The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds

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Abstract

The foraging behaviour of Australian honeyeaters is reviewed in terms of diet, foraging selectivity, foraging flight mode, quality and quantity of nectar encountered per flower, flower densities encountered and effect of predation. At the same time comparisons are made between honeyeaters and hummingbirds. These two groups of birds are superficially similar. Both feed on nectar and insects. Both tend to have long curved bills and tongues adapted for removal of nectar from flowers. Both tend to feed at long, red flowers. However, on close inspection, honeyeaters and hummingbirds are quite dissimilar. For example, many honeyeaters include fruit in their diets. Hummingbirds almost never eat fruit. Honeyeaters appear to be considerably less nectarivorous and more insectivorous than hummingbirds. Honeyeaters are, for the most part, larger than hummingbirds and they usually perch while feeding whereas hummingbirds usually hover. Honeyeaters but not hummingbirds often flock while feeding. Predation appears to be considerably more important for honeyeaters than for hummingbirds. Territorial defense of flowers seems common in hummingbirds but uncommon in honeyeaters. These differences are discussed in detail and explanations are offered for them wherever possible.

Introduction

The major aim of this paper is to review the literature on the foraging behaviour of Australian honeyeaters. At the same time

attempts will be made to point out areas where information is scarce and further data seem warranted. The topics that will be considered are for the most part simply convenient subdivisions of the foraging process such as dietary composition and dietary selectivity. As will be seen, however, they do not cover all possible aspects of foraging behaviour. Instead, they cover only those aspects for which available data justify a review and some general comments. Treatment of presently neglected aspects of foraging must await the acquisition of more data.

The secondary aim of this paper is to make comparisons wherever appropriate between the foraging behaviour of Australian honeyeaters and that of hummingbirds. Such comparisons appear to be invited by the following: (a) the similar habits of both families of birds of feeding on flower nectar (see below); (b) the apparent coevolution that appears to have occurred between both bird families and the respective plant species that they visit and pollinate (Gilbert 1923; Sargent 1928; Hindwood 1944; Keast 1959; Wakefield 1960; Mees 1967; Keighery 1975; Paton & Ford 1977); and (c) the large and growing body of literature on hummingbird feeding ecology (e.g. Feinsinger & Chaplin 1975; Hainsworth & Wolf 1972a; Pyke 1978b; Wolf *et al.* 1971). As will be seen, however, nectar is not by any means the only component of the diets of the two families of birds and the relative importance of nectar appears to differ between the families. Consideration of both similarities and dissimiliarities will hopefully increase the level of understanding of the biology of both honeyeaters and hummingbirds.

There are other birds in the world which are, at least partly, nectarivorous. They include the sunbirds (Nectarinidae), the sugarbirds (Promeropidae) and the honeycreepers (Drepanididae) (Percival 1965). None of these other groups of birds will be compared, however, with Australian honeyeaters in this paper as available

data on these other birds are presently insufficient for the purpose. For the same reason, this paper will deal only with those honeyeater species which occur in Australia and not with the remainder of the meliphagids, most of which occur in New Guinea. The family Meliphagidae contains altogether about 167 species of which about seventy occur in Australia (Keast 1976; Schodde 1975). In this paper the taxonomic classification of the Meliphagidae by Schodde (1975) will be adopted.

Diets

The diets of honeyeaters consist mostly of nectar from flowers, 'insects' (insects plus occasional spiders) and fruit (see below). Included in the diets on rare occasions are sap oozing from tree wounds (Hindwood 1932; Darnell-Smith 1910) and sap oozing from unripe fruits (Ford 1976a). In addition honeyeaters sometimes feed extensively on honeydew, lerps and manna (D. C. Paton, personal communication). The importance of these food types varies considerably from one species to another. The painted honeyeater (*Grantiella picta*), for example, appears to be essentially a frugivore specializing on mistletoe berries and only occasionally feeding on nectar and/or insects (Eddy 1966; Chisholm 1940, 1944). The green-backed honeyeater (*Glycichaera fallax*), on the other hand, appears to be completely insectivorous (Officer 1964; Holland 1972). Whereas virtually all species are known to include some nectar in their diets, no species is completely nectarivorous and all eat some insects (see below). This would be expected since nectar is, except for very small quantities of free amino acids and proteins (Baker & Baker 1973a,b; 1975), an energy source whereas insects provide energy *and* necessary protein. Nectar is, however, a major food source to most honeyeaters (see below).

For a good understanding of the importance of the different food types to the various honeyeater species some quantification of the diet of each species is necessary. One way of doing this is to tabulate feeding observations from the literature for each honeyeater species and to note the relative frequencies of reports of nectar, insect, and fruit feeding. The results of an extensive literature survey are presented in this man-

ner in Table 1. These results are also summarized in Table 2 for most genera. Genera are omitted where data are few. This is admittedly a very crude approach to the diets of these birds but the following conclusions can be drawn from Tables 1 and 2:

(1) There appears to be a relationship between the diet of a species and the genus to which the species belongs. The genera *Myzomela, Certhionyx, Acanthorhynchus, Phylidonyris, Lichmera* and *Melithreptus*, feed largely on nectar and insects and seldom eat fruit. The genera *Lichenostomus, Meliphaga, Xanthotis, Manorina, Entomyzon, Xanthomyza, Plectorhyncha, Acanthagenys* and *Anthochaera* include fruit as well as nectar and insects in their diets. As mentioned above, *Grantiella picta* is essentially frugivorous and *Glychichaera fallax* is probably entirely insectivorous. Data are extremely scarce for some species (see Table 1).

(2) There appears to be a relationship between diet and body size. Most of the species which include a significant proportion of fruit in their diet are relatively large. With the exception of *Grantiella picta* these species range in size from *Lichenostomus chrysops* (average wing length: 82 mm; Keast 1976) to *Philemon corniculatus* (average wing length: 160 mm; Keast 1976). By comparison, those species which rely essentially on nectar and insects tend to be small.

The smallest of these species is *Myzomela erythrocephala* (average wing length: 60 mm; Keast 1976) while the largest is *Certhionyx variegatus* (average wing length: 90 mm; Keast 1976). There is no apparent relationship between diet and bill length. (See Table 2 and Figure 1 of Keast 1976).

Relatively recently, several authors have attempted to provide more accurate quantitative assessments of the diets of honeyeaters (Keast 1968b, 1975, 1976; Keast & Condon 1968; Recher & Abbott 1970b; Ford & Paton 1976a,b, 1977; Recher 1977; Halse 1978; Crome 1978). Two methods have been employed. One consists of recording the kind of feeding behaviour being employed each time an individual of a particular species is seen feeding (Keast 1968; Keast 1975; Keast 1976; Ford & Paton 1976a,b; Recher 1977; Crome 1978). These data are then converted into the percentages of feeding *observations* that were of nectar, insect or fruit feeding. The second method con-

TABLE 1. Feeding observations on Australian honeyeater species (Numbers in food category columns refer to numbered articles in bibliography)

