

BIRD-POLLINATED PLANTS IN WESTERN AUSTRALIA

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Bird-pollination is found throughout Western Australia, but reaches its zenith (in terms of numbers) in the southern heathlands. Over 608 species in 70 genera are modally pollinated by birds in South Western Australia. Bird-flowers in Western Australia are often yellow or white and not tubular. Geanthous pollination is relatively common. Variable levels of self-fertility are encountered, but mechanical autogamy is rare. The Myrtaceae are used to illustrate the continuing evolution of bird-pollination in this region.

INTRODUCTION

Bird-pollination is one of the major pollination syndromes of the flora of South Western Australia. Adaptations to birds as pollinators have had profound influences on the nature of the flora of this region. Some aspects of these influences will be discussed with especial reference to the family Myrtaceae.

Geographical occurrence of bird-pollination

Keighery (in press a) surveyed the occurrence of bird-pollination in the tropics and desert regions of Western Australia. In both regions the actual and percentage figures (7.4% of the flora, or 87 species for the tropics, and 5.6% or 54 species for the desert) are low compared to temperate Western Australia (*ca* 15% or 608 species). Within temperate Western Australia the largest concentration of bird-pollinated species are found in the southern heathlands (the Stirling/Eyre Provinces of Beard (1970); Figure 1). The number of species of plants (287) primarily pollinated by birds found in this region is over twice that of any other comparable area of temperate Western Australia.

The reasons for the preponderance of bird-pollinated species in this region are numerous and interlocked. First, the area is diverse in restricted species, especially with regard to the Proteaceae (Speck, 1958), *Eucalyptus* (Chippendale & Wolf, 1981), Rutaceae (Hopper, 1979) and Epacridaceae (Keighery, unpub. data). These groups contain many bird-pollinated species. Studies have shown that an appreciable number of the endemics of the region, for example, Stirling Ranges (Keighery, 1979) and the Fitzgerald River National Park (Keighery, 1981a), are bird-pollinated. Secondly, the climate of the southern coast is often cold and wet, and unsuitable for insect activity. However, growing seasons are long, up to 10-11 months in some areas (Beard, 1979), enabling long flowering seasons and a continuous supply of pollen and nectar during the year. Probably due to these factors, the region contains high numbers of sedentary and nomadic honeyeaters (Wooley, 1981; Keighery, unpub. data). Adequate soil water levels may also partially eliminate the costs of providing large amounts of nectar for vertebrate pollinators. Finally, studies in the Perth region (Table 1) are showing that woodlands and heaths contain the largest numbers of bird-pollinated species. Bird-pollinated plants are uncommon in foreshore regions, swamps and salt lakes where wind-pollination predominates. Beard (1972, 1979, 1981) has demonstrated that woodlands and heaths are the common vegetation formations of southern temperate Western Australia, and George *et al.* (1979) have demonstrated that these heathlands contain more species per unit area than any other vegetation type.

