

Nectar sources used by birds in monsoonal north-western Australia: a regional survey

Donald C. Franklin^A and Richard A. Noske

Cooperative Research Centre for the Sustainable Development of Tropical Savannas and
Science Faculty, Northern Territory University, Darwin, NT 0909, Australia.

^ACorresponding author; PO Box 987, Nightcliff, NT 0814, Australia; email: monsoon@topend.com.au

Abstract. We document the flora that provides nectar for birds in monsoonal north-western Australia, and examine the relationship between floral morphology and bird morphology in the region. Twenty-four regular nectarivores (21 honeyeaters, two lorikeets, one white-eye) and 29 opportunist species have been observed probing the flowers of 116 species of plants from 28 families. Amongst the nectar sources, the Myrtaceae is dominant in both the number of species and frequency of use, followed distantly by the Proteaceae and Loranthaceae. Variation between bird species in patterns of use of different floral structures primarily reflected the habitats occupied rather than shared or co-evolved morphology. Woodland birds made particular use of staminiferous cups, mangal specialists particular use of open sepaliferous and petaliferous flowers, and forest specialists and habitat generalists intermediate use of these flower types. Bird-flower relationships in monsoonal Australia may be generalised because of a combination of the dominance of mass-flowering myrtaceous trees, aridity during past glacials that may have eliminated specialists from the system, and perhaps also because many nectar sources are shared with bats.

Introduction

In monsoonal north-western Australia, a variety of nectar sources (Brooker *et al.* 1990; Brown *et al.* 1997) support a considerable diversity of avian nectarivores (Morton and Brennan 1991), but the relationship between the two has received little attention (Franklin 1997). Brooker *et al.* (1990) demonstrated that the region lacks the guild of very long-billed small to medium honeyeaters that is prominent in parts of southern Australia. As elsewhere in Australia, some nectarivore species track nectar resources through space and time (Morton and Brennan 1991; Franklin and Noske 1999). Knowledge of fluctuations in resource availability is scant and mostly localised (Brooker *et al.* 1990; Woinarski and Tidemann 1991; Franklin and Noske 1998), although Woinarski *et al.* (in press) provide an overview of seasonal patterns of nectar production across the Northern Territory.

In this paper we investigate patterns of choice of flower species by avian nectarivores in monsoonal north-western Australia at a broad geographic scale by combining data collected during formal studies, opportunistic observations, the unpublished observations of other observers and records from the literature. Nectar sources are characterised according to taxonomy, phenology, habitat and floral structures, and birds by their weight and bill length. We then examine the relationship between bird morphology and the floral structures they utilise.

Study area

North-western Australia (north of c. 18°S and west of the Queensland border) experiences intensely seasonal rainfall and moderate to high temperatures throughout the year. The wet season lasts from November to April with a peak during the monsoon period in January and February. Mean annual rainfall varies from c. 600 mm at its inland limits to above 1600 mm in the north. In most areas, seasonal saturation of the soil is a reliable annual event (McDonald and McAlpine 1991) that underlies a fundamental annual rhythm of plant growth and flowering (Nix 1976; Williams *et al.* 1997, 1999).

The complex variety of habitats that occur in the study area have been described in detail by Beard (1979) and Wilson *et al.* (1990) and in more general terms by Dunlop and Webb (1991) and Brock (1993). More than 99% of the woody vegetation is floristically and structurally heterogeneous woodland frequently dominated by eucalypts (*Corymbia* and *Eucalyptus*, Myrtaceae), or eucalypt-dominated open forest. Other woody vegetation types include monsoon rainforest, riparian *Melaleuca* forests and mangal (mangrove forests), but each comprises no more than 0.4% of the landscape in monsoonal areas of the Northern Territory (calculated from Wilson *et al.* 1990) and even less in the Kimberley region of Western Australia (Beard 1979; Russell-Smith *et al.* 1992).

Broad patterns of habitat choice amongst the nectarivorous birds of the study area are described by Keast (1968), Blakers *et al.* (1984) and Woinarski *et al.* (1988).

Methods

Data collection

Records of birds probing flowers were collected during formal ornithological studies and opportunistically throughout the year from March 1985 to October 1998 at a range of sites in monsoonal areas of north-western Australia. For each record, we noted the bird species, the flower species, the date and the location. These records have been supplemented extensively by those of other resident observers, and by published records (mostly Brooker *et al.* 1990 and Brown *et al.* 1997).

Morphometrics were recorded for birds captured at Palmerston (12°30'S, 130°57'E), Berry Springs (12°45'S, 131°02'E), Yinberrie Hills (14°08'S, 132°05'E) and in smaller numbers at other locations in northern and north-western areas of the Northern Territory. Captured birds were weighed to 0.1 g on an electronic balance, and bill lengths from the tip to the base of the skull measured to 0.1 mm by using vernier callipers.

Data analysis

Records were vetted to the following standard of independence: no more than one record of each bird-flower combination was allowed for each month of each year at each study site or area of observation.

Flower species were classified as having one of eight flower/inflorescence structural types (Table 1), as occurring in one or more of four broad habitats (woodland/eucalypt forest, riparian *Melaleuca* forest, monsoon rainforest and mangal), one or more of six growth habits (large tree, small tree, shrub, woody parasite, climber, herb) and to one or more of a range of flower colours from our experience with the species concerned and by consulting Guymer (1988), Wheeler (1992), Brock (1993) and Dunlop *et al.* (1995a). Bird species were classed as either *opportunist* or *regular* nec-

tarivores. Opportunist nectarivores are defined as those whose use of nectar in the monsoonal tropics is highly seasonal (Franklin 1999), whereas regular nectarivores either display strong morphological and ecological specialisation to nectarivory (honeyeaters—Meliphagidae, lorikeets—Loriidae) or consume at least some nectar throughout the year (yellow white-eye *Zosterops luteus*, Zosteropidae; Noske 1996; the present study). Our use of the term *regular nectarivore* is in no way intended to imply an absolute dependence on nectar or even an absence of seasonal variation in levels of usage.

A paucity of records in our database indicates either that a nectar source is not very attractive to birds or that its use may have been poorly documented. Sources, the use of which is reasonably well documented (arbitrarily set at >10 non-urban records by regular nectarivores) and that frequently attract larger nectarivores (arbitrarily, where >25% of the non-urban records of regular nectarivores are of species weighing more than 50 g) are classed as 'main' sources.

Patterns of use of floral structure classes by regular nectarivore species for which there were more than 24 non-urban records were compared by two methods. Proportional rate of use of each class was compared with the corresponding proportional rates for all the species combined, low rates of usage being identified as less than 50% of the group rate and high rates of usage identified as greater than 150% of the group rate. A simple measure of niche breadth of each bird species (uncorrected for differences in habitat use) is provided by summing the number of floral structure classes for which the proportional rate was greater than 50% of the group rate. Furthermore, bird species were classified according to their proportionate use of floral structure classes, by using the Bray-Curtis measure of dissimilarity and flexible UPGMA with $\beta = -0.1$ (Belbin 1994). The Bray-Curtis coefficient was selected because it emphasises the most abundant variables (Krebs 1989). The contributions of variables to the groupings distinguished were assessed with Kruskal-Wallis tests (Zar 1984).

Bird names follow Christidis and Boles (1994). Plant names follow Dunlop *et al.* (1995b), Wheeler (1992) and Guymer (1988), with amendments to *Eucalyptus* from Hill and Johnson (1995).

Table 1. Structural flower/inflorescence classes describing the flowers that were used by birds in the Top End of the Northern Territory

Structural class	Bird-use characteristics	Top End examples
1. Staminiferous flowers arranged in brush or spherical inflorescence	flowers often small, but aggregation enables rapid feeding	<i>Banksia, Melaleuca, Terminalia</i>
2. Staminiferous open cup, flowers solitary or in umbels or corymbs	nectar is readily accessible, flowers often robust, mostly generalised vertebrate-pollination syndrome	<i>Corymbia, Eucalyptus, Syzygium, Xanthostemon</i>
3. 'Shaving brush' ^A —flower solitary, both petaliferous and prominently staminiferous, not open	bat-pollination syndrome, requires deep insertion of bill	<i>Planchonia, Sonneratia</i>
4. Tubular corolla	requires deep insertion of bill, bird-pollination syndrome	Loranthaceae, <i>Lysiphylloides, Helicteres</i>
5. 'Gullet-shaped' ^A	most require deep insertion of bill, bird-pollination syndrome	<i>Grevillea</i>
6. 'Flag-shaped' ^A	may require deep insertion of bill	Fabaceae, <i>Hypoestes</i>
7. Small (<10 mm long or across) petaliferous or sepaliferous flower	mostly insect-pollination syndrome, nectar amounts small	<i>Lophostemon, Verticordia, mangroves except Sonneratia</i>
8. Large (>10 mm) showy petaliferous flowers	some insect, some bird-pollination syndrome	<i>Bombax, Brachychiton, Cordia, Gardenia</i>

^A *sensu* Armstrong (1979).