Honeyeater species	Nectar	No. of obs.	Insects	No. of obs.	Fruit	No. of obs.
Myzomela sanguinolenta	14, 34, 40, 71, 95, 99, 128, 148, 152, 205, 206	11	39, 40, 148, 152, 162 205	6	162	1
Myzomela erythrocephala	119, 172, 205	3	172, 205, 262	3		0
Myzomela obscura	14, 65, 95, 162, 172, 173, 174, 205, 262, 287	10	66, 162, 172, 173, 205, 262	6	162	1
Certhionyx variegatus	95, 148	2	162	1	162	1
Certhionyx niger	22, 23, 29, 48, 89, 90, 95, 113, 128, 133, 134 148, 174, 184, 201	15	23, 89, 90, 113, 162, 202	6	162	1
Certhionyx pectoralis	95, 119, 142, 148, 172, 235	6	13, 172, 262	3		0
Acanthorhynchus superciliosus	5, 113, 143, 164, 182, 227, 235, 266, 267	9	113, 267			
Acanthorhynchus tenuirostris	16, 17, 45, 47, 71, 75, 85, 86, 88, 90, 92, 93, 95, 99, 128, 153, 162, 164, 181, 205, 230, 259, 279, 289	23	52, 53, 90, 97, 128, 153, 162, 205	8	162	1
Conopophila whitei		0		0	59, 65	2
Conopophila rufogularis	148, 172, 174, 205	4	13, 21, 36, 95, 172, 205, 262	7	205	1
Ramsayornis fasciatus	172, 173, 205, 236, 271	5	162, 262	2		0
Ramsayornis modestus	174	1				
Phylidonyris melanops	17, 88, 90, 95, 97, 99, 113, 122, 153, 194, 205, 208, 219, 246, 254, 260	16	53, 81, 95, 97, 113, 162, 205, 219, 246	9		0
Phylidonyris albifrons	95, 148, 152, 184, 189, 203, 208, 221, 225, 237, 263	11	97, 120, 148, 152, 162, 192, 203, 221, 252, 263	10	162	1
Phylidonyris nigra	28, 37, 46, 113, 127, 152, 155, 166, 203, 219, 220, 222	12	52, 53, 113, 124, 152, 162, 203, 219, 220, 222	10		0

Honeyeater species	Nectar	No. of obs.	Insects	No. of obs.	Fruit	No. of obs.
Phylidonyris novaehollandiae	3, 37, 88, 90, 92, 97, 127, 128, 151, 152, 153, 190, 203, 205, 208, 220, 256, 259	18	52, 53, 54, 90, 92, 147, 151, 152, 153, 162, 190, 203, 205, 220	14	205	1
Phylidonyris pyrrhoptera	62, 72, 76, 86, 88, 90, 97, 153, 153, 205, 208	11	53, 54, 72, 90, 152, 153, 162, 205	8	205	1
Grantiella picta	125, 206, 218	3		0	13, 49, 50, 59, 78, 95, 125, 129, 148, 177, 201, 205, 218, 272	14
Trichodere cockerelli	172	1	172	1		0
Lichmera indistincta	14, 46, 87, 94, 95, 106, 113, 124, 128, 141, 143, 148, 151, 155, 156, 162, 173, 174, 182, 205, 223, 224, 235, 236, 287	25	21, 52, 106, 113 151, 162, 261	7		0
Glycichaera fallax		0	135, 205	2		0
Melithreptus affinus	95, 150, 205	3	95, 150, 162, 205	4	95, 162, 205	3
Melithreptus lunatus	73, 90, 122, 128, 131, 150, 160, 162, 203, 205, 208, 256	12	73, 90, 97, 131, 148, 150, 162, 203, 205, 229	10	162	1
Melithreptus albogularis	34, 131, 150, 172, 205	5	13, 131, 150, 162, 172, 205, 262	7		0
Melithreptus brevirostris	71, 88, 90, 97, 113, 122, 150, 153, 165, 203, 206, 208, 254, 256	14	52, 53, 88, 90, 113, 150, 153, 203, 229, 269	10		0
Melithreptus validirostris	150, 205	2	95, 150, 162	3	205	1
Melithreptus gularis	3, 90, 98, 128, 150, 162, 197, 205, 208, 256	10	13, 54, 90, 98, 128, 150, 162, 197, 205, 264	10		0

Lichenostomus penicillatus	51, 55, 87, 90, 91, 130, 149, 174, 188, 205, 208, 254, 256, 259, 265, 273	16	21, 52, 54, 55, 90, 91, 147, 149, 152, 162, 174, 188, 198, 199, 205, 229, 265	17	162, 188, 198	3
Lichenostomus flavescens	104, 174, 205, 236	4	13, 162, 172, 205	4		0
Lichenostomus fuscus	17, 24, 127, 128, 136, 203, 205, 254	8	12, 54, 128, 152	4	128	1
Lichenostomus plumulus	25, 91, 180	3	52, 91, 162	3		0
Lichenostomus ornatus	91, 203, 205, 208	4	91, 162, 192, 203, 205	5		0
Lichenostomus keartlandi	87, 91	2	87, 91, 148, 162	4		0
Lichenostomus cratitius	37, 88, 90, 91, 153, 162, 205, 208	8	54, 90, 91, 97, 153, 162, 205, 229	8	162	1
Lichenostomus melanops	17, 45, 63, 121, 122, 127, 128, 137, 140, 200, 203, 205, 276	13	52, 53, 63, 121, 128, 137, 165, 200, 203, 205, 276, 277	12	165	1
Lichenostomus flavicollis	240	1	162, 203, 240	3	162	1
Lichenostomus leucotis	91, 104, 153, 208, 222	5	52, 53, 91, 124, 153, 162, 222, 252	8	162	1
Lichenostomus flavus	172	1	61, 172, 205	3		0
Lichenostomus unicolor	174	1	162, 262	2	152, 162, 262	3
Lichenostomus fasciogularis	76, 132	2	132	1		0
Lichenostomus versicolor	–		–		–	
Lichenostomus virescens	87, 90, 91, 116, 143, 155, 196, 205, 236, 270, 278	11	13, 53, 90, 91, 162, 172, 174, 194, 196, 205, 227	11	13, 53, 54, 91, 116,, 148, 162, 196, 205, 228	10
Lichenostomus frenatus	27, 95, 205	3	205	1		0
Lichenostomus chrysops	51, 71, 87, 90, 94, 122, 128, 205, 208, 212, 256	11	52, 71, 87, 90, 94, 128, 152, 162, 205	9	128, 162, 203, 204, 205, 289	6
Meliphaga albilineata	262	1	234, 262	2	234, 261, 262	3

Honeyeater species	Nectar	No. of obs	Insects	No. of obs.	Fruit	No. of obs
Meliphaga gracilis	66	1	66	1	66, 172	2
Meliphaga notata	205	1	205	1	44, 148, 172, 205	4
Meliphaga albilineata	33, 66, 115, 145, 205	5	26, 52, 66, 115, 162, 203, 205	7	33, 52, 53, 66, 71, 75, 95, 115, 145, 152, 162, 203,205	13
Xanthotis flaviventer	173, 205	2	172, 205	2	205	1
Xanthotis macleayana	14, 34, 66, 205	4	66, 205	2	66, 205	2
Manorina melanotis		0	4, 43, 162, 252	4	162	1
Manorina flavigula	90, 100, 205, 208, 237	5	13, 21, 52, 55, 90, 101, 162, 198, 199, 202, 205, 262	12	162, 174, 199	3
Manorina melanocephala	48, 77, 90, 191, 203, 205, 256	7	48, 52, 77, 90, 147, 152, 162, 191, 203, 205	10	162, 191, 203, 205	4
Manorina melanophrys	177, 205	2	162, 203, 205, 245, 253, 275	6		0
Entomyzon cyanotis	115, 170, 172, 203 205	5	54, 115, 170, 172, 203, 205, 262	7	54, 115, 170, 203, 205	5
Xanthomyza phrygia	41, 95, 127, 128, 148, 162, 163, 205	8	41, 52, 58, 128, 162, 163, 185, 203, 205	9	128, 162, 203, 205	4
Philemon citreogularis	123, 148, 162, 168, 174, 205, 236, 271	8	21, 54, 123, 148, 162, 168, 172, 187, 205, 262	10	54, 71, 162, 187, 205	5
Philemon corniculatus	14, 17, 46, 148, 156, 203, 205, 221	8	128, 148, 156, 162, 203, 205, 221	7	6, 52, 71, 156, 162, 203, 204, 205	8
Philemon argenticeps	13, 14, 148, 156, 172, 205, 262	7	13, 148, 156, 172, 262	5	205	1
Philemon buceroides	148, 186	2	148, 186, 207	3	186	1
Plectorhyncha lanceolata	79, 95, 129, 174, 178, 179, 205, 206 208	9	54, 95, 129, 162, 192, 203, 205	7	95, 129, 162, 205	4

