

PREFERENTIAL FORAGING BY HONEYEATERS IN THE JARRAH FOREST OF WESTERN AUSTRALIA

BRIAN G. COLLINS & JAMES GREY

Curtin University of Technology, Kent Street, Bentley, 6102, Western Australia

SUMMARY

COLLINS, B.G. & GREY, J. 1988. Preferential foraging by honeyeaters in the jarrah forest of Western Australia. *Ostrich suppl.* 14:39–47.

Individual *Dryandra sessilis* plants are patchily distributed in jarrah forest habitats, sometimes occurring in dense clumps but often widely spaced. These plants can differ considerably in terms of their canopy volumes and the number of nectar-producing inflorescences that they bear. Honeyeaters forage preferentially at *D. sessilis* inflorescences, selecting those that are youngest and produce the most nectar. The frequency with which honeyeaters visit particular plants is significantly and positively correlated with the number of productive inflorescences present, birds visiting more inflorescences, spending more time foraging for nectar and making a greater number of probes per inflorescence at plants with greater numbers of inflorescences. By behaving in this manner, birds enhance their foraging efficiencies. Birds identify appropriate plants and inflorescences by means of the number of flowers open and colour cues.

INTRODUCTION

The most abundant Australian nectarivorous birds are honeyeaters (Meliphagidae), which occupy habitats that range from coastal heath to mallee scrub and eucalypt forest (Blakers *et al.* 1984). All 67 species are thought to make some use of nectar, although the relative importance of nectar as a food resource varies between species, and with location and time of year (Pyke 1980; Paton 1982; Collins 1985; Collins *et al.* 1989).

Several studies have documented the diversity of birds and nectar-producing plants within communities (Ford & Paton 1982; Collins & Newland 1986; Paton 1986), yet only a few have shown how patchy the distribution of nectar can be (Paton & Ford 1983; Collins 1985; Collins *et al.* 1989). Nectar availability varies both temporally and spatially. For instance, the amount of nectar present in individual flowers is often greatest around dawn, with standing crop volumes decreasing throughout the day (Ford 1979; Collins & Briffa 1983; Collins 1985). Volumes also vary according to floral age, with younger flowers generally producing more nectar than older ones (Collins 1985; Collins *et al.* 1989). Total nectar availability in a particular habitat fluctuates throughout the year, with its level depending upon the species in flower and the numbers of flowers per plant (Collins 1985; Paton 1986). The extent to which nectar availability varies spatially is determined by the distributions and densities of plant species in flower, and the abundance of floral age-classes on individual plants (Collins 1985; Collins *et al.* 1989).

Considerable empirical evidence suggests that honeyeaters (Paton & Ford 1983; Collins 1985; Collins & Newland 1986; Collins *et al.* 1989), in addition to sunbirds and sugarbirds (Gill & Wolf 1977; Collins 1983), often forage selectively for nectar. These birds generally prefer plant species, patches of a species, individual plants and flowers that make foraging energetically most rewarding (Paton & Ford 1983; Collins 1985; Collins *et al.* 1989). Nevertheless, relatively little quantitative evidence has been obtained in an effort to explain how nectarivores identify the most profitable nectar-sources in their natural habitats.

It has been suggested that visual cues such as colour and morphology are especially important means by which birds identify appropriate sources of nectar (Gill & Wolf 1975; Stiles 1976; Collins 1983). For instance, honeyeaters visiting *Banksia ilicifolia* inflorescences easily distinguish between yellow and red colour morphs, rapidly and reliably switching their foraging preferences between the most rewarding morphs (Lamont & Collins 1988). This paper identifies morphological features that serve as cues for selective foraging by honeyeaters at a particular proteaceous plant species, *Dryandra sessilis*, in Jarrah forest habitats of Western Australia, and illustrates how the birds respond to variations in some of these features.

STUDY AREA AND METHODS

Investigations were undertaken within the Kar-net section of the State Jarrah Forest, approximately nine km south of Jarrahdale (32 21S, 116 3E), Western Australia, between 1984 and 1986. Climatic conditions during this period were typically mediterranean, with hot, dry summers and cool, wet winters (Wykes 1985). The major study site used had an area of approximately 8.5 ha, and contained relatively open sclerophyllous vegetation, dominated by *Eucalyptus marginata* (Jarrah) and *E. calophylla* (Marri), with an understorey bush layer comprising *Dryandra sessilis*, *Calothamnus rupestris* and *Banksia grandis*. Ground cover was provided by small shrubs such as *Grevillea wilsonii* and *Adenanthos barbiger* (Collins 1985; Wykes 1985; Collins & Newland 1986; Collins *et al.* 1989).

Individual *D. sessilis* plants were typically open, with heights and diameters ranging from 2–4 m. Inflorescences were erect capitula comprising approximately 100 tightly-packed flowers, each of which was gullet-shaped, yellow, had a nectary-stigma length of 22–25 mm and a diameter of 102 mm.

Honeyeaters most commonly seen foraging at *D. sessilis* were Western Spinebills *Acanthorhynchus superciliosus*, Little Wattlebirds *Anthochaera chrysoptera* and New Holland Honeyeaters *Phylidonyris novaehollandiae*. These

TABLE 1
CANOPY VOLUMES OF INDIVIDUAL *DRYANDRA SESSILIS*
PLANTS AT OBSERVATION SITES, AND DISTANCES TO NEAREST NEIGHBOURS

Observation site	Canopy volume (m ³)			Distance to nearest neighbour (m)	
	N	Range	x±s.d.	Range	x±s.d.
1	50	0,1–23,0	3,3±4,6	0,1– 7,2	1,7±1,5
2	24	0,2–28,3	6,8±7,9	1,0–26,0	3,3±4,9
3	44	0,1–14,9	2,1±3,3	0,5– 9,0	2,1±2,0
4	28	0,1–29,4	3,9±7,1	0,5– 8,5	3,0±1,9

birds typically perched on stems adjacent to inflorescences that they probed for nectar, and rarely alighted on the inflorescences or involucre bracts.