Results

Our database comprises 2282 records of 53 species of nectarivorous birds feeding at the flowers of 116 plant species. Of these records, 1590 (70%) were collected by the authors, 354 (16%) by other observers and 338 (15%) were obtained from the literature. Forty-nine percent of records were obtained from non-urban areas close to Darwin, 18% from the southern Top End (mostly Katherine and Victoria River areas), 14% from the north-eastern Top End (Kakadu, Arnhem Land, Groote Eylandt), 7% from the Kimberley in Western Australia, 4% from urban areas and 8% were not attributed to a locality. The 1883 dated records were collected in all months of the year but more frequently in the dry season (peak monthly total of 245 records in June) than the wet season (minimum monthly total of 80 records in December).

The birds

Ninety-two percent (2089) of all records were of regular nectarivores, comprising 21 species of honeyeaters, two lorikeets, and one white-eye (Table 2). Honeyeaters ranged in weight from 7.5 g (red-headed honeyeater, $n = 426$) to 98 g (blue-faced honeyeater, $n = 23$) (Fig. 1), and ssp. *ammitophila* of the helmeted friarbird, which we have not weighed, may be even larger. In general, bill length in honeyeaters increased

with increasing body weight, but divergence from the regression line illustrated (Fig. 1) suggests that there may be two distinct guilds of honeyeaters; those with moderately long bills compared with body weight and those with short bills compared with body weight. The distinction appears particularly marked amongst the 10 species of honeyeater (plus yellow white-eye) that weighed less than 13 g, with the three myzomelid species (*Myzomela*, *Certhionyx*) and the brown honeyeater having relatively long bills. There was only one honeyeater species (white-gaped honeyeater) in the range of 22–55 g, and no 'long-billed' honeyeaters in the range 13–55 g. The lorikeet species weighed 117 g (rainbow lorikeet, $n = 27$) and 53 g (varied lorikeet, $n = 11$). Details of the 29 species of opportunist nectarivores are provided by Franklin (1999).

The flowers

The 116 plant species comprise 113 indigenous and three naturalised species from 28 families (Appendix, summarised in Table 3). Myrtaceae was by far the most speciose family, with the eucalyptoid genera *Corymbia* and *Eucalyptus* dominant, followed by *Melaleuca* and *Syzygium*. Proteaceae and Loranthaceae, the former represented by numerous *Grevillea* and one *Banksia* species and the latter by *Amyema* and four other mistletoe genera, were also prominent.

Table 2. Regular nectarivores recorded feeding at flowers in monsoonal north-western Australia

Species	Species abbreviation	No. of records
Lorikeets, Psittacidae		
Rainbow lorikeet, <i>Trichoglossus haematodus</i>	RLK	172
Varied lorikeet, <i>Psitteuteles versicolor</i>	VLK	77
Honeyeaters, Meliphagidae		
Spiny-cheeked honeyeater, <i>Acanthagenys rufogularis</i>	HFB	3
Helmeted friarbird, <i>Philemon buceroides</i>	SCF	21
Silver-crowned friarbird, <i>P. argenteiceps</i>	LFB	161
Little friarbird, <i>P. citreogularis</i>	BFH	195
Blue-faced honeyeater, <i>Entomyzon cyanotis</i>	YTM	78
Yellow-throated miner, <i>Manorina flavigula</i>		42
White-lined honeyeater, <i>Meliphaga albilineata</i>		16
Singing honeyeater, <i>Lichenostomus virescens</i>	SHE	19
White-gaped honeyeater, <i>L. unicolor</i>	WGH	92
Grey-fronted honeyeater, <i>L. plumulus</i>	GFH	19
Yellow-tinted honeyeater, <i>L. flavescens</i>	YTH	43
Black-chinned honeyeater, <i>Melithreptus gularis</i>	BCH	14
White-throated honeyeater, <i>M. albogularis</i>	WTH	118
Brown honeyeater, <i>Lichenostomus indistincta</i>	BRH	356
Bar-breasted honeyeater, <i>Ramsayornis fasciatus</i>	BBH	74
Rufous-banded honeyeater, <i>Conopophila albogularis</i>	RBH	44
Rufous-throated honeyeater, <i>C. rufogularis</i>	RTH	85
Banded honeyeater, <i>Certhionyx pectoralis</i>	BDH	109
Black honeyeater, <i>C. niger</i>	DHE	1
Dusky honeyeater, <i>Myzomela obscura</i>	RHH	166
Red-headed honeyeater, <i>M. erythrocephala</i>		167
White-eyes, Zosteropidae	YWE	25
Yellow white-eye, <i>Zosterops luteus</i>		

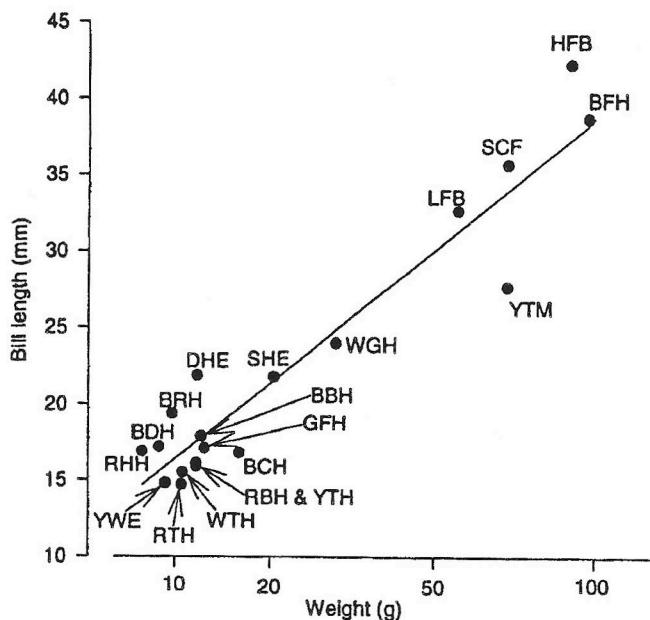


Fig. 1. Relationship between mean weight and mean bill length for Top End honeyeaters. Abbreviations are as in Table 2. Measurements for the helmeted friarbird (HFB) are from ssp. *gordoni*—examination of museum skins shows ssp. *ammitophila* to be substantially larger.

Nectar sources attractive to a range of both small and large nectarivore species ('main' nectar sources) were concentrated particularly in *Corymbia* and *Eucalyptus*, with a wide taxonomic scatter of other species notably including the woodland trees *Banksia dentata*, *Grevillea decurrens*, *G. pteridifolia*, *Melaleuca nervosa*, *Planchonia careya* and *Xanthostemon paradoxus*, the riparian forest trees *Melaleuca leucadendra* and *M. viridiiflora*, the mistletoe *Amyema sanguinea*, the rainforest tree *Bombax ceiba* and the mangrove *Sonneratia alba*. Sources notably attractive to small, but not or infrequently to large nectarivores, include the woodland trees *Brachychiton megaphyllus*, *Erythrophleum chlorostachys*, *Lysiphyllum cunninghamii* and *Terminalia grandiflora*, the woodland shrub *Grevillea dryandri*, the mistletoes *Decaisnina signata* and *Amyema mackayensis*, the riparian or swamp trees of the genus *Lophostemon* and the mangroves *Aegiceras corniculatum*, *Bruguiera exaristata*, *Ceriops tagal* and *Rhizophora stylosa*.

Most nectar sources were small or large trees (Table 3). Climbers and herbs were infrequent nectar sources and were mostly used by small honeyeaters. All adequately documented plants with eucalyptoid staminiferous open cup flowers were 'main' nectar sources, as also were the two sources with shaving-brush flowers. Small petaliferous, small sepaliferous, tubular and flag-shaped flowers were rarely used by larger nectarivores, the myrtaceous shrub *Verticordia cunninghamii* being a notable exception. White and cream were the most common flower colours, followed

Table 3. Summary of characteristics of 116 nectar sources of monsoonal north-western Australia

Details of plant species and their characters are given in Appendix. Totals for Habitat, Growth habit and Flower colour may be greater than the number of species because some species belong in more than one category. A = species with >10 non-urban records of regular nectarivores; B = species with >10 non-urban records of regular nectarivores, >25% of which are for nectarivores >50 g (see Methods)

Character	Number of nectar source species			
	Total	A	B	%B/A
Speciose families				
Myrtaceae	45	25	22	88
Proteaceae	12	5	4	80
Loranthaceae	9	4	2	50
Fabaceae	6	1	0	0
Combretaceae	5	1	0	0
Rhizophoraceae	4	3	0	0
Sterculiaceae	4	1	0	0
Apocynaceae	3	0	0	—
Caesalpiniaceae	3	2	0	0
Verbenaceae	3	0	0	—
Speciose genera				
<i>Corymbia</i> (Myrtaceae)	17	10	10	100
<i>Grevillea</i> (Proteaceae)	11	4	3	75
<i>Eucalyptus</i> (Myrtaceae)	10	6	6	100
<i>Melaleuca</i> (Myrtaceae)	6	5	3	60
<i>Amyema</i> (Loranthaceae)	4	3	2	67
<i>Syzygium</i> (Myrtaceae)	4	0	0	—
<i>Terminalia</i> (Combretaceae)	4	1	0	0
<i>Brachychiton</i> (Sterculiaceae)	3	1	0	0
<i>Xanthostemon</i> (Myrtaceae)	3	1	1	100
Habitat				
Woodland	73	31	24	77
Mangal	12	6	1	17
Riparian forest	15	8	5	63
Monsoon rainforest	28	2	1	50
Growth habit				
Large tree	40	18	14	78
Small tree	57	27	7	26
Shrub	23	9	5	56
Woody parasite	9	4	2	50
Climber	4	0	0	—
Herb	2	0	0	—
Flower/inflorescence class				
1. Staminiferous brush inflorescence	15	9	5	56
2. Staminiferous open cup flower	34	17	17	100
3. Shaving brush flower	4	2	2	100
4. Tubular flower	14	6	2	33
5. Gullet-shaped flower	11	4	3	75
6. Flag-shaped flower	7	1	0	0
7. Other small flower	22	5	1	20
8. Other large flower	8	2	1	50
Flower colour				
White or cream or yellow	80	32	24	75
Orange or red	31	15	7	47
Green	12	4	1	25
Pink or mauve or purple	9	3	3	100
Total no. of plant species	116	46	32	70

by yellow, orange and red. Few flowers were solely green, the colour most often occurring in mistletoes and mangroves in tandem with yellow, orange or red.