Acanthagenys rufogularis	87, 90, 128, 148, 162, 195, 203, 205, 208, 254	10	57, 90, 148, 162, 195, 202, 203, 205	8	57, 71, 148, 162, 194, 195, 203, 205	8
Anthochaera chrysoptera	2, 15, 46, 64, 85, 90, 97, 122, 127, 143, 152, 155 159, 162, 183, 193, 203, 205, 208, 221, 256, 288	22	53, 71, 85, 90 152, 153, 162, 164, 183, 193, 203, 205, 221	13	15, 71 162, 205	4
Anthochaera paradoxa	85, 152, 162, 205, 240	5	85, 152, 162, 164, 205	5	162	1
Anthochaera carunculata	2, 12, 45, 64, 74, 80, 88, 90, 100, 128, 138, 147, 148, 152, 153, 162, 203, 205, 208, 221, 238, 239, 256	23	53, 74, 80, 90, 97, 128, 148, 152, 153, 162, 164, 203, 205, 221	14	74, 162, 194, 203, 204, 205, 228	7

TABLE 2. Summary of feeding observations on Australian honeyeater genera.*

Honeyeater genus	Percentages of feeding records			
	Nectar	Insects	Fruit	*n*
Myzomela	59	37	5	41
Certhionyx	66	29	6	35
Acanthorhynchus	74	23	2	43
Lichmera	78	22	0	32
Phylidonyris	56	51	3	122
Melithreptus	48	44	5	95
Grantiella	18	0	82	17
Lichenostomus	43	44	13	215
Meliphaga/Xanthotis	26	28	46	54
Manorina	32	50	18	44
Entomyzon/Xanthomyza	34	42	24	38
Philemon	36	36	28	69
Plectorhyncha/Acanthagenys	41	33	26	46
Anthochaera	52	35	13	92

*Genera listed in approximate order of increasing size (see Keast, 1976).

sists of following individual birds for fairly short periods of time and recording the amounts of time spent in the three feeding categories (Keast & Condon 1968; Recher & Abbott 1970b; Halse 1978). The average percentages of feeding *time* spent in the feeding categories are then calculated for each species. Both of these methods contain biases since, for example, a bird that is nectar-feeding may be more or less likely to be noticed by a human observer than one that is feeding on insects. The two methods however, should be roughly equivalent and should be particularly useful when comparing different species or the same species at different times. A summary of the data so far obtained for honeyeaters using these methods is presented in Table 3. In the following discussion the two forms of data are lumped as no significant overall difference was found between them.

The following conclusions can be drawn from Table 3:

(1) Different studies of the same species yield quite different estimates of the relative dietary importance of nectar, insects and fruit. *Lichenostomus leucotis*, for example, was found by Recher & Abbott (1970) to spend an average of 28% of feeding time taking nectar but Keast & Condon (1968) did not record any nectar-feeding by this species.

(2) Despite the fact that eleven of the species in Table 3 were included above in the group of honeyeaters that feed to a significant extent on fruit, only two of these species and none of the others were recorded as feeding on fruit. The two exceptions, *Lichenostomus virescens* and *Meliphaga lewinii/gracilis* were observed taking fruit on 5 and 21% of occasions, respectively (Ford & Paton 1976a; Crome 1978). These observations suggest that, for all but a few honeyeater species, fruit plays a negligible dietary role. This view is somewhat reinforced by noting that many of the records of fruit-eating in honeyeaters come either from stomach contents analyses where presence or absence of various food types are recorded (e.g. Cowles 1967; Morgan 1919, 1930, 1932; Lea & Gray 1936; Macgillivray 1914; White 1917a,b; Barnard 1914; Cleland 1910, 1911, 1912) or from observations of honeyeaters feeding in gardens or orchards (e.g. Wolstenholme 1929; Norton 1922; McNamara 1937; Dickison 1935; Barry 1928; Austin 1907). More quantitative data are needed before the importance of fruit will be clear.

(3) Honeyeater species belonging to the same genus tend to be somewhat similar with respect to the relative contributions of nectar and insects to their diets and consistent inter-generic differences are apparent. Treating each estimate of the relative dietary importance of nectar as a separate data point, the average dietary contributions of nectar are 17% for the genera *Meliphaga* and *Xanthotis*, 22% for *Lichenostomus*, 28% for *Manorina*, 31% for *Melithreptus*, 39% for *Acanthorhynchus*, 38% for

TABLE 3. Summary of Honeyeater feeding record data

| Honeyeater species | Method* | Time of year† | Percentage of feeding observations and feeding time | | | |
			Nectar	Insects	Fruit	Source
Myzomela obscura	0	All year	26	74	0	Crome (1978)
Certhiomyx niger	0	All year	50	50	0	Ford (1978b)
Certhiomyx niger	t	Sept.	93	7	0	Halse (1978)
Acanthorhynchus superciliosus	t	Sept.	54	46	0	Halse (1978)
Acanthorhynchus tenuirostris	0	All year	27	73	0	Keast (1976)
	0	All year	54	46	0	Ford & Paton (1977)
	t	Dec.	20	80	0	Keast & Condon (1968)
Phylidonyris melanops	0	All year	42	58	0	Ford (1978b)
	t	Dec.	100	0	0	Keast & Condon (1978)
Phylidonyris nigra	0	Mainly Mar. to Oct.	22	78	0	Recher (1977)
	t	May to Oct.	98	2	0	Recher & Abbott (1970b)
	t	Sept.	72	28	0	Halse (1978)
Phylidonyris novaehollandiae	0	Sept.	90	10	0	Keast (1975)
	0	All year	59	41	0	Ford & Paton (1977)
	0	Mainly Mar. to Oct.	22	78	0	Recher (1977)
	t	Dec.	60	40	0	Keast & Condon (1968)
Phylidonyris pyrrhoptera	t	Dec.	15	85	0	Keast & Condon (1968)
Lichmera indistincta	0	Sept.	20	80	0	Keast (1975)
	t	Sept.	99	1	0	Halse (1978)
Melithreptus lunatus	0	All year	24	76	0	Ford & Paton (1977)
Melithreptus brevirostris	0	All year	35	65	0	Ford & Paton (1977)
	t	Dec.	2	98	0	Keast & Condon (1968)
	t	Sept.	97	3	0	Halse (1078)
Melithreptus gularis	0	All year	18	82	0	Ford & Paton (1977)
Melithreptus spp.	0	Spring	10	90	0	Keast (1968b)
Lichenostomus penicillatus	0	All year	31	69	0	Ford & Paton (1976a)
Lichenostomus plumulus	0	All year	12	88	0	Ford & Paton (1976a)

Honeyeater species	Method*	Time of year†	Percentage of feeding observations and feeding time			
			Nectar	Insects	Fruit	Source
Lichenostomus ornatus	0	All year	24	76	0	Ford & Paton (1976a)
Lichenostomus keartlandi	0	All year	35	65	0	Ford & Paton (1976a)
Lichenostomus cratitius	0	All year	38	62	0	Ford & Paton (1976a)
	t	Dec.	0	100	0	Keast & Condon (1968)
Lichenostomus leucotis	0	All year	11	89	0	Ford & Paton (1976a)
	t	Dec.	0	100	0	Keast & Condon (1968)
	t	May to Oct.	28	72	0	Recher & Abbott (1970b)
Lichenostomus virescens	0	All year	26	69	5	Ford & Paton (1976a)
Lichenostomus chrysops	0	All year	38	62	0	Ford & Paton (1976a)
Meliphaga lewinii and *M. gracilis*	0	All year	18	61	21	Crome (1978)
Xanthotis macleayana	0	All year	16	79	5	Crome (1978)
Manorina flavigula	0	All year	30	70	0	Ford (1978b)
Manorina melanocephala	0	All year	25	75	0	Ford (1978b)
Acanthagenys rufogularis	0	All year	50	50	0	Ford (1978b)
Anthochaera chrysoptera	0	All year	79	21	0	Ford (1978b)
	t	Dec.	0	100	0	Keast (1976)
Anthochaera carunculata	0	All year	15	85	0	Keast (1976)
	0	All year	67	33	0	Ford & Paton (1977)
	t	Dec.	15	85	0	Keast & Condon (1968)

*'0' indicates percentages of feeding observations 't' indicates percentages of feeding times.