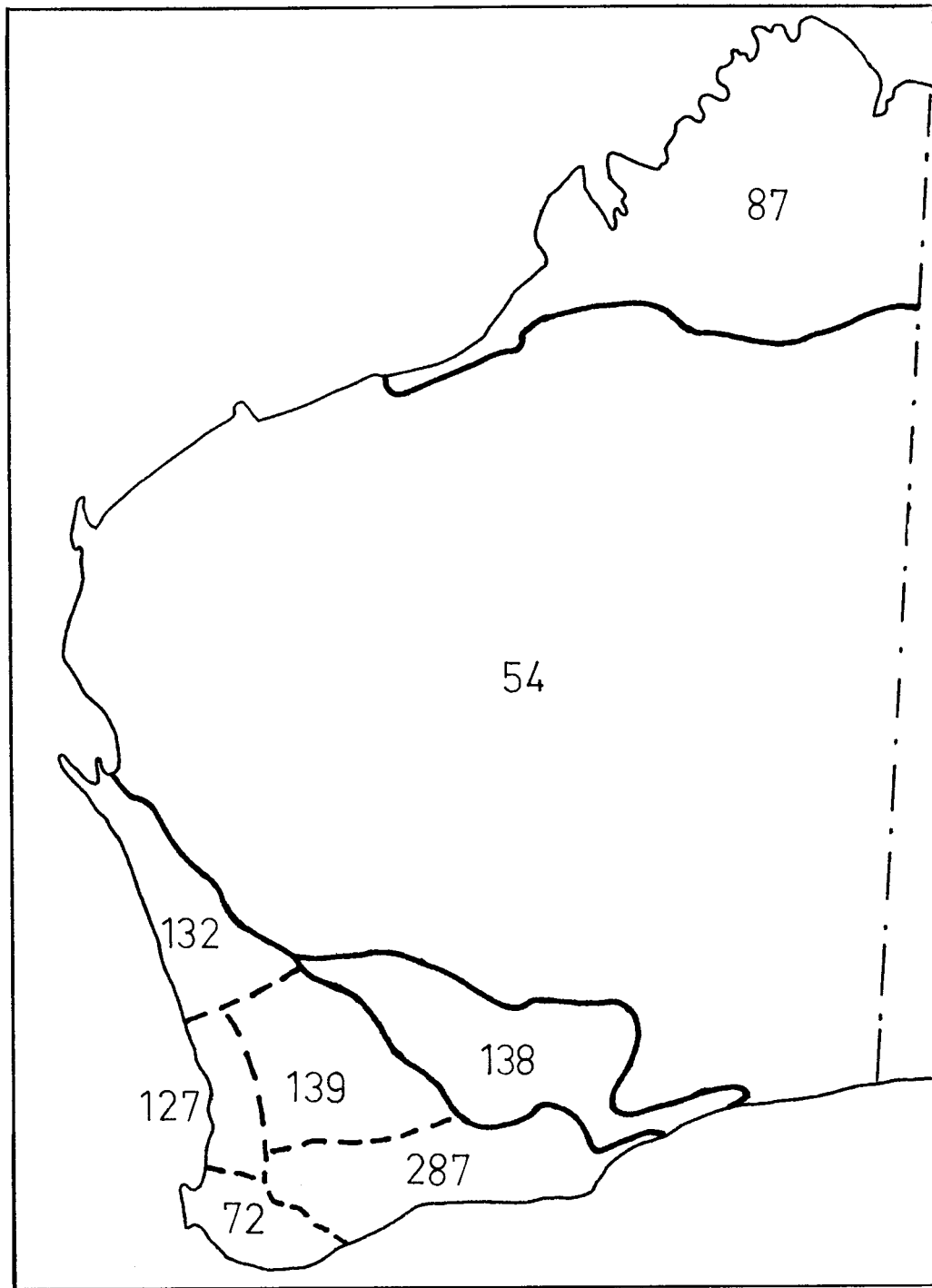


Figure 1. Actual numbers of species of plants primarily pollinated by birds in each phytogeographical region of Western Australia.

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TABLE 1
Percentage of pollination types in various habitats
in the Perth area

Pollination Syndrome Habitat/Locality	Insect	Bird	Wind	Total Species Numbers
FORE DUNES (Yalgorup National Park)	66.7 (20)*	3.3 (1)	30.0 (9)	30
STABLE DUNES (Yalgorup National Park)	83.0 (73)	4.5 (4)	12.5 (11)	88
LIMESTONE HEATH (Yalgorup National Park)	78.6 (103)	8.4 (11)	13.0 (17)	131
TUART WOODLAND (Yalgorup National Park)	80.8 (147)	6.6 (12)	12.6 (23)	182
PAPERBARK SWAMP (Yanchep)	66.7 (18)	— (—)	33.3 (9)	27
SEDGELAND SWAMP (Yanchep)	72.5 (29)	2.5 (1)	25.0 (10)	40
JARRAH (10 ha quadrat, Yanchep National Park)	62.5 (20)	12.5 (4)	25.0 (8)	32
BANKSIA WOODLAND (10 ha quadrat, Melaleuca Park)	10.4 (71)	74.0 (10)	15.6 (15)	96
Garden Island (Consolidated dunes)	67.3 (70)	5.7 (6)	27.0 (28)	104

*species numbers given in brackets

Taxonomic occurrence

Keighery (1980a) listed some 570 species in temperate Western Australia that are primarily pollinated by birds. Since that paper was compiled several new and significant changes can be noted. Crisp (1980) has foreshadowed the splitting of *Brachysema* (*Fabaceae*) into three genera: *Brachysema*, *Bugesia* and *Leptosema*, all of which are entirely bird-pollinated. Continuing studies (Keighery, unpub. data) on nectivorous birds have listed brown honeyeaters (*Lichmera indistincta* (Vig. & Horsf.)) feeding on *Scaevola tomentosa* Gaud. (*Goodeniaceae*) in the Geraldton region; New Holland honeyeaters (*Phylidonyris novaehollandiae* Latham) have been observed feeding on *Andersonia grandiflora* Stschegl. (*Epacridaceae*—*A. setifolia* Benth. also has a similar floral morphology) and *Kingia australis* R Br. (*Liliaceae* or *Xanthorrhoeaceae*) in the Stirling Ranges; *Utricularia menziesii* R.Br. (*Lentibulariaceae*) has been observed being visited by brown honeyeaters (Perth region) and New Holland honeyeaters (Stirling Ranges). This appears to be the only record of bird-pollination in the family *Lentibulariaceae*.

These new generic records, continuing observations and new taxonomic treatments raise to 70 genera and 608 species of plants adapted to bird-pollination in the flora of South Western Australia. There seems little doubt that this number will rise as observations continue, but few new generic records can be expected. The most significant families for bird-pollinated species remain the *Myrtaceae*, *Proteaceae*, *Myoporaceae*, *Epacridaceae*,

Fabaceae, Loranthaceae, Rutaceae and Haemodoraceae.