Many 'main' nectar sources flowered in a single discrete annual period (Fig. 2), in some cases with demonstrably similar timing in different regions of the study area (Fig. 2b, c, e). More complex patterns are also evident. Fern-leaved grevillea, *Grevillea pteridifolia*, an important dry season nectar source in many areas of northern Australia, had a single dry season flowering peak at Berry Springs, but in some districts a second, apparently discrete population flowered several months earlier (Fig. 2f). Weeping paperbark *Melaleuca leucadendra*, a large tree dominant along many perennial streams, had flowering peaks at the beginning and again at the end of the wet season (Fig. 2j). Bridal tree *Xanthostemon paradoxus* was in many districts an important early wet season nectar source but displayed marked regional variation in its flowering times such that some flowering was recorded in all months of the year (Fig. 2k). In Darwin Harbour, star mangrove *Sonneratia alba* had two discrete annual flowering peaks, one during the early to mid-wet season and another brief but heavy peak at the end of the wet (Fig. 2l).

By far the greatest variety of nectar sources was to be found in the woodlands (Table 3). For its very small relative area, monsoon rainforest contained a considerable diversity of nectar sources, but only few were sufficiently documented to enable determination of the importance of their contribution. The few nectar sources in riparian forest featured a high proportion of 'main' nectar sources, particularly *Melaleuca* spp., while only one mangrove species, the seaward fringe tree *Sonneratia alba*, was a 'main' source of nectar. At all taxonomic levels up to at least family, the flowers used in mangals and monsoon rainforests differ markedly from those of woodland and riparian habitats (Appendix).

Patterns of use of floral structures

A range of bird species was recorded by using plants of all floral structure classes, but there were marked differences between species in their patterns of use (Table 4). Three regular nectarivores, the brown, dusky and white-gaped honeyeaters, used all eight floral structure classes at greater than 50% of the group rate, while at the other extreme, the varied lorikeet and banded honeyeater made frequent use of only a restricted subset of classes (2 and 3 classes greater than 50% of the group rate, respectively). Niche breadth values were generally low amongst lorikeets and moderate amongst large honeyeaters, but highly variable amongst the small honeyeaters.

Brush inflorescences were selected most frequently by bar-breasted and rufous-banded honeyeaters, reflecting their use of paperbarks (*Melaleuca*) in riparian forest. Staminiferous cups were visited by all species except the yellow white-eye, but most prominently by both lorikeets, all large honeyeaters and the woodland-inhabiting yellow-tinted, rufous-throated and banded honeyeaters. Tubular flowers were exploited by

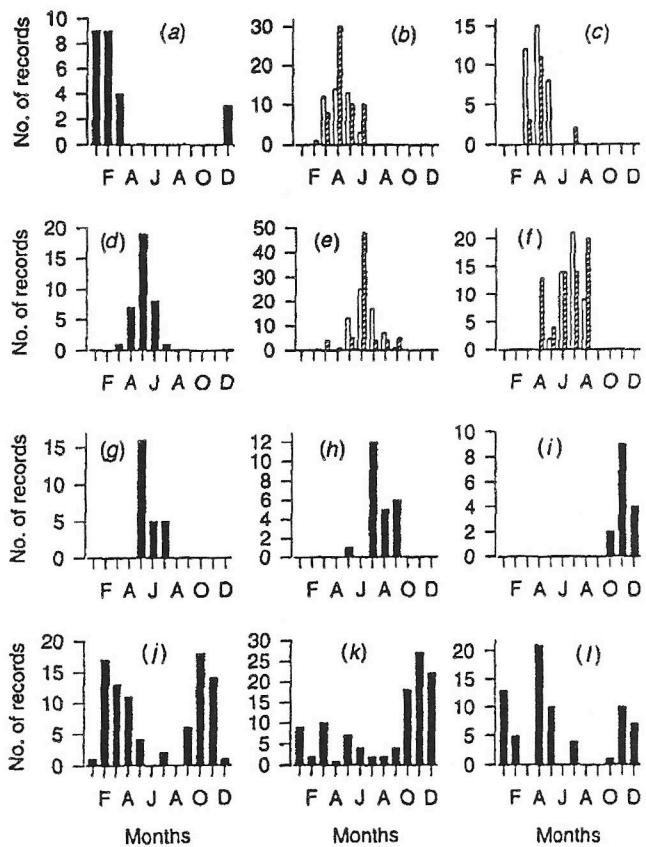


Fig. 2. Flowering times of some 'main' nectar sources in monsoonal north-western Australia, as indicated by the months when regular nectarivores were recorded feeding at them in non-urban areas. All qualifying records (solid bars); records from Berry Springs (open bars) (Franklin and Noske 1998); all records other than from Berry Springs (hatched bars). (a) *Grevillea decurrens*; (b) *Corymbia polycarpa*; (c) *Banksia dentata*; (d) *Eucalyptus phoenicea*; (e) *Eucalyptus miniata*; (f) *Grevillea pteridifolia*; (g) *Eucalyptus pruinosa*; (h) *Lysiphyllo cunninghamii*; (i) *Eucalyptus tectifica*; (j) *Melaleuca leucadendra*; (k) *Xanthostemon paradoxus*; (l) *Sonneratia alba*.

most honeyeaters but rarely by lorikeets. The blue-faced honeyeater, and to a lesser extent the friarbirds and several smaller honeyeaters, made particular use of gullet-shaped (most *Grevillea*) flowers. Small petaliferous or sepaliferous flowers and 'other large flowers' were mostly visited by small honeyeaters and especially by the mangal-inhabiting yellow white-eye and red-headed honeyeater. The few records of use of flag-shaped flowers were mostly by smaller honeyeaters. There was no obvious pattern to the fairly small number of records of the use of shaving-brush flowers.

A classification of bird species by their use of flower structure classes identified three distinct but morphologically heterogeneous groups of birds (Fig. 3). The first, most distinct group comprised the two small mangal specialists, the red-headed honeyeater and yellow white-eye, which made much use of small and large open petaliferous or sepaliferous

Table 4. Use of floral structure classes by regular nectarivores
 Only species for which there are more than 24 non-urban records are included. Bird-name abbreviations are as in Table 2. Values for bird species are proportions of the set of records for that bird species. Italicised proportions are >50%, and proportions in bold font >150% of the proportion of all records (column 1) for that floral structure (see Methods—Data analysis)

Floral structure class (proportion of all records)	RLK	VLK	SCF	LFB	BFH	YTM	WGH	YTH	WTH	BRH	BBH	RBH	RTH	BDH	DHE	RHH	YWE
1. Brush inflorescences (0.223)	<i>0.208</i>	<i>0.158</i>	<i>0.185</i>	<i>0.198</i>	<i>0.243</i>	<i>0.214</i>	<i>0.148</i>	<i>0.146</i>	<i>0.272</i>	<i>0.246</i>	<i>0.448</i>	<i>0.400</i>	<i>0.222</i>	<i>0.106</i>	<i>0.269</i>	<i>0.215</i>	<i>0.167</i>
2. Staminitiferous cups (0.413)	<i>0.585</i>	<i>0.763</i>	<i>0.573</i>	<i>0.503</i>	<i>0.473</i>	<i>0.595</i>	<i>0.239</i>	<i>0.512</i>	<i>0.482</i>	<i>0.260</i>	<i>0.269</i>	<i>0.086</i>	<i>0.556</i>	<i>0.731</i>	<i>0.333</i>	<i>0.076</i>	<i>0.000</i>
3. Shaving-brush flowers (0.052)	<i>0.044</i>	<i>0.013</i>	<i>0.064</i>	<i>0.041</i>	<i>0.048</i>	<i>0.148</i>	<i>0.000</i>	<i>0.009</i>	<i>0.067</i>	<i>0.000</i>	<i>0.286</i>	<i>0.000</i>	<i>0.010</i>	<i>0.058</i>	<i>0.089</i>	<i>0.042</i>	
4. Tubular flowers (0.069)	<i>0.013</i>	<i>0.013</i>	<i>0.051</i>	<i>0.059</i>	<i>0.054</i>	<i>0.095</i>	<i>0.148</i>	<i>0.244</i>	<i>0.061</i>	<i>0.082</i>	<i>0.060</i>	<i>0.086</i>	<i>0.086</i>	<i>0.048</i>	<i>0.096</i>	<i>0.057</i>	<i>0.042</i>
5. Gullet-shaped flowers (0.104)	<i>0.094</i>	<i>0.039</i>	<i>0.127</i>	<i>0.123</i>	<i>0.162</i>	<i>0.048</i>	<i>0.159</i>	<i>0.049</i>	<i>0.070</i>	<i>0.143</i>	<i>0.164</i>	<i>0.029</i>	<i>0.086</i>	<i>0.087</i>	<i>0.109</i>	<i>0.032</i>	<i>0.042</i>
6. Flag-shaped flowers (0.011)	<i>0.000</i>	<i>0.000</i>	<i>0.006</i>	<i>0.011</i>	<i>0.000</i>	<i>0.000</i>	<i>0.034</i>	<i>0.024</i>	<i>0.009</i>	<i>0.020</i>	<i>0.000</i>	<i>0.000</i>	<i>0.037</i>	<i>0.000</i>	<i>0.013</i>	<i>0.006</i>	<i>0.000</i>
7. Other flowers small (0.090)	<i>0.044</i>	<i>0.000</i>	<i>0.013</i>	<i>0.027</i>	<i>0.014</i>	<i>0.000</i>	<i>0.091</i>	<i>0.024</i>	<i>0.088</i>	<i>0.135</i>	<i>0.060</i>	<i>0.057</i>	<i>0.012</i>	<i>0.019</i>	<i>0.083</i>	<i>0.354</i>	<i>0.542</i>
8. Other flowers large (0.037)	<i>0.013</i>	<i>0.013</i>	<i>0.032</i>	<i>0.016</i>	<i>0.014</i>	<i>0.026</i>	<i>0.034</i>	<i>0.000</i>	<i>0.009</i>	<i>0.047</i>	<i>0.000</i>	<i>0.057</i>	<i>0.000</i>	<i>0.038</i>	<i>0.171</i>	<i>0.167</i>	
No. of classes >50%	4	2	6	5	5	8	4	6	8	5	5	5	3	8	6	5	
Number of records	159	76	157	187	74	42	88	41	114	342	67	35	81	104	156	158	24