Within the study area, four observation sites containing mainly *D. sessilis* bushes were randomly selected. Distances between adjacent *D. sessilis* plants that were likely to flower during the current year were measured at each site, and the relative positions of the plants mapped. All plants were labelled with numbered aluminium tags. The height and two crown diameters, taken approximately at right angles to each other, were measured for each plant and used to calculate its canopy volume. Assuming that the plant's shape was roughly spheroidal (Briffa & Lamont pers. comm.), canopy volume = 0,5236 × height (m) × crown diam. 1 (m) × crown diam. 2 (m).

Numbered aluminium tags were attached to 20 randomly selected, unopened individual *D. sessilis* inflorescences on different bushes within the study sites in May, 1984. Morphological and colour changes associated with floral development were noted. During visits in June and July, the numbers of *D. sessilis* inflorescences belonging to each age-class (based on morphological and colour characteristics) were counted for individual, marked plants on two successive days at each observation site. The percentage frequencies of different age-classes were calculated on each occasion, lumping data for all four sites.

Approximately 220 unopened *D. sessilis* inflorescences were selected at random on several different plants outside the observation sites, in June and July, 1984, and labelled with numbered aluminium tags. Inflorescences were inspected daily at dusk until pollen presentation was first observed. Sub-samples of 10 inflorescences were picked at that time, and then at dawn, noon and dusk on subsequent days. Nectar was removed from each picked inflorescence using a motor-driven aspirator, and its volume measured with calibrated micropipettes (Collins & Briffa 1983). The equivalent sucrose concentrations (w/w) of nectar samples were measured using a National temperature-compensated refractometer. Concentrations and volumes were combined to estimate the energy values of all samples (Collins & Newland 1986; Collins *et al.* 1989).

The frequencies with which honeyeaters visited inflorescences of particular age-classes were recorded opportunistically throughout the study area during June, 1984. Honeyeater preferences for particular plants within each obser-

vation site were recorded for three hours in the morning, commencing half an hour before sunrise, and two hours during late afternoon, finishing half an hour after sunset. Observations were made during June and July on days just before or after flower counts were recorded for individual plants. On each occasion, birds were watched from a fixed point which had been chosen because it gave a clear view of all plants concerned, yet was not located within the site. For each visit to a plant, the identification number of the plant, total time spent foraging at the plant, number of inflorescences visited on the plant and the number of probes at each inflorescence, were recorded. Whenever possible, the next plant visited after probing a particular inflorescence, and the distance travelled to that plant, were also recorded.

In June 1986, floral abundance and New Holland Honeyeater preferences for *D. sessilis* plants at Site 2 were again recorded over a period of two days. At the end of this time, half of the 1–4 day-old inflorescences on the six most frequently visited plants were removed. Plant preferences were then monitored for a further two days. Similar experiments were conducted at Site 4, except that canopy volumes (but not the numbers of inflorescences) for the six most frequently visited plants were reduced by pruning branches from these plants after the control period. Since canopy volumes were not measured before or after pruning, the extent to which volumes were reduced cannot be quantified.

RESULTS

Plant distribution and dimensions

The distribution of *Dryandra sessilis* within the study area was extremely patchy, with plants abundant in some parts and absent from others (plants per 20 m² quadrat: \bar{x} = 7,7, s.d. 10,0, range 0–33, N = 15). Sites chosen for observations of honeyeater foraging included high and low density areas (Fig. 1). Plants were generally most widely spaced at Sites 2 and 4, and closest together at Sites 1 and 3 (Table 1).

Canopy volumes of individual plants were extremely variable at all observation sites, with values varying from 0,1 to almost 30 m³ (Table 1). Nevertheless, mean canopy volumes were least for Sites 1 and 3, the locations where distances between nearest-neighbour plants were also least.