FLORAL CHARACTERISTICS OF BIRD-POLLINATED PLANTS IN WESTERN AUSTRALIA

Faegri & van der Pijl (1971), Grant & Grant (1968) and Ford *et al.* (1979) have summarized the syndrome of bird-pollinated flowers in considerable detail, and these need not be repeated. However, Australian bird-flowers depart considerably from these "norms", and such differences are considered in more detail below.

Colour

Table 2 gives the basic floral colours (stamens, petals or bracts) of the southwest Australian flora. While it is true that the predominant colour of bird-flowers is red (49%), yellow and white constitute an equally important colour group. Noting flower colours in terms of numbers: black: 2 species, white: 148, yellow: 132, orange: 25, red: 274, purple: 3, green: 15 and brown: 9. Perhaps the most unusual colours are black, brown and purple, though these are relatively rare.

Another unusual aspect of flower colour is that the flowers of some species are relatively inconspicuous and hidden. Dull coloured flowers have been documented in bird-pollinated Eastern Australian Rutaceae by Armstrong (1979). This characteristic is widespread in Western Australian members of the genus *Adenanthos* (*A. cunninghamii*, *A. sericeus*, *A. cygnorum*, *A. velutinus*, *A. stictus*, *A. teges* and *A. cuneatus*) where the flowers are dull coloured and hidden in the foliage. These taxa are, however, regularly visited by birds and cannot be considered inbreeding. More intensive studies on the breeding systems and possible evolution of this unusual group of species are clearly warranted.

TABLE 2
Percentage flower colours of the south eastern flora

Colour	A	B	C	D
White	22	27	24.3	148
Yellow	28	31	21.7	157
Red	20	22	49.2	247
Blue or purple	14	15	0.5	3
Green	4	5	2.5	15
Brown	12	1	1.5	9

A: including anemophilous species (McComb, 1968); B: entomophilous species (McComb, 1968); C: ornithophilous species only; D: ornithophilous species total numbers.

Shape

Unlike hummingbird-flowers which are predominantly tubular, the most common flower shape in southern western Australia is a brush flower (Table 3), often bowl-shaped as in *Eucalyptus*. Tubular flowers have developed in the Rutaceae. Cleistopetalous tubular flowers are characteristic of the genera *Astroloma* and *Cosmelia* (Epacridaceae). These narrow, tubular flowers are rarely visited by insects, nor by the larger-billed honeyeaters (except in a nectar thieving role), and can only be utilized by the smaller, slender-billed honeyeaters. Specific relationships may have developed in the genus *Astroloma* (*Cosmelia* is visited by honeyeaters, but it is autogamous), in contrast to the normal catholic relationships of honeyeaters and plants. The spurred flower of *Utricularia menziesii*, and the slender

elongated gullet of *Microcorys* may also be restrictive for the large-billed honeyeaters. Further studies are being carried out on a range of species of *Astroloma*.

TABLE 3
Structural Blossom (Pollen presentation/pickup)
Classes of Western Australian Bird Flowers

Brush:	<i>Dasypogon, Kingia, Xanthorrhoea</i> <i>Banksia, Dryandra</i> <i>Amyema, Lysiana, Nuytsia</i> <i>Albizia, Acacia</i> <i>Chorilaena, Diplolaena</i> <i>Siegfriedia, Pimelea</i> <i>Beaufortia, Callistemon, Calothamnus, Darwinia,</i> <i>Eremaea, Eucalyptus, Kunzea, Lamarchea,</i> <i>Melaleuca, Regelia, Verticordia</i>
(tubular/gullet) (gullet/brush)	<i>Anigozanthos, Macropidia</i> <i>Adenanthos, Grevillea, Hakea, Lambertia</i>
Tubular:	<i>Blancoa, Conostylis</i> <i>Correa</i> <i>Drummondita, Eriostemon, Nematolepis, Muiriantha,</i> <i>Rhabdinothermum</i> <i>Astroloma, Cosmelia</i> <i>Andersonia, Brachyloma, Styphelia</i>
(closed)	
Tubular/Gullet: (with spur)	<i>Lechenaultia, Scaevola</i> <i>Utricularia</i>
Gullet:	<i>Lambertia, Brachysema</i> <i>Leptosema, Bugesia</i> <i>Hemiandra, Hemigenia, Prostanthera, Microcorys</i> <i>Eremophila</i>
Flag Blossom:	<i>Bossiaea, Brachysema, Burtonia, Cupulanthus,</i> <i>Clianthus, Daviesia, Jansonia, Kennedia,</i> <i>Nemcia, (Oxylobium), Templetonia</i>

Position

Perhaps one of the most surprising aspects of bird-pollinated flowers in Western Australia are the number which are prostrate or pollinated by birds standing on the ground (Table 4). Currently at least 73 species, distributed in 21 genera have flowers positioned near the ground, and honeyeaters frequently feed on these species. The positioning of flowers on the ground cannot be considered as a departure from the bird-pollination syndrome (towards mammal-pollination) in south western Australia, as has been suggested for Southern African Proteaceae by Rourke & Wiens (1980).