†Locations of studies: Keast & Condon (1968): Kangaroo Is., S.A.; Recher & Abbott (1970): Brisbane Water Nat. Pk., N.S.W.; Ford & Paton (1976a) Near Adelaide and on Kangaroo Is., S.A.; Ford & Paton (1977): Near Adelaide, S.A.; Ford (1978): Near Adelaide, S.A.; Keast (1975): Yundurup, W.A.; Keast (1976): East and south Australia; Crome (1978): Near Innisfail, Qld.; Halse (1978): Near Perth, W.A.

Anthochaera and *Acanthagenys*, 56% for *Myzomela* and *Certhionyx*, 57% for *Phylidonyris*, and 60% for *Licherma*. Thus, as noted by Keast (1976), the genera *Acanthorhynchus*, *Anthochaera*, *Acanthagenys*, *Myzomela*, *Certhionyx*, *Phylidonyris* and *Lichmera* tend to have relatively pronounced nectar components of their diets while the genera *Meliphaga*, *Xanthotis*, *Lichenstomus*, *Manorina* and *Melithreptus* tend to be rather less nectarivorous.

It is not possible to determine from Table 3 the extent to which location and season affect honeyeater diets. Such effects would however, be expected and some indication of their existence can be gained from the literature. Keast (1968), for example, stated that members of the genus *Melithreptus* are more nectarivorous in autumn and winter than in spring and summer.

At this point it is possible to compare the diets of honeyeaters with the diets of hummingbirds, the best known family of nectarivorous birds. One difference is immediately apparent. Hummingbirds do not, except under very unusual circumstances (Smith 1926) feed on fruit, and they rarely feed on tree sap (Wright & Wright 1918). Instead, they feed virtually entirely on nectar and 'insects' (i.e. insects plus spiders) (Wagner 1946; Bent 1940; Skutch 1972). Hence, at this level, a hummingbird diet is essentially the same as the diets of most honeyeaters. A more quantitative comparison reveals differences, however.

Quantitative data on hummingbird diets come from two sources. One source is 'time budget' studies in which individual birds are followed closely for long periods of time and the fractions of time spent by each bird in various activities are calculated. These activities are usually categorized as sitting, aggressive interactions, nectar feeding and insect feeding (e.g. Pearson 1954; Stiles 1971; Wolf & Hainsworth 1971; Wolf 1975; Carpenter 1976) though sometimes a single 'feeding' category is used (e.g. Schemske 1975). In cases where nectar and insect feeding are separated the relative times devoted by the birds to these two kinds of feeding are readily calculated. A summary of available time-budget data for hummingbirds is presented in Table 4. The second source of data on hummingbirds' diets consists of data on the relative numbers of insect and nectar feeding observations for each species (Snow & Snow 1972; Lack 1976). This

source is the same as the principal source of data on honeyeater diets that is described above. Table 5 contains a summary of these data for hummingbirds.

These two sources of data on hummingbirds should differ greatly in terms of biases. Selection for study of hummingbirds which can be followed for long periods of time creates a bias towards the selection of birds which are defending small, flower-based territories containing relatively high flower densities (see Table 4). Non-territorial birds are likely to encounter lower flower densities (Colwell 1973; Feinsinger & Chaplin 1975; Stiles 1975; Linhart 1973; Wolf *et al*. 1976; Feinsinger 1976). If energy is of principal importance to the birds, then the relative dietary importance of nectar should increase as the encountered flower density increases since the net rate of energy intake from nectar should increase as flower density increases. Hence nectar should contribute more to the diets of territorial birds than to those of nonterritorial birds. Nectar should therefore appear to be a more important dietary component in the time budget studies than in the studies which present data from accumulated feeding observations and which should tend to include a closer-to-random sample of territorial and nonterritorial birds.

Despite differences in the two sources in terms of biases, a consistent dietary pattern is apparent. Tables 4 and 5 show that, with the exception of nesting females, hummingbirds spend the vast majority of their feeding time taking nectar rather than insects. The nesting females studied by Carpenter (1976), on the other hand, spend about twice as much time taking insects as taking nectar. Excluding these nesting females, the average percentage of feeding time spent taking nectar in Table 4 is 89%. Including them, the average is 84%. The average percentage of feeding records that were of nectar feeding is, from Table 5, 86%. Thus hummingbirds appear to be, in general, considerably more nectarivorous than even the most nectarivorous genera of honeyeaters which were seen taking nectar on an average of only about 60% of feeding observations (see above). Despite differences in potential biases, the results of Tables 4 and 5 are extremely similar.

It is possible, however, that the above analysis has exaggerated the difference between hummingbirds and honeyeaters in terms of dietary

TABLE 4. Summary of time budget data on foraging by hummingbirds

| Hummingbird species | Sex | Situation | Percentage of feeding time | | Source |
			Nectar	Insects	
Calypte anna	♂	Breeding territory	88	12	Stiles (1971), Fig.2
Calypte anna	♂	Breeding territory	88	12	Stiles (1971), Fig.2
Calypte anna	♂	Breeding territory	86	14	Stiles (1971), Fig.2
Calypte anna	♂	Non-breeding territory	91	9	Stiles (1971), Fig.1
Calypte anna	♂	Non-breeding territory	96	4	Pearson (1954)
Eulampis jugularis	♂	Mistletoe territory	95	5	Wolf & Hainsworth (1971)
Eulampis jugularis	♂	Myrtaceae territory	98	2	Wolf & Hainsworth (1971)
Eulampis jugularis	♂	*Inga* sp.	79	21	Wolf & Hainsworth (1971)
Eulampis jugularis	♂	Banana territory	94	6	Wolf & Hainsworth (1971)
Eulampis jugularis	♂	*Heliconia* sp.	85	16	Wolf & Hainsworth (1971)
Eulampis jugularis	♂	*Inga Hibiscus* territory	95	5	Wolf & Hainsworth (1971)
Calypte anna	♂	*Fuchsia* territory	97	5	Wolf & Hainsworth (1971)
Eulampis jugularis	♂	*Heliconia caribea* territory	78	22	Wolf (1975)
		Musa sp. territory	94	6	Wolf (1975)
		Inga vera	60	40	Wolf (1975)
		Ichnosiphon sp.	98	2	Wolf (1975)
Ensifera ensifera	?	Non-territorial	100	0	Hainsworth & Parker (unpublished data)
Colibri coruscans	?	Territorial, caring for young	92	8	Hainsworth (1975)
	?	Territorial, without young	97	3	Hainsworth (1975)
Oreotrochilus estella	♀	Territorial, in-cubating or brooding	28	72	Carpenter (1976)
Oreotrochilus estella	♀	Territorial, feeding young	39	61	Carpenter (1976)
	♂	Non-territorial, non-breeding	96	4	Carpenter (1976)
Oreotrochilus estella	♂ & ♀	Territorial, non-breeding	67	33	Carpenter (1976)
		Average:	84	16	