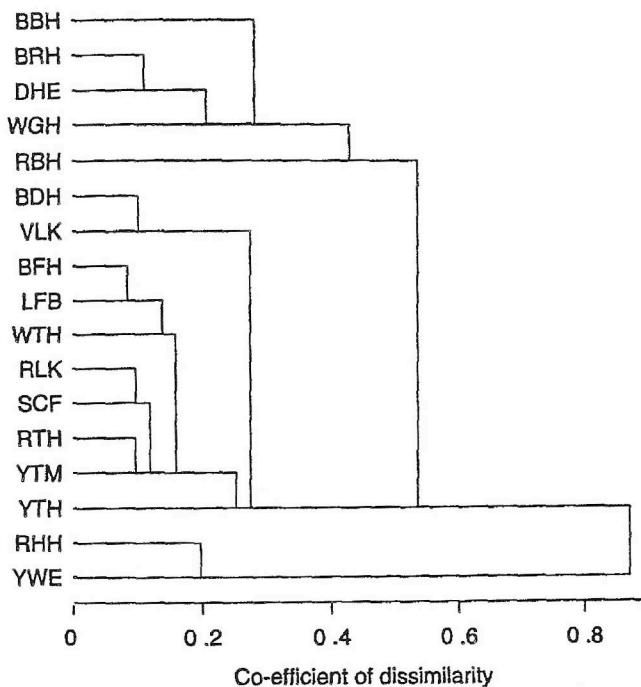


Fig. 3. Dendrogram of avian nectarivores grouped by the proportional use of different floral structures. Floral structures are as in Table 1 and bird-name abbreviations as in Table 2.

flowers, some use of brush inflorescences and little use of anything else (Table 5). The second group, all primarily woodland species, comprised all lorikeets and larger honeyeaters plus the banded, rufous-throated, white-throated and

yellow-tinted honeyeaters. These made particularly frequent use of staminiferous cup flowers. Within the woodland group, the banded honeyeater and varied lorikeet formed a distinct subgroup that made even greater use of staminiferous cups and relatively little use of other flower types except brush inflorescences. The third group comprised a loose collection of five small-medium-sized honeyeaters that associate particularly with riparian and/or other forest vegetation or are catholic in their choice of habitat, and that make use of a moderate to wide variety of floral structures.

Discussion

Survey bias and relative significance of habitats

Our records were collected extensively rather than intensively, emphasising regional rather than local patterns, but with some concentration of records at sites close to Darwin and in the Katherine area. Sampling bias was inevitable. In particular, we note a shortage of records from more arid areas of the monsoonal tropics. Balanced representation of the main habitat types is even more problematic, because habitats that occupy a small part of the landscape may make a large contribution to the diversity of nectar sources or seasonally to the maintenance of nectarivore assemblages. In this study, almost twice as many nectar source species were identified in monsoon rainforest as in either riparian forest or mangal, even though these environments occupy similarly small portions of the landscape and survey effort was greater in the latter two. However, there is no indication that monsoon rainforest contributes substantially at a landscape

Table 5. **Floral structure classes utilised by three bird groups**

See Table 1 for more details of floral structure classes. Bird groups from Fig. 3 (Group 1, $n = 5$, BBH, BRH, DHE, WGH, RBH; Group 2, $n = 10$, BDH, VLK, BFH, LFB, WTH, RLK, SCF, RTH, YTM, YTH; Group 3, $n = 2$, RHH, YWE; abbreviations as in Table 2). Values for each floral structure class–bird group combination are: first line, median proportion of use; second line, range (minimum–maximum) of proportion of use. Kruskal–Wallis comparisons are between medians of the three bird groups. Probabilities have been calculated using the χ^2 approximation with two degrees of freedom in all cases. * $P < 0.05$; ** $P < 0.01$; n.s., not significant

Floral structure class	Bird Group 1	Bird Group 2	Bird Group 3	H (Kruskal–Wallis)
1. Brush inflorescences	0.27 0.15–0.45	0.20 0.11–0.27	0.19 0.17–0.22	3.6 n.s.
2. Staminiferous cups	0.26 0.09–0.33	0.56 0.47–0.76	0.04 0–0.08	12.4 **
3. Shaving-brush flowers	0.07 0–0.29	0.01 0–0.06	0.07 0.04–0.09	4.6 n.s.
4. Tubular flowers	0.09 0.06–0.15	0.06 0.01–0.24	0.05 0.04–0.06	4.4 n.s.
5. Gullet-shaped flowers	0.14 0.03–0.16	0.09 0.04–0.16	0.04 0.03–0.04	4.2 n.s.
6. Flag-shaped flowers	0.01 0–0.03	0 0–0.04	0 0–0.01	0.8 n.s.
7. Other flowers small	0.08 0.06–0.14	0.02 0–0.09	0.45 0.35–0.54	10.7 **
8. Other flowers large	0.04 0–0.06	0.01 0–0.03	0.17 0.17–0.17	8.6 *

level to the seasonal maintenance of nectarivore assemblages, whereas riparian forests clearly do (Woinarski *et al.* *in press*). This paradox is discussed further below.

In this study, survey effort in riparian forest, monsoon rainforest and mangal was in all cases much greater than the proportionate spatial contribution of these environments to the landscape. However, the environment that occupies most of the landscape—woodland—is well represented by most of the records. The 116 nectar source species identified in this study are most unlikely to be a complete listing for the region, with most additional species likely to be found in woodland and monsoon rainforest. However, given that all main environments are represented in the sample and that availability and use of floral structures appears to be primarily related to these environments rather than any confounding cross-environment factors, we do not believe that these sampling biases would have had any substantial effect on our conclusions.

The considerable diversity of nectar sources found in the monsoonal Australian woodlands reflects both their vast dominance in the landscape and their considerable floristic variability (Beard 1979; Wilson *et al.* 1990). Mass-flowering woodland trees, particularly the myrtaceous *Corymbia*, *Eucalyptus* and one species each of *Melaleuca* and *Xanthostemon*, are a feature both of the landscape and the nectar sources used by birds within them. The intensity of flowering of many of these sources is unreliable from year to year (Setterfield and Williams 1996; Franklin and Noske 1998; Williams *et al.* 1999). Most honeyeater and lorikeet species occur in the woodlands and at least nine species may be regarded as woodland specialists (Keast 1968; Blakers *et al.* 1984; Woinarski *et al.* 1988; D. C. Franklin and R. A. Noske, pers. obs.). All nine made extensive use of the myrtaceous nectar sources, and two species, the varied lorikeet and banded honeyeater, obtained nectar from little else; not surprisingly, these two are also the most mobile (Keast 1968; Woinarski and Tidemann 1991; Franklin 1996). Nectar availability in many woodland areas peaks during the dry season (Franklin and Noske 1999; Woinarski *et al.*, *in press*), and it is at this time and in this habitat that many birds that are not normally nectarivorous become so (Franklin 1999).

Riparian *Melaleuca* (paperbark) forests contained a limited range of nectar sources, and in any one area there is unlikely to be a year-round continuity of nectar availability (e.g. Franklin and Noske 1998). However, at least five sources were mass-flowering and utilised by large nectarivores, and the concentration of nectarivorous birds in riparian forest at the time of flowering is often dramatic. Many woodland and forest species visit riparian forest at such times, and movements between this and other habitats were suggested by Morton and Brennan (1991) and later demonstrated by banding (Franklin and Noske 1998). The bar-breasted honeyeater is the sole nectarivorous riparian forest specialist, although the rufous-banded honeyeater also displays a marked preference for this habitat.