Thus bird-pollinated flowers in Western Australia depart from the typical syndrome in shape (bowl-shaped flowers, brush or cleistopetalous flowers are common), colour (yellow and white are common), possession of smell (Ford *et al.*, 1979) and position (geanthous flowers are frequent).

BREEDING SYSTEMS

Studies carried out to date (Table 5) suggest that most bird-pollinated species are at least modally outbreeding. Many species (for example, *Grevillea, Eucalyptus*) have the capacity to set some seed following self-pollination. However, long term studies on some self-fertile taxa in the genus *Eucalyptus* (Pryor, 1976) have shown a decrease in selfed seed viability during storage and inbreeding depression occurring in selfed progeny. This also appears to be true in *Banksia* and *Grevillea* (Keighery, unpub. data), and most Myrtaceae (Rye, 1980) where selfed seed set is consistently lower than crossed.

TABLE 4
Bird Pollinated Species which can be pollinated by
Birds standing on the ground

HAEMODORACEAE	<i>G. plurijuga</i> (prostrate form)
* <i>Anigozanthos bicolor</i> (spp.)	* <i>G. saccata</i>
* <i>A. humilis</i>	<i>G. tenuiloba</i>
* <i>A. kalbarriensis</i>	* <i>G. thelemanniana</i>
* <i>A. viridis</i> (spp.)	<i>G. thrsoides</i>
* <i>Blancoa canescens</i>	FABACEAE
* <i>Conostylis androstemma</i>	<i>Bossiaea dentata</i>
* <i>C. bealiana</i>	* <i>Brachysema praemorsum</i>
PROTEACEAE	<i>Bugesia</i> (* <i>Brachysema macrocarpum</i>)
<i>Banksia blechnifolia</i>	* <i>Clianthus formosus</i>
<i>B. goodii</i>	<i>Cupulanthus bracteolus</i>
<i>B. lullfitzii</i>	* <i>Kennedia prostrata</i>
* <i>B. petiolaris</i>	* <i>Leptosema chambersii</i>
<i>B. prostrata</i>	(+ several other species still
* <i>B. repens</i>	in <i>Brachysema</i>)
(prostrate forms of <i>B. media</i> / <i>B. grandis</i>)	RUTACEAE
<i>Dryandra arctotidis</i>	* <i>Muiriantha hassellii</i>
<i>D. bipinnatifida</i>	MYRTACEAE
* <i>D. calophylla</i>	* <i>Balaustion microphyllum</i>
<i>D. cirsioides</i>	* <i>B. pulcherrimum</i>
<i>D. ferruginea</i>	* <i>Darwinia citriodora</i>
* <i>D. fraseri</i>	<i>D. repens</i>
<i>D. longifolia</i>	* <i>D. sanguinea</i>
* <i>D. nana</i>	<i>D. thymoides</i>
* <i>D. nivea</i>	<i>D. virescens</i>
<i>D. obtusa</i>	* <i>Verticordia mitchelliana</i>
* <i>D. runcinata</i>	EPACRIDACEAE
<i>D. tenuifolia</i>	* <i>Andersonia grandiflora</i>
* <i>D. tridentifera</i>	* <i>Astroloma ciliatum</i>
* <i>Grevillea bipinnatifida</i>	<i>A. humifusum</i>
* <i>G. brachystylis</i> (prostrate form)	* <i>A. pallidum</i>
* <i>G. brownii</i>	* <i>A. prostratum</i>
* <i>G. dryandri</i>	CHLOANTHACEAE
* <i>G. dryandroides</i>	* <i>Chloanthes coccinea</i>
* <i>G. eriostachya</i> (desert)	* <i>Pityrodia exserta</i>
* <i>G. fasciculata</i> (prostrate form)	* <i>P. uncinata</i>
<i>G. nana</i>	
* <i>G. nudiflora</i>	
<i>G. patentiloba</i>	

*observed being visited by nectivorous birds.

Only two species of bird-pollinated plants (*Cupulanthus bracteolus* (F. Muell.) Hutch. and *Cosmelia rubra* R.Br.) are autogamous and habitually self-pollinating. Both are monotypic genera confined to the Eyre district of southern western Australia. *Cupulanthus* has dull brown-red flowers and is rarely visited by birds, but *Cosmelia* produces ample nectar in large red attractive flowers and is regularly visited by birds. Rye (1980) reported that *Darwinia oederioides* (Turcz.) Benth. and *Darwinia pimelioides* Cayzer & Wakefield are largely autogamous but retain many of the attractive features of closely related bird-pollinated species. James (1958) showed that some *Callistemon* species in New South Wales are apomictic, and preliminary evidence suggests that apomixis also occurs in *Calothamnus*.

