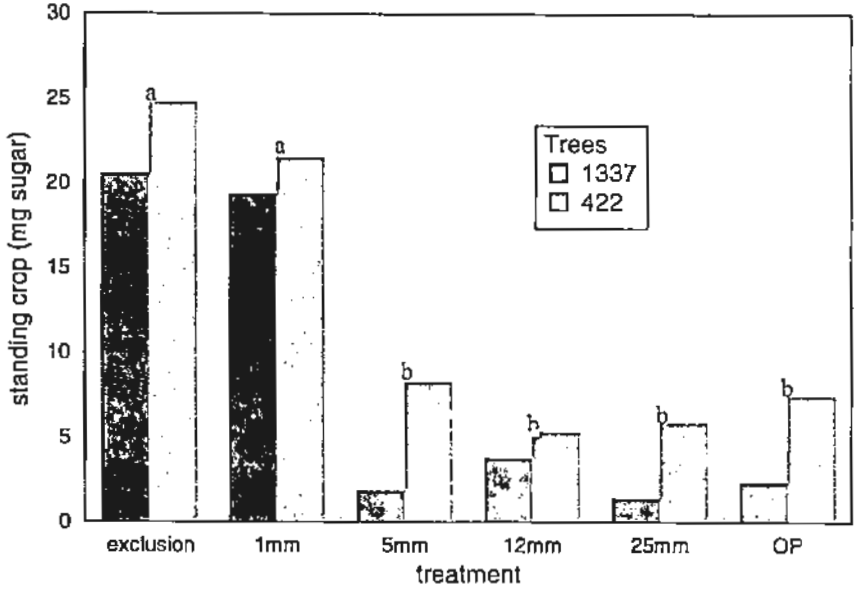


FIGURE 9.9

Nectar sugar remaining in flowers at the end of the day in flowers subjected to various caging treatments on two trees of *E. globulus*. The treatments are as follows: exclusion = enclosing flowers in bags to prevent animals from accessing flowers; 1mm, 5mm, 12mm and 25 mm = enclosing flowers in cages of these aperture sizes; and OP = open-pollinated flowers accessible to all flower visitors. Letters denote significant differences between treatments as determined by Student-Newman-Keuls Method following 2-Way ANOVA on $\log_{10}$ data.

Two-Way Analysis of Variance indicated that both tree and exclosure treatment significantly ($P < 0.0001$) affected nectar standing crops after 24 hours. For each treatment, standing crops were always greater on tree 422 than tree 1337 (Figure 9.9). Flowers from which all animals were excluded for one day accumulated large quantities of nectar on both trees (Figure 9.9). The amount of nectar consumed from flowers enclosed in cages with 1 mm

apertures was not statistically significant (Figure 9.9). However, statistically significant quantities of nectar were consumed from all other treatments. These findings are consistent with observations of nectar always accumulating in flowers in the 1 mm mesh (Plate 9.3), but rarely in the other cages or open-pollinated treatment, during the experiment into seed production. There were no statistically significant differences in the quantities of nectar consumed between flowers enclosed in cages of 5 mm, 12 mm and 25 mm aperture diameters, and exposed flowers (Figure 9.9). Therefore, birds did not decrease nectar standing crops below the levels resulting from insects accessing flowers (Figure 9.9).

Honey bees comprised over 90% of the insects seen on both trees; the remainder being flies (Tables 9.12 and 9.13). As for the fecundity experiment, honey bees frequently foraged inside the cages of 5 mm, 12 mm and 25 mm aperture diameter, indicating that they were responsible for most nectar consumption. Flies would have consumed very little nectar in the cages because of their low abundances on the experimental region of the tree (Tables 9.12 and 9.13) and their tendency not to enter cages (Table 9.8). A small number of insects were still foraging when the flowers were harvested, but activity had declined greatly in the last two hours of the experiment (Tables 9.12 and 9.13).

Time	T_A (°C)	RH (%)	Insect species			
			Apis mellifera	*Calliphora stygia*	*Calliphora* sp.2	Muscidae sp.1
1028	16.4	48	5		1	
1102	16.6	55	2			
1237	18.1	40	8			
1310	15.1	63	10			
1332	17	53	9	1		
1445	16.9	40	3	1		1
1518	16.1	52	8			
1700	14	50	2	1		
		% total	90.38	5.77	1.92	1.92

TABLE 9.12

Numbers of insects seen foraging on flowers in the vicinity of the exclosure experiment during one minute spot counts on tree 1337, ambient temperature (T_A) and relative humidity (RH), at the given times.

Time	T_A (°C)	RH (%)	Insect species			
			Apis mellifera	*Calliphora stygia*	Muscidae sp.1	Syrphidae sp.1
1124	18.5	45	13	1		
1157	18.1	51	15	1		1
1352	18.3	45	8			
1425	17.1	45	5			
1535	18.4	47	18	1		1
1608	16.9	48	1			
1639	16.5	53	3	1	1	
1804	15.1	61	1			
		% total	90.14	5.63	1.41	2.82

TABLE 9.13

Numbers of insects seen foraging on flowers in the vicinity of the exclosure experiment during one minute spot counts on tree 422, ambient temperature (T_A) and relative humidity (RH), at the given times.

Time	T_A (°C)	RH (%)	Bird species				
			green rosella	yellow wattlebird	little wattlebird	black-headed honeyeater	New Holland honeyeater
0837-0907	11.4	60	0	1625	3155	70	7020
1031-1101	16.4	48	0	955	2020	0	2325
1239-1309	18.1	40	40	280	1830	0	895
1447-1517	16.9	40	0	0	985	0	1625
		% total	0.18	12.53	35.01	0.31	51.98

TABLE 9.14

Ambient temperature, relative humidity, and amounts of time (seconds) birds spent foraging on flowers during 30 minute periods on tree 1337.

Time	T_A (°C)	RH (%)	Bird species		
			yellow wattlebird	little wattlebird	yellow-throated honeyeater
0749-0819	8.5	67	20	3715	105
1126-1156	18.5	45	5	5165	0
1354-1424	18.3	45	0	2500	0
1537-1607	18.4	47	0	3825	0
		% total	0.16	99.15	0.68

TABLE 9.15

Ambient temperature, relative humidity, and amounts of time (seconds) birds spent foraging on flowers during 30 minute periods on tree 422.

Little wattlebirds were common on both trees, with New Holland honeyeaters and yellow wattlebirds also being frequent visitors to tree 1337 (Tables 9.14 and 9.15). Little wattlebirds were occasionally seen feeding from

flowers in the vicinity of the experiment on tree 422, but all birds remained higher in the canopy of tree 1337. Birds continued to forage at least until within two hours of flower harvest on both trees, although foraging activity declined through the day on tree 1337 (Tables 9.14 and 9.15).

9.3.1.7 Pollinator efficiency

If it is assumed that the nectar consumption patterns on trees 1337 and 422 were typical of those on the trees where the effects of exclosures on fecundity were examined, the most economical pollination services across all trees occurred in the bag with 1 mm apertures and open-pollinated flowers (Table 9.16). The high pollinator efficiency behind 1 mm apertures was apparent in SC trees, but not SI trees. In contrast, high pollinator efficiency in open-pollinated flowers when compared to other treatments was very apparent in SI trees, but to a lesser extent in SC trees (Table 9.16).

The least economical pollination services across all trees occurred in the bag with 5 mm apertures (Table 9.16). This is because of particularly inefficient pollination services in SC trees rather than in SI trees (Table 9.16). This may have been because of the removal of pollen from the bodies of insects, particularly honey bees (diameter 5-6 mm), as they squeezed through the 5 mm openings. At the end of the experiment, pollen was visible on the mesh.

Caging treatment	Group of trees SC	SI	all
1mm	1.45	0.16	0.59
5mm	0.39	0.25	0.30
12mm	0.74	0.25	0.42
25mm	0.99	0.19	0.46
OP	0.95	0.39	0.57

TABLE 9.16

Pollinator efficiencies (pollinator effectiveness per percentage of nectar standing crop consumed) for various treatments within different caging treatments. Pollinator effectiveness was determined from eight SI trees and four SC trees in 1998-99 (Figs 9.6 – 9.8). Nectar consumption was determined from two trees (1337 and 422) in spring 2000 (Fig. 9.9).

9.3.1.8 Associations between avian flower visitors and pollination

Fitting pollinator effectiveness scores for branches of open-pollinated flowers as vectors to the ordination plots of the same branches, based on the proportional bird species compositions in the trees, provided no evidence of differences between birds in their effectiveness as pollinators. None of the pe scores for the numbers of seeds per flower, seeds per capsule, or capsules per flower were significantly associated with the ordination plots for all trees or SI trees (Table 9.17).

Pollinator effectiveness	all trees	SI trees
Capsules / flower	$P > 0.39$	$P > 0.43$
Seeds / capsule	$P > 0.57$	$P > 0.49$
Seeds / flower	$P > 0.31$	$P > 0.08$

TABLE 9.17

Significance of pollinator effectiveness scores for three fecundity variables as vectors, fitted to the ordination plots of OP branches according to their proportional bird visitor composition on the entire canopy at the time of flowering on the OP, for all 11 trees (see Fig. 9.2) and eight SI trees (see Fig. 9.3). Tree 849 was excluded because no birds were observed feeding on its flowers (Table 9.7).

9.3.1.9 Associations between insect flower visitors and pollination

Vector fitting of pollinator effectiveness (pe) scores for experimental branches of flowers accessible to large insects, to the ordination plots of the same branches according to their mean flower visitation rates by insect species, provided little evidence of differences between insects in their effectiveness as pollinators. None of the pe scores for the numbers of seeds per flower, seeds per capsule, or capsules per flower were significantly associated with the ordination plot for SI trees (Table 9.18). Similarly, for SC trees, pe scores for the numbers of seeds per flower and seeds per capsule were not significantly associated with the ordination plot. However, pe for capsules per flower was significantly associated with the ordination plot for SC trees (Table 9.18). This was positively associated with cockchafer beetles (Pmac and Pruf) and negatively associated with honey bees (Am) in the plane described by the two axes that contained most of the variation between experimental branches (Fig. 9.4).

Pollinator effectiveness	SC trees	SI trees
Capsules / flower	$P < 0.01$	$P > 0.52$
Seeds / capsule	$P > 0.20$	$P > 0.74$
Seeds / flower	$P > 0.28$	$P > 0.78$

TABLE 9.18

Significance of pollinator effectiveness scores for three fecundity variables as vectors, fitted to the ordination plots of 5 mm, 12 mm, 25 mm and OP treatments according to their mean insect visitation rates, for four SC trees (see Fig. 9.4) and eight SI trees (see Fig. 9.5).

9.3.1.10 Effects of tree-related factors on insect flower visitors

	Tree-related factors						
Insect taxa	Distance	Height	Aspect	#Flowers	Diameter	Peakint	Peakdate
Apis mellifera	**0.0001 -**	0.6961	0.9483	0.2599	0.0136	0.8210	0.0200
Bombus terrestris	0.1546	0.0338	0.9909	0.1036	0.2296	0.1737	0.6949
Total exotic bees	**0.0001 -**	0.6422	0.9486	0.2365	0.0120	0.8570	0.0191
Exoneura spp.	0.8010	0.6900	0.5458	0.1656	0.0596	0.3620	0.1696
Leioproctus (Leioproctus) spp.	0.6124	0.0615	0.8740	0.8617	0.3472	0.8073	0.7336
*Hylaeus (Euprosopis) honestus**	0.6886	0.0627	0.4542	0.9221	0.9475	0.8662	0.8201
Hylaeus (Gnathoprosopoides) bituberculatus	0.1969	**0.0004 -**	0.0739	0.9762	0.0122	0.3899	0.0454
Hylaeus (Prosopisteron) spp.	0.6456	0.8558	0.1549	0.7329	0.2277	0.0798	0.1574
Homalictus (Homalictus) spp.	0.5668	0.6508	0.3103	0.9065	0.5576	0.9670	0.2544
small *Lasioglossum (Chilalictus)*	0.0466	0.6862	0.9796	0.5933	0.4132	**0.0002 -**	0.0711
large *Lasioglossum (Chilalictus)*	0.1997	0.1408	0.5899	0.2148	0.7703	0.4958	0.8942
Lasioglossum (Parasphecodes) spp.	0.1547	0.6713	0.4615	0.6085	0.3034	0.3353	0.6598
Total native bees	0.8078	0.0541	0.8953	0.6961	0.1588	0.3507	0.3600
Gasteruption spp.	0.6158	0.0175	0.8330	0.4515	0.5125	0.6056	0.9633
Thynnus zonatus	0.6739	**0.0003 -**	0.7375	0.8220	0.8710	0.7402	0.4753
Total wasps	0.5827	**0.0003 -**	0.6597	0.8823	0.7345	0.8013	0.3470
unidentified small ants	0.5390	**0.0001 -**	0.0244	0.4642	0.2517	0.1847	0.4731
Total ants	0.5858	**0.0001 -**	0.0245	0.4910	0.2572	0.1783	0.4598
Anthomyiidae	**0.0007 -**	0.1703	0.1405	**0.0010 -**	**0.0004 +**	0.4144	0.0536
Calliphora stygia	0.1520	0.0324	0.9979	0.5558	0.0556	0.9821	0.3987
Calliphora sp.2	0.1213	0.8895	0.8113	0.4647	0.0046	0.3115	0.0015
Sepsidae	0.3810	0.3348	0.0024	0.0759	0.4373	0.6298	0.3664
Syrphidae sp.1	0.2019	0.6527	0.8738	0.0081	0.1436	0.0843	0.2852
Psilota sp.	0.1203	0.5111	0.1808	0.5374	0.0170	0.5270	0.0146
Total flies	0.3931	0.4052	0.9919	0.0048	0.6793	0.5814	0.0514
Chauliognathus lugubris	0.4589	0.0250	0.5860	0.4611	0.7401	0.4932	0.2466
Chauliognathus nobilitatus	0.7134	0.0884	0.6137	0.2502	0.6818	0.4446	0.5846
Cerambycidae	0.1522	**0.0001 -**	0.3037	0.7479	0.2650	0.9522	0.3746
Eleale sp.	0.2725	**0.0001 -**	0.2229	0.5865	0.1872	0.9655	0.5703
Mordellistena spp.	0.6970	0.8720	0.6710	0.5073	0.1818	0.6082	0.3792
Phyllotocus macleayi	0.8336	0.6488	0.0058	0.0065	0.5037	0.0040	0.0265
Phyllotocus rufipennis	0.8093	0.4358	0.0053	0.0071	0.7826	0.0303	0.0858
Total beetles	0.7144	0.3552	0.0174	0.0234	0.5978	0.0062	0.0238
Total insects	0.2579	0.8058	0.0340	0.0632	0.7982	0.0041	0.1195