The range of nectar sources available in the mangals reflects the limited floristic diversity of these habitats. *Sonneratia alba* and possibly also *Bruguiera gymnorhiza* are the only species attractive to larger nectarivores. *Bruguiera exaristata* is bird-pollinated (R. A. Noske, unpubl. data) but attracts only smaller nectarivores, as do the other mangrove species. Nevertheless, a continuity of nectar resources throughout the year may be obtained by local movements between tidal zones and mangal fringe habitats, permitting the highly nectarivorous red-headed honeyeater to persist exclusively in the habitat (Noske 1996).

The nectar resources of the rainforests of monsoonal Australia remain poorly documented, but we believe that they are generally not especially attractive to nectarivorous birds, many flowers being either unattractive to birds and/or not mass-flowering. It is possible that the prevalence of bird-dispersed fleshy-fruited trees in monsoon rainforest (Bach 1998; O. Price, pers. comm.) has mitigated evolutionary pressure towards vertebrate (i.e. long-distance) pollen dispersal mechanisms, a situation contrasting with other environments in monsoonal Australia (see also Ford 1985). It is noteworthy, that monsoon rainforest is the only one of the four main woody environments to lack an endemic nectarivorous species, although ssp. *gordoni* of the helmeted friarbird is restricted to coastal vine-thicket and adjacent mangals and the dusky honeyeater is perhaps more frequent in rainforests than other habitats. Furthermore, although the occurrence of nectarivorous birds in monsoon rainforest is often seasonal, it is not consistently related to nectar availability (Woinarski *et al.* 1989; Woinarski 1993). Two of the nectarivores that do frequently occur in monsoon rainforest, the helmeted friarbird and white-gaped honeyeater, may be as much frugivorous as nectarivorous (Schodde *et al.* 1979; R. A. Noske and D. C. Franklin, unpubl. data and pers. obs.). The limited extent and extreme patchiness of monsoon rainforest in north-western Australia (Russell-Smith *et al.* 1992), its probably even greater spatial restriction during past glacials (Ford 1982), and the marked seasonality of its floral resources (Bach 1998) may have combined to prevent the evolution or persistence of monsoon rainforest nectarivores.

Phylogenetic affinities of the flora

The predominance of plants with derived Australian affinities (the ‘autochthonous’ subelement of Nelson 1981, e.g. dry-fruited Myrtaceae, Proteaceae, Loranthaceae) rather than tropical or relictual rainforest affinities in the flowers visited by birds in north-western Australia demonstrates an underlying similarity to that of southern Australia (Ford *et al.* 1979; Paton 1986; Brown *et al.* 1997). It reflects the relative abundance of plant genera in the north-western Australian landscape (Dunlop and Webb 1991; Bowman *et al.* 1993) rather than the predominantly tropical affinities of the flora (Bowman *et al.* 1988). The paradox is attributable, in large

part, to the strong association of the autochthonous Australian flora with the woodland habitats that comprise the vast majority of the study area, and the concentration of flora with tropical affinities in the geographically minute but species-rich monsoon rainforests.

However, there are also important differences in the taxonomic composition of the flora used by birds in north-western and south-eastern Australia. Eucalypts (*Eucalyptus* and *Corymbia*) are especially prominent in monsoonal Australia (38% of all records), as they are in the south-west of Western Australia (28% of records, Brown *et al.* 1997). Of the 31 species of eucalypts recorded in the Darwin area (Dunlop *et al.* 1995a), we have records of birds feeding at the flowers of 22, and most of the remainder are uncommon and thus inadequately surveyed, suggesting that most species are visited by birds. Although eucalypts are equally dominant in the vegetation of monsoonal north-western and temperate south-eastern Australia, many species in the latter area are primarily visited and pollinated by insects (House 1997). An inter-regional comparison of nectar sugar volumes, concentrations and composition in eucalypts might be an informative exercise.

Melaleuca species in northern Australia are mostly trees and 'main' nectar sources (14% of all records), features that are not characteristic of temperate or arid Australian members of the genus (pers. obs.). *Xanthostemon* is another important myrtaceous nectar source in north-western Australia (see also Woinarski and Tidemann 1991) that is absent from southern Australia. Monsoon rainforest and mangal nectar source species are generally absent from southern Australia. Some 'main' nectar sources in the woodlands have tropical (e.g. east Asian) affinities, examples being the nut tree *Terminalia grandiflora* (Combretaceae) and cocky apple *Planchonia careya* (Lecythidaceae).

Notable absentees from the nectar sources used by birds in monsoonal Australia that are typical of temperate Australia include the Epacridaceae, *Xanthorrhoea* (Xanthorrhoeaceae), *Callistemon* (Myrtaceae) and *Adenantheros* and *Dryandra* (Proteaceae). The important arid-zone avian nectar source genus *Eremophila* (Myoporaceae) is also virtually absent, several species occurring marginally and infrequently along the arid fringe of the monsoonal woodlands. There is only one species of *Banksia* in north-western Australia, a small tree of swamp woodlands, in marked contrast to the variety of *Banksia* species in the heathlands and heathy woodlands of south-eastern and especially south-western Australia.

Floral structures and pollination syndromes

There have been very few field studies of pollination in monsoonal Australia, so that pollination syndromes are of necessity mostly inferred from floral structures. Although such inferences may prove incorrect in specific cases

(Ollerton 1998), we see no reason to doubt their general utility. The range of floral structures represented in the nectar sources used by birds in north-western Australia does not differ markedly from that elsewhere in Australia, but the minor structural differences and differences occurring in relative abundance at the landscape scale suggest a significant and unique impact of the zoogeographic history and/or past and current climate on the evolution of bird-flower interactions in the region.

Exclusive and even semi-exclusive ornithophily is poorly represented in the monsoonal Australian flora. There is a modest diversity of plant species with tubular flowers, but these tend to have short corolla tubes or corollas split along the side, and are visited by most species of honeyeaters regardless of bill length, though rarely by lorikeets. Flag-shaped flowers are rarely visited by birds. Gullet-shaped flowers are moderately prominent, but the most prominent of these, *G. pteridifolia*, holds its nectar in a readily accessible external cup, a characteristic shared with the subtropical *G. robusta* (Nicolson 1995). Eucalypts with relatively closed flowers that exclude insects, such as occur in south-western Australia (House 1997), are apparently absent.

The flowers of several 'main' nectar sources including, most prominently, the dry season flowering Darwin woollybutt *Eucalyptus miniata*, scarlet gum *E. phoenicea* and *G. pteridifolia*, are orange, a colour that is often associated with bird pollination (Vickery 1992), but display no structural adaptation to exclude non-avian visitors. It is quite probable, that these species are in part dependant on morphologically unspecialised opportunist avian nectarivores for pollination (Franklin 1999). Many northern Australian eucalypts have large, robust flowers, and most of the corymbiform eucalypts that comprise the majority of the species bear their flowers externally to foliage, traits related to flying-vertebrate pollination rather than birds *per se* (House 1997). Transport of the pollen of two corymbiform eucalypts by bats has been demonstrated in north-western Australia (McCoy 1990).

At least three of the eight floral structure classes recognised in this study may bear no particular relation to pollination by birds. Shaving-brush flowers are a tropical phenomenon and apparently an adaptation to bat pollination (Armstrong 1979) from which birds may be nectar thieves or incidental foragers. The flowers of *P. careya* and *S. alba* open in the late afternoon and are mostly shed during the following morning, and notwithstanding high rates of visitation by birds, pollination of *S. alba* is mostly by bats (R. A. Noske and T. J. Martin, unpubl. data). Even though small petaliferous or sepaliferous flowers and large petaliferous flowers are well represented in the nectar sources used by birds in monsoonal Australia, most are likely to be insect-pollinated. With a few notable exceptions, most were visited by small nectarivorous birds but not by larger species, and in many cases infrequently so. The diversity and abundance of particularly small avian nectarivores (by Australian standards) combined

with the large size of some tropical insects may have promoted some convergence of plant usage.

Fruit and blossom bats (Pteropodidae) are prominent consumers of nectar in north-western Australia, sharing many flower species with nectarivorous birds. Although the timing of their arrival in Australia is unclear (Hand 1984), it may well coincide with the development of the Australian tropical savannas during the Miocene (Dunlop and Webb 1991), a period also of diversification among the eucalypts (Wardell-Johnson *et al.* 1997). Fruit and blossom bats may have been a selective force in the evolution of vertebrate-pollination syndromes in the Australian tropics as in other tropical regions (Crome and Irvine 1986; Bawa 1990), and their prevalence may have mitigated against the evolution of highly-specific bird-pollination syndromes. The role of non-flying mammals such as the sugar glider *Petaurus breviceps* in the evolution of pollination syndromes in north-western Australia is unknown, but if current abundance is a measure of influence then that influence is likely to have been much less than that of the Pteropodidae.

