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# FORAGING AND NECTAR USE IN NECTARIVOROUS BIRD COMMUNITIES

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*Abstract.* Nectar-feeding birds, such as honeyeaters, sunbirds, and sugarbirds, usually occupy habitats in which distributions of particular plant species, individual plants, and flowers are patchy. The contribution that each plant species makes to the overall nectar pool is dependent upon plant density, floral abundance, and amount of nectar produced per flower. Nectar availability can be variable: some flowers contain considerable quantities of nectar, youngest flowers usually being most productive, while others are empty. In Australian and southern African habitats, we found interspecific partitioning of nectar resources. The largest species of nectarivore at a given site generally foraged selectively at the most rewarding nectar sources, relying on the most productive plant species and the youngest flowers available. Dominance hierarchies within nectarivore communities helped to sustain partitioning, although incompatibilities between bill and floral morphologies sometimes prevented particular species from utilizing part of the nectar pool. Preliminary observations suggested that intraspecific differences in use of nectar also occurred.

*Key Words:* Nectarivorous birds; honeyeaters; sunbirds; sugarbirds; foraging; nectar; resource partitioning; community ecology; Australia; Africa.

Nectarivorous birds are abundant in many parts of the world. The most prominent of these are honeyeaters (Meliphagidae) of Australasia, sunbirds (Nectariniidae) and sugarbirds (Promeropidae) of Africa, and hummingbirds (Trochilidae) of northern and neotropical America (Johnsgard 1983, Maclean 1985, Collins and Rebelo 1987, Collins and Paton 1989). Evidence concerning the extent to which these birds use nectar is circumstantial in most cases, although the efficiency and extent of its uptake have been measured precisely for several species (e.g., Wolf et al. 1972, Gill and Wolf 1978, Ford 1979, Collins et al. 1984, Paton and Carpenter 1984). There is a similar dearth of quantitative data regarding the importance of arthropods, fruits, and other potentially useful foods in the diets of nectarivores (e.g., Skead 1967, Johnsgard 1983, Maclean 1985), although a few detailed investigations have confirmed that honeyeaters ingest a variety of materials (e.g., Pyke 1980, Collins and Briffa 1982, Paton 1986). It has been suggested that arthropods are used primarily to provide protein and minerals (e.g., Pyke 1980, Paton 1982). Nectar contains a variety of carbohydrates, as do fruits, and in most instances appears to be the major source of energy for nectarivorous birds (e.g., Hainsworth and Wolf 1976, Baker and Baker 1983, Collins and Paton 1989).

Nectarivorous bird communities in many parts of North America and Africa are simple, often comprising only one or two types of bird that forage for nectar from a small number of plant species at any given time (e.g., Carpenter 1983, Paton and Carpenter 1984). Community organization is considerably more complex in the neotropics, and in most Australian habitats, where numbers of competing nectarivores and potential nectar sources are much greater (e.g., Feinsinger 1976, Ford and Paton 1982, Kodric-Brown et al. 1984, Collins and Newland 1986). Several comprehensive studies have documented the diversity of plants and birds within such habitats, often providing considerable information relating to nectar production and partitioning of nectar between different species of nectarivore (e.g., Wolf et al. 1976; Feinsinger 1978, 1983; Feinsinger and Colwell 1978; Snow and Snow 1980; Ford and Paton 1982; Collins and Briffa 1982; Collins and Newland 1986). Nevertheless, little attention has been paid to intraspecific variations in the use of available nectar. Even when such differences have been discussed, small sample sizes have usually been involved, and comparisons limited to territorial male and female birds (e.g., Gill and Wolf 1975b; Wolf 1975; Carpenter 1976; Gass 1978, 1979; Wolf et al. 1976). Almost no data have been supplied for individuals within the same species which differ in age or position within dominance hierarchies (e.g., Gass 1979, Craig 1985, Newland and Wooller 1985).

Most studies of foraging activity by nectarivores other than territorial hummingbirds have produced composite data derived from many observations of (often unmarked) birds, each made over a relatively short period of time (e.g., Collins and Briffa 1