TABLE 9.19

The significance of tree-related factors as predictors of visitation rates by each insect taxon to each experimental branch using individual regressions, after the effects of all other tree-related factors (Table 9.5) have been removed. Taxa whose visitation rates were statistically significant predictors of fecundity have the *P*-value in bold, with the direction of the

association given as + (positive) or - (negative). The *P*-value designated as the level of significance (0.05) was adjusted, using the Bonferroni method, to 0.00147. Only insects observed on at least three experimental branches were analysed. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of *E. globulus* in Tasmania (Hingston and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999).

Individual regressions of the residuals of each tree-related factor as predictors of the residuals of the mean flower visitation rates by insects on each experimental branch, after controlling for the effects of the other tree-related factors, revealed some statistically significant associations (Table 9.19). *Hylaeus (Gnathoprosopoides) bituberculatus* (Smith), *Thynnus zonatus*, small ants, Cerambycidae, *Eleale* sp., total wasps, and total ants were all more common on flowers nearer to the ground (Table 9.19). Anthomyiidae and honey bees, indeed all exotic bees, were more abundant when flowering conspecifics were nearby (Table 9.19). Anthomyiidae were also more abundant on larger flowers, and when there were fewer flowers on the experimental branch. Small species of *Lasioglossum (Chilalictus)* visited flowers more frequently when flowering intensity was low. However, aspect of the experimental branch on the tree, and date of peak flowering on the experimental branch, did not significantly influence visitation rates by any insect taxa (Table 9.19).

9.3.1.11 Effects of tree-related factors on seed set per flower

Individual regressions of the residuals of each tree-related factor as predictors of the residuals of pe score for the numbers of seeds per flower on each experimental branch, after controlling for the effects of the other tree-related factors, also revealed some statistically significant associations (Table 9.20). However, statistically significant associations were only apparent on SC trees, not on SI trees. Fecundity on SC trees was greater when flowering conspecifics were nearby, flowers were smaller, and on branches nearer to the ground. In contrast, no tree-related factor enhanced fecundity in SI trees. When all trees were investigated, fecundity was greater when the intensity of

flowering on the tree was greater (Table 9.20). Pollinator effectiveness scores for the numbers of seeds per flower were not related to aspect of the experimental branch on the tree, date of peak flowering on the experimental branch, or the number of flowers on the experimental branch (Table 9.20).

Trees	Tree-related factors						
	Distance	Height	Aspect	#Flowers	Diameter	Peakint	Peakdate
all	0.1067	0.8843	0.0855	0.4254	0.1842	**0.0017 +**	0.0098
SC	**0.0001 -**	**0.0001 -**	0.8857	0.9542	**0.0001 -**	0.0723	0.2970
SI	0.1567	0.7535	0.8053	0.6698	0.0638	0.3337	0.3683

TABLE 9.20

The statistical significance of each tree-related factor as predictors of the pollinator effectiveness scores for the numbers of seeds produced per flower on each experimental branch determined using individual regressions, after the effects of the other tree related factors, site and caging treatment have been removed (Table 9.5). Factors that were significant predictors of fecundity have the *P*-value in bold, with the direction of the association given as + (positive) or - (negative). The *P*-value designated as the level of significance (0.05) was adjusted, using the Bonferroni method, to 0.00714.

9.3.1.12 Effects of individual insect taxa on seed set per flower

Comparisons of the effects of tree-related factors on insect visitation rates (Table 9.19) and pe scores for the numbers of seeds per flower (Table 9.20) on each branch provide some insight into the relationships between insect taxa and pollinator effectiveness. Several insect taxa were associated with tree-related factors that were also positively associated with pe scores for the numbers of seeds per flower on SC trees (Table 9.21). However, none of these relationships occurred more than once for any insect taxon. Moreover, Anthomyiidae and this fecundity score were positively associated via distance to the nearest flowering conspecific, but negatively associated via flower diameter. The only statistically significant relationship by an insect with the tree-related factor associated with pe scores for the numbers of seeds per flower on all trees was in the opposite direction. Hence, small species of *Lasioglossum (Chilalictus)* were negatively associated with fecundity on all trees.

Tree-related factor	Correlations	
	significantly negative	significantly positive
Distance	Near pe seeds/flower SC trees *Apis mellifera*, Anthomyiidae, exotic bees	Far
Height	Low pe seeds/flower SC trees *Hylaeus (Gnathoprosopoides) bituberculatus.* *Thynnus zonatus*, small ants, Cerambycidae, *Eleale* sp., wasps, ants	High
Aspect	North	South
#Flowers	Few Anthomyiidae	Many
Diameter	Small pe seeds/flower SC trees	Large Anthomyiidae
Peakint	Light small *Lasioglossum (Chilalictus)* spp.	Heavy pe seeds/flower all trees
Peakdate	Early season	Late season

TABLE 9.21

Pollinator effectiveness scores for the numbers of seeds produced per flower, and visitation rates by insect taxa, that were significantly predicted by tree-related factors (summary of Tables 9.19 and 9.20). Tree-related factors are detailed in Table 9.5.

Individual regressions of residuals of pe scores for the numbers of seeds produced per flower as functions of the residuals of insect visitation rates revealed very few statistically significant relationships (Table 9.22). Only the visitation rates of bees similar to *Hylaeus (Euprosopis) honestus* (Smith), and the beetles *Phyllotocus rufipennis* and *Mordellistena* spp., were significantly associated with increased fecundity in SI trees. No visitation rates were statistically significant predictors of fecundity on all trees or SC trees (Table 9.22).

Insect taxon	all trees	SI trees	SC trees
Apis mellifera	0.0884	0.3146	0.0265
Bombus terrestris	0.7317	0.6533	
Total exotic bees	0.0851	0.3049	0.0265
Exoneura spp.	0.7670	0.9116	
Leioproctus (Leioproctus) spp.	0.8394	0.7582	0.0160
*Hylaeus (Euprosopis) honestus**	0.0016	**0.0001 +**	
Hylaeus (Gnathoprosopoides) bituberculatus	0.9945		
Hylaeus (Prosopisteron) spp.	0.8574	0.6001	0.2465
Homalictus (Homalictus) spp.	0.2730	0.1352	0.9373
small *Lasioglossum (Chilalictus)* spp.	0.8995	0.8851	
large *Lasioglossum (Chilalictus)* spp.	0.8433	0.7666	0.0945
Lasioglossum (Parasphecodes) spp.	0.8601	0.6292	
Total native bees	0.8066	0.6602	0.0060
Gasteruption spp.	0.0152	0.0108	
Thynnus zonatus	0.0064	0.2313	0.5160
Total wasps	0.0036	0.1661	0.5160
unidentified small ants	0.0779	0.3232	0.4999
Total ants	0.0791	0.3265	0.4999
Anthomyiidae	0.7002	0.3152	0.0146
Calliphora stygia	0.0353	0.0523	
Calliphora sp.2	0.5708	0.8828	0.8461
Sepsidae	0.6612		
Syrphidae sp.1	0.8636	0.3547	0.1199
Psilota sp.	0.7036	0.9323	
Total flies	0.3575	0.8146	0.1214
Chauliognathus lugubris	0.5582	0.6523	0.2258
Chauliognathus nobilitatus	0.0204	0.6901	
Cerambycidae	0.4007	0.1675	
Eleale sp.	0.1411	0.0248	0.0329
Mordellistena spp.	0.0038	**0.0001 +**	
Phyllotocus macleayi	0.9428		0.9954
Phyllotocus rufipennis	0.0974	**0.0008 +**	0.4599
Total beetles	0.8970	0.3306	0.3486
Total insects	0.7601	0.3216	0.0150

TABLE 9.22

The statistical significance of visitation rates by each insect taxon to each experimental branch as predictors of the pollinator effectiveness scores for the numbers of seeds produced per flower on each experimental branch determined using individual regressions, after the effects of all tree-related factors were removed (Table 9.5). Taxa whose visitation rates were significant predictors of fecundity have the *P*-value in bold, with the direction of the association given as + (positive) or - (negative). The *P*-value designated as the level of significance (0.05) was adjusted, using the Bonferroni method, to 0.00147 for all trees, 0.00161 for self-incompatible trees, and 0.00238 for self-compatible trees. Empty cells represent cases where the insect taxon was recorded on less than three experimental branches, as these were not included in the analysis. *Some bees attributed to *Hylaeus (Euprosopis) honestus* may have been *Hylaeus (Hylaeorhiza) nubilosus* or *Hylaeus (Prosopisteron) quadratus* as they are superficially similar and are all known to visit flowers of *E. globulus* in Tasmania (Hingston

and Potts 1998). However, *H. (Euprosopis) honestus* is more common than the other two species in Tasmania (Hingston and Potts 1998, Hingston 1999).

9.3.2 *Experiment 2*

9.3.2.1 Flower visitors

Flowers of dwarf precocious trees were visited by a wide variety of insects (Table 9.23), and occasional New Holland honeyeaters. The most common insect visitors were the exotic bees, namely *Apis mellifera* and *Bombus terrestris* (L.), although small ants were abundant on some flowers (Table 9.23). Paired t-tests revealed no significant differences in insect visitation rates between caged and uncaged flowers on the four trees, whether at the level of total insects, functional groups or morphospecies (Table 9.23).

9.3.2.2 Pollinator effectiveness

Flowers exposed to insects only, or insects and birds, were not fully pollinated. Two-Way Analysis of Variance indicated that the numbers of seeds per capsule and seeds per flower on the four trees were almost significantly different between the three treatments, with fecundity from flowers receiving supplemental outcross pollen being much higher than those pollinated by insects or insects plus birds (Table 9.24). Moreover, the difference in all three fecundity measures between flowers visited only by insects and those receiving supplementary outcross pollen became statistically significant following inclusion of the fecundity data from trees 1018 and 1021 (Table 9.25). Hence, flowers receiving supplementary outcross pollen produced significantly more capsules per flower, seeds per capsule, and seeds per flower than did those exposed to insects only (Table 9.25). The number of seeds produced per flower after exposure to insects was less than that produced from flowers receiving supplementary outcross pollen on all six trees (Table 9.26).