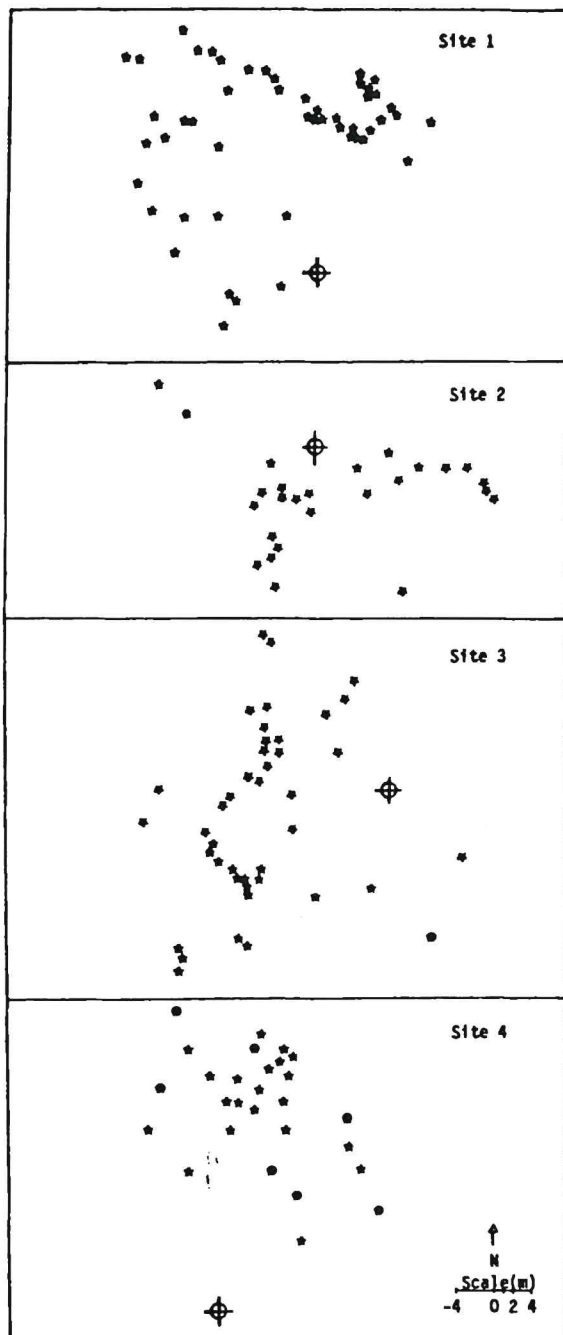


FIGURE 1

Spatial distribution of *Dryandra sessilis* plants at observation sites in the jarrah forest. Individual plants are denoted by *, and observation (viewing) points by O.

Floral development

D. sessilis inflorescences observed in this study comprised 79–127 individual flowers ($\bar{x} = 94,1$, s.d. = 11,3, $N = 20$). The outermost flowers usually opened first, with an average of 21,2 flowers (22,5% of total) opening on the first day. After 2, 3 and 4 days, the corresponding numbers were 66,9 (71,1%), 93,1 (98,9%) and 94,1 (100,0%), respectively. As each flower opened, the perianth ruptured and withered, exposing an erect, thin (c.1mm) style with sub-terminal pollen

TABLE 2
OBSERVABLE CHANGES IN *DRYANDRA SESSILIS* INFLORESCENCES AFTER OPENING OF FIRST FLOWER

Time after opening of first flower (days)	Appearance of inflorescence
1	Approximately 23% of outer flowers open, all perianths light yellow
2	Approximately 71% of outer flowers open, all perianths light yellow
3	Approximately 99% of outer flowers open, all perianths light yellow
4	All flowers open, outer perianths dark yellow
5	Most perianths dark yellow, some brown
6	Most perianths brown
7+	All perianths dark brown, becoming increasingly withered.

presenter and stigmatic groove. Apart from morphological changes such as these, distinct alterations to perianth colour occurred for all or some flowers after the third day (Table 2). The colour and disposition of involucre bracts at the base of each inflorescence remained constant during floral development. Variations in the appearance of inflorescences during floral development were so clearcut that age-classes of 1–2, 3–4, 5–6 and 7+ days could readily be distinguished. The relative overall frequencies of day 1–2 and day 3–4 inflorescences were similar in June and July, 1984, both exceeding those of older flowers (Table 3).

Floral abundance

Some *D. sessilis* plants within the observation sites bore more than 60 inflorescences when observed in June or July 1984, others none (Table 4). The abundance of various age-classes of inflorescence also varied considerably between plants. Nevertheless, the overall abundances of particular age-classes were generally greatest at Site 2, and least at Site 3 in both June and July.

Nectar availability

Nectar availability in *D. sessilis* inflorescences varied throughout the day, regardless of floral age or time of year (Fig. 2). In general, the mean nectar energy content per inflorescence was greater at dawn than at noon or dusk. Overall availability of nectar was also greater on days 1 and 2 than for older inflorescences. In June 1984, nectar production continued until inflorescences were approximately 7 days old, although production virtually ceased within three days of initial pollen presentation in July.

TABLE 3
OVERALL PERCENTAGE FREQUENCIES OF *DRYANDRA SESSILIS* INFLORESCENCES BELONGING TO DIFFERENT AGE-CLASSES AT ALL OBSERVATION SITES. ABSOLUTE NUMBERS OF INFLORESCENCES ARE INDICATED IN PARENTHESES

Age-class of inflorescence (days)	Percentage frequency of inflorescences	
	June	July
1–2	34,2 (379)	32,8 (311)
3–4	34,9 (386)	31,5 (299)
5–6	20,8 (230)	23,2 (220)
7+	10,1 (112)	12,5 (119)

TABLE 4

FLORAL ABUNDANCE ON INDIVIDUAL *DRYANDRA SESSILIS* PLANTS AT SEPARATE OBSERVATION SITES. NUMBERS OF INFLORESCENCES PER AGE-CLASS ARE INDICATED IN PARENTHESES

Time of year	Observation site	Floral age (days)	Floral abundance (inflor./plant)	
			Range	$\bar{x} \pm s.d.$
June	1	1-2	0-26 (145)	2,9±5,1
		3-4	0-20 (133)	2,7±4,7
		5-6	0-17 (96)	1,9±3,4
		7+	0-8 (54)	1,1±1,8
	2	1-2	0-30 (132)	5,5±7,7
		3-4	0-16 (111)	4,7±4,9
		5-6	0-12 (71)	3,0±3,4
		7+	0-10 (36)	1,5±2,4
	3	1-2	0-9 (48)	1,1±2,1
		3-4	0-8 (70)	1,6±2,4
		5-6	0-3 (26)	0,6±0,9
		7+	0-4 (9)	0,2±0,7
	4	1-2	0-7 (54)	1,9±2,4
		3-4	0-21 (72)	2,6±4,6
		5-6	0-8 (37)	1,3±2,0
		7+	0-4 (13)	0,5±1,0
July	1	1-2	0-12 (118)	2,4±3,4
		3-4	0-15 (116)	2,3±3,5
		5-6	0-10 (78)	1,6±2,4
		7+	0-7 (45)	0,9±1,6
	2	1-2	0-24 (101)	4,2±6,1
		3-4	0-19 (96)	4,0±5,1
		5-6	0-16 (86)	3,6±4,5
		7+	0-5 (40)	1,7±2,0
	3	1-2	0-5 (45)	1,0±1,5
		3-4	0-6 (50)	1,1±1,8
		5-6	0-6 (38)	0,9±1,4
		7+	0-3 (15)	0,3±0,7
	4	1-2	0-10 (47)	1,7±2,7
		3-4	0-7 (37)	1,3±2,1
		5-6	0-5 (18)	0,6±1,2
		7+	0-3 (19)	0,7±0,9