TABLE 5. Summary of hummingbird feeding record data

Hummingbird species	Percentages of feeding observations		
	Nectar	Insects	Source
Glaucis hirsuta	69	31	Snow & Snow (1972)
Phaethornis guy	92	8	Snow & Snow (1972)
Phaethornis longuemareus	92	8	Snow & Snow (1972)
Anthracothorax nigricollis	62	38	Snow & Snow (1972)
Florisuga mellivora	85	15	Snow & Snow (1972)
Chrysolampis mosquitos	91	9	Snow & Snow (1972)
Chlorestes notatus	86	14	Snow & Snow (1972)
Amazilia chionopectus	87	13	Snow & Snow (1972)
Saucerottia tobaci	93	7	Snow & Snow (1972)
Glaucis hirsuta	87	13	Snow (1973)
Phaethornis superciliosus	96	4	Snow (1973)
Phaethornis ruber	90	10	Snow (1973)
Anthracothorax mango	76	24	Lack '1976)
Trochilus polytmus	87	13	Lack (1976)
Mellisuga minima	92	8	Lack (1976)
Average:	86	14	

importance of nectar. It could be argued as mentioned above, that the time budget studies overrate the general importance of nectar. It could also be argued that the records of hummingbird feeding were all obtained on tropical islands where nectar sources are readily available throughout the year and should therefore be compared with similar data on tropical honeyeaters or with honeyeater data obtained only at times of moderate to high nectar availability. Furthermore in Australian honeyeaters, both sexes are involved as a rule, in nesting activities such as feeding the young (Officer 1964), whereas, in hummingbirds, it is almost invariably just the female who performs these tasks (Wolf & Stiles 1970). Since growing nestlings require insect protein, it follows that comparisons should be made only between birds of similar nesting status. The hummingbird data could be biased relative to the honeyeater data towards a greater representation of non-nesting birds and hence of nectar in the diet. Many more data are necessary to clarify this issue.

Dietary selectivity

Honeyeaters, like other animals, appear to be selective in their foraging. They do not take nectar from all available plant species but tend, like other nectar-feeding birds, to take nectar from

plants which have red or orange flowers (Sargent 1928; personal observations) and which produce moderate to high nectar volumes (Ford 1978b; Paton & Ford 1977; personal observations) and many of which have long tubular-shaped flowers (Ford 1976b; Ford 1978b; Paton & Ford 1977; personal observations). This does not necessarily mean that honeyeaters have a preference for, say, red flowers as their selection could be based solely on nectar content of flowers and their tendency to feed on such coloured flowers could arise from the correlation between flower colour and nectar content. The reverse could also be true. Hummingbirds appear to select plant species on the basis of the energy content of the nectar and to use such plant traits as flower colour, only as easily changeable cues (Bene 1941, 1945; Grant 1966; Stiles 1976). Honeyeaters may forage in similar fashion. Both honeyeaters and hummingbirds sometimes feed on plants which have flowers which are neither tubular nor red (Sargent 1928; Grant & Grant 1968).

Different species of honeyeaters tend to select different plant species when foraging for nectar in the same place (Ford 1976b; Ford & Paton 1977; Ford 1979; Keast & Condon 1968; Paton & Ford 1977; Recher & Abbott 1970b). Though data are scant (Recher & Abbott 1970b; Ford & Paton 1977; Ford 1979), both bill length and body size appear to be involved in determining these differences. Recher & Abbott (1970b)

explained the differences in plant preferences shown by *Lichenostomus leucotis* and *Phylidonyris nigra* on the basis of bill length, the shorter-billed *L. leucotis* having more difficulty reaching the nectar in some situations. Ford & Paton (1977) have found that the small, short-billed species (*Lichenomstomus, Melithreptus*) (bill length <16 mm) tended to feed on open cup-shaped flowers (*Eucalyptus*), the small to medium sized, medium-billed species, (*Acanthorhynchus, Phylidonyris*) (bill length between 16 and 21 mm) fed from a wide-range of plants, including both those with short, open flowers and those with long tubular flowers (e.g. *Epacris, Astroloma*) and the large long-billed species (*Anthochaera*) (bill lengths >21 mm) concentrated on short, open flowers (*Eucalyptus, Xanthorrhoea*) and various *Banksia* species which have flowers that are effectively of medium length. Ford (1979) found a similar pattern but also found that *Acanthorhynchus tenuirostris* had a greater preference for long, tubular flowers than the larger but shorter-billed *Phylidonyris novaehollandiae*. Paton & Ford (1977) found that honeyeaters are quite generalised in their nectar-feeding behaviour and did not note any selectivity patterns. Terborgh & Diamond (1970) argue that several honeyeater species in New Guinea are opportunistic in their nectar foraging.

Plant preferences of honeyeaters should be based on both bill length and body size. Firstly, bill length relative to corolla length should affect the amount of nectar that can be removed from a flower, the rate at which this nectar can be removed and the time required to insert and remove the bill, just as it does in hummingbirds (Hainsworth & Wolf 1976; Hainsworth 1973; Wolf & Hainsworth 1971). Secondly, as honeyeaters almost always perch while taking nectar, the speed with which they move between flowers on a plant may be greatly affected by their size. For example, many plants with long, tubular flowers have their flowers attached to slender, flexible stems which bend considerably under the weight of a large honeyeater (e.g. *Epacris, Astroloma*). While attempting to feed on such tubular flowers a large honeyeater such as *Anthochaera* spp. would be expected, as was observed by Paton & Ford (1977), to be slow and clumsy. On the other hand, in situations where the flower-supporting stems are relatively stiff and where several flowers can be reached by

a bird without changing perching positions, larger honeyeaters may be able either to reach more flowers without changing perches or to move the head between the flowers more quickly than smaller honeyeaters. Members of the plant genus *Eucalyptus* often offer this sort of nectar-feeding situation (personal observations) and so perhaps it is not surprising that these plants appear to be preferred by the large *Anthochaera* spp. (Ford & Paton 1976b; Ford 1979). In fact Ford (1979) found that the rates of flower visitation of various honeyeater species on two species of *Eucalyptus* were positively correlated with honeyeater body size in both cases (see Table 3 of Ford 1979).

Some additional insights into the relative importance of bill length and body size can be gained by further examination of the data presented in Table 3 of Ford (1979). Data on rates of flower visitation are given for several honeyeater species feeding on *Astroloma conostephioides*, a plant with long, tubular flowers arranged in small aggregations on somewhat flexible stems. The average corolla length is 20.9 mm (Paton & Ford 1977). In this case the two honeyeater species with bill lengths less than 13 mm (*Lichenostomus chrysops*, and *Melithreptus brevirostris*) both had equally low visitation rates (24 and 25 flowers/min respectively) as might be expected since their rate of nectar removal from the flowers would probably have been reduced by the long distance that they would have to extend their tongues to reach the nectar (Wolf & Hainsworth 1971; Hainsworth 1973; Hainsworth & Wolf 1976). Amongst the three species which had longer bills (*Phylidonyris novaehollandiae*, bill length 19.7 mm; *P. pyrrhoptera*, 17.1 mm; *Acanthorhynchus tenuirostris*, 22.5 mm (Ford 1979) and which would all have had no difficulty in reaching the nectar, the two larger species (*Phylidonyris* spp.) had equally high visitation rates (34 flowers/min each) whereas the smaller *Acanthorhynchus* had a low visitation rate (26 flowers/min). This suggests that, for those species readily able to reach the nectar of *A. conostephioides*, the flower visitation rate may largely depend on the abilities of each species to move the head from one flower to another, possibly without changing perches. Ford (1979) also presents data for two honeyeater species (*P. novaehollandiae* and *A. tenuirostris*) feeding on *Epacris impressa*. This plant has quite flexible stems from which are borne

medium length tubular flowers. The average corolla length is 13.7 mm (Paton & Ford 1977). In this case both honeyeater species have bills longer than the flowers and the small *Acanthorhynchus* has a visitation rate of 50% higher than the larger *Phylidonyris*. *P. novaehollandiae* weighs about twice as much as *A. tenuirostris* (Ford 1979). Hence, it appears that, in this case, the visitation rate may depend largely on agility. The above tentative suggestions do, however, require considerably more investigation.