Insect visitors		Tree number				Data	P
Family	Species	1023	1026	1029	1037		
Apidae	*Apis mellifera*	0	0.014	0.020	0.020	raw	0.174
		0.028	0.128	0.011	0.071		
	Bombus terrestris	0	0.012	0	0.034	raw	0.578
		0	0.034	0.011	0.020		
	Total exotic bees	**0**	**0.026**	**0.020**	**0.054**	**raw**	**0.183**
		0.028	**0.162**	**0.022**	**0.091**		
Anthophoridae	*Exoneura* spp.	0	0	0	0.017	raw	0.746
		0.004	0.003	0	0.004		
Colletidae	*Hylaeus*	0	0.002	0	0.031	rank	0.500
	(Prosopisteron) spp.	0	0	0	0		
Halictidae	*Homalictus* spp.	0	0	0	0.014	rank	1.000
		0	0	0	0.001		
	small *Lasioglossum*	0	0.011	0.007	0.020	raw	0.315
	(Chilalictus) spp.	0	0	0.011	0.001		
	large *Lasioglossum*	0	0	0	0	rank	1.000
	(Chilalictus) spp.	0	0	0	0.001		
	Total native bees	**0**	**0.012**	**0.007**	**0.082**	**raw**	**0.392**
		0.004	**0.003**	**0.011**	**0.008**		
Vespidae	*Vespula* spp.	0	0.004	0	0	rank	1.000
		0	0.002	0	0		
	Total wasps	**0**	**0.004**	**0**	**0**	**rank**	**1.000**
		0	0.002	0	0		
Formicidae	unidentified small	0	0.002	0	0.388	raw	0.912
	ants	0	0.002	0.319	0		
	Myrmecia pilosula	0	0.002	0	0.014	raw	0.505
		0.004	0	0	0		
	Total ants	**0**	**0.004**	**0**	**0.401**	**raw**	**0.900**
		0.004	**0.002**	**0.319**	**0**		
Diptera	unidentified small	0.005	0.002	0	0.017	rank	1.000
	flies	0	0	0	0.012		
Calliphoridae	*Calliphora stygia*	0	0	0	0	rank	1.000
		0	0.002	0	0		
	Calliphora sp.2	0	0	0	0	rank	1.000
		0	0.002	0	0		
Sepsidae	sp.1	0	0	0	0	rank	1.000
		0	0	0	0.001		
Syrphidae	sp.1	0	0	0.013	0	rank	1.000
		0	0	0	0.001		
	Total flies	**0.005**	**0.002**	**0.013**	**0.017**	**raw**	**0.242**
		0	**0.003**	**0**	**0.015**		
Coleoptera	unidentified small	0	0	0	0.020	rank	1.000
	beetles	0	0	0	0		
Cleridae	*Eleale* sp.	0	0	0	0.007	rank	1.000
		0	0	0	0.001		
Lycidae	*Metriorrhynchus*	0	0	0	0.024	rank	1.000
	spp.	0	0	0	0		
Mordellidae	*Mordellistena* spp.	0	0	0	0.007	rank	1.000
		0	0	0	0		
	Total beetles	**0**	**0**	**0**	**0.058**	**rank**	**1.000**
		0	**0**	**0**	**0.001**		
	Total insects	**0.005**	**0.047**	**0.040**	**0.612**	**raw**	**0.969**
		0.036	**0.172**	**0.352**	**0.116**		

TABLE 9.23

Mean visitation rates (visits per 5 minutes) by insect taxa to flowers of *E. globulus* either caged within chicken-wire or uncaged on four trees. For each tree, the visitation rate by each

insect to caged flowers is placed above the visitation rate to uncaged flowers. *P*-values derived from paired t-tests of treatments using trees as replicates (raw data) or Wilcoxon Signed Rank Tests due to non-normal data (rank data).

Fecundity variable	insects	insects & birds	supplements	*P*
capsules / flower	0.537	0.629	0.858	0.188
seeds / capsule set	10.7	11.8	22.3	0.0729
seeds / flower	6.16	7.69	20.4	0.0637

TABLE 9.24

Mean fecundity for flowers exposed to insects only, insects plus birds, or receiving supplementary outcross pollination, from four trees of *E. globulus*. All comparisons conducted using 2-Way ANOVA on the means from each tree.

Fecundity variable	insects	supplements	*P*
capsules / flower	0.471	0.792	0.0253
seeds / capsule set	11.7	24.0	0.0203
seeds / flower	5.68	19.42	0.0269

TABLE 9.25

Mean fecundity for flowers exposed to insects only or receiving supplementary outcross pollination from six trees of *E. globulus*. All comparisons conducted using paired t-tests on the means from each tree.

There were no statistically significant associations between flower visitation rates by insects and seed production on the six trees. None of the residuals of visitation rates by insect species, functional groups, or total insects were significant predictors of the residuals of the pe scores for the numbers of seeds per flower exposed only to insects (Table 9.26). This was in spite of the fact that both visitation rates by insects and pe scores for the numbers of seeds per flower varied widely across the six trees (Table 9.26).

Insect visitor		Tree number						P
Family	Species	1018	1021	1023	1026	1029	1037	
Apidae	*Apis mellifera*	0.051	0	0	0.014	0.020	0.020	0.047
	Bombus terrestris	0.003	0	0	0.012	0	0.034	0.267
	Total exotic bees	**0.054**	**0**	**0**	**0.026**	**0.020**	**0.054**	**0.661**
Anthophoridae	*Exoneura* spp.	0.001	0	0	0	0	0.017	0.629
Colletidae	*Hylaeus (Prosopisteron)* spp.	0	0	0	0.002	0	0.031	0.558
Halictidae	small *Lasioglossum (Chilalictus)* spp.	0.0001	0	0	0.011	0.007	0.020	0.500
	Total native bees	**0.004**	**0**	**0**	**0.012**	**0.007**	**0.082**	**0.591**
	Total wasps	**0.001**	**0**	**0**	**0.004**	**0**	**0**	**0.397**
Formicidae	unidentified small ants	0.013	0	0	0.002	0	0.388	0.623
	Myrmecia pilosula	0.006	0	0	0.002	0	0.014	0.657
	Total ants	**0.019**	**0**	**0**	**0.004**	**0**	**0.401**	**0.624**
Diptera	unidentified small flies	0	0	0.005	0.002	0	0.017	0.335
	Total flies	**0**	**0**	**0.005**	**0.002**	**0.013**	**0.017**	**0.552**
	Total insects	**0.078**	**0**	**0.005**	**0.047**	**0.040**	**0.612**	**0.672**
	pe seeds / flower	42.9	14.5	8.0	78.9	19.4	74.6	

TABLE 9.26

Mean visitation rates (visits / 5 min) by insect species, functional groups and total insects recorded from at least two trees to flowers of *E. globulus* caged within chicken-wire on six trees, the pollinator effectiveness scores for the numbers of seeds per flower (pe s/f) for each cage, and the *P*-values for individual regressions of the residuals of pe s/f as a function of the residuals of visitation rates. Residuals calculated by removing the effects of the numbers of flowers on the tree and the date of peak flowering within the cage. The *P*-value designated as the level of significance (0.05) was adjusted, using the Bonferroni method, to 0.00357.

9.4 Discussion

9.4.1 Pollen limitation

Open-pollinated flowers of *E. globulus* were consistently not fully fertilized within its natural distribution. In Experiment 1, open-pollinated flowers produced significantly fewer seeds than flowers receiving supplementary outcross pollen in the lower branches of trees (Table 9.27). A similar trend was apparent in Experiment 2 (Table 9.27), although the low number of replicates prevented these differences from reaching statistical significance. Comparisons between flowers receiving these two treatments in a Chilean *E. globulus* plantation also found statistically significant pollen limitation,

apparent as reduced numbers of capsules per flower, seeds per capsule and seeds per flower (Harbard *et al.* 1999, Table 9.27). However, this contrasts with the absence of statistically significant differences in these three measures of fecundity, between open-pollinated flowers and those receiving outcross pollen after emasculation and isolation in an earlier study of 11 *E. globulus* trees at Hobart Airport (Hardner and Potts 1995, Table 9.27). This may be because Hardner and Potts (1995) used a different procedure to the other two studies for manual outcross pollination. Hardner and Potts (1995) raised the possibility that their emasculation and bagging technique may have damaged the flowers, thereby confounding the comparison. The differences between the two Tasmanian studies may also be a consequence of most of the trees in Experiment 1 being completely self-incompatible (SI), whereas most of the trees studied by Hardner and Potts (1995) were self-compatible (SC) (see below).

Fecundity variable	Experiment 1, SI trees	Experiment 1, SC trees	Experiment 2	Harbard *et al.* (1999)	Hardner & Potts (1995)
capsules / flower	41.3	111.5	73.3	33.3	140.0
seeds / capsule	47.1	66.6	52.9	77.8	83.3
seeds / flower	25.3	69.1	37.7	26.0	104.4

TABLE 9.27

Mean pollinator effectiveness scores for open-pollinated flowers in both experiments, and those calculated from two previous studies of *E. globulus*. All pollinator effectiveness scores were calculated as the fecundity from open-pollinated flowers as a percentage of that from flowers receiving supplementary outcross pollen, except Hardner and Potts (1995) where they were calculated as percentages of fecundity from bagged emasculated flowers receiving manual cross pollinations. All studies were conducted in southeastern Tasmania, except Harbard *et al.* (1999) which was carried out in a Chilean plantation.

Seed production from open-pollinated flowers in the lower branches of *E. globulus* trees was limited by the amounts of outcross pollen deposited on stigmata, more than by the total quantities of pollen deposited. This was apparent from statistically significant increases in seed production in open-pollinated flowers after application of supplementary outcross pollen in SI trees but not in SC trees (Table 9.27). However, seed set from open-pollinated flowers on SC trees was still only 69.1% of that resulting from

outcross pollen supplementation (Table 9.27). Although this may reflect some limitation in the total quantity of pollen deposited, this is unlikely because large quantities of pollen can be deposited on stigmata during single contacts by pollinators (Chapter 6) and flowers are usually visited hundreds of times. Pollen limitation in SC trees most probably resulted from insufficient outcross pollen deposition in conjunction with preferential outcrossing in these partially SC trees (Potts and Cauvin 1988, Hardner and Potts 1995).

The degree of pollen limitation in both of my experiments and that of Harbard *et al.* (1999) is far more severe than that in *E. nitens* (Tibbits 1989, Chapter 5). This suggests that *E. globulus* flowers within 5 m of the ground incur consistently severe pollination deficits (Thomson 2001), with pollen limitation being almost as great within its natural distribution as in an extralimital Chilean population (Table 9.27). Because all of the daily nectar production in Tasmanian *E. globulus* is often consumed on fine days (Chapter 4), this pollination shortfall cannot be attributed to insufficient flower visitors. Rather, it must reflect the presence of large numbers of inefficient pollinators together with low numbers of efficient pollinators.

9.4.2 Effectiveness of various animals as pollinators

The flowers of *E. globulus* were visited by animals encompassing a size range from insects small enough to pass through 1 mm mesh up to birds too large to pass through a 25 mm mesh. Both birds and insects pollinated flowers of *E. globulus*, consistent with the results of single visits to flowers (Chapter 6), and the conclusions of Ford *et al.* (1979) that large flowered eucalypts are able to exploit both birds and insect as pollinators. However, none of the size classes of flower visitors were particularly effective pollinators in the lower branches of SI trees, as every size class contributed less than 13% of the maximum possible seed set.

9.4.2.1 Effectiveness of insects as pollinators

Insects that were small enough to pass through the 1 mm mesh provided little, if any, pollination services to *E. globulus*. However, they may be able to deposit outcross pollen on stigmata. Evidence for this came in the form of occasional seed production from flowers enclosed in the 1 mm mesh on apparently SI trees. Hence, although single flower visits by very small insects did not result in seed set (Chapter 6), multiple insect visits may result in the deposition of sufficient compatible pollen to initiate seed set (Keys *et al.* 1995, Olsen 1997). However, the production of a small number of seeds from flowers enclosed within 1 mm mesh, on trees that produced no seeds in exclusion bags, may have been the result of some of these trees having some self-compatibility.

Even if this seed set within 1 mm mesh was caused by deposition of outcross pollen, this cannot be attributed with certainty to xenogamous pollination by small insects. It is possible that outcross pollen was transported into the tree by other animals, and secondarily transferred to stigmata by small insects via geitonogamous or autogamous pollination (Heinrich 1975, DeGrandi-Hoffman and Martin 1995, DeGrandi-Hoffman and Watkins 2000). Alternatively, outcross pollen may have been transported into the canopy above the experimental branches by other vectors, and then fell through the 1 mm mesh onto the stigmata. Evidence that pollen transfer can be transferred to stigmata low in the canopy by falling from above comes from the negative association between pollinator effectiveness for seeds per flower and height in the canopy in SC trees but not SI trees, and the much greater pollinator efficiency in the 1 mm mesh on SC than SI trees. Therefore, although *Eucalyptus* pollen is not suited to transport by wind (Ashton 1975, Pryor 1976, Eldridge *et al.* 1993), pollen may be transferred by gravity between flowers on the same tree or near neighbours (Eldridge 1970).

The greatest contribution to seed production per flower, in both SI and SC trees, in Experiment 1 was from insects that were too large to pass through the 1 mm mesh. However, these large insects were inefficient pollinators

because they visited flowers on an average of approximately once every 5 minutes in Experiment 1 and consumed most of the nectar on fine days (see also Chapter 4), while providing only 14.1% and 40.8% of the maximum possible pollination services to SI and SC trees, respectively. Constant exposure to insects also resulted in only 29.2% of the maximum possible seed set in Experiment 2. Hence, permanent exposure to insects resulted in much lower seed set than did a single flower visit by a swift parrot, which resulted in an average of 76% of maximum possible seed set (Chapter 6). Although there is a possibility that insects visited more flowers per foraging bout within cages than to uncaged flowers (Paton and Turner 1985), thereby making them appear less effective outcross pollinators, this did not have a dramatic effect because fecundity from open-pollinated flowers was not significantly greater than that within cages in either experiment. The inability of insects to fully pollinate flowers is likely to be the result of inefficient pollination when they were active, rather than their inability to forage during inclement weather (Christensen 1971, Ford *et al.* 1979, Hopper 1981, Houston *et al.* 1993), because unpollinated stigmata appear to remain receptive for several days (Chapter 6).

As the western honey bee was the most abundant anthophilous insect in both experiments, and was responsible for most nectar consumption (see also Chapter 4) without being a statistically significant predictor of pe s/f, it must be a very inefficient pollinator. Honey bees visited each flower in Experiment 1 on average several hundred times before it senesced, but still facilitated less seed set than a single visit by a swift parrot (Chapter 6). Therefore, introduction of honey bee hives to *E. globulus* seed orchards where all nectar is consumed is likely to reduce seed set, by competitive displacement of more efficient bird-pollinators such as the swift parrot (Paton 1993, Roubik 1996, Paton 1997, Irwin and Brody 1998, see Section 6.4.1).