Mean nectar energy availability per *D. sessilis* plant can be estimated crudely by summing the products of the numbers of inflorescences present that belong to particular age-classes and mean nectar availabilities for these classes. Estimates ranged from 0,0-3052,4 J/plant in June to 0,0-1803,8 J/plant in July 1984 (Table 5). Energy availability was least at Site 3 in both months, and greatest at Site 2.

Inflorescence and plant preferences

Little Wattlebirds foraged almost exclusively at day 1-2 and day 3-4 *D. sessilis* inflorescences, especially the former (Table 6). New Holland Honeyeaters had similar preferences, although older inflorescences were occasionally used by this species. Since inflorescences in day 1-2 and

TABLE 6

PERCENTAGE FREQUENCIES OF VISITS TO DIFFERENT AGE-CLASSES OF *DRYANDRA SESSILIS* INFLORESCENCE BY LITTLE WATTLEBIRDS AND NEW HOLLAND HONEYEATERS IN JUNE. ABSOLUTE NUMBERS OF VISITS ARE INDICATED IN PARENTHESES

Age-class of inflorescence (days)	Percentage frequency of visits by	
	Little Wattlebirds	New Holland Honeyeaters
1-2	68,1 (64)	71,0 (149)
3-4	31,9 (27)	25,7 (54)
5-6	0,0 (0)	2,4 (5)
7+	0,0 (0)	0,9 (2)

day 3-4 age-classes were equally abundant, both species of honeyeater showed a preference for younger inflorescences.

Some plants at each site received no visits by Little Wattlebirds or New Holland Honeyeaters during observation periods in June or July. Others were visited on many occasions, some up to 19 times in a five hour period (Table 7). In general, plants were visited most frequently by honeyeaters at Site 2, and least frequently at Sites 3 and 4. Similar, but sometimes less pronounced, differences occurred between sites with respect to the mean number of inflorescences encountered per visit to a plant, time spent foraging at inflorescences per visit and number of times birds probed each inflorescence visited (Table 7).

When overall frequencies of visits by Little Wattlebirds and New Holland Honeyeaters to *D. sessilis* plants are related to characteristics of these plants and aspects of foraging behaviour at their inflorescences, several consistent trends become apparent (Table 8). Frequency of visitation is significantly and positively correlated with the number of 1-4 day-old inflorescences probed per visit, time spent foraging per plant and number of probes made per inflorescence. Characteristics of nearby plants appear to have relatively little impact upon the popularity of particular plants.

Manipulation of canopy volumes and inflorescence counts

Removal of inflorescences from the six plants that previously were visited most frequently by New Holland Honeyeaters at Site 2 led to a significant reduction in the popularity of these plants (Table 9; Fig. 3; $t = 2,87, P < 0,02$). Never-

TABLE 5

TOTAL NECTAR ENERGY AVAILABILITY PER *DRYANDRA SESSILIS* PLANT FOR EACH OBSERVATION SITE. N DENOTES NUMBERS OF PLANTS AT EACH SITE

Time of year	Observation site	N	Total nectar energy availability (J/plant) ^a	
			Range	$\bar{x} \pm s.d.$
June	1	50	0,0-3 052,4	361,4±618,1
	2	24	0,0-2 810,5	604,8±761,7
	3	44	0,0-1 108,4	163,1±262,0
	4	28	0,0-1 491,7	371,6±320,6
July	1	50	0,0- 964,0	186,4±266,1
	2	24	0,0-1 803,8	300,3±436,6
	3	44	0,0- 387,7	78,6±109,4
	4	28	0,0- 741,1	130,0±191,0

^a The value for each plant was calculated as the sum of the products of inflorescence counts per age-class and mean nectar availability at dawn, noon and dusk for those age-classes.