Honeyeater body size may also affect the plants included in their diets through its effect on the outcome of interspecific interactions (Ford 1979). Larger species are usually dominant over small species (Immelmann 1961; Ford 1979). Hence the smaller species may be excluded, partially or completely, from some nectar-sources (Ford 1979).

Different species of hummingbirds also tend to feed on different plant species (e.g. Stiles 1975; Feinsinger 1976; Wolf *et al*. 1976; Snow & Snow 1972; Colwell 1973; Lack 1976). Just as in the case of honeyeaters, however, no general explanation for these differences has emerged. Snow & Snow (1972) and Stiles (1975) found correlations between the bill length and shape of each hummingbird species and the average length and shape of the corollas of their nectar sources. Wolf *et al*. (1976) found a correspondence between bill length and corolla length for several hummingbird species. Several authors have found that some short-billed hummingbird species do not visit certain plants with long corollas that are visited by long-billed species (e.g. Colwell 1973; Lack 1976). Interspecific aggressive interactions have also been found to affect the plant species fed upon by each hummingbird species, some bird species being completely or partially excluded from some nectar sources by other birds (e.g. Feinsinger & Chaplin 1975; Colwell 1973; Wolf *et al*. 1976; Lyon 1976; Feinsinger 1976; Linhart 1973). The wing disc loading, or ratio of body weight to area swept out by the wings, may tend to be higher in territorial species and sexes of hummingbirds than in non-territorial birds (Feinsinger & Chaplin 1975). In other words, heavy hummingbird species tend to be territorially dominant over lighter species (all other things being roughly equal) (Stiles & Wolf 1970), whereas, for similiarly weighted species, the small-winged species tend to be dominant over the larger-winged species. Data are not presently available on the relationship between hummingbird body size and flower visitation rates, though it might be expected that little relationship will occur since most hummingbirds almost invariably hover while taking nectar (Wagner 1946) and do not face any problems of bending flower stems. Hence the same factors that affect honeyeater selectivity with respect to plant nectar sources also appear to affect hummingbird selectivity with the possible addition of bill shape and exception of body size as it affects visitation rates.

Honeyeaters are also likely to be selective in their foraging on insects and on fruits. It might be expected, for example, that those species with large, thick bills would tend to feed on larger fruit and/or insects than the species with short, thin bills. There are apparently, however, no data available on this aspect of honeyeater foraging. The same also appears to be true for insect foraging by hummingbirds.

Hummingbirds, while foraging for nectar from a single plant species, appear to forage preferentially in patches of higher flower density (personal observations) and on plants with the highest number of flowers (e.g. Pyke 1978b). This would be expected if, as has been postulated (e.g. De Benedictus *et al*. 1978; Pyke 1978b) hummingbirds forage in such a way as to maximize their net rate of energy gain. No similar data are available for honeyeater foraging.

Flight mode while foraging for nectar

Honeyeaters and hummingbirds differ also in terms of their flight mode while feeding on nectar. Most honeyeaters almost invariably perch while taking nectar from a flower. A few relatively small species have, however, been observed hovering at flowers. These include *Acanthorhynchus tenuirostris* (Campbell 1900; Mattingley 1919; Hindwood 1944; Salter 1957; Gannon 1962; Officer 1964; Leach 1929; personal observations) (average weight, 10.8 g: Paton & Ford 1977), *A superciliosus* (Leach 1929) (approximately same size as *A. tenuirostris*), *Certhionyx niger* (Berney 1938) (average weight 7.8 g: Ford 1978a). *Myzomela sanguinolenta* (North 1906) (approximately same size as *C. niger*) and *Lichmera indistincta* (Halse 1978) (approximately same size as *C. niger*).

Most hummingbirds, on the other hand, hover while feeding on nectar (Wagner 1946). A few relatively large hummingbird species, however, often perch while taking nectar. These include *Oreotrochilus estella* (Wolf *et al.* 1975; Carpenter 1976) (average weight, 8.4 g: Carpenter 1976), *Eutoxeres aguila* (Wolf *et al.* 1975) (average weight, 10–11.5 g: Hainsworth & Wolf 1972). Perching while taking nectar has also been observed for *Atthis heliosa* (Wagner 1946), the smallest of all hummingbirds (average weight 2.7 g: Lyon 1976). The size distributions of honeyeaters and hummingbirds are almost disjunct, there being very few hummingbird species weighing more than 9 g on average (Carpenter 1976) and no Australian honeyeaters weighing less than about 7 or 8 g on average. The smallest Australian honeyeater species, *Myzomela erythrocephala*, is about the same size as *Certhionyx niger* which has an average weight of 7.8 g (Ford 1978a). Thus, the largest hummingbird and the smallest honeyeater species, weigh about 9 g and include almost all the species which exhibit both hovering and perching modes of nectar feeding. In other words, treating hummingbirds and Australian honeyeaters as one large group of nectarivorous birds, there appears to be a size threshold of about 9 g with species larger than this threshold favouring the perching mode with species smaller than the threshold favouring hovering. Species near the threshold size show a tendency to be flexible with respect to the two feeding modes.

Assuming that nectarivorous birds forage for nectar in such a way that their net rates of energy gain are maximized, it is perhaps surprising that some of them hover while feeding, since this is considerably more costly than perching in terms of energy (Wolf *et al.* 1975). A possible explanation for the existence of the hovering mode of feeding is, however, that a hovering bird is able to visit flowers more rapidly than a perching bird. If this were the case, the increased gross rate of energy gain resulting from hovering rather than perching could outweigh the increased rate of energy expenditure. Since the difference between the rates of energetic expenditure of hovering and perching birds becomes larger as body weight increases, such a trade-off between rate of flower visitations and energetic cost is less likely to favour hovering as a bird's body weight increases. Hence this trade-off

could also explain the apparent threshold phenomenon described above.

Some data are available on the rates of flower visitation of honeyeaters and hummingbirds. Ford (1978b) measured the rates of flower visitation for a total of twenty honeyeater-plant species combinations. The average of these rates is 33 flowers/min (see Table 3 of Ford 1978b). Ford (1978b) also *estimated* flower visitation rates for *Phylidonyris novaehollandiae* feeding on seven plant species, each of which has flowers so close together in inflorescences that it is very difficult to tell when a bird has moved its bill from one flower to another. The average of these rates is 51 flowers/min (see Table 3 of Ford 1978b). This average is, as would be expected, higher than the previous average of rates which were all obtained for plants with relatively distinct flowers. By comparison, the available data of this kind for hummingbirds are very meagre and are summarized in Table 6. All of the plants listed in this table have distinct flowers with inter-flower distances that are similar to the plants for which Ford (1978b) was able to *measure* the visitation rates of honeyeaters (personal observations). The average of the hummingbird rates is 41 flowers/min which is somewhat higher than the average of Ford's (1978b) measured rates. The difference is not, however, significant ($P > 0.1$, t-test). Hence, honeyeaters as a group *may*, as postulated above, tend to have higher rates of flower visitation than hummingbirds as a group. More data, especially on hummingbirds, are required to settle the issue.