The inefficiency of honey bees as pollinators appears to be the result of them mostly depositing self-pollen. Pollinator efficiency was much higher in SC

trees than SI trees in all caging treatments in Experiment 1 except the 5 mm mesh, because honey bees and other insects of similar size provided much poorer pollination services within the 5 mm mesh than other treatments they visited on SC trees. Therefore, large proportions of self-pollen were deposited on stigmata in all treatments visited by these insects except the 5 mm mesh. Because honey bees were the major flower visitors, and large quantities of pollen were removed from honey bees' bodies as they squeezed tightly through the 5 mm mesh, it is highly likely that they were responsible for most self-pollination. More evidence of honey bees depositing mostly self-pollen comes from them being able to deposit large quantities of pollen via a single stigma contact, contacting stigmas on approximately 50% of visits to female-phase flowers (Chapter 6), and visiting flowers hundreds of times while facilitating no more than 14.1% of the maximum possible seed set on SI trees. In addition, stigmatic contact by honey bees did not increase seed set above levels occurring in flowers they visited without stigmatic contact, further suggesting that they deposited mostly self-pollen (Chapter 6). This finding is similar to that in the largely SI *Callistemon rugulosus* DC (Myrtaceae) for which fruit set in flowers visited by honey bees only was comparable to that from bagged flowers that were self-pollinated, but much lower than from cross-pollinated flowers (Paton 1993, 1997).

The propensity for honey bees to deposit mostly self-pollen can be attributed to the frequent tendency of individuals to confine their foraging to very small areas for long periods of time (Butler *et al.* 1943, Grant 1950, Hodgson 1976a, Paton 1993, 1997). The impact that this behaviour has on rates of xenogamous pollen transfer would be exacerbated by the large numbers of flowers on trees of *E. globulus* (de Jong *et al.* 1993, Klinkhamer and de Jong 1993). Regular grooming of pollen from the bodies of honey bees (e.g. Free 1968, Bernhardt and Weston 1996) also reduces their capacity to transfer pollen between plants because such behaviour reduces pollen carryover (Thomson and Plowright 1980, Thomson 1986).

The deposition of large quantities of self-pollen on stigmata of *E. globulus* by honey bees, together with grooming of pollen from their bodies, reduces the amount of pollen available for more effective pollinators to deposit as outcross pollen (Wilson and Thomson 1991, de Jong *et al.* 1993, Klinkhamer and de Jong 1993). Although such pollen wastage by honey bees on SI trees was not sufficient to cause a statistically significant negative correlation between honey bee abundance and pollinator effectiveness scores on these flowers that were not visited by large numbers of effective pollinators, it is possible that honey bees may reduce seed set in the upper canopy where effective bird pollinators are more common (Chapter 8) by reducing the amount of pollen available for cross-pollination. This is possible because Ellis and Sedgley (1992) found that animals removed most pollen from three other *Eucalyptus* species within one day of anther dehiscence, and pollen removal by honey bees reduced seed set in some other bird-pollinated plant species because less pollen was available for birds to transfer (Pyke 1990, Paton 1993, 1997).

Although single honey bee visits to flowers of *E. globulus* at peak stigmatic receptivity resulted in 6.8% of the maximum possible seed set (Chapter 6), exposure to several hundred visits by honey bees in Experiment 1 resulted in only 14.1% and 40.8% of maximum possible seed set in SI and SC trees, respectively. This indicates that the value of honey bee flower visits declines rapidly with increased numbers of visits, especially on fully SI trees, suggesting that they may deposit such high proportions of self-pollen that this interferes with outcross pollen. Self-pollen on eucalypt stigmata can germinate and the pollen tubes then penetrate ovules (Ellis and Sedgley 1992). In such plants with post-zygotic self-incompatibility mechanisms, the deposition of self-pollen can reduce seed set by fertilising ovules that subsequently abort, thereby making them unavailable for fertilization by compatible outcross pollen (Waser and Price 1991, Ramsey *et al.* 1993, Ramsey 1995, Ramsey and Vaughton 2000). However, not all ovules are penetrated by pollen tubes in eucalypts, even when the numbers of pollen tubes reaching the base of the style exceeds the number of ovules, leading

Ellis and Sedgley (1992) to conclude that ovule pre-emption has little impact on fecundity. Nevertheless, deposition of self-pollen could reduce the number of outcross pollen tubes reaching the ovules because pollen tubes can compete for space in the lower style of eucalypts (Ellis and Sedgley 1992). Although rates of self-pollen deposition by honey bees were not sufficient to cause a statistically significant negative correlation between honey bee abundance and pollinator effectiveness scores on these flowers that were not visited by large numbers of effective pollinators, it is possible that honey bees may reduce the capacity of flowers to be fully pollinated by animals that deposit greater proportions of outcross pollen.

Therefore, in most situations, addition of honey bee hives to seed orchards of *E. globulus* would be of little value in enhancing seed production. By depositing high proportions of self-pollen, honey bees would only make major contributions to seed set when trees were self-compatible and more effective bird pollinators were scarce. Although the deposition of large quantities of self-pollen by honey bees on highly SC trees could facilitate abundant seed set, the quality of the resultant offspring would be poor because of inbreeding depression manifesting as reduced growth rates and increased mortality in young trees of *E. globulus* (Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995).

This conclusion contrasts with the claim by Moncur *et al.* (1995) that deployment of honey bee hives increases seed production in *E. globulus*. Their claim was based on observations of greater numbers of seeds per capsule in a Tasmanian seed orchard following a year when honey bee hives were deployed than in the previous year when no hives were introduced (Moncur *et al.* 1993). However, the numbers of capsules produced per flower were not determined, hence, the numbers of seeds produced per flower could not be calculated (Moncur *et al.* 1993). More importantly, their results were confounded by the 'with hives' and 'without hives' treatments being conducted in different years (Moncur *et al.* 1993). As flowering intensity in eucalypts varies enormously between years (Ashton 1975, Brown 1989,

Moncur 1993, Moncur *et al.* 1994), and this influences seed production (Carpenter 1976, Andersson 1988), any increase in seed set in years when hives were added may not have been caused by the actions of honey bees (Paton 1996). Furthermore, seed production is also affected by the activity levels of other pollinators, environmental conditions and seed predation levels (Eldridge *et al.* 1993), which may also vary between seasons and therefore confounded their findings. Because of inadequate experimental design their results should only be regarded as correlations based on two data points. Even if it were valid to draw conclusions of cause and effect from correlations based on two data points, such conclusions could not be drawn because no evidence of increases in numbers of honey bees in these areas after introduction of hives was obtained (Moncur *et al.* 1993). As feral populations of honey bees are widespread in Australia (Oldroyd *et al.* 1995, Oldroyd 1998), and the number of feral honey bees increased rapidly following removal of managed hives (Schaffer *et al.* 1983), it cannot be assumed that the introduction of hives by Moncur *et al.* (1993) increased the numbers of honey bees in these areas (Paton 1996).

In addition to honey bees, five other insect taxa were common flower visitors in both experiments without being statistically significant predictors of pe s/f, suggesting that they were also not particularly effective pollinators. These insects were the bumble bee *Bombus terrestris*, the native bees *Exoneura* spp., small *Lasioglossum (Chilalictus)* spp. and *Hylaeus (Prosopisteron)* spp., and small ants. Further evidence of bumble bees being poor pollinators, of comparable inefficiency to honey bees, comes from them facilitating almost identical mean seed set per single visit as honey bees (Chapter 6) and their generally larger body mass than honey bees that should result in them removing at least as much nectar as honey bees per flower visit. This casts doubts on the sweeping statement, made by proponents for introduction of this bumble bee to the Australian mainland, that it will be an efficient pollinator of native plants (Goodwin and Steiner 1997). The absence of seed production from single visits to flowers of *E. globulus* by native bees (Chapter

6) also provides more evidence that they are also poor pollinators of *E. globulus*.

Although insects were generally inefficient as pollinators of *E. globulus*, there was some evidence that a few taxa may be effective pollinators. Visitation rates by three insect taxa were statistically significant predictors of pollinator effectiveness for the numbers of seeds per flower (pe s/f) in SI trees in Experiment 1. These were the native hylaeine bees resembling *Hylaeus (Euprosopis) honestus*, and the beetles *Phyllotocus rufipennis* and *Mordellistena* spp. These bees may have included *Hylaeus (Hylaeorhiza) nubilosus* (Smith) and *H. (Prosopisteron) quadratus* (Smith) because these superficially similar species have been recorded visiting *E. globulus* in Tasmania (Hingston and Potts 1998), but have been attributed to *H. (Euprosopis) honestus* because it appears to be the most common of these three species in Tasmania (Hingston and Potts 1998, Hingston 1999). These bees and beetles were not observed in sufficient numbers during Experiment 2 to confirm this association. However, single flower visits by hylaeine bees or beetles did not facilitate any seed set (Chapter 6), suggesting that the observed correlations are not the result of these insects being particularly effective pollinators.

9.4.2.2 Effectiveness of birds as pollinators

Birds did not significantly enhance the numbers of seeds produced per flower, above the levels resulting from continuous exposure to insects, on the lower branches of *E. globulus* in Experiment 1 or in the dwarf precocious trees used in Experiment 2. This finding is atypical for plants whose flowers or extrafloral nectaries are visited by both birds and insects. In 15 of the 16 plant species where this has been studied previously, exposure to birds significantly enhanced pollination (Carpenter 1976, Waser 1978, 1979, Whelan and Burbidge 1980, Collins *et al.* 1984, Coetzee and Giliomee 1985, Ramsey 1988, Reid *et al.* 1988, Vanstone and Paton 1988, Vaughton 1992, Paton 1993, Vaughton 1996, Paton 1997, Dalgleish 1999). This difference can be attributed to the low visitation rates by birds to the experimental flowers in this study. Birds tended to forage far more frequently higher in the

canopies in Experiment 1 (see also Chapter 8), where outcrossing rates and the numbers of seeds per capsule in *E. globulus* are higher (Patterson *et al.* 2001). This argument is supported by the contributions by birds to fruit set in the related *Metrosideros collina* in Hawaii increasing significantly (approximately double) with height in the canopy across the range from 1 - 13 m above the ground (Carpenter 1976). Hence, although uncaged flowers and those within 25 mm mesh were able to be visited by birds, it cannot be certain that such visits took place on all of these flowers in Experiment 1. In fact, only those on tree 523 were actually seen being visited by birds. On this SI tree, treatments visited by small honeyeaters were the only ones in which seeds developed, with the pollinator effectiveness for numbers of seeds per flower being 19.6% for the 25 mm mesh cage and 59.1% for open pollinated flowers. These values are far greater than the means for these treatments on SI trees, suggesting that these birds enhanced pollination.

Even at the low visitation rates observed here, birds may have had some beneficial effect on pollination. Exposure to birds enhanced the numbers of seeds per flower by 11.2% of the maximum possible seed set in SI trees and 17% in SC trees in Experiment 1, and 24.8% in the small trees in Experiment 2. Hence, the increase in seed set after exposure to birds was almost as large as the increase after exposure to large insects on SI trees, and almost half that facilitated by large insects on SC trees. Unlike large insects, birds did not consume measurable quantities of nectar from flowers in the lower branches, resulting in pollinator efficiency on SI trees being highest in flowers exposed to birds. This suggests that birds enhanced outcrossing. In addition, the more regular visits by birds to flowers in Experiment 2 than in Experiment 1 were associated with a proportionally greater increase in seed set, suggesting that the New Holland honeyeaters that occasionally visited the flowers in Experiment 2 were able to pollinate flowers. Although these increases in pollinator effectiveness and efficiency may have been caused by some insects, particularly flies and beetles, that were reluctant to pass through the 5 mm and 12 mm meshes, they are unlikely to have made a major

contribution to seed set because single visits to flowers by these insects did not result in the production of any seeds (Chapter 6).

9.4.3 Effects of tree-related factors on seed set per flower

Pollinator effectiveness scores for the numbers of seeds per flower (pe s/f) were influenced by tree-related factors on SC trees far more than on SI trees. For SC trees, pe s/f was greater in small flowers. This may reflect a greater likelihood of autogamous pollination on small flowers, either with or without the assistance of a flower-visiting animal, because of the closer proximity of anthers and stigma this entails. The presence of flowering conspecifics nearby, and lower positions in the canopy also increased pe s/f in SC trees, but did not in SI trees. The tendency for these factors to enhance transfer of self pollen but not outcross pollen may reflect inbreeding between related near-neighbours when flowering conspecifics are nearby (Moran *et al.* 1989, Watkins and Levin 1990, Hardner *et al.* 1998, Skabo *et al.* 1998), and increased amounts of pollen rain accumulating towards the base of the canopy (Eldridge 1970), respectively.