Past climatic fluctuations may also have rendered the survival of specialised bird-flower relationships difficult in the Australian monsoonal tropics. Arid phases during the Pleistocene may have been particularly severe (Nix and Kalma 1974), which is likely to have induced greater seasonal fluctuations in, and reduced the availability and predictability of nectar resources. For birds, the ability to survive, at least periodically, on alternative resources such as insects, may have been at a premium. However, we note that the limited data available for tropical rainforest in New Guinea, a system thought to have been subject to much less extreme climatic fluctuations during the Pleistocene (Nix and Kalma 1974), also demonstrates a quite generalised relationship between birds and flowers (Brown and Hopkins 1995). In contrast, bird-flower relationships are somewhat more highly evolved in southern Australia (e.g. Hopper and Burbidge 1986) and much more highly coevolved in the New World (Stiles 1981).

In view of the general lack of specialised bird-flower systems in north-western Australia, it is perhaps not surprising that patterns of use of different floral structures by birds in monsoonal Australia bear only limited relationship to the size and bill-shape of the birds, appearing more strongly related to the habitats they occupy. Nor is it surprising to note that the 'long-billed' honeyeaters of north-western Australia are shorter-billed, in proportion to body mass, than a number of species in southern Australia (Brooker *et al.* 1990), where tubular and other flowers specialised to pollination by birds occur (e.g. Paton and Ford 1977; Hopper and Burbidge 1986). The differences that occur in bill length in north-western Australia, including the possibility that there are two distinct guilds based on relative bill length, may well relate to differences in relative dependence on nectar as noted in southern Australia by Ford and Paton (1977), but there are insufficient

data on diets to test this hypothesis. Even in flowers accessible to both short- and long-billed honeyeaters, long bills enable more rapid extraction; however, the trade-off is that they reduce the efficiency of non-nectar foraging (Paton and Collins 1989). More intriguing but less explicable is the large number of very small honeyeater species in north-western Australia and the relative lack of medium-sized species.

Acknowledgments

We are grateful to John Woinarski, John Estbergs, Doug Robinson, Denise Goodfellow, Hilary Thompson, Ian Rowley, Owen Price, Chris Bach, Dave Hooper and Terry Barnes for contributing their observations of birds at flowers. John Woinarski, Hugh Ford and David Cheal patiently read and helpfully commented on earlier drafts of this paper. The Bioregional Assessment Unit of the Parks and Wildlife Commission of the Northern Territory provided facilities for data analysis and preparation of the manuscript.

References

- Armstrong JA (1979) Biotic pollination mechanisms in the Australian flora—a review. *New Zealand Journal of Botany* 17, 467–508.
- Bach CS (1998) Resource patchiness in space and time: phenology and reproductive traits of monsoon rainforests in the Northern Territory. PhD Thesis, Northern Territory University, Darwin.
- Bawa KS (1990) Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21, 399–422.
- Beard JS (1979) 'The vegetation of the Kimberley area. Explanatory notes to map sheet 1 of vegetation survey of Western Australia 1:1 000 000 series: Kimberley.' (University of Western Australia Press: Nedlands, WA)
- Belbin L (1994) 'PATN. Pattern analysis package.' (CSIRO: Canberra, ACT)
- Blakers M, Davies SJF, Reilly PN (1984) 'The atlas of Australian birds.' (Melbourne University Press: Carlton, Vic.)
- Bowman DMJS, Wilson BA, Dunlop CR (1988) Preliminary biogeographic analysis of the Northern Territory vascular flora. *Australian Journal of Botany* 36, 503–517.
- Bowman DMJS, Woinarski JCZ, Menkhorst KA (1993) Environmental correlates of tree species diversity in Stage III of Kakadu National Park, Northern Australia. *Australian Journal of Botany* 41, 649–660.
- Brock J (1993) 'Native plants of northern Australia.' (Reed: Chatswood, NSW)
- Brooker MG, Braithwaite RW, Estbergs JA (1990) Foraging ecology of some insectivorous and nectarivorous species of birds in forests and woodlands of the wet-dry tropics of Australia. *Emu* 90, 215–230.
- Brown ED, Hopkins MJG (1995) A test of pollinator specificity and morphological convergence between nectarivorous birds and rainforest tree flowers in New Guinea. *Oecologia* 103, 89–100.
- Brown EM, Burbidge AH, Dell J, Edinger D, Hopper SD, Wills RT (1997) 'Pollination in Western Australia: a database of animals visiting flowers.' (WA Naturalists Club: Perth, WA)
- Christidis L, Boles WE (1994) 'The taxonomy and species of birds of Australia and its territories.' (Royal Australasian Ornithologists Union: Hawthorn East, Vic.)
- Crome, FHJ, Irvine AK (1986) 'Two bob each way': the pollination and breeding system of the Australian rainforest tree *Syzygium cormiflorum* (Myrtaceae). *Biotropica* 18, 115–125.
- Dunlop CR, Leach GJ, Cowie ID (1995a) 'Flora of the Darwin region. Vol. 2. Northern Territory Botanical Bulletin No. 20.' (Conservation Commission of the Northern Territory: Darwin, NT)

- Dunlop CR, Leach GJ, Latz PK, Barritt MJ, Cowie ID, Albrecht DE (1995b) 'Checklist of the vascular plants of the Northern Territory, Australia.' (Conservation Commission of the Northern Territory: Darwin, NT)
- Dunlop CR, Webb LJ (1991) Flora and vegetation. In 'Monsoonal Australia: landscape, ecology and man in the northern lowlands'. (Eds C Haynes, MG Ridpath, MAJ Williams) pp. 41–60. (A. A. Balkema: Rotterdam)
- Ford HA (1985) Nectar-feeding birds and bird pollination: why are they so prevalent in Australia yet absent from Europe? *Proceedings of the Ecological Society of Australia* 14, 153–158.
- Ford HA, Paton DC (1977) The comparative ecology of ten species of honeyeaters in South Australia. *Australian Journal of Ecology* 2, 399–407.
- Ford HA, Paton DC, Forde N (1979) Birds as pollinators of Australian plants. *New Zealand Journal of Botany* 17, 509–519.
- Ford J (1982) Origin, evolution and speciation of birds specialised to mangroves in Australia. *Emu* 82, 12–23.
- Franklin D (1996) A massive aggregation of the varied lorikeet. *Eclectus* 1, 6–7.
- Franklin DC (1997) The foraging behaviour of avian nectarivores in a monsoonal Australian woodland over a six-month period. *Corella* 21, 48–54.
- Franklin DC (1999) Opportunistic nectarivory: an annual dry season phenomenon among birds in monsoonal northern Australia. *Emu* 99, 135–141.
- Franklin DC, Noske RA (1998) Local movements of honeyeaters in a subcoastal vegetation mosaic in the Northern Territory. *Corella* 22, 97–103.
- Franklin DC, Noske RA (1999) Birds and nectar in a monsoonal woodland: correlations at three spatio-temporal scales. *Emu* 99, 15–28.
- Guymer GP (1988) A taxonomic revision of *Brachychiton* (Sterculiaceae). *Australian Systematic Botany* 1, 199–323.
- Hand S (1984) Bat beginnings and biogeography: a southern perspective. In 'Vertebrate zoogeography and evolution in Australasia (animals in space and time)'. (Eds M Archer, G Clayton) pp. 853–904. (Hesperian Press: Marrickville, NSW)
- Hill KD, Johnson LAS (1995) Systematic studies in the eucalypts 7. A revision of the bloodwoods, genus *Corymbia* (Myrtaceae). *Telopea* 6, 185–504.
- Hopper SD, Burbridge AH (1986) Speciation of bird-pollinated plants in south-western Australia. In 'The dynamic partnership: birds and plants in Southern Australia'. (Eds HA Ford, DC Paton) pp. 20–31. (The Flora and Fauna of South Australia Handbooks Committee: Adelaide, SA)
- House SM (1997) Reproductive biology of eucalypts. In 'Eucalypt ecology: individuals to ecosystems'. (Eds JE Williams, JCZ Woinarski) pp. 30–55. (Cambridge University Press: Cambridge)
- Keast A (1968) Seasonal movements in the Australian honeyeaters (Meliphagidae) and their ecological significance. *Emu* 67, 159–209.
- Krebs CJ (1989) 'Ecological methodology.' (Harper Collins: New York)
- McCoy M (1990) Pollination of eucalypts by flying foxes in Northern Australia. In 'Flying fox workshop'. (Ed. JM Slack) pp. 33–37. (NSW Agriculture and Fisheries: Wollongbar, NSW)
- McDonald NS, McAlpine J (1991) Floods and droughts: the northern climate. In 'Monsoonal Australia: landscape, ecology and man in the northern lowlands'. (Eds CD Haynes, MG Ridpath, MAJ Williams) pp. 19–29. (A. A. Balkema: Rotterdam)
- Morton SR, Brennan K (1991) Birds. In 'Monsoonal Australia: landscape, ecology and man in the northern lowlands'. (Eds C Haynes, MG Ridpath, MAJ Williams) pp. 133–149. (A. A. Balkema: Rotterdam)
- Nelson EC (1981) Phytogeography of southern Australia. In 'Ecological biogeography of Australia'. (Ed. A Keast) pp. 733–759. (Dr. W. Junk: The Hague)
- Nicolson SW (1995) Direct demonstration of nectar reabsorption in the flowers of *Grevillea robusta* (Proteaceae). *Functional Ecology* 9, 584–588.
- Nix HA (1976) Environmental control of breeding, post-breeding dispersal and migration of birds in the Australian region. In 'Proceedings of the 16th International Ornithological Congress, Canberra, Australia, 12–17 August 1974'. (Eds HJ Frith, JH Calaby) pp. 272–305. (Australian Academy of Science: Canberra, ACT)
- Nix HA, Kalma JD (1974) Climate as a dominant control in the biogeography of northern Australia and New Guinea. In 'Bridge and barrier: the natural and cultural history of Torres Strait'. (Ed. D Walker) pp. 61–91. (Australian National University: Canberra, ACT)
- Noske RA (1996) Abundance, zonation and foraging ecology of birds in mangroves of Darwin Harbour, Northern Territory. *Wildlife Research* 23, 443–474.
- Ollerton J (1998) Sunbird surprise for syndromes. *Nature* 394, 726–727.
- Paton DC (1986) Honeyeaters and their plants in south-eastern Australia. In 'The dynamic partnership: birds and plants in Southern Australia'. (Eds HA Ford, DC Paton) pp. 9–19. (The Flora and Fauna of South Australia Handbooks Committee: Adelaide, SA)
- Paton DC, Collins BG (1989) Bills and tongues of nectar-feeding birds: a review of morphology, function and performance, with intercontinental comparisons. *Australian Journal of Ecology* 14, 473–506.
- Paton DC, Ford HA (1977) Pollination by birds of native plants in South Australia. *Emu* 77, 73–85.
- Russell-Smith, J, McKenzie, NL, Woinarski JCZ (1992) Conserving vulnerable habitat in northern and north-western Australia: the rainforest archipelago. In 'Conservation and development issues in Northern Australia'. (Eds I Moffatt, A Webb) pp. 63–68. (North Australia Research Unit, Australian National University: Darwin, NT)
- Schodde R, Mason IJ, McKean JL (1979) A new subspecies of *Philemon buceroides* from Arnhem Land. *Emu* 79, 24–30.
- Setterfield SA, Williams RJ (1996) Patterns of flowering and seed production in *Eucalyptus miniata* and *E. tetrodonta* in a tropical savanna woodland, northern Australia. *Australian Journal of Botany* 44, 107–122.
- Stiles FG (1981) Geographical aspects of bird-flower coevolution, with particular reference to central America. *Annals of the Missouri Botanic Gardens* 68, 323–351.
- Vickery RK (1992) Pollinator preferences for yellow, orange, and red flowers of *Mimulus verbenaceus* and *M. cardinalis*. *Great Basin Naturalist* 52, 145–148.
- Wardell-Johnson GW, Williams JE, Hill KD, Cumming R (1997) Evolutionary biogeography and contemporary distribution of eucalypts. In 'Eucalypt ecology: individuals to ecosystems'. (Eds JE Williams, JCZ Woinarski) pp. 92–128. (Cambridge University Press: Cambridge)
- Wheeler JR (ed.) (1992). 'Flora of the Kimberley region.' (Department of Conservation and Land Management: Como, WA)
- Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D (1997) Leaf phenology of woody species in a north Australian tropical savanna. *Ecology* 78, 2542–2558.
- Williams RJ, Myers BA, Duff GA, Eamus D (1999). Reproductive phenology of woody species in a north Australian tropical savanna. *Biotropica* 31, 626–636.
- Wilson FA, Brocklehurst PS, Clark MJ, Dickinson KJM (1990) Vegetation survey of the Northern Territory, Australia. Conservation Commission of the Northern Territory Technical Report No. 49, Darwin, NT.
- Woinarski JCZ (1993) A cut-and-paste community: birds of monsoon rainforests in Kakadu National Park, Northern Territory. *Emu* 93, 100–120.
- Woinarski JCZ, Tidemann SC (1991) The bird fauna of a deciduous woodland in the wet-dry tropics of northern Australia. *Wildlife Research* 18, 479–500.