The clearest understanding of the relative advantages of hovering and perching while taking nectar is likely to come from studies of bird species which may engage in either feeding mode. *Acanthorhynchus tenuirostris* would be an excellent honeyeater species of this kind as it is often fairly common, appears to hover more often than other honeyeater species (see above), and adapts fairly readily to an aviary situation (personal observations).

Nectar quality and quantity

The nectar-foraging behaviours of both honeyeaters and hummingbirds are likely to be affected by the quality and quantity of nectar in the flowers they visit. It is therefore of interest to

TABLE 6. Rates of flower visitation for hummingbirds

| Hummingbird species | Visitation rate | | |
	Plant species	Flowers/min.	Source
Colibri coruscans	*Mutisia accuminata*	14	Hainsworth (1975)
Eugenes fulgens	*Centropogon talamancensis*	28	Wolf *et al*. (1976)
Selasphorus platycercus	*Ribes pinetorum*	41	Brown *et al*. (unpublished)
S. platycercus and	*Ipomopsis aggregata*	53	Pyke (1978b)
S. rufus	*Aquilegia formosa* and *Castilleja* sp.	~56*	Gass (1974)
S. platycercus	*Penstemon barbatus*	56	Hainsworth & Wolf (unpublished data)
S. sasin and *S. rufus*	*Castilleja* spp., *Penstemon bridgesii* *Ipomopsis aggregata*, *Aguililegia formosa*	20	Carpenter (1978)
S. rufus	*Rhamnus purshiana*	~60†	Gass (1978)
		Average: 41 flowers/min.	

*Depends on average nectar volume per flower (Gass, 1974).
†Rate 'often greater than 1 flower/sec.' (Gass, 1978).

TABLE 7. Energy content per flower encountered by hummingbirds

Hummingbird species	Plant species	Mean calories/ flower	Source
Eugenes fulgens	*Centropogon talamancensis*	2.86	Wolf *et al*. (1976)
Selasphorus platycereus and *S. rufus*	*Penstemon barbatus*, *Ipomopsis aggregata*\and *Castilleja integra*	1.61	Kodric-Brown & Brown (1978)
S. platycerus and *S. rufus*	*Ipomopis aggregata*	3.3	Watt *et al*. (1974)
Various species	*Ribes pinetorum*	0.25	Brown *et al* (unpublished)
"	*Chilopsis linearis*	0.63	"
S. flammula	*Salvia* sp.	1.34	Hainsworth & Wolf (1972)
S. platycerus and *S. rufus*	*Ipomopsis aggregata*	2.68	Pyke (1978)
S. sasin	*Penstemon bridgesii*	1.1	Carpenter (1978)
and *S. rufus*	*Ipomopsis aggregata*	0.2	(Calculated from Fig.1)
"	*Aquilegia formosa* (per spur)	1.1	"
"	*Castilleja linariaefolia*	1.2	"
"	*C. minoiata*	0.9	"
S. rufus	*Rhamnus purshiana*	0.24	Gass (1978)
Various species (Mexico)	13 different species	8.84	Cruden (1976)
S. platycerus and *S. rufus* (Colorado)	*Aquilegia elegantula* (per spur)	7.17	Pyke (unpublished)
"	*Castilleja miniata*	1.28	"
"	*C. linaerifolia*	1.00	"
Various species (Arizona)	*Fouquieria splendens*	1.26	"
	Castilleja integra	5.40	"
		Average: 4.80 calories ($n = 31$)	

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TABLE 8. Sugar concentrations in nectars from plants visited by honeyeaters near Sydney, N.S.W.

Plant species		Mean sugar concentrations (% by weight)	Sample size
(a)	Native species		
	Epacris longiflora	16	11
	Lambertia formosa	19	20
	Styphelia triflora	23	8
	Grevillea punicea	29	5
	G. banksii	17	6
	Callistemon linearis	26	3
	C. citrinus	17	1
	C. linearifolius	17	1
	Blandfordia nobilis	30	7
(b)	Cultivated species		
	Grevillea poorinda	16	3
	Anigozanthos viridus	19	5
	Correa decumbeus	19	1
	Calothamnus sp.	17	1
	Kennedia rubicunda	27	1
	Callistemon viminalis	15	2

Average: 20.4% ($n = 15$)

review what is known about nectar encountered by these two families of birds and to compare the two families on the basis of nectar.

Honeyeaters appear to encounter considerably more sugar, and hence obtain more calories, per flower than hummingbirds. Paton & Ford (1977), Ford (unpublished) and Pyke (unpublished) measured the mean caloric content of flowers of a variety of plants that are important nectar sources to honeyeaters. Treating the mean for each plant species as a single data point the average caloric content per flower was 9.4 calories for thirteen species considered by Paton & Ford (1977), 7.4 calories for twenty-two species of Ford (unpublished) and 12.0 calories for three species of Pyke (unpublished). Combining these data, the overall average is 8.4 calories/flower ($n = 38$). The available data of this kind for plants frequented by hummingbirds are summarized in Table 7. Except for the data of Cruden (1976), the highest of the mean caloric contents per flower of these plants is only 7.2 calories. The overall average, treating each plant species of each study as a single observation, is 4.8 calories which is about half the average value for flowers encountered by honeyeaters. That honeyeaters encounter more energy per flower than the smaller hummingbirds is in accord with a general tendency for the body weight of an animal and the average energy encountered per flower to be positively correlated (Faegri & van der Pijl 1971; Proctor & Yeo 1972; Heinrich & Raven 1972; Heinrich 1975; Pyke 1978a). Such a correlation is presumably the outcome of plant-animal coevolution and explanations for it must be sought in terms of advantage for both individual plants and individual animals (Pyke 1978a, 1979).

The sugar concentrations of the nectars encountered by honeyeaters and hummingbirds are much more similar than the energy contents per flower discussed above. Ford (unpublished) measured the sugar concentration in nectars from twenty-four species of plants frequented by honeyeaters and growing in South Australia. The average of these nectar concentrations is 21.7% by weight of sucrose equivalents (see Hainsworth & Wolf 1972a; Ford 1979 for discussions of the methods of determining sugar concentration). During the period from October 1977 to May 1978, using the same methods as above, I measured the nectar sugar concentrations in honeyeater frequented plants growing near Sydney, New South Wales. These data are presented in Table 8. The average of these sugar concentrations is 20.4% by weight of sucrose equivalents ($n = 15$). Combining the two sets of data the overall average sugar concentration for

plants visited by honeyeaters is 21.2% ($n = 39$, s.d. $= 5.8$, s.e. $= 0.9$). The considerably greater amount of data for plants frequented by hummingbirds is summarized in Table 9. The overall average concentration for the hummingbird plants is 24.3% ($n = 197$). The standard deviation, calculated from all species for which data on nectar concentration are available, is 9.4 ($n = 155$). Thus the average nectar concentration in flowers of honeyeater plants is slightly less than that in flowers of hummingbird plants. The difference is statistically significant ($P<0.01$, Student t-test) but could possibly be due to biases in the data sources. The mean nectar concentration for temperate hummingbird plants (27.5 ± 1.2, $n = 61$) is also significantly greater than that for honeyeater plants, all of which have so far come from temperate parts of Australia ($P < 0.01$, student t-test).

The average sugar concentration for the various groups of hummingbird plants are all very similar and, contrary to the suggestion of Baker (1975), there is no significant difference between lowland tropical and highland tropical species ($P > 0.10$, student t-test). The average for the temperate species is, however, significantly greater than that for all tropical species ($P = 0.02$, Student t-test).