Greater pe s/f in SC, but not SI, trees when conspecifics were flowering nearby, suggestive of inbreeding between related near neighbours, is contrary to the increased outcrossing rates in *E. globulus* in denser stands observed by Hardner *et al.* (1996). This relationship is very complex and likely to be variable, as both the probability of receiving xenogamous pollen (Stucky 1985, House 1997) and the proportions of xenogamous pollen that carry the same genes as the receiving tree should be negatively correlated with distance to the nearest flowering conspecific in natural stands (Watkins and Levin 1990, Hardner *et al.* 1998, Skabo *et al.* 1998). Consequently, the effects of isolation distance will depend upon the genetic structure of the *E. globulus* population, with xenogamous inbreeding increasing when the genetic diversity of the population is low. This may explain the lack of concordance between my study and that of Hardner *et al.* (1996), as my study comprised a large proportion of ornamental plantings whereas Hardner *et al.* (1996) investigated natural stands. If each ornamental planting studied here

comprised mainly the offspring of one tree, this would have increased the likelihood of inbreeding via xenogamy. Inbreeding may also be greater in ornamental plantings if the trees were grown from seed collected from low in the canopy, as outcrossing rates can be lower near the base of the canopy (Patterson *et al.* 2001).

Pollinator effectiveness scores for the numbers of seeds per flower on all trees in Experiment 1 were greater when flowering intensity was high. This may be because of increased numbers of foraging bouts and longer foraging bouts on plants that provide more rewards for pollinators (Paton and Ford 1983, Klinkhamer *et al.* 1989, de Jong *et al.* 1993, Klinkhamer and de Jong 1993, Robertson and Macnair 1995). Paton and Ford (1983) found that the number of visits to individual flowers of *Eucalyptus cosmophylla* F. Muell. and *Correa schlechtendalii* Behr. by New Holland honeyeaters increased with the numbers of flowers on the plants. However, by encouraging longer foraging bouts, high flowering intensity promotes self-pollination through geitonogamy which should reduce pollinator effectiveness in this partially self-incompatible species (Paton and Ford 1983, Klinkhamer *et al.* 1989, de Jong *et al.* 1993, Klinkhamer and de Jong 1993, Robertson and Macnair 1995). Therefore, when flowering intensity was high on these experimental trees, the effect of greater numbers of foraging bouts in enhancing outcrossing rates, together with longer foraging bouts increasing flower-visitation frequencies, appeared to outweigh the effect of increased geitonogamous selfing resulting from longer foraging bouts (see Paton and Ford 1983). Aggressive interactions between birds that facilitate shorter foraging bouts may have contributed to this situation (Chapter 8).

9.4.4 Flower visiting animals and their abundances at flowers

Of the 16 bird species recorded visiting *E. globulus* flowers in this study, most have been observed doing so at other times (Thomas 1980, Brown 1989, Hingston 1997, Hingston and Potts 1998, Chapters 6, 7 and 8). However, these are the only records of eastern spinebills *Acanthorhynchus tenuirostris* (Latham) feeding on *E. globulus* nectar.

The longitudinal variation in anthophilous bird communities in Experiment 1 is consistent with other studies on *E. globulus* (Hingston and Potts 1998, Chapter 8). As in the other study into bird communities on flowering *E. globulus* south of Hobart (Chapter 8), the Derwent Estuary tended to be the major boundary between different communities. In both studies, musk lorikeets were restricted to the eastern shore while yellow wattlebirds, the smaller honeyeaters and swift parrots were restricted to the western shore. However, this boundary was more clearcut in this study because only one species, the little wattlebird, was observed on both sides of the estuary. In contrast to the other study (Chapter 8), noisy miners were never seen on the western shore. In addition, eastern rosellas, which were common flower-feeders on both sides of the estuary during the other study (Chapter 8), were not observed feeding on flowers at all during this study.

The observed diversity and relative abundances of insect visitors to flowers of *E. globulus* is generally similar to that observed in other studies of *E. globulus* in Tasmania (Hingston and Potts 1998, Chapter 6), and to that recorded from other eucalypts in Victoria (Ashton 1975, Bond and Brown 1979, Horskins and Turner 1999). All studies on *E. globulus* found honey bees to be the most frequent flower visitors (see also Chapter 4), and that native bees and beetles were also common but butterflies were absent (Hingston and Potts 1998, Chapter 6). Similar observations were made on *E. regnans* F. Muell. and *E. costata* F. Muell. in Victoria where the majority of all insect visits were by honey bees (Ashton 1975, Bond and Brown 1979, Horskins and Turner 1999), while native bees and ants were also common on *E. costata* (Horskins and Turner 1999). All studies into *E. globulus* found that *Leioproctus* and *Hylaeus (Prosopisteron)* were the most common native bee taxa, and that Colletidae outnumbered other families of bees (Hingston and Potts 1998, Chapter 6). In contrast, *Lasioglossum* and *Hylaeus* were the most common native bees recorded from *E. costata*, although Colletidae was still the most species-rich family of bees on the flowers (Horskins and Turner 1999). The high species richness but low numbers of individuals of flies

observed in this study is also consistent with other studies of *E. globulus* (Hingston and Potts 1998, Chapter 6).

However, the relative abundances of beetle taxa recorded by Hingston and Potts (1998) differed from this study. *Mordellistena* was by far the most common genus of beetles observed by Hingston and Potts (1998), including at Tinderbox, but was very uncommon during this study and not recorded at all from Tinderbox despite sampling three of the trees observed in the previous study. The other beetles that were common at Tinderbox in the study of Hingston and Potts (1998), namely *Chauliognathus lugubris*, *Phyllotocus rufipennis* and *Eleale* sp., were also uncommon there during this study. This was particularly so for the latter two species, with *P. rufipennis* only recorded rarely from one replicate and *Eleale* sp. not recorded at all from Tinderbox in this study. Thus, beetle numbers appear to vary between years as well as between sites and within flowering seasons (Hingston and Potts 1998). Such variation is typical of insect pollinator communities, as the compositions of bee communities fluctuate widely between years at particular localities (Williams *et al.* 2001).

Differences between insect assemblages at flowers were largely the result of differing abundances of honey bees, native bees and beetles, as was the case in the study conducted one year earlier (Hingston and Potts 1998). However, as in the earlier study, there was an absence of major geographic variation between anthophilous insect assemblages. This was largely because honey bees were widespread and abundant in both studies.

9.5 Conclusions

The flowers of *E. globulus* were visited by an enormous variety of insects and birds, with all size classes apparently able to pollinate the flowers. However, flowers within 5 m of the ground were not fully fertilized, especially on SI trees. Therefore, stigmata on these flowers did not receive enough outcross pollen for maximal seed set to occur, or the quantities of self-pollen deposited were so great that they interfered with outcross pollen, suggesting

that no size class comprised large numbers of effective outcrossing pollinators in the lower branches of the trees.

The consistently severe pollination deficit in *E. globulus* within its natural range, at a level comparable to that in an extralimital Chilean population, suggests that pollination services to these experimental flowers were inferior to those to which *E. globulus* has evolved (Thomson 2001). This pollination deficit may be a consequence of recent deterioration in the quality of pollination services to *E. globulus* (Thomson 2001), or pollination services in the experimental flowers within 5 m of the ground being inferior to those higher in the canopy to which *E. globulus* has evolved. The former explanation could easily be attributed to the introduction of honey bees because they are inefficient pollinators (see also Chapter 6) that often consume most of the nectar (see also Chapter 4) and therefore may have displaced more efficient pollinators. The swift parrot, which is known to be a very effective pollinator of *E. globulus* (Chapters 6 and 7), has declined in abundance to the point where it is now classified as endangered under Australia's *Environment Protection and Biodiversity Conservation Act 1999*. The latter explanation could be true, because pollination services near the tops of *E. globulus* trees are superior to those near the ground (Patterson *et al.* 2001), and birds are effective pollinators (Chapters 6 and 7) that seldom visit the flowers within 5 m of the ground but are frequent visitors higher in the canopy (see also Chapter 8). As honey bees may be displacing birds from the flowers of *E. globulus* (Chapter 4), these explanations are not mutually exclusive. Prior to the introduction of honey bees, that are now the major nectar consumers in the lower canopy (see also Chapter 4), birds that preferentially forage in the tops of trees (Chapter 8) would have depleted nectar standing crops in the upper canopy early in the day while nectar standing crops remained high in the lower canopy. This would probably have resulted in some birds, particularly larger species (Chapter 8), foraging more frequently in the lower canopy later in the day thereby increasing pollination services to flowers such as those investigated here.

Chapter 10

What animals are the most effective pollinators of *Eucalyptus globulus* subsp. *globulus* and *E. nitens*?

Abstract

Seeds of *Eucalyptus globulus* and *E. nitens* are being collected increasingly from commercial seed orchards to grow plantation stock. Management practices that benefit populations of animals that are effective outcross pollinators of these two species should enhance both the numbers of seeds produced from seed orchards and the fitness of plantation trees grown from such seeds. The bird pollinators of *E. globulus* require alternative food sources at times when nectar and pollen from *E. globulus* is not available, and some also require old-growth eucalypt forest for nest sites. The insect pollinators of *E. nitens* are vulnerable to broad-spectrum insecticides. Therefore, shifts away from broad-spectrum insecticides in favour of biological or target specific insecticides to control insect pests should benefit their populations. The deployment of colonies of exotic social bees appears to be of no direct benefit to *E. nitens* pollination because they rarely visit the flowers, and is of little benefit to seed production of *E. globulus* because they are poor pollinators of this species. Indeed, increasing numbers of honey bees or bumble bees in seed orchards of *E. globulus* could even reduce seed production as a result of the displacement of more effective bird pollinators through competition for nectar and pollen, reducing the amount of pollen available for transfer by birds, or by depositing such large quantities of self-pollen that this interferes with outcross pollen deposited by more effective bird pollinators.

10.1 Introduction

Eucalyptus globulus Labill. subsp. *globulus* (hereafter *E. globulus*) and *E. nitens* (Deane & Maiden) Maiden are both grown extensively in plantations for wood production in temperate regions of the world (Eldridge *et al.* 1993,

Tibbits *et al.* 1997). Plantation stock are grown mostly from seeds, that are being increasingly supplied from seed orchards comprising elite trees with characteristics desired by the forest industry (Eldridge *et al.* 1993, Tibbits *et al.* 1997).

The production of seeds in *Eucalyptus* is dependent mainly upon pollen transfer between flowers (allogamy). This is because of the absence of parthenocarpy in this genus (Griffin *et al.* 1987), as well as the partial barrier to pollen transfer between anthers and stigma of the same flower (autogamy) that 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 (Griffin 1982, Eldridge *et al.* 1993).

Seed production in these eucalypts is dependent on the quality, as well as the quantity, of pollen transferred to conspecific stigmata. Seed set per capsule following hand self-pollination is generally lower than from open-pollinations (Potts and Cauvin 1988, Hardner and Potts 1995) and hand cross-pollinations (Potts and Cauvin 1988, Tibbits 1989, Hardner and Potts 1995). Thus, both *E. globulus* (Potts and Cauvin 1988, Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995, 1998) and *E. nitens* (Tibbits 1989, Potts *et al.* 1992) produce fewer seeds after self-pollination than after outcrossing.

Self pollination, through autogamy or geitonogamy, may also reduce the quality of seeds in self-compatible species (Primack and Silander 1975, Potts and Cauvin 1988). Selfing in *E. nitens* reduced seed viability and increased seedling abnormalities and mortality compared to outcrossing (Tibbits 1988). In contrast, selfing in *E. globulus* reduced seed viability (Hardner and Potts 1995), but not seedling survival rates, compared to outcrossing (Hardner and Potts 1995, Hardner *et al.* 1998). However, inbreeding depression in *E. globulus*, in the form of reduced growth rates and increased mortality, became more evident as the offspring aged in field trials (Potts *et al.* 1992,

Hardner and Potts 1995, Hardner *et al.* 1995). Reduced growth rates in progeny from open pollination compared to outcross pollination were also recorded in both of these species, with this being more pronounced in *E. globulus* than in *E. nitens* (Hodge *et al.* 1996).

Hence, the output from seed orchards of these two species, both in terms of quantities of seeds produced and the quality of the resultant trees, should be enhanced by the presence of large numbers of animals that are effective outcrossing pollinators. For this reason, seed orchards and the surrounding areas need to be managed in ways that benefit populations of these animals. This chapter synthesizes findings relating to the pollinators of *E. globulus* and *E. nitens*, and discusses management options that may benefit the most effective pollinators.

10.2 Interspecific differences between *E. globulus* and *E. nitens*

The different floral forms of the closely related species *E. nitens* and *E. globulus* are associated with enormous differences in nectar production levels (Chapter 4), that result in the flowers of the two species being used by different animals as food sources. The small flowers of *E. nitens* produce little nectar (Chapter 4) and, accordingly, are visited exclusively by small insects (Chapter 5). European honey bees *Apis mellifera* L. and bumble bees *Bombus terrestris* (L.), being larger and more energy demanding insects, were rarely seen visiting flowers of *E. nitens*, and birds were never seen attempting to feed from these flowers (Chapter 5). In contrast, the large flowers of *E. globulus* produced copious nectar (Chapters 4 and 9), rendering them attractive to energy demanding birds and exotic bees, as well as the less energy demanding smaller insects (Hingston and Potts 1998, Chapters 4, 6 and 9). Hence, flowers of *E. nitens* are pollinated exclusively by small insects, whereas flowers of *E. globulus* may potentially be pollinated by a much broader range of anthophiles ranging from tiny insects up to large birds.