TABLE 5
Breeding systems of south western Australian bird pollinated plants

Taxon	Breeding System	Reference*
HAEMODORACEAE		
<i>Blancoa canescens</i>	obligate outbreeding	Keighery, 1981b
<i>Anigozanthos</i> (10 species)	low seed set on selfing	Hopper, 1978
<i>A. flavidus</i>	self-fertile	
<i>Macropidia fuliginosa</i>	obligate outbreeding	Hopper, 1978
XANTHORRHOACEAE		
<i>Xanthorrhoea</i> (4 species)	self-fertile, but low to variable seed set	Keighery, in press b
<i>Kingia australis</i>	obligate outbreeding	Keighery, in press b
PROTEACEAE		
<i>Adenanthos</i> (5 species)	Modally outbreeding, low seed set on selfing	
<i>Banksia</i>	7 species obligate outbreeding, some modally outbreeding, several highly self-fertile	Keighery, 1980b
<i>Grevillea</i> (11 species)	modally outbreeding, low seed set on selfing	
<i>Hakea</i> (7 species)	self-fertile	
<i>Lambertia multiflora</i>	self-fertile	
LORANTHACEAE		
<i>Amyema</i>	self-fertile	Blakely, 1922
<i>Lysiana</i>	self-fertile	Blakely, 1922
<i>Nuytsia</i>	self-fertile	
PITTOSPORACEAE		
<i>Billardiera</i> (2 species)	self-fertile	
FABACEAE		
<i>Bossiaea dentata</i>	self-fertile	
<i>Brachysema</i> (3 species)	self-fertile	
<i>Bugesia</i> (1 species)	self-fertile	
<i>Cupulanthus bracteolosus</i>	self-fertile	
<i>Clianthus formosus</i>	some populations obligate outbreeding, some self-fertile	
<i>Daviesia epiphylla</i>	partially self-fertile	
<i>Kennedia</i> (all species)	self-fertile	Silisbury & Brittan (1960)
<i>Templetonia retusa</i>	self-fertile	
RUTACEAE		
<i>Chorilaena</i> (1 species)	outbreeding	Armstrong, 1979
<i>Diplolaena</i> (4 species)	outbreeding	Armstrong, 1979
<i>Nematolepis</i> (1 species)	outbreeding	Armstrong, 1979
RHAMNACEAE		
<i>Siegfriedia</i>	outbreeding	
MYRTACEAE	see Tables 6, 7	
EPACRIDACEAE		
<i>Astroloma</i> (4 species)	some outbreeding, some self-fertile	
<i>Cosmelia</i> (1 species)	autogamous	
CHLOANTHACEAE		
<i>Pityrodia</i> (2 species)	outbreeding	
LAMIACEAE		
<i>Prostanthera</i> (2 species)	outbreeding	
MYOPORACEAE		
<i>Eremophila</i> (15 species)	partially self-fertile	
GOODENIACEAE		
<i>Lechenaultia</i> (2 species)	outbreeding	

*author's data where no reference stated

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Odd polyploidy has been found in some species of *Melaleuca* (Brighton & Ferguson, 1976) and studies are needed to determine if these taxa reproduce asexually (vegetative or pseudogamy). Field studies are needed on the *Darwinia* and *Melaleuca* species.

Vegetative reproduction is relatively rare. James (1958) reported that rhizomes are a common means of producing new individuals in *Callistemon pachyphyllus* (a New South Wales species). A number of genera in the Northern Territory (*Eucalyptus*, *Syzygium* (Eugenia), *Melaleuca*, *Lophostemon* (Tristania) and *Xanthostemon*) possess rhizomes capable of replacing aerial parts destroyed by fire (Lacey, 1974). *Eucalyptus tetradonta* F. Muell., a common species in the western Kimberley region possesses rhizomes, and a similar habit. All of the above genera form clones of short non-reproductive stems, which in the absence of fire give rise to a single sexually reproducing tree. *Utricularia menziesii* R.Br. produces daughter plants via budding of new tubers. However, in general terms, dependence on vegetative reproduction rather than sexual reproduction appears rare. Species perennate via rhizomes, lignotubers or tubers rather than reproduce using these structures.

Dioccy is unknown in bird-pollinated plants, perhaps because of the cost of producing attractive male flowers. Andromonoecy is, however, relatively common (Rye, 1980) and probably serves to increase the pollen supply and attractiveness of the inflorescence.