- Woinarski JCZ, Tidemann SC, Kerin S (1988) Birds in a tropical mosaic: the distribution of bird species in relation to vegetation patterns. *Australian Wildlife Research* 15, 171–196.
- Woinarski JCZ, Press AJ, Russell-Smith J (1989) The bird community of a sandstone plateau monsoon forest at Kakadu National Park, Northern Territory. *Emu* 89, 223–231.

Woinarski JCZ, Connors GT, Franklin DC, (in press). Thinking honeyeater: nectar maps for the Northern Territory, Australia. *Pacific Conservation Biology*.

Zar JH (1984) 'Biostatistical analysis. 2nd Edn.' (Prentice-Hall: New Jersey)

Manuscript received 26 November 1998, accepted 11 August 1999

Appendix. Characteristics of plant species the flowers of which are used by birds in monsoonal north-western Australia

An asterisk indicates a naturalised alien species. The number of bird species (no. bird spp.) and number of records (no. records) feeding at the flowers are for non-urban situations, with the number of additional records from urban situations in brackets (when >0). 'Percentage large' is the percentage of non-urban records that were of nectarivores weighing >50 g (lorikeets, friarbirds, blue-faced and spiny-cheeked honeyeater and yellow-throated miner), calculated for nectar source species for which there are 10 or more non-urban records. Habitats are as defined in the *Study area*: m = mangal; r = riparian forest; v = monsoon rainforest; w = woodland. (Growth) habits are: cl = climber; h = herb; lt = large tree (>10 m); sh = shrub; st = small tree (3–10 m); wp = woody parasite. Flower types correspond to and are explained in Table 1

Species	Family	No. bird spp.	No. records	Percentage large	Habitat	Habit	Flower type	Flower colour
<i>Adansonia gregorii</i>	Bombacaceae	7	7	—	w	lt	3. shaving	cream
<i>Aegiceras corniculatum</i>	Myrsinaceae	6	17	0	m	sh/st	7. small	white
<i>Albizia lebbeck</i>	Mimosaceae	2	2	—	v	lt	1. brush	cream
<i>Alphitonia excelsa</i>	Rhamnaceae	3	5	—	rvw	st	7. small	cream
<i>Alstonia actinophylla</i>	Apocynaceae	4	4	—	vw	lt	7. small	cream
<i>Amyema mackayensis</i>	Loranthaceae	6	19	0	m	wp	4. tubular	green/red
<i>A. miquellii</i>	Loranthaceae	1	1	—	w	wp	4. tubular	red
<i>A. sanguinea</i>	Loranthaceae	9	12	67	w	wp	4. tubular	red, yellow
<i>A. villiflora</i>	Loranthaceae	8	13	39	w	wp	4. tubular	green/orange
<i>Asteromyrtus symphyocarpa</i>	Myrtaceae	9	13 (1)	31	r	sh/st	1. brush	yellow
<i>Avicennia marina</i>	Verbenaceae	3	6	—	m	st	7. small	orange
<i>Banksia dentata</i>	Proteaceae	12	57	49	rw	sh/st	1. brush	yellow
<i>Barringtonia acutangula</i>	Lecythidaceae	5	8	—	r	st	1. brush	red
<i>Bombax ceiba</i>	Bombacaceae	11	17	59	v	lt	8. large	red
<i>Brachychiton megaphyllus</i>	Sterculiaceae	11	23	22	w	sh/st	4. tubular	red
<i>B. paradoxum</i>	Sterculiaceae	1	1	—	w	st	4. tubular	red
<i>B. viscidulus</i>	Sterculiaceae	1	1	—	w	st	4. tubular	red
<i>Bruguiera exaristata</i>	Rhizophoraceae	4	46	0	m	st	8. large	orange/green
<i>B. gymnorhiza</i>	Rhizophoraceae	3	3	—	m	st/lt	8. large	green/orange
<i>Cajanus</i> sp.	Fabaceae	2	3	—	w	sh	6. flag	yellow
<i>Calytrix</i> sp.	Myrtaceae	1	2	—	?	?	?	?
<i>Capparis quiniflora</i>	Capparaceae	2	2	—	v	cl/sh/st	3. shaving	white
* <i>Centrosema pubescens</i>	Fabaceae	1	1	—	w	cl	6. flag	mauve
<i>Ceriops tagal</i>	Rhizophoraceae	5	29	14	m	sh/st	7. small	white or orange
<i>Corymbia arnhemensis</i>	Myrtaceae	1	1	—	w	lt	2. stamin.	creamy-white
<i>C. bleeseri</i>	Myrtaceae	10	32	69	w	lt	2. stamin.	white
<i>C. confertiflora</i>	Myrtaceae	11	23	48	w	lt	2. stamin.	cream
<i>C. dichromophloia</i>	Myrtaceae	4	5	—	w	lt	2. stamin.	creamy-white
<i>C. ferruginea</i>	Myrtaceae	3	4	—	w	lt	2. stamin.	white
<i>C. foelscheana</i>	Myrtaceae	12	23	39	w	st	2. stamin.	cream
<i>C. grandifolia</i>	Myrtaceae	1	1	—	w	lt	2. stamin.	cream
<i>C. jacobsiana</i>	Myrtaceae	2	2	—	w	st	2. stamin.	white
<i>C. kombolgiensis</i>	Myrtaceae	2	2	—	w	lt	2. stamin.	creamy-white
<i>C. latifolia</i>	Myrtaceae	7	11	55	w	lt	2. stamin.	creamy-white
<i>C. polycarpa</i>	Myrtaceae	16	124 (20)	48	w	lt	2. stamin.	creamy-white
<i>C. polysciada</i>	Myrtaceae	7	13	54	w	st/lt	2. stamin.	cream
<i>C. porrecta</i>	Myrtaceae	11	11	46	w	st	2. stamin.	cream
<i>C. ptychocarpa</i>	Myrtaceae	12	17 (1)	53	r	st/lt	2. stamin.	red, pink or white
<i>C. sp. (papuana complex)</i>	Myrtaceae	12 (1)	22 (5)	41	r	lt	2. stamin.	creamy-white
<i>C. sp. (setosa complex)</i>	Myrtaceae	2	2	—	w	st	2. stamin.	red, pink or white
<i>C. sp. (terminalis complex)</i>	Myrtaceae	12 (1)	27 (3)	26	w	st/lt	2. stamin.	creamy-white
<i>Cordia subcordata</i>	Boraginaceae	1	2	—	v	st	8. large	orange
<i>Crotalaria cunninghamii</i>	Fabaceae	4	4	—	w	sh	6. flag	yellow-green
<i>Cupaniopsis anarcardoides</i>	Sapindaceae	1	1	—	v	st	7. small	white or green-yellow
<i>Decaisnina petiolata</i>	Loranthaceae	4	4	—	w	wp	4. tubular	yellow