10.3 Pollinators of *E. globulus*

All of my experiments that assessed the effectiveness of flower visitors as pollinators of *E. globulus* indicated that insects were not particularly effective (Chapters 6 and 9). Single visits to flowers by honey bees, bumble bees, or native insects did not result in the production of statistically significant quantities of seeds (Chapter 6). Even flowers exposed to high densities of insects throughout their lives in two other experiments produced few seeds in comparison to those receiving supplementary outcross pollination (Chapter 9). The ineffectiveness of insects as pollinators was most apparent on self-incompatible trees (Chapter 9), suggesting that they seldom transferred pollen between trees. Such a finding is not unexpected, as flowers that produce enough nectar to render them attractive to birds should contain so much nectar that smaller animals, such as insects, would be satiated after visiting a small number of flowers (Heinrich and Raven 1972, Doull 1973, Ford *et al.* 1979, Heinrich 1983, Paton 1986a). For this reason, insects would not need to engage in frequent movements between flowers and trees (Ford *et al.* 1979, Eldridge *et al.* 1993, Paton 1993, 1997). Although abundant honey bees may deposit large quantities of self-pollen on stigmata of *E. globulus*, hundreds of visits to individual flowers on trees with some self-compatibility did not facilitate full seed set (Chapter 9). Moreover, the fitness of offspring resulting from such self-pollination would be reduced by inbreeding depression (Potts *et al.* 1992, Hardner and Potts 1995, Hardner *et al.* 1995).

In contrast, single visits to flowers of *E. globulus* by swift parrots *Lathamus discolor* (Shaw) resulted in the production of statistically significant quantities of seeds, indicating that they are very effective pollinators (Chapter 6). Seed production following a single flower visit by a swift parrot (Chapter 6) was greater than from flowers visited hundreds of times by honey bees and other insects (Chapter 9). Although the pollinator effectiveness of other bird species was not sufficiently assessed by this method to determine whether they are also effective pollinators (Chapter 6), the available evidence suggests they are. Birds commenced, and spent more time, foraging in the upper

halves of canopies than the lower halves (Chapter 8). Because outcrossing rates and the numbers of seeds per capsule are greater in the upper, than the lower, sections of canopies (Patterson *et al.* 2001), these observations are consistent with birds being major contributors to the deposition of outcross pollen (Chapter 8). Moreover, birds carry large loads of eucalypt pollen on their bill and adjacent feathers, which indicates that they can pollinate *E. globulus* (Chapter 7). However, the pollen loads carried by the Meliphagidae (honeyeaters) were significantly smaller than those carried by swift parrots, suggesting that the Meliphagidae are not as effective at pollination (Chapter 7). In addition, the broad hypanthium of *E. globulus* is likely to allow the long-billed Meliphagidae to take nectar without always contacting stigmata (Paton and Ford 1977), in contrast to swift parrots that almost always contacted stigmata (Chapter 6). These effects may be counterbalanced somewhat by the often shorter foraging bouts of the Meliphagidae than by swift parrots, which could enhance outcrossing by the former (Chapter 8). Consequently, the maintenance of large populations of swift parrots, and probably other anthophilous birds, in seed orchards of *E. globulus* would enhance seed production.

Birds may also provide pollination services to *E. globulus* in seed orchards outside Australia. This is because specialised nectarivorous birds occur in most temperate regions of the world: other Meliphagidae species occur in New Zealand; hummingbirds (Trochilidae) occur in North and South America; and sunbirds (Nectariniidae) occur in South Africa, the Middle East and Eastern Asia (Ford 1985). Europe is the only continent with a temperate climate that lacks specialised nectarivorous birds (Ford 1985). However, my observations of birds not usually regarded as nectarivorous taking nectar from *E. globulus* (Chapters 8 & 9), and records of native European birds feeding on nectar (Ford 1985), indicate that birds would also be potential pollinators of *E. globulus* in Europe. Indeed, the chiffchaff *Phylloscopus collybita* has been observed visiting flowers of eucalypts in Europe in a way that should effect pollination (Ford 1985), and several European bird species

visit the similar flowers of the related *Metrosideros excelsa* in New Zealand (Schmidt-Adam *et al.* 2000).

However, the tendency for birds to forage preferentially in the upper parts of canopies (Chapter 8) means that they provide little pollination service to flowers in the lower parts of canopies (Chapter 9). This problem may be overcome by collecting seeds only from high in the canopies (Patterson *et al.* 2001), manually cross-pollinating the flowers in the lower parts of the canopies (Harbard *et al.* 1999, Williams *et al.* 1999, Trindade *et al.* 2001), or pruning trees in seed orchards to prevent them from becoming so tall that flowers near the bottom of the canopy are rarely visited by birds.

It is not known whether mammals are effective pollinators of *E. globulus*. Although mammalian visits to flowers of *E. globulus* appear to have been negligible in this study (Chapters 4 and 9), the large quantities of nectar and pollen could be attractive to mammals such as gliders (Smith 1982, Turner 1984, Howard 1989, Goldingay 1990). Research into the effectiveness of mammals as pollinators of *E. globulus* would be worthwhile, as it may be possible to encourage large populations of these animals in seed orchards.

10.4 Pollinators of *E. nitens*

A diverse array of small insects use the flowers of *E. nitens* as a food source, including numerous taxa of beetles, native bees and flies, as well as a few wasps, ants and moths (Chapter 5). There was little evidence that some of these insect taxa are better pollinators of *E. nitens* than others (Chapter 5). Indeed, flowers of *E. nitens* appear to be highly allophilic, and can probably be effectively pollinated by most of these insects. As a result, the maintenance of large populations of wild anthophilous insects in seed orchards of *E. nitens* would assist seed production (Chapter 5).

The evidence that a wide variety of insects pollinate *E. nitens* in Tasmania (Chapter 5) indicates that effective pollinators should be present in seed orchards of *E. nitens* throughout the world. However, this was not the case

in South Africa where flowers of *E. nitens* that were exposed to flower visitors did not produce significantly more capsules or seeds than those from which visitors were excluded (Jones *et al.* 2001). This was probably because *E. nitens* bloomed at a time of year when the weather was cold and wet in South Africa and, therefore, not conducive to insect activity (Jones *et al.* 2001).

10.5 Implications for management

The reluctance of domesticated social bees to visit flowers of *E. nitens* (Chapter 5), and their inability to effectively cross-pollinate flowers of *E. globulus* (Chapters 6 and 9), means that the deployment of hives in seed orchards is unlikely to enhance seed set in either species (cf. Moncur *et al.* 1993, 1995). Hence, high levels of seed production in both species require wild pollinator populations.

Indeed, social bees may displace more effective bird pollinators from *E. globulus* as a result of competition for the frequently limited nectar resource (Chapter 4), thereby reducing seed production (McDade and Kinsman 1980, Paton 1993, 1997, Irwin and Brody 1998). As honey bees and bumble bees also collect pollen from *E. globulus* (A. Hingston pers. obs.), and most pollen is removed within the first day after anthesis in eucalypts (Ellis and Sedgley 1992), pollenivorous birds such as swift parrots and musk lorikeets *Glossopsitta concinna* (Shaw) (Gartrell *et al.* 2000, Gartrell and Jones 2001) may also suffer as a result of competition for this resource. The removal of pollen by these bees also reduces the quantity of pollen available for outcross pollination by more effective bird pollinators (Wilson and Thomson 1991, de Jong *et al.* 1993, Klinkhamer and de Jong 1993, Chapter 9), which may lead to lower seed set (Pyke 1990, Paton 1993, Vaughton 1996, Paton 1997). The large quantities of self-pollen that appear to be deposited on stigmata of *E. globulus* by honey bees may also reduce the capacity for outcross pollen deposited by birds to fertilize ovules through competition between pollen tubes for ovules or space in the style (Chapter 9). This potential for introduced social bees to reduce the capacity for more effective pollinators to

facilitate seed set may account for the more severe pollen limitation in the exotic bee-visited *E. globulus* (Chapter 9) than in *E. nitens* which is not regularly visited by exotic bees (Chapter 5). This, together with the rapid invasion of Tasmanian native vegetation by bumble bees within nine years of their introduction (Hingston *et al.* 2002), casts doubts into the wisdom of efforts to have this species introduced to the Australian mainland (e.g. Goodwin and Steiner 1997).

Bird pollinators that facilitate seed production in *E. globulus* are also threatened by habitat destruction. When a pollinator lives longer than the duration of a single species' flowering, other plants with different flowering seasons are necessary for the maintenance of the pollinator population in the area (Heinrich and Raven 1972, Faegri and van der Pijl 1979, Augspurger 1980, Williams and Batzli 1982). An example of such mutualism between sequentially flowering plants that shared the same pollinator was found by Waser and Real (1979). When drought led to poor flowering of *Delphinium nelsonii*, the population of hummingbirds that pollinated both *D. nelsonii* and *Ipomopsis aggregata* was adversely affected. This in turn resulted in poor seed set in the latter self-incompatible species (Waser and Real 1979).

Although pollinator populations in agricultural situations may be enhanced by growing other food plants in the vicinity (Patten *et al.* 1993), these plant mutualisms are not restricted to co-occurring plants because anthophilous birds move between habitats as they follow floral resources (Christensen 1971, Ford *et al.* 1979, Paton 1980, Hopper 1981, Brown 1989, Brereton 1996, Paton 1997, McGoldrick and Mac Nally 1998). 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 central Victoria, the understorey genera of *Astroloma, Grevillea, Callistemon* and *Banksia* provided reliable sources of nectar throughout the year for New Holland honeyeaters *Phylidonyris novaehollandiae* (Latham), while *Eucalyptus* species were unreliable nectar sources due to their inconsistent flowering (Paton

1985). In the case of *E. globulus* in Tasmania, the provision of nectar sources for its bird pollinators would be achieved primarily by ensuring that abundances of *Banksia marginata* Cav. and the diversity of ornithophilous eucalypts are maintained (Hingston and Potts 1998). Accordingly, the swift parrot recovery plan aims to identify and protect other eucalypt species in Tasmania and the southeastern Australian mainland which provide floral resources outside their breeding season (Brereton 1996).

Although able to forage in young regrowth forest, swift parrots require mature forest on nearby dry ridges for roosting and breeding (Brown 1989, Taylor 1991) with the most frequently used areas occupying at least 100 ha (Brereton 1997). In fact, both swift parrots and musk lorikeets *Glossopsitta concinna* (Shaw) 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 (Brown 1989, Schodde and Tidemann 1990, Brereton 1996), suggests that pollinator activity would be enhanced in proximity to mature eucalypt forest. Hence, Brown (1989) recommended that mature forest be retained within 5 km of *E. globulus* plantations so that nest sites were available near food sources during the breeding season.

Wild insect pollinators, such as those needed for seed production in *E. nitens*, are vulnerable to insecticides, habitat destruction, disease, and introduced predators and competitors (Kevan *et al.* 1990a, Kevan 1991, 1999). Of these, the effects of insecticide use are of greatest concern (Chapter 5). The use of broad-spectrum insecticides in eucalypt production forests and plantations is a common and widespread practice (Davies and Cook 1993, Greener and Candy 1994, Beveridge and Elek 1999, Elek and Beveridge 1999). Although the impacts of broad-spectrum insecticides on insect pollinators and seed set have not been investigated widely in *Eucalyptus*, cypermethrin is highly toxic to the flower-visiting soldier beetle *Chauliognathus lugubris* (Fabricius) (Greener and Candy 1994), and the harmful impacts of insecticides on pollinators and seed production have been well documented in other

systems (Kevan 1975, Johansen 1977, Thaler and Plowright 1980, Kevan 1986, Kevan *et al.* 1990a, Kevan 1991, 1999). Hence, the encouragement of biological control agents and the use of target-specific insecticides, in place of broad-spectrum insecticides (Greener and Candy 1994, Beveridge and Elek 1999, Elek and Beveridge 1999), is likely to benefit pollination of *E. nitens*.

The breeding sites used by the insects that pollinate *E. nitens* are many and varied, but dead wood stands out as being of particular importance. The larvae of many beetle taxa feed on dead wood, both dry standing wood and damp wood on the ground (Lawrence and Britton 1991). For this reason, obsessions with tidiness in seed orchards of *E. nitens* may be counterproductive. Indeed, if some trees are to be removed from seed orchards, it may be beneficial to ringbark some of these and leave them standing, or to fall others and leave the trunks on the ground. The holes made by beetle larvae in dry standing wood are subsequently used as nesting sites by many species of solitary bees (Cardale 1993). Nesting sites for bees are particularly important if they are to be encouraged into seed orchards as, unlike most other insects, their foraging activities at flowers are associated with collecting pollen and nectar to provision their larvae (Cardale 1993). Other sites used by solitary bees for nesting include relatively bare and well-drained soil, and the small hollow stems of plants such as ferns and reeds (Cardale 1993).