CONTINUED EVOLUTION: THE MYRTACEAE AS A CASE STUDY

The family Myrtaceae in southern western Australia consists of ca 547 species distributed in 30 genera. Table 6 suggests that bird-pollination has arisen independently several times within the family. In the Chamelaucioids ("nut" fruited Myrtaceae), bird-pollination has only arisen in the closely related genera *Darwinia* and *Verticordia*. The largely lepidopteran pollinated Calytricinae (*Calytrix*, *Calythropsis*, *Lhotskya* and *Wehlia*) have not given rise to any taxa pollinated by birds. Neither have the small flowered Thryptomeninae (*Micromyrtus*, *Corynanthera* and *Thryptomene*). Within *Verticordia* only three species (*V. helichrysantha* Turcz, *V. mitchelliana* C.A. Gardn. in sect. *Verticordia* and *V. grandis* Drumm. in section *Catocalypta*) of a total 53 species are known to be bird-pollinated, suggesting a relatively recent adaptation for this genus. *Darwinia*, on the other hand, has many divergent floral morphologies for bird-pollination. Evidence suggests that bird-pollination may be basic for this genus.

In the Leptospermoideae the *Baeckea* sub-alliance (*Astartea*, *Baeckea*, *Balaustion*, *Hypocalymma* and *Scholtzia*) contains the south-western endemic genus *Balaustion*, both species of which are bird-pollinated (Keighery, in press c). The *Leptospermum* sub-alliance contains the genera *Leptospermum*, *Agonis* and *Kunzea*. The genus *Kunzea* contains two species *K. baxteri* (Klotzsch.) Schauer and *K. pulchella* (Lindl.) George which are bird-pollinated. The *Calothamnus* sub-alliance contains the genera *Calothamnus*, *Beaufortia*, *Regelia*, *Phymatocarpus* and *Eremaea*. Bird-pollination is basic to the genus *Calothamnus*, and is also known for species of *Beaufortia*, *Regelia* and *Eremaea*. The genera *Callistemon*, *Conothamnus*, *Lamarchea* and *Melaleuca* occur also in this sub-alliance. Bird-pollination is basic to *Callistemon* and *Lamarchea* and occurs sporadically in *Melaleuca*.

The *Eucalyptus* alliance contains *Eucalyptus*, *Symphomyrtus* and *Eudesmia* in Western Australia. Bird-pollination is probably basic to this group, but the often small, open flowers allow access for a wide range of pollinators. However, adaptation to birds as pollinators has occurred repeatedly in this genus. Closer adaptation can be shown in the following characters: larger flower sizes; red and yellow colours versus white; pendulous flowers (for example, *Eucalyptus caesia*); tubular flowers (for example, *forrestiana*); synandry giving tubular flowers (*E. beardiana*, *E. aff leptopoda*), and aggregation giving ball-like flowers

TABLE 6
Pollination syndromes: South Western Myrtaceae

Western Australian Myrtaceae	Self-comp	Beetle	Fly	Bee	Moth	Butterfly	Bird	Mammal
LEPTOSPERMOIDEAE								
Chamelaucium alliance								
Chamelaucium sub-alliance								
<i>Actinodium</i>	*	*	*	*	*	*	#	#
<i>Chamelaucium</i>	*	*	*	**	#	#	#	#
<i>Darwinia</i>	*	?	?	*	#	#	***	?
<i>Pileanthus</i>	#	?	*	***	#	#	#	#
<i>Verticordia</i>	*	*	*	***	?	?	*	?
<i>Calytrix</i>	*	?	**	*	*	***	#	#
<i>Lhotskya</i>	**	?	**	*	*	**	#	#
<i>Calythropsis</i>	**	?	**	*	*	**	#	#
<i>Wehlia</i>	**	?	**	*	*	**	#	#
<i>Micromyrtus</i>	***	*	*	***	#	?	#	#
<i>Corynanthera</i>	***	?	?	***	#	?	#	#
<i>Thryptomene</i>	***	?	*	***	#	?	#	#
Baeckea sub-alliance								
<i>Astartea</i>	***	*	*	**	?	?	#	#
<i>Baeckea</i>	***	*	*	**	?	?	#	#
<i>Balaustion</i>	**	#	#	#	#	#	**	#
<i>Hypocalymma</i>	*	*	*	**	*	?	#	#
<i>Scholtzia</i>	***	*	*	**	?	?	#	#
Leptospermum alliance								
Calothamnus sub-alliance								
<i>Beaufortia</i>	**	?	?	**	?	?	**	*
<i>Phymatocarpus</i>	**	*	*	**	?	?	#	#
<i>Calothamnus</i>	**	#	#	#	#	#	***	*
<i>Regelia</i>	**	*	*	**	*	#	*	#
<i>Eremaea</i>	**	*	*	*	?	?	**	?
<i>Melaleuca</i>	***	*	*	*	*	*	*	?
<i>Callistemon</i>	***	#	#	#	#	#	***	?
<i>Calothamnus</i>	***	?	*	**	?	?	#	#
<i>Lamarchea</i>	***	#	#	#	#	#	***	#
<i>Eucalyptus</i>	***	*	*	*	*	*	***	*
Leptospermum sub-alliance								
<i>Agonis</i>	**	*	*	*	*	?	#	#
<i>Leptospermum</i>	**	*	**	*	*	?	#	#
<i>Kunzea</i>	**	*	*	**	*	?	*	?