Appendix. (continued)

Species	Family	No. bird spp.	No. records	Percentage large	Habitat	Habit	Flower type	Flower colour
<i>D. signata</i>	Loranthaceae	11	19	16	vw	wp	4. tubular	red/green
<i>Dendrophthoe odontocalyx</i>	Loranthaceae	6	7	—	w	wp	4. tubular	yellow/orange
<i>Diplatia furcata</i>	Loranthaceae	7	7	—	w	wp	4. tubular	green
<i>Erythrophleum chlorostachys</i>	Caesalpiniaceae	8	12	0	w	lt	1. brush	cream
<i>Erythrina</i> sp.	Fabaceae	7	11	18	w	st	6. flag	red
<i>Eucalyptus bigalerita</i>	Myrtaceae	6 (6)	7 (10)	—	w	lt	2. stamin.	creamy-white
<i>E. camaldulensis</i>	Myrtaceae	6 (6)	8 (11)	—	r	lt	2. stamin.	cream
<i>E. herbacea</i>	Myrtaceae	2	2	—	w	st	2. stamin.	cream
<i>E. houseana</i>	Myrtaceae	3	4	—	w	lt	2. stamin.	cream
<i>E. miniata</i>	Myrtaceae	17	172 (4)	52	w	lt	2. stamin.	orange
<i>E. phoenicea</i>	Myrtaceae	13	46 (3)	33	w	st	2. stamin.	orange
<i>E. pruinosa</i>	Myrtaceae	13	26	31	w	st	2. stamin.	cream or pale yellow
<i>E. tectifica</i>	Myrtaceae	11	24	50	w	st/lt	2. stamin.	creamy-white
<i>E. tetrodonta</i>	Myrtaceae	12	40	78	w	lt	2. stamin.	creamy-white
<i>E. tintinnans</i>	Myrtaceae	6	12	42	w	st	2. stamin.	cream
<i>Gardenia megasperma</i>	Rubiaceae	3	3	—	w	sh/st	8. large	white
<i>Grevillea agrifolia</i>	Proteaceae	3	4	—	w	sh	5. gullet	green
<i>G. angulata</i>	Proteaceae	1	1	—	w	sh	5. gullet	green
<i>G. decurrens</i>	Proteaceae	9	27	30	w	sh	5. gullet	pink
<i>G. dryandri</i>	Proteaceae	7	15	20	w	sh	5. gullet	red
<i>G. heliosperma</i>	Proteaceae	9	15	40	w	st	5. gullet	pink
<i>G. mimosoides</i>	Proteaceae	3	3	—	w	st	5. gullet	cream
<i>G. parallela</i>	Proteaceae	5	5	—	w	st	5. gullet	white
<i>G. pteridifolia</i>	Proteaceae	21	136 (3)	45	w	st	5. gullet	orange
<i>G. refracta</i>	Proteaceae	3	6	—	w	st	5. gullet	orange
<i>G. versicolor</i>	Proteaceae	0 (5)	0 (5)	—	w	sh	5. gullet	cream to yellow
<i>G. wickhamii</i>	Proteaceae	1	3	—	w	sh/st	5. gullet	red
<i>Grewia breviflora</i>	Tiliaceae	2	3	—	v	sh/st	7. small	yellow
<i>Helicteres isora</i>	Sterculiaceae	2	2	—	v	sh	4. tubular	orange
<i>Hypoestes floribunda</i>	Acanthaceae	1	1	—	vw	h	6. flag	pink
* <i>Ipomoea quamoclit</i>	Convolvulaceae	1	1	—	mv	cl	8. large	red
<i>Leea rubra</i>	Leeaceae	1	1	—	mv	sh	7. small	red
<i>Livistona eastonii</i>	Arecaceae	1	1	—	w	st	7. small	cream or yellow
<i>L. humilis</i>	Arecaceae	2	2	—	w	sh	7. small	cream or yellow
<i>Lophostemon grandiflorus</i>	Myrtaceae	6	10	0	r	lt	7. small	cream
<i>L. lactifluus</i>	Myrtaceae	6	17	0	r	st	7. small	cream
<i>Lumnitzera racemosa</i>	Combretaceae	3	7	—	m	st	7. small	red
<i>Lysiphyllo cunninghamii</i>	Caesalpiniaceae	12	29	17	w	st	4. tubular	red
<i>Lysiana spathulata</i>	Loranthaceae	3	3	—	w	wp	4. tubular	green/red
<i>Melaleuca argentea</i>	Myrtaceae	6 (2)	7 (10)	—	r	lt	1. brush	cream
<i>M. cajaputi</i>	Myrtaceae	10	63	8	r	lt	1. brush	cream
<i>M. dealbata</i>	Myrtaceae	14	31	19	r	st/lt	1. brush	cream
<i>M. leucadendra</i>	Myrtaceae	18	91	41	r	lt	1. brush	cream
<i>M. nervosa</i>	Myrtaceae	14	30	37	w	st	1. brush	cream
<i>M. viridisflora</i>	Myrtaceae	14	76	50	r	lt	1. brush	white or cream
<i>Melicope elleryana</i>	Rutaceae	6	9	—	v	lt	7. small	cream or pink
<i>Parsonia velutina</i>	Apocynaceae	1	1	—	v	cl	7. small	green/yellow
<i>Peltophorum pterocarpum</i>	Caesalpiniaceae	0 (1)	0 (2)	—	v	lt	8. large	yellow
<i>Planchonia careya</i>	Lecythidaceae	12	29	38	w	sh/st	3. shaving	white
<i>Rhizophora stylosa</i>	Rhizophoraceae	6	39	8	m	st/lt	7. small	white
<i>Scaevola taccada</i>	Goodeniaceae	1	1	—	m	sh	8. large	white
<i>Schefflera actinophylla</i>	Araliaceae	1 (9)	1 (9)	—	v	st	7. small	red
<i>Sesbania formosa</i>	Fabaceae	1	2	—	rv	lt	6. flag	white
<i>Sonneratia alba</i>	Sonneratiaceae	9	71	30	m	st	3. shaving	white
* <i>Stachytarpheta</i> sp.	Verbenaceae	1	1	—	vw	h	7. small	purple
<i>Syzygium armstrongii</i>	Myrtaceae	0 (1)	0 (1)	—	rv	lt	2. stamin.	white
<i>S. eucalyptoides</i>	Myrtaceae	2	2	—	w	sh/st	2. stamin.	white
<i>S. nervosum</i>	Myrtaceae	6	6	—	v	lt	2. stamin.	cream
<i>S. suborbiculare</i>	Myrtaceae	8 (1)	8 (3)	—	vw	st/lt	2. stamin.	white
<i>Terminalia australis</i>	Combretaceae	5	5	—	w	st	1. brush	cream

Appendix. (continued)

Species	Family	No. bird spp.	No. records	Percentage large	Habitat	Habit	Flower type	Flower colour
<i>T. ferdinandiana</i>	Combretaceae	4	4	—	w	st	1. brush	cream
<i>T. grandiflora</i>	Combretaceae	12	36	19	w	st	1. brush	cream
<i>T. microcarpa</i>	Combretaceae	2	2	—	v	lt	1. brush	cream
<i>Timonius timon</i>	Rubiaceae	1	1	—	vw	st/lt	7. small	white
<i>Verticordia</i> sp. ^a	Myrtaceae	6	13	39	w	sh	7. small	white
<i>Vigna vexillata</i>	Fabaceae	1	1	—	w	cl	6. flag	pink, yellow or purple
<i>Vitex glabrata</i>	Verbenaceae	2	2	—	vw	st	7. small	cream
<i>Wrightia pubescens</i>	Apocynaceae	3	3	—	v	st	7. small	white
<i>Xanthostemon paradoxus</i>	Myrtaceae	21	141	50	w	st	2. stamin.	bright yellow
<i>X. psidioides</i>	Myrtaceae	3	3	—	v	st	2. stamin.	cream
<i>X. umbrosus</i>	Myrtaceae	4	4	—	v	st	2. stamin.	cream

^aMost (or all) records are of *V. cunninghamii*.