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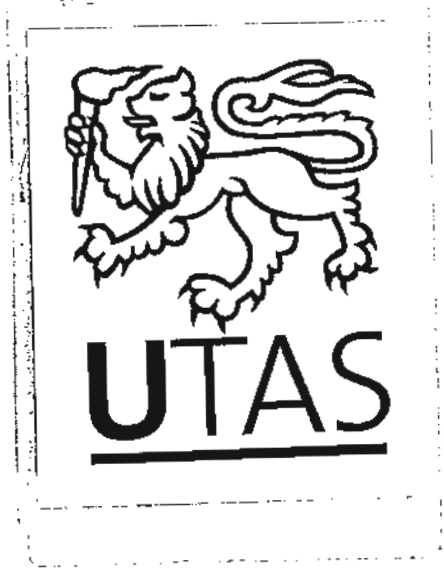

Appendices

Time	930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700	1730	1800	1830
number of flowers	171	171	166	166	161	161	156	156	151	151	145	145	140	140	134	134	128	128	122
air temperature (℃)	13.1	13.6	13.9	14	14.4	15.3	15.4	15.6	16.3	16	16.6	16.4	16.6	16.9	17	16.8	16.9	16.3	15.9
relative humidity	75	73	73	75	74	72	68	62	66	65	70	67	66	69	67	67	70	71	72
Apis mellifera	1	2	2	1	2	11	12	10	7	11	5	3	8	7	4	4	4	8	0
Leioproctus spp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum (Chilalictus) spp.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0
Lasioglossum (Parasphecodes) spp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Calliphora spp.	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0

APPENDIX 1

Numbers of unbagged experimental flowers, weather conditions, and numbers of insects seen during 1 min spot counts on *E. globulus* tree 1339 during nectar measurements on 31 Oct. 2000. See Chapter 4.

Time	630	700	730	800	830	900	930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630
number of flowers	265	265	260	260	255	255	250	250	245	245	239	239	233	233	229	229	224	224	219	219	215
air temperature (°C)	12.3	15.4	17.3	17.8	18.4	19.9	18.6	18.3	17.9	18.8	18.5	19.4	18.8	18.4	18.9	18	17.6	18.1	17.4	16.4	14.9
relative humidity	100	100	86	82	66	66	64	73	78	80	65	59	57	60	61	69	56	67	67	67	73
Apis mellifera	3	2	8	26	42	31	30	30	30	26	24	21	30	21	18	26	21	25	7	14	11
Exoneura spp.	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Hylaeus (Prosopisteron) spp.	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0
Homalictus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lasioglossum (Parasphecodes) spp.	0	0	0	0	1	0	1	1	1	1	0	0	1	0	2	0	0	0	0	0	0
Gasteruption spp.	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0
Ichneumonidae	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Thynnus zonatus	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calliphora spp.	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0
Odontomyia sp.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Syrphidae sp.1	0	1	0	0	1	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Atoichus bicolor	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Chauliognathus lugubris	25	35	37	32	45	43	45	43	34	32	51	42	43	42	45	51	34	38	38	46	29
Cerambycidae	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0

APPENDIX 2

Numbers of unbagged experimental flowers, weather conditions, and numbers of insects seen during 1 min spot counts on *E. globulus* tree 1338 during nectar measurements on 19 Nov. 2000. See Chapter 4.

Time	600	630	700	730	800	830	900	930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700
number of flowers	228	228	223	223	218	218	213	213	208	208	203	203	198	198	193	193	188	188	183	183	178	178	173
air temperature (°C)	7.9	8.3	9.9	9.6	10.6	10.3	12.5	12.8	12.6	12.9	15.9	17.6	19.1	16.6	21.4	22.4	22.9	20.9	18.4	18.1	17.9	16.1	13.4
Apis mellifera	0	0	0	0	0	1	4	5	2	7	11	16	6	21	32	24	15	23	12	2	13	2	0
Bombus terrestris	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum (Parasphecodes) spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
Thynnidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Muscidae	0	0	0	0	0	0	0	0	0	0	0	2	2	0	3	0	2	2	4	2	0	0	0
Syrphidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	1	0	0	0

APPENDIX 3

Numbers of unbagged experimental flowers, weather conditions, and numbers of insects seen during 1 min spot counts on *E. globulus* tree 297 during nectar measurements on 11 Sept. 2001. See Chapter 4. No humidity measurements were taken because the hygrometer failed.

Time	600	630	700	730	800	830	900	930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700	1730	1800
number of flowers	271	271	266	266	261	261	254	254	249	249	244	244	239	239	234	234	229	229	223	223	217	217	211	211	206
air temperature (°C)	8	7.4	8.1	7.9	9.4	10	11.5	13.1	15.6	14.8	17.3	17.5	18	18.4	17	16.9	17.8	17.4	17.9	17.3	18.1	17.9	16.8	16.5	16
relative humidity	100	100	100	100	88	82	78	72	63	64	50	50	51	44	63	65	62	66	66	70	67	69	76	76	83
Apis mellifera	0	0	0	0	0	0	0	0	3	0	4	5	7	6	1	1	4	2	7	4	4	2	0	1	0
Homalictus spp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Lasioglossum (Chilalictus) spp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ichneumonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sphecidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus sp.	0	0	0	0	0	0	0	2	3	1	0	2	0	0	0	0	1	1	0	2	0	0	1	0	2
Calliphora spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Muscidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	1	0	2	0	0
Sepsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Syrphidae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0
Atoichus brevior	0	0	0	0	0	0	0	1	1	1	0	3	2	0	2	5	1	0	0	2	0	2	3	1	1

APPENDIX 4

Numbers of unbagged experimental flowers, weather conditions, and numbers of insects seen during 1 min spot counts on *E. globulus* tree 335 during nectar measurements on 11 Oct. 2001. See Chapter 4.

Time	600	630	700	730	800	830	900	930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700
number of flowers	312	312	307	307	302	302	297	297	291	291	286	286	281	281	276	276	271	271	266	266	261	261	256
air temperature (°C)	8.3	8.4	10.9	10.9	10.9	10.9	11.6	13.9	14.6	15.4	16.6	18.5	18.6	19.4	20.6	22.9	23	23.1	24.6	22.8	20.4	21.9	20.9
relative humidity	89	87	64	70	68	74	73	68	62	57	53	51	42	41	40	39	36	36	38	42	43	40	42
Apis mellifera	0	0	0	0	0	0	0	1	1	4	5	4	8	2	3	4	1	2	0	2	1	0	1
Lasioglossum (Chilalictus) spp	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Calliphora spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Syrphidae sp.1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Syrphidae sp.5	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 5

Numbers of unbagged experimental flowers, weather conditions, and numbers of insects seen during 1 min spot counts on *E. globulus* tree 341 during nectar measurements on 22 Oct. 2001. See Chapter 4.

Code	Orchard	Tree	Height (m)	Aspect (°)	Date	# capsules/flower			# seeds/capsule			# seeds/flower		
						OP	supp	pe	OP	supp	pe	OP	supp	pe
H1a	Hastings	1	3.6	10	17/01/99	0.69	0.75	91.83	2.45	4.91	49.91	1.69	3.68	45.83
H1b	Hastings	1	4.1	10	17/01/99	0.67	0.75	89.25	3.45	5.11	67.50	2.31	3.83	60.24
H1c	Hastings	1	3.8	270	17/01/99	0.92	1.00	91.67	5.27	5.07	104.07	4.83	5.07	95.39
H1d	Hastings	1	4.1	180	17/01/99	0.80	0.78	102.73	2.50	4.57	54.69	2.00	3.56	56.18
H2a	Hastings	2	2.2	350	17/01/99	0.36	0.44	82.09	0.63	2.75	22.90	0.23	1.22	18.80
H2b	Hastings	2	3.7	10	17/01/99	0.64	0.43	149.14	1.55	1.33	116.25	0.99	0.57	173.38
H2c	Hastings	2	2.5	70	17/01/99	0.61	0.86	71.56	0.50	1.08	46.15	0.31	0.93	33.03
H2d	Hastings	2	2	110	17/01/99	0.38	0.86	44.56	1.00	1.08	92.31	0.38	0.93	41.13
H3a	Hastings	3	3.5	10	17/01/99	0.33	0.18	180.33	3.11	5.50	56.46	1.02	1.00	101.81
H3b	Hastings	3	4.1	70	17/01/99	0.57	0.58	96.89	3.25	6.29	51.70	1.84	3.67	50.10
H3c	Hastings	3	3.7	80	17/01/99	0.40	0.80	49.48	3.16	4.50	70.18	1.25	3.60	34.72
H4a	Hastings	4	3	330	17/01/99	0.50	0.64	77.78	2.85	1.44	197.31	1.43	0.93	153.46
H4b	Hastings	4	2.8	40	17/01/99	0.62	0.83	74.74	1.70	4.70	36.17	1.06	3.92	27.03
H4c	Hastings	4	3	90	17/01/99	0.71	0.69	102.60	1.37	3.68	37.17	0.97	2.53	38.13
H4d	Hastings	4	4.2	170	17/01/99	0.58	0.71	82.15	2.62	2.85	91.80	1.52	2.02	75.42
B1a	Bream Ck	2.5	1.2	40	24/01/99	0.26	0.67	38.94	0.74	0.50	148.15	0.19	0.33	57.69
B1c	Bream Ck	2.5	3.3	220	24/01/99	0.17	0.25	66.24	0.83	1.44	57.97	0.14	0.37	38.40
B1d	Bream Ck	2.5	3	20	24/01/99	0.10	0.52	18.70	0.63	0.33	187.50	0.06	0.17	35.06
B3b	Bream Ck	6.20	1.5	170	24/01/99	0.16	0.27	59.41	2.06	1.25	165.00	0.33	0.33	98.02
B3c	Bream Ck	6.20	3.1	150	24/01/99	0.31	0.73	42.10	1.70	1.64	103.62	0.52	1.20	43.62
B3d	Bream Ck	6.20	3.7	350	24/01/99	0.12	0.65	18.60	1.54	1.91	80.59	0.19	1.24	14.99
B4w	Bream Ck	2.10	1.5	110	18/01/00	0.39	0.24	167.09	1.43	1.75	81.99	0.56	0.41	137.00
B4y	Bream Ck	2.10	4	330	18/01/00	0.34	0.36	95.60	1.22	1.67	73.33	0.42	0.60	70.11
B4z	Bream Ck	2.10	5	120	18/01/00	0.46	0.69	66.16	0.65	2.78	23.48	0.30	1.92	15.53
B5w	Bream Ck	1.6	1.4	330	18/01/00	0.74	0.56	132.60	1.35	1.40	96.43	0.99	0.78	127.86
B5x	Bream Ck	1.6	2.3	180	18/01/00	0.62	0.63	98.59	2.36	1.59	148.57	1.46	1.00	146.48
B5y	Bream Ck	1.6	4	20	18/01/00	0.74	0.71	104.13	1.85	2.20	84.09	1.38	1.57	87.56
B5z	Bream Ck	1.6	5	120	18/01/00	0.49	0.57	86.88	2.33	1.94	120.20	1.15	1.10	104.43
W2b	Wycombe	10.11	1.7	100	27/01/99	0.23	0.21	109.20	2.35	2.25	104.44	0.54	0.47	114.05
W3	Wycombe	9.18	2.1	70	27/01/99	0.30	0.17	177.46	2.24	2.25	99.47	0.66	0.38	176.53
W4a	Wycombe	8.32	1.9	180	27/01/99	0.12	0.25	46.00	1.70	1.33	127.17	0.20	0.33	58.50
W6b	Wycombe	11.46	1.2	180	27/01/99	0.03	0.26	11.34	1.50	2.43	61.76	0.04	0.63	7.01
W7y	Wycombe	6.44	2.1	70	24/01/00	0.35	0.31	113.30	1.55	2.00	77.50	0.54	0.62	87.81
W7z	Wycombe	6.44	2.3	0	24/01/00	0.40	0.59	67.69	1.10	4.00	27.50	0.44	2.36	18.62
W4z	Wycombe	8.32	2.4	310	24/01/00	0.40	0.21	191.83	2.95	3.75	78.73	1.19	0.79	151.03
W8y	Wycombe	7.25	1.6	280	24/01/00	0.40	0.30	134.83	1.70	4.25	40.00	0.69	1.28	53.93
W2z	Wycombe	10.11	2	240	24/01/00	0.34	0.14	254.52	3.30	7.20	45.83	1.14	0.97	116.66
K1c	Kingsclere	4.7	3.6	220	29/01/99	0.31	0.48	63.94	2.84	2.36	120.24	0.87	1.13	76.88
K2b	Kingsclere	2.6	1.7	350	29/01/99	0.59	0.70	84.56	3.20	1.50	213.33	1.88	1.04	180.39
K2c	Kingsclere	2.6	3.4	140	29/01/99	0.64	0.54	118.59	3.00	4.00	75.00	1.92	2.15	88.94
K2d	Kingsclere	2.6	3.7	350	29/01/99	0.79	0.41	193.28	4.30	2.33	184.29	3.40	0.95	356.19
K3a	Kingsclere	2.3	1.1	320	29/01/99	0.44	0.59	74.42	2.37	0.90	260.16	1.04	0.53	195.85
K3b	Kingsclere	2.3	0.8	210	29/01/99	0.47	0.50	94.40	2.50	3.00	83.33	1.18	1.50	78.67
K3c	Kingsclere	2.3	2.1	320	29/01/99	0.47	0.95	49.20	1.91	4.10	46.66	0.90	3.90	22.95
K3d	Kingsclere	2.3	3.3	120	29/01/99	0.84	1.00	84.29	4.45	4.00	111.25	3.75	4.00	93.77
K4w	Kingsclere	3.1	1.2	340	30/01/00	0.62	0.80	77.10	0.95	2.55	37.32	0.59	2.04	28.78
K4x	Kingsclere	3.1	3.6	40	30/01/00	0.57	0.89	64.15	1.10	2.00	55.00	0.63	1.78	35.28
K3w	Kingsclere	2.3	1.2	60	30/01/00	0.53	0.41	130.54	2.30	1.67	138.00	1.23	0.68	180.15
K3x	Kingsclere	2.3	1.3	210	30/01/00	0.71	0.59	120.16	2.95	3.87	76.24	2.09	2.28	91.60
K3y	Kingsclere	2.3	2.4	170	30/01/00	0.90	0.86	93.55	3.75	2.30	163.04	3.01	1.97	152.53
K3z	Kingsclere	2.3	3.6	40	30/01/00	0.77	0.79	97.41	2.15	4.64	46.37	1.65	3.64	45.17
K2w	Kingsclere	2.6	1.2	330	30/01/00	0.79	0.70	112.75	3.40	2.47	137.45	2.70	1.74	154.97
K2y	Kingsclere	2.6	3.7	30	30/01/00	0.79	0.78	101.93	2.50	2.14	116.67	1.98	1.67	118.92
K2z	Kingsclere	2.6	3.6	130	30/01/00	0.75	0.81	93.33	3.05	4.85	62.89	2.30	3.92	58.69
h2	Huntsman	2	2.2	100	1/02/99	0.18	0.35	52.57	2.96	2.86	103.48	0.54	1.00	54.40