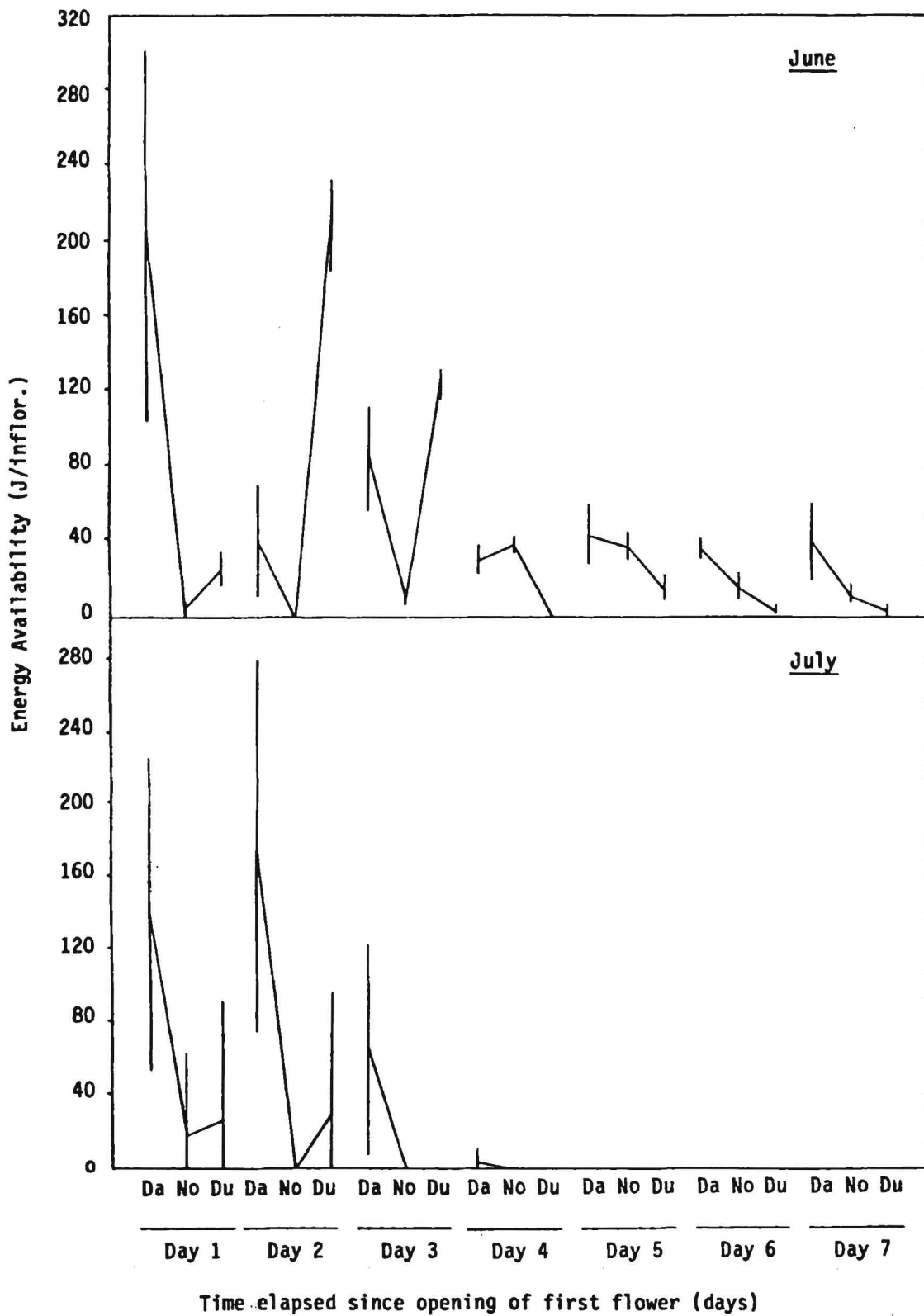


FIGURE 2

Nectar energy availability in *Dryandra sessilis* inflorescences of various ages at different times of day during June and July. Da, No and Du represent dawn, noon and dusk, respectively. Mean values are connected by solid angled lines, vertical lines represent + s.e., N=10 in each case.