Since both honeyeaters and hummingbirds are important pollinators of the plants they visit, the rate of nectar production per flower, the average standing crop of energy per flower and the sugar concentration of the nectar should all represent the outcome of a long coevolutionary process involving both plants and animals. I have discussed elsewhere the adaptive nature of the observed patterns in terms of flower energy content (Pyke 1978a, 1979). The adaptive significance of nectar concentration has, however, received scant attention (Baker 1975).

Flower density

Another factor which would be expected to have an influence on the foraging behaviour of nectarivorous birds is the density (or total number) of flowers in a bird's foraging area. For both honeyeaters and hummingbirds, however, there are few data presently available on the densities of flowers encountered. (Honeyeaters: Ford,

unpublished; Hummingbirds: Lyon 1976; Gass *et al.* 1976; Kodric-Brown & Brown 1978). Consequently it is not possible to make quantitative comparisons between the flower densities usually encountered by honeyeaters and hummingbirds. My own observations, however, suggest that hummingbirds usually encounter higher flower densities than do honeyeaters. The often-extensive and densely-flowering plant patches in which North American hummingbirds defend territories seem to have few counterparts in Australia (personal observations). Perhaps it is for this reason that territoriality in hummingbirds has been reported so frequently and has been extensively studied many times (e.g. Armitage 1955; Cody 1968; Wolf 1969, 1975; Stiles 1971; Wolf & Hainsworth 1971; Lyon 1976; Stiles & Wolf 1970; Gass *et al.* 1976; Kodric-Brown & Brown 1978; Pitelka 1942) whereas territoriality in Australian honeyeaters is seldom mentioned (Bell 1966; Recher & Abbott 1970b; Baldwin 1972). This also provides a possible explanation for the apparently higher dietary importance of nectar to hummingbirds as compared with honeyeaters. Reliance on nectar as the source of energy, for both honeyeaters and hummingbirds, may be greater for territorial individuals than for non-territorial ones.

Predation

Predation, or rather, potential predation may also affect behaviour in general and foraging behaviour in particular. In the case of hummingbirds there are extremely few reports of predation attempts (Mayr 1969), and most authors have simply not considered predation, focussing instead on the energetic aspects of hummingbird behaviour (Hainsworth 1978; Wolf & Hainsworth 1971; Wolf *et al.* 1972; Gass *et al.* 1976; De Benedictus *et al.* 1978; Pyke 1978b). In the case of honeyeaters, however, there appear to be a greater number of reports of predation attempts (Gilbert 1923; Slater 1961; Leach 1928; Chaffer 1944; Kaveney 1958; Czechura 1971; Lord 1948). Hence predation risk could affect various aspects of honeyeater foraging, such as the tendency of a bird to feed in exposed situations, and should not be neglected without careful consideration.

TABLE 9. Sugar concentrations in nectars from plants visited by hummingbirds

Plant species	Location	Mean nectar concentration (% by weight)	Source
(a) Tropical highland habitats			
9 species	Mt Pichincha, Canada	28%	Hainsworth & Wolf (1976) (Table 2)
11 species	Villa Mills, Costa Rica (3100 m)	17%	Hainsworth & Wolf (1972a) (Table 2)
12 species	Cerro de la Muerte, Costa Rica (3100 m)	20%	Wolf et al. (1976) (Appendix 1)
10 species	Mountains, Costa Rica (1000–2000 m)	21%	Baker (1975) (Table 3)
Salvia sp.	Villa Mills, Costa Rica (3100 m)	33%	Hainsworth & Wolf (1972b)
Tropaeolum sp.	" "	33%	"
Passiflora mollisima	Marcapata, Peru (2800 m)	31%	Hainsworth & Parker (Unpublished data)
Mutisia accuminata	Tamboraque, Peru (3000 m)	28%	Hainsworth (1977)
	All tropical highland species: 22.3% (n = 46)		
(b) Tropical lowland habitats			
29 tree and leaves species	Costa Rica	21%	Baker (1977) (Table 2)
11 species	Villa Mills, Costa Rica (3100 m)	37%	Hainsworth & Wolf (1972a) (Table 2)
9 species	La Selva, Costa Rica (140 m)	31%	Stiles (1975) (Table 5)
12 species	La Selva, Costa Rica (140 m)	20%	Baker (1975) (Table 3)
8 species	Guanacaste, Costa Rica (100 m)	24%	"
	All tropical lowland species: 25.0% (n = 69)		

(c) *Tropical island habitats*

9 species				
Mandevilla hirsuta	Jamaica	21%		Percival (1974) (Table 1)
Hamelia patens	Trinidad	39%		Feinsinger & Colwell (1978)
Heliconia wagneriana	Trinidad	19%		Feinsinger & Colwell (1978)
	Trinidad	32%		Feinsinger & Colwell (1978)

All tropical island species: 23.3% (n = 12)

(d) *Temperate habitats*

21 species	California	21%		Baker (1975) (Table 3)
13 species	Arizona (700–2900 m)	35%		Hainsworth (1973) (Table 3)
13 species	Mexico	21.1%		Cruden (1976) (Table 6)
Ipomopsis aggregata	Gothic, Colorado (3000–)	18%		Pyke (unpublished)
Aquilegia elegantula	"	47%	33% (n=3)	"
Castilleja miniata	"	35%		"
Echinocereus triglochidiatus	Arizona (300–1600 m)	29%		Pyke (unpublished)
Castilleja integra	"	38%		"
C. lanata	"	44%		"
Penstemon eatoni	"	32%		"
Salvia Henryi	"	50%	37% (n=11)	"
S. Greggii	"	53%		"
Stachys coccinea	"	42%		"
Fouquieria splendens	"	21%		"
Beloperone californica	"	39%		"
Anisacanthus thurberi	"	35%		"
Mimulus cardinalis	"	23%		"

All temperate species: 27.5% (n = 61)

(e) *Other*

9 non-native species	Berkeley, California	22.0%	Baker (1975) (Table 3)

All species from all habitats: 24.6% (n = 197)

Perhaps the apparent difference in predation intensity between hummingbirds and honeyeaters is due to their different sizes. Hummingbirds are not only smaller than honeyeaters, but are also, as a group, the smallest sized birds in the world (Grant & Grant 1968). As a result, they could be unprofitable as dietary items to the avian predators with which they occur. Honeyeaters, on the other hand, are similar in size to most other Australian birds and so might be expected to be included profitably in the diets of several Australian avian predators.

This apparent difference in predation intensity may also explain the different extents to which honeyeaters and hummingbirds travel as flocks. Virtually all Australian honeyeater species have been observed moving in a flock whereas there are almost no reports of hummingbird flocking (Butler 1967). This difference in flocking would be expected if flocking is, as has been suggested (e.g. Hindwood 1937; Buskirk 1976; Hamilton 1971; Lazarus 1972; Pulliam 1973; Siegfried & Underhill 1975; Vine 1971; Willis 1973), an anti-predator adaptation on the part of individual birds.

Conclusion

The best known aspect of the foraging behaviour of Australian honeyeaters is the composition of their diets. Not only are the diets known qualitatively but quantitative data are also available for many species on the relative importance of the three major dietary components, namely insects, nectar and fruit. These quantitative data permit objective comparisons to be made between different genera of honeyeaters and also between honeyeaters and hummingbirds.

Much less is known, however, about other aspects of the foraging behaviour of honeyeaters. It is possible only to make a few general statements concerning selectivity with respect to nectar sources, hovering versus perching while taking nectar and nectar volumes and concentrations usually encountered by Australian honeyeaters. Once again it is the existence of quantitative observations which permits these generalizations. In terms of the density of flowers encountered by nectar-feeding honeyeaters and the effect of predation risk on foraging behaviour only suggestions are possible as quan-

titative observations are lacking. Clearly much more quantitative data for all aspects of honeyeaters behaviour and ecology are needed.

Acknowledgments

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