* present in at least one species; ** present in several species; *** widespread to almost universal in genus; ? presently unrecorded; # unknown or not present in genus; Classification based on Briggs & Johnson (1979).

(for example, *E. conferruminata*).

Table 7 indicates how floral characters limiting insect visitation/pollination are spread through the different subgenera of *Eucalyptus* found in Western Australia. Several of these floral adaptations—tubular flowers, synandrous flowers, aggregations and very large flowers are either totally or almost totally confined to Western Australia, suggesting that closer adaptations to birds as pollinators is a major evolutionary force in this region.

In summation, bird-pollination occurs in 12 genera spread throughout the Myrtaceae of Western Australia. It appears to be basic in 6 genera (*Darwinia*, *Balaustion*, *Calothamnus*, *Callistemon*, *Lamarchea* and *Eucalyptus*) and minor in the other 6 (*Verticordia*, *Kunzea*, *Regelia*, *Beaufortia*, *Eremaea* and *Melaleuca*). Genera with bird-pollination as a basic pollination syndrome can be large and diverse (*Darwinia* and *Eucalyptus*) suggesting that it may have considerable antiquity in the region. However,

TABLE 7
Bird-pollination in Western Australian *Eucalyptus* species

Birds have been observed feeding on most *Eucalyptus* species, but most taxa are considered open-pollinated because of their small cup-shaped white flowers, which are easily accessible for insects. However, throughout the genus, species (or groups of species) have morphological attributes which limit access or stigma contact for small non-vertebrate pollinators. These species are shown in **bold** face in the Table. They deserve further study, to determine the relative importance of insects or vertebrates as pollinators. They also demonstrate how a large genus may only have superficially similar flowers which can serve different pollinators.

Taxon†	Floral characters limiting insect pollination
Subgenus <i>Blakella</i> Series <i>Clavigerae</i> <i>*papuana</i> , <i>grandiflora</i> , <i>confertiflora</i> <i>clavigera</i> , <i>*aspera</i>	
Subgenus <i>Corymbia</i> Series <i>Setosae</i> <i>*setosa</i> , <i>ferruginea</i> , <i>abbreviata</i> , <i>*zygophylla</i> , <i>perfoliata</i> Series <i>Ptychocarphae</i> <i>*ptychocarpa</i>	large flowers (large gap stigma-anthers), pink colour
Series <i>Gummiferae</i> Subseries <i>Dichromophloinae</i> <i>collina</i> , <i>bleseri</i> , <i>foelscheana</i> , <i>*latifolia</i> , <i>*dichromophloia</i> , <i>terminalis</i> Subseries <i>Polycarpinae</i> <i>polycarpa</i> , <i>cliftoniana</i> Subseries <i>Ficifolinae</i> <i>*ficifolia</i> Subseries <i>Gummiferinae</i> <i>*calophylla</i> , <i>*haematoxylon</i> <i>nesophila</i>	large flowers, red colour
Subgenus <i>Eudesmia</i> Series <i>Tetragonae</i> <i>*tetragona</i> , <i>*gittinsii</i> <i>*eudesmioides</i> , <i>*erythrocorys</i> Subseries <i>Ebbanoesinae</i> <i>ebbanoensis</i> Subseries <i>Jucundinae</i> <i>*jucunda</i> , <i>*roycei</i> Subseries <i>Odontocarpinae</i> <i>*gongylocarpa</i> , <i>odontocarpa</i> <i>gamophylla</i> Series <i>Baileyanae</i> <i>lirata</i> Series <i>Miniatae</i> <i>*miniata</i> , <i>*phoenicea</i> Series <i>Tetrodontae</i> <i>tetrodonta</i>	large flowers, yellow colour large flowers, yellow colour large flowers, pink colour
Subgenus <i>Monocalyptus</i> Series <i>Preissianae</i> <i>megacarpa</i> , <i>*preissiana</i> , <i>*coronata</i> <i>*acies</i> , <i>aquilina</i> , <i>ligulata</i> , <i>*calcicola</i> , <i>brevistylis</i> Series <i>Diversifoliae</i> <i>*pachyloma</i> , <i>diversifolia</i> , <i>patens</i> , <i>*todtiana</i> Series <i>Marginatae</i> <i>*buprestium</i> , <i>*sepulcralis</i> , <i>exilis</i> , <i>*pendens</i> , <i>*marginata</i> , <i>*staeri</i> , <i>insularis</i> Series <i>Jacksonianae</i> <i>*jacksonii</i>	large flowers, yellow colour