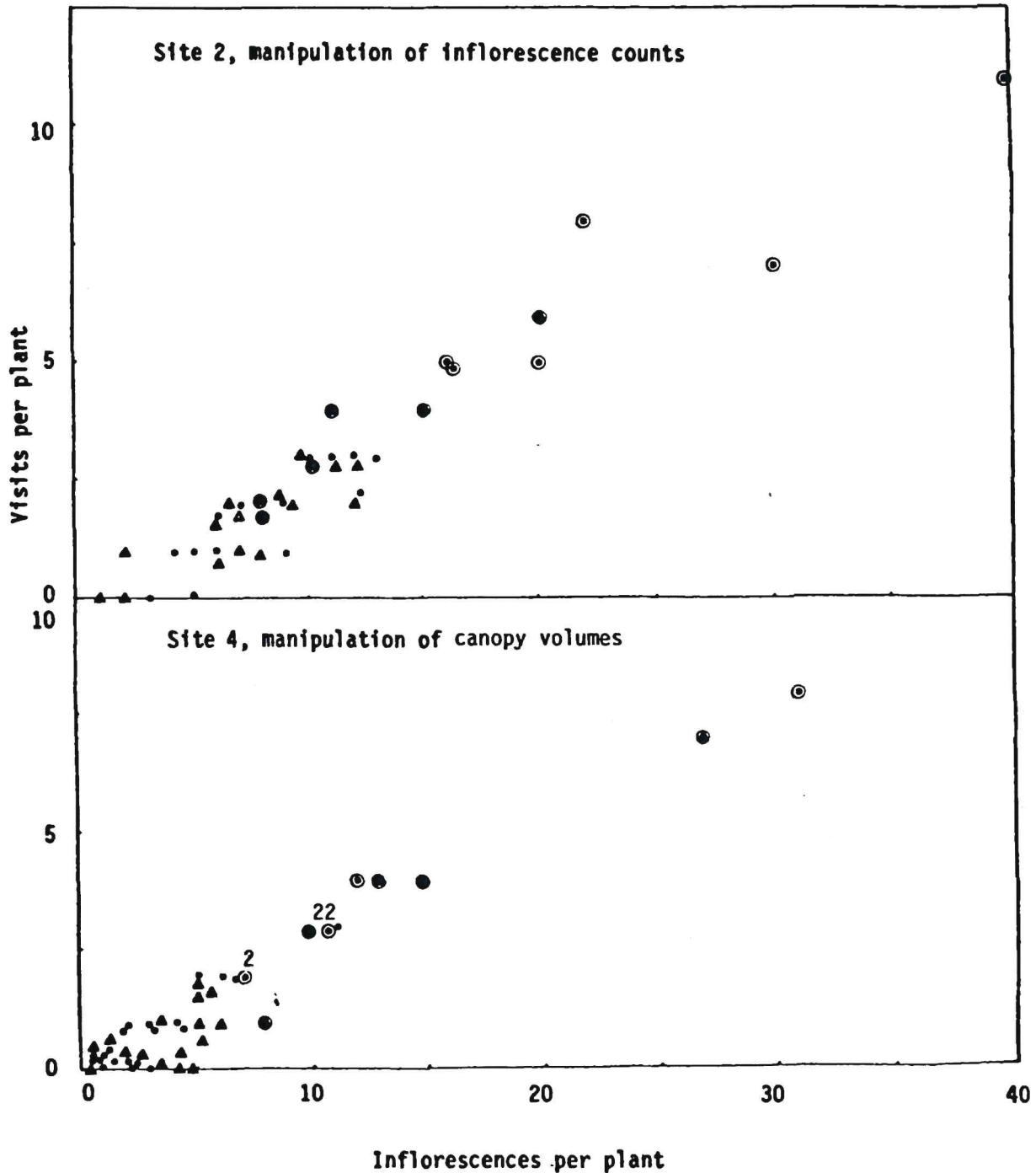


FIGURE 3

Frequencies of visits by New Holland Honeyeaters to *Dryandra sessilis* plants, some of whose inflorescence counts or canopy volumes were modified and denote data gathered prior to and during experimental periods, respectively, at Sites 2 and 4. Values for plants whose canopy volumes or inflorescence counts were altered are circled. The number 2 alongside circled data points indicates that values for two plants were identical.

theless, the slope of the linear regression line relating the overall incidence of visits by honeyeaters to the number of inflorescences per plant did not change significantly ($t = 1,02$, $P > 0,05$). Reduction in the canopy volumes of the six most "attractive" plants at Site 4 did not appreciably alter the frequencies with which they were visited ($t = 0,00$, $P > 0,05$), nor did it significantly change the slope of the regression line fitted to data points ($t = 1,14$, $p > 0,05$).

DISCUSSION

The results of this and other studies (Collins 1985; Wykes 1985; Collins *et al.* 1989) indicate that *Dryandra sessilis* has an extremely patchy distribution within the jarrah forest. Plants often occur in dense clumps, but are sometimes considerable distances apart. In either case, the number of inflorescences present at any given time can vary significantly between plants (Collins 1985;

TABLE 7
FORAGING BEHAVIOUR OF HONEYEATERS VISITING INDIVIDUAL *DRYANDRA SESSILIS* PLANTS

Bird species, site and time of year	visits/plt. ^a		Foraging behaviour				probes/inflor ^d	
			inflor./visit ^b		sec./visit ^c			
	Range	x±s.d.	Range	x±s.d.	Range	x±s.d.	Range	x±s.d.
New Holland Honeyeater								
June 1 Site 1	0,0-19,0	1,2±4,0	1,0-2,5	1,8±0,5	3,0-23,5	15,1±7,4	3,0-18,2	12,2±5,6
June 2 Site 2	0,0-11,0	1,2±3,1	1,0-3,2	2,1±1,1	9,5-36,8	20,8±11,6	6,0-26,5	15,2±9,0
June 3 Site 3	0,0-10,0	0,4±1,7	2,0-2,7	2,4±0,4	19,4-31,0	23,7±6,4	15,0-22,8	17,1±5,0
June 4 Site 4	0,0-2,0	0,3±0,6	1,0-2,5	1,9±0,5	8,2-25,8	17,0±7,8	7,0-19,0	12,9±5,7
July 28 Site 1	0,0-7,0	0,8±1,9	1,3-2,1	1,7±0,3	6,7-23,6	14,2±6,3	5,0-18,0	10,7±4,8
July 27 Site 2	0,0-3,0	0,4±0,9	1,0-2,3	1,9±0,5	9,5-25,5	17,9±5,8	7,3-19,7	13,5±4,7
July 26 Site 3	0,0-16,0	1,1±3,3	1,0-2,9	2,1±0,7	9,0-29,9	19,0±7,5	6,0-18,0	11,0±4,2
Little Wattlebird								
June 2 Site 2	0,0-9,0	1,2±2,2	1,4-2,7	1,9±0,5	13,9-31,2	19,6±5,9	100-24,0	15,7±5,1
June 4 Site 4	0,0-4,0	0,4±1,0	1,0-3,0	2,0±0,9	7,2-30,3	18,7±8,7	5,5-19,0	12,3±5,3
July 28 Site 1	0,0-7,0	0,7±1,7	1,0-2,6	1,9±0,5	7,7-24,8	16,4±6,1	6,0-18,6	11,9±4,1
July 27 Site 2	0,0-10,0	1,4±2,7	1,0-3,0	1,8±0,6	6,9-31,5	19,1±7,7	5,2-24,0	13,3±6,7
June 25 Site 4	0,0-9,0	1,1±2,5	1,3-2,7	2,0±0,5	8,6-25,4	15,7±6,2	6,0-18,3	11,0±4,4

^a Sample size for each site/day was the number of plants present (range 24-50)
^b Sample size for each site/day was the number of plants visited (range 3-11)
^c Sample size for each site/day was the number of visits (range 3-11)
^d Sample size for each site/day was the number of inflorescences probed (range 3-11)

Collins & Newland 1986). The availability of nectar is also variable, with the amount present per inflorescence depending upon floral age and other factors such as soil moisture and air temperature.