Code	Orchard	Tree	Height (m)	Aspect (°)	Date	# capsules/flower			# seeds/capsule			# seeds/flower		
						OP	supp	pe	OP	supp	pe	OP	supp	pe
h3a	Huntsman	3	2.6	320	1/02/99	0.79	0.75	105.81	3.10	2.33	132.65	2.46	1.75	140.36
h3b	Huntsman	3	4.2	30	1/02/99	0.58	0.81	71.94	3.53	2.71	130.32	2.05	2.19	93.75
h3c	Huntsman	3	3.6	110	1/02/99	0.82	0.67	122.97	3.47	2.58	134.47	2.85	1.72	165.36
h3d	Huntsman	3	3.8	170	1/02/99	0.79	0.53	150.32	4.43	2.70	164.02	3.50	1.42	246.55
h4a	Huntsman	4	4.2	300	1/02/99	0.54	0.53	101.62	1.42	1.67	85.26	0.76	0.88	86.65
h4b	Huntsman	4	4.2	30	1/02/99	0.15	0.20	76.92	0.95	3.00	31.58	0.15	0.60	24.29
h4c	Huntsman	4	3.3	70	1/02/99	0.63	0.71	89.74	1.30	3.00	43.33	0.82	2.12	38.89
h4d	Huntsman	4	3.1	150	1/02/99	0.29	0.44	67.23	1.11	2.86	38.68	0.33	1.25	26.01
h5a	Huntsman	5	1.6	80	9/02/99	0.57	0.62	91.95	1.20	1.11	108.00	0.68	0.69	99.31
h5b	Huntsman	5	1.4	150	9/02/99	0.64	0.38	170.98	2.29	2.33	97.96	1.47	0.88	167.49
h6a	Huntsman	6	1.7	50	9/02/99	0.51	0.64	80.37	0.61	0.43	142.03	0.31	0.27	114.15
h6b	Huntsman	6	1.5	150	9/02/99	0.68	0.45	149.22	1.10	0.80	137.50	0.75	0.36	205.18
h1z	Huntsman	1	2	290	1/02/00	0.34	0.27	125.32	1.50	1.50	100.00	0.51	0.41	125.32
h3w	Huntsman	3	3.1	150	1/02/00	0.99	0.93	106.43	3.00	3.69	81.25	2.96	3.43	86.48
h3x	Huntsman	3	1.8	250	1/02/00	0.98	1.00	98.40	3.05	3.65	83.63	3.00	3.65	82.29
h3y	Huntsman	3	3.8	20	1/02/00	0.92	1.00	92.39	2.85	3.83	74.35	2.63	3.83	68.69
h3z	Huntsman	3	3.2	330	1/02/00	0.95	1.00	95.11	3.35	4.29	78.06	3.19	4.29	74.24
h8y	Huntsman	8	3.3	30	1/02/00	0.97	0.80	120.69	1.80	3.00	60.00	1.74	2.40	72.41
h8z	Huntsman	8	2.6	300	1/02/00	0.85	0.88	97.02	1.25	3.36	37.23	1.06	2.94	36.12

APPENDIX 6

Locations of branches of *E. nitens* flowers used in the data analysis, the dates when insects were surveyed and supplementary outcross pollinations were conducted, the fecundity from flowers that were open-pollinated (OP) or received supplementary outcross pollen (supp), and the pe scores for the open-pollinated flowers. See Chapter 5.

Species	Date	Side of head	0-5.5mm	5.6-11mm	11.1-16.5mm	16.6-22mm
crescent honeyeater	13-Oct-98	forehead	109	81	12	24
		chin	173	33	11	18
		lore	118	25	14	12
		lore	1	24	2	6
New Holland honeyeater	13-Oct-98	forehead	800	459	69	18
		chin	317	500	225	59
		lore	377	210	341	39
		lore	85	464	227	117
New Holland honeyeater	13-Oct-98	forehead	77	139	47	51
		chin	194	178	158	123
		lore	265	213	36	40
		lore	33	52	55	10
New Holland honeyeater	13-Oct-98	forehead	193	586	76	119
		chin	133	33	52	172
		lore	248	421	37	32
		lore	159	70	45	50
New Holland honeyeater	13-Oct-98	forehead	55	195	13	24
		chin	40	631	89	28
		lore	546	57	16	14
		lore	13	21	14	18
New Holland honeyeater	13-Oct-98	forehead	143	72	15	39
		chin	49	217	46	32
		lore	1928	604	14	26
		lore	113	39	36	19
New Holland honeyeater	14-Nov-98	forehead	16	53	24	23
		chin	24	12	9	90
		lore	12	65	33	30
		lore	120	22	9	150
New Holland honeyeater	27-Oct-98	forehead	2	11252	724	256
		chin	2482	3611	1576	338
		lore	216	2467	3244	446
		lore	47	43	5477	293
New Holland honeyeater	15-Oct-98	forehead	14	50	3	35
		chin	4	9	64	72
		lore	110	16	53	27
		lore	57	363	22	55
New Holland honeyeater	15-Oct-98	forehead	1	2	78	264
		chin	182	2046	1036	159
		lore	26	1045	2248	226
		lore	1383	47	137	118
New Holland honeyeater	15-Oct-98	forehead	12	22	16	3
		chin	1	2	14	29
		lore	1	1	0	55
		lore	2	4	9	44
New Holland honeyeater	1-Oct-99	forehead	26	159	327	34
		chin	93	13	269	164
		lore	161	209	178	42
		lore	55	46	158	102

Species	Date	Side of head	0-5.5mm	5.6-11mm	11.1-16.5mm	16.6-22mm
New Holland	5-Oct-99	forehead	833	686	130	65
honeyeater		chin	12	615	293	101
		lore	102	63	68	59
		lore	172	40	97	141
New Holland	8-Oct-99	forehead	55	116	47	5
honeyeater		chin	7	4	57	197
		lore	9	19	23	33
		lore	25	19	50	40
yellow	27-Oct-98	forehead	37	227	40	27
wattlebird		chin	128	146	34	37
		lore	12	7	17	130
		lore	17	112	108	139
yellow	13-Oct-99	forehead	867	488	542	323
wattlebird		chin	2950	824	99	103
		lore	108	173	182	216
		lore	796	182	201	88
yellow	13-Oct-99	forehead	804	52	101	89
wattlebird		chin	11	53	132	94
		lore	86	83	38	22
		lore	91	98	93	137
swift	15-Nov-98	forehead	64	76	53	43
parrot		chin	837	1240	2920	606
		lore	20	72	535	66
		lore	47	100	451	282
swift	16-Oct-98	forehead	776	1103	234	66
parrot		chin	4626	6635	4089	1148
		lore	966	2061	850	517
		lore	4831	3809	698	368
swift	16-Oct-98	forehead	422	60	202	234
parrot		chin	2040	5577	8797	2124
		lore	201	169	482	460
		lore	520	1955	742	573
swift	27-Oct-98	forehead	26	583	447	58
parrot		chin	1050	1851	1094	360
		lore	39	552	419	108
		lore	94	244	182	55
swift	28-Oct-98	forehead	49	112	15	17
parrot		chin	297	1358	1726	1516
		lore	16	21	40	62
		lore	18	63	1487	166
swift	30-Sep-99	forehead	536	355	37	9
parrot		chin	1386	1361	947	184
		lore	103	538	190	88
		lore	602	740	161	79
swift	30-Sep-99	forehead	41	48	635	353
parrot		chin	148	357	112	48
		lore	22	333	106	40
		lore	52	416	96	142
swift	1-Oct-99	forehead	365	436	227	206
parrot		chin	891	510	632	1262
		lore	335	720	326	267
		lore	675	789	174	145

Species	Date	Side of head	0-5.5mm	5.6-11mm	11.1-16.5mm	16.6-22mm
swift	5-Oct-99	forehead	262	200	22	37
parrot		chin	2890	821	2481	73
		lore	1811	579	349	20
		lore	5728	437	171	83
swift	5-Oct-99	forehead	44	261	22	14
parrot		chin	2401	2132	253	81
		lore	30	108	164	74
		lore	93	128	155	99
swift	5-Oct-99	forehead	242	248	25	29
parrot		chin	1600	1923	607	173
		lore	197	205	157	80
		lore	925	722	99	48
swift	5-Oct-99	forehead	174	240	551	51
parrot		chin	10190	2655	1173	311
		lore	1217	5511	496	71
		lore	180	83	33	33
swift	5-Oct-99	forehead	4529	6900	363	100
parrot		chin	3288	5260	1945	643
		lore	2474	910	340	725
		lore	2520	2188	396	492
swift	8-Oct-99	forehead	288	115	26	38
parrot		chin	818	3157	506	200
		lore	136	178	107	47
		lore	841	369	328	60
swift	19-Oct-99	forehead	968	460	222	164
parrot		chin	44	172	337	142
		lore	1649	1516	1355	183
		lore	1691	2552	261	134
swift	19-Oct-99	forehead	204	1754	2678	305
parrot		chin	2168	1819	747	243
		lore	214	1935	871	398
		lore	1080	727	562	137
swift	20-Oct-99	forehead	884	759	314	27
parrot		chin	4327	3991	1499	677
		lore	386	668	279	77
		lore	170	851	235	114
swift	20-Oct-99	forehead	1899	1086	162	71
parrot		chin	1449	854	738	461
		lore	981	1994	329	356
		lore	243	427	182	113
swift	20-Oct-99	forehead	1847	2390	688	199
parrot		chin	1579	14757	5539	3167
		lore	4041	862	569	116
		lore	1926	1520	205	131
swift	21-Oct-99	forehead	78	547	854	72
parrot		chin	1593	1553	425	239
		lore	1637	1808	122	72
		lore	133	382	57	67

APPENDIX 7

Numbers of eucalypt pollen grains in different regions of the bills and heads of birds mistnetted near flowering trees of *E. globulus*, and the date of capture. Distances are measured from the bill tip. See Chapter 7.

Tree	excl.	1mm	5mm	12mm	25mm	OP	supp
330	0.00	0.00	2.78	2.36	3.88	1.57	10.10
341	0.00	0.00	0.00	0.00	0.00	0.00	2.91
349	0.00	0.08	0.42	0.38	0.58	0.20	1.36
532	0.00	0.00	0.45	0.78	0.67	2.53	8.22
523	0.00	0.00	0.00	0.00	5.81	17.47	29.58
524	0.00	0.00	2.51	2.04	0.00	1.71	3.94
411	0.00	0.20	0.77	0.71	0.39	1.59	3.06
850	0.00	0.00	0.08	0.63	0.18	0.70	2.39
340	2.85	1.21	8.25	9.91	9.46	9.71	16.25
845	2.25	1.68	1.08	2.10	5.18	5.58	13.00
846	0.13	0.13	0.21	0.70	1.30	0.97	0.63
849	0.75	0.44	0.90	1.44	0.86	1.25	2.93
795	0.00	0.00	0.00	0.62	0.00	1.36	0.00
844	0.00	0.00	0.00	0.00	0.00	0.00	0.00

APPENDIX 8

Mean numbers of seeds per flower in each caging treatment on each tree in Experiment 1 from Chapter 9.

Tree	birds	insects	OP	supp
1018	0.00	6.61		15.41
1019	0.00	0.83		0.00
1021	0.45	2.83		19.50
1022	1.86	0.00		0.00
1023		2.13	4.36	26.63
1025			0.00	3.71
1026		5.26	7.13	6.67
1027	0.00	0.00		0.00
1028	0.00	0.00		0.00
1029		6.60	14.71	34.00
1030	0.00	0.00		0.00
1033	0.00	0.00		0.00
1037		10.67	4.56	14.30

APPENDIX 9

Mean numbers of seeds per flower in each caging treatment on each tree in Experiment 2 from Chapter 9.