Taxon†	Floral characters limiting insect pollination
Subgenus Telocalyptus Series Degluptae <i>brachyandra</i>	
Subgenus Symphyomyrtus Series Guilfoyleanae <i>*guilfoylei</i> Series Diversicolores <i>*diversicolor</i> Series Cornutae <i>*gomphocephala</i> <i>*cornuta, *burdettiana, *lehmanii</i> <i>*conferruminata, newbeyi, bennettiae</i> <i>*macrocera, megacornuta</i>	flowers aggregated into ball-flowers
Series Occidentalinae <i>occidentalis</i> <i>sargentii</i>	
Series Erythronemae <i>*cylindriflora, *erythronema, dielsii,</i> <i>cerasiformis</i>	large pendulous red flowers
Series Reduncae <i>*wandoom, *redunca, *xanthonema,</i> <i>*gardneri, desmondensis</i>	
Series Accedentes <i>*laeliae, *accedens, trivalvis,</i> <i>prominens</i>	
Series Grossae <i>*grossa, *stricklandii, carnei</i>	large yellow flowers
Series Salubres <i>*salubris, *campaspe, *diptera, *effusa</i>	
Series Kruseanae <i>*kruseanae</i>	
Series Loxophlebeae <i>*loxophleba</i>	
Series Cneorifoliae <i>*doratoxylon, *decurva, *goniantha,</i> <i>*falcata, *decipiens, micranthera,</i> <i>angustissima</i>	
Series Bakerianae <i>jutsonii</i>	
Series Cladocalyces <i>brockwayii</i>	
Series Oleosae <i>*longicornis, grasbyi, *oleosa, kochii,</i> <i>peeneri, *transcontinentalis, socialis,</i> <i>cooperana, *flocktoniae, balladoniensis</i>	
Series Salmonophloiae <i>*salmonophloia</i>	
Series Macrocarpae Subseries Leptopodinae <i>*leptopoda, oxymitra</i>	
Subseries Orbifoliae <i>*ewartiana, *orbifolia</i> <i>*websterana, *crucis,</i> <i>*caesia</i>	large pendulous red flowers
Subseries Macrocarpinae <i>*lanepolei, *beardiana, *drummondii,</i> <i>*macrocarpa, *oldfieldii, burracoppinensis,</i> <i>rameliana, pyriformis, *youngiana,</i> <i>pachyphylla, kingsmillii</i>	synandrous pendulous flower large, red
Series Calycogonae <i>*gracilis, *calycogona, celastroides</i>	

Taxon†	Floral characters limiting insect pollination
Series Foecundae <i>rigidula</i> , * <i>foecunda</i> , <i>formanii</i> , * <i>uncinata</i> , <i>albida</i>	
Series Dumosae * <i>woowardii</i> , * <i>sheathiana</i> , <i>dongarrensis</i> , <i>striaticalyx</i> , <i>fraseri</i> , <i>dumosa</i> , * <i>conglobata</i> , <i>kondininensis</i> , <i>clelandii</i> , * <i>lesouefii</i> , <i>georgei</i>	
Series Torquatae * <i>rugosa</i> , * <i>melanoxylon</i> , <i>merrickiae</i> , <i>leptocalyx</i> , * <i>comitae-vallis</i> , * <i>concinna</i> , <i>griffithsii</i> , * <i>corrugata</i> , * <i>torquata</i> , <i>deflexa</i>	
Series Incrassatae * <i>incrassata</i> , * <i>stoatei</i> , * <i>tetraptera</i> , * <i>forrestiana</i>	large red pendulous flowers
Series Dundasianae <i>ovularis</i> , * <i>oraria</i> , * <i>dundasii</i>	
Series Albae <i>alba</i> , <i>bigalerita</i> , <i>brevifolia</i> , <i>mooreana</i> , <i>leucophloia</i> , <i>houseana</i> , * <i>apodophylla</i> , <i>herbertiana</i> , <i>cupularis</i>	
Series Tereticornes * <i>camaldulensis</i> , * <i>rudis</i>	
Series Oliganthae <i>patellaris</i> , <i>oligantha</i> , <i>fitzgeraldii</i> , <i>tectifica</i> , <i>argillacea</i> , * <i>microtheca</i>	
Series Largiflorentes <i>normantonensis</i> , <i>lucasii</i>	
Series Intertextae <i>intertexta</i>	
Series Pruinosaes <i>jensenii</i> , <i>pruinosa</i> ,	

* observed being visited by nectariferous birds.

† classification based on Pryor & Johnson (1971).

the diversity in flower form shown in these large genera suggests that adaptations to birds as pollinators are still actively evolving.

Data on the close relatives of bird-pollinated taxa in *Verticordia*, *Darwinia*, *Kunzea*, *Beaufortia* and *Eremaea* suggests that the bird-pollinated taxa are derived from taxa which were bee-pollinated (Table 6) not moth-pollinated as has been suggested for other groups (Grant & Grant, 1968). Moth and butterfly pollination is relatively rare in south western Australia (Keighery, unpub. data). The pollination of the Fabaceae of Western Australia also shows a clear bee/bird dichotomy (Keighery, 1982) with no evidence of moth pollination preceding bird-pollination. Further studies on this aspect of the evolution of bird-pollination are planned, and Western Australia appears to provide an ideal laboratory to study all aspects of bird-pollination.

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