One consequence of spatial variation in the floral and nectar environments is that nectarivores are provided with foraging options from which they might choose. Previous studies have demonstrated that nectarivorous birds such as honeyeaters (Paton & Ford 1983; Collins 1985; Collins *et al.* 1989) and sunbirds (Gill & Wolf 1977; Collins 1983) are often selective in their use of plants. Almost invariably, the larger species of

nectarivore present make greatest use of the most productive plant species. For example, Little Wattlebirds and New Holland Honeyeaters forage almost exclusively at plants such as *D. sessilis* and *Calothamnus rupestris* in the jarrah forest, whereas smaller Western Spinebills use less rewarding species (Collins *et al.* 1989). In addition, honeyeaters usually forage most frequently in regions where the densities of their preferred plant species are greatest (Collins & Newland 1986; Collins *et al.* 1989). By behaving in this manner, the birds should reduce the cost of movement between plants and flowers, and thus maximise their rates of net energy intake. Evi-

TABLE 8

SIGNIFICANCE MATRICES BASED ON PARTIAL CORRELATION COEFFICIENTS RELATING THE INCIDENCE OF VISITS BY HONEYEATERS TO INDIVIDUAL *DRYANDRA SESSILIS* PLANTS TO CHARACTERISTICS OF THESE PLANTS AND ASPECTS OF FORAGING BEHAVIOUR AT PLANTS. *** DENOTES P < 0.001, ** P < 0.01, * P < 0.05, N.S. NOT SIGNIFICANT

Bird species, site and time of year	Plant or foraging characteristic ^a							
	In	Cv	Nn	Ni	Nb	Ip	Tf	Pi
New Holland Honeyeater								
June 1 Site 1	***	***	N.S.	N.S.	N.S.	***	***	***
June 2 Site 2	**	N.S.	N.S.	*	N.S.	***	***	***
June 3 Site 3	***	***	***	***	**	***	***	***
June 4 Site 4	***	**	N.S.	N.S.	N.S.	***	***	***
July 28 Site 1	***	***	*	N.S.	N.S.	***	***	***
July 27 Site 2	***	***	N.S.	N.S.	N.S.	***	***	***
July 26 Site 3	***	**	N.S.	N.S.	N.S.	***	***	***
Little Wattlebird								
June 2 Site 2	***	***	N.S.	**	.	***	***	***
June 4 Site 4	***	**	N.S.	N.S.	N.S.	***	***	***
July 28 Site 1	***	***	N.S.	N.S.	N.S.	***	***	***
July 27 Site 2	***	***	N.S.	N.S.	N.S.	***	***	***
July 25 Site 3	***	***	N.S.	N.S.	N.S.	***	***	***

^a In = number of 1-4 day-old inflorescences on host plant, Cv = canopy volume of host plant, Nn = distance of host to nearest neighbour, Ni = number of 1-4 day-old inflorescences on neighbour, Nb = canopy volume of neighbour, Ip = number of inflorescences probed per visit to host, Tf = time spent foraging at host, Pi = number of probes per inflorescence of host.

TABLE 9

FLORAL ABUNDANCE AND VISITS BY NEW HOLLAND HONEYEATERS FOR INDIVIDUAL *DRYANDRA SESSILIS* PLANTS BEFORE AND AFTER CANOPY VOLUMES OR INFLORESCENCE COUNTS ALTERED N = 6 IN EACH CASE

Site and treatment	Before treatment				After treatment			
	inflor./plt.		visits/plt.		inflor./plt.		visits/plt.	
	Range	x±s.d.	Range	x±s.d.	Range	x±s.d.	Range	x±s.d.
Site 2 . . . half 1-4 day inflorescences removed from six largest plants after 2 days	16-40	24.8±8.7	5-11	6.8±2.4	8-20	12.0±4.7	2-6	3.5±1.5
Site 4 . . . canopy volumes of six largest plants reduced after 2 days	7-31	13.2±9.0	2-8	3.7±2.3	8-27	13.8±6.9	1-7	3.7±2.0

dence from other investigations has shown that nectarivorous birds often choose between particular plants or flowers (inflorescences) of a given species. For instance, Paton & Ford (1983) have demonstrated that New Holland Honeyeaters prefer *Eucalyptus cosmophylla* and *Correa schlectendalii* plants in south-eastern Australia that bear the greatest numbers of flowers. In Kenya, it has been shown that Golden-winged *Nectarinia reichenowi* and Malachite *N. famosa* Sunbirds select *Leonotis nepitifolia* inflorescences that offer the richest nectar rewards (Gill & Wolf 1977). Data presented in this paper also indicate that Little Wattlebirds and New Holland Honeyeaters generally choose the most rewarding nectar sources offered by *D. sessilis* in jarrah forest habitats. The foraging efficiencies of both honeyeater species are clearly enhanced by selection of young inflorescences, and plants with relatively high numbers of these (Table 10).

The frequency of visits by honeyeaters to *D. sessilis* is not only correlated with the number of productive inflorescences per plant, but also with total time spent visiting inflorescences on each plant, number of inflorescences visited per plant and the number of probes made at each inflorescence. These observations are independent of the site at which data were recorded, and coincide with predictions based on theoretical considerations, which assume that birds were

endeavouring to maximize net energy intake (Pyke 1984). Providing inflorescences offer reasonable nectar rewards, it would be advantageous for birds if they maximized the amount of time spent on particular plants and inflorescences, and minimized the frequency with which they shifted to other plants.

It has been suggested that birds identify the most rewarding plants or inflorescences by means of morphological and/or colour cues (Stiles 1976; Collins 1983; Collins & Rebelo 1987). For instance, honeyeaters that visit *Banksia ilicifolia* inflorescences in banksia woodlands of Western Australia are able to differentiate between yellow and red colour morphs, switching their foraging preferences according to the relative nectar rewards available (Lamont & Collins 1988). With *D. sessilis*, morphological changes that occur during the first 1-4 days after an inflorescence begins to open are quite noticeable. Beyond that time, changes in both colour and morphology occur. The fact that honeyeaters forage selectively at the youngest and most productive inflorescences clearly indicates that they are again able to distinguish between different types of inflorescence.

Manipulative experiments reported in this paper were designed to test hypotheses based on empirical data, which suggested that the frequencies with which honeyeaters visited particular *D. sessilis* plants were related to the number of

TABLE 10

FORAGING EFFICIENCIES FOR HONEYEATERS VISITING *DRYANDRA SESSILIS* IN THE JARRAH FOREST (MODIFIED AFTER COLLINS ET AL. 1989).

Age of flower/time of day	Standing crop (J/inflor.)	energy	Nectarivore ^a species	Foraging efficiency (J) ^b		
				A	B	C
Day 1/dawn	603		N.H.H.	594	587	581
			L.W.	589	568	548
Day 4/dawn	60		N.H.H.	51	44	38
			L.W.	46	25	5

^a N.H.H. and L.W. denote New Holland Honeyeaters and Little Wattlebirds respectively.

^b Foraging efficiency is the difference between energy intake, assuming 100% ingestion of available nectar when an inflorescence is visited by a bird, and the energy expended in flying to the inflorescence and extracting this nectar; efficiencies have been calculated for situations in which birds had to fly different distances in order to harvest nectar; flight times used were: (A) 0.5, (B) 2.0 and (C) 3.5 s; mean extraction times were: N.H.H. 12.5 and L.W. 6.7 s.

productive inflorescences present, and the canopy volumes of these plants. These experiments have confirmed that plant popularity is reduced if inflorescences are removed. However, reductions in canopy volume did not produce similar changes. This discrepancy could be explained in several ways. The reductions in canopy volume that were effected may have been less than those necessary to produce an appreciable change in honeyeater behaviour. Alternatively clearing some of the foliage may have made inflorescences more obvious than usual, thus countering any effect that reduced canopy volume might have had. It is also possible that the spatial distribution of inflorescences, which remained unaltered, was more important than the actual volumes of shapes of individual plants.

ACKNOWLEDGMENTS

We are grateful for financial assistance from the Australian Research Grants Committee and the Southern African Ornithological Society. Valuable technical assistance was provided by Vaughan Monamy.

REFERENCES

- BLAKERS, M., DAVIES S.J.J.F & REILLY, P.N. 1984. The atlas of Australian birds. Melbourne: Melbourne University Press.
- COLLINS, B.G. 1983. Pollination of *Mimetes hirtus* (Proteaceae) by Cape Sugarbirds and Orange-breasted Sunbirds. *J. S. Afr. Bot.* 49: 124–142.
- COLLINS, B.G. 1985. Energetics of foraging and resource selection by honeyeaters in forest and woodland habitats of Western Australia. *N.Z.J. Zool.* 12: 577–587.
- COLLINS, B.G. & BRIFFA, P. 1983. Seasonal and diurnal variations in the energetics and foraging activities of the brown honeyeater, *Lichmera indistincta*. *Aust. J. Ecol.* 8: 103–111.
- COLLINS, B.G., GREY, J & McNEE, S. 1989. Foraging and nectar use in nectarivorous bird communities. *Studies in Avian Biology*. (in press).
- COLLINS, B.G. & NEWLAND, C. 1986. Honeyeater population changes in relation to food availability in the Jarrah forest of Western Australia. *Aust. J. Ecol.* 11: 63–76.
- COLLINS, B.G. & REBELO, T. 1987. Pollination biology in the Proteaceae of Australia and southern Africa. *Aust. J. Ecol.* 12: 387–421.
- FORD, H.A. 1979. Interspecific competition in Australian honeyeaters—depletion of common resources. *Aust. J. Ecol.* 4: 145–164.
- FORD, H.A. & PATON, D.C. 1982. Partitioning of nectar sources in an Australian honeyeater community. *Aust. J. Ecol.* 7: 149–159.
- GILL, F.B. & WOLF, L.L. 1975. Foraging strategies and energetics of East African sunbirds at mistletoe flowers. *Am. Nat.* 109: 491–510.
- GILL, F.B. & WOLF, L.L. 1977. Nonrandom foraging by sunbirds in a patchy environment. *Ecology* 58: 1284–1296.
- LAMONT, B.B. & COLLINS, B.G. 1988. Flower colour change in *Banksia ilicifolia*: a signal for pollinators. *Aust. J. Ecol.* 13: 129–135.
- PATON, D.C. 1982. The diet of the New Holland honeyeater, *Phylidonyris novaehollandiae*. *Aust. J. Ecol.* 7: 279–298.
- PATON, D.C. 1986. Food supply, population structure and behaviour of New Holland Honeyeaters *Phylidonyris novaehollandiae* in woodland near Horsham, Victoria. In KEAST, A., RECHER, H.F., FORD, H. & SAUNDERS, D. (Eds). Birds of eucalypt forests and woodlands. Sydney: Surrey Beatty: 219–230.
- PATON, D.C. & FORD, H.A. 1983. The influence of plant characteristics and of pollination in Australian plants. In JONES, C.E. & LITTLE, R.J. (Eds). Handbook of experimental pollination biology. New York: Van Nostrand Reinhold: 235–248.
- PYKE, G.H. 1980. The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. *Aust. J. Ecol.* 5: 343–369.
- PYKE, G.H. 1984. Optimal foraging theory: a critical review. *Ann. Rev. Ecol. Syst.* 5: 523–575.
- STILES, F.G. 1976. Taste preferences, colour preferences and flower choice in hummingbirds. *Condor* 78: 10–26.
- WYKES, B.J. 1985. The jarrah forest avifauna and its re-establishment after bauxite mining. School of Biology bulletin, Number 11. Perth: Western Australian Institute of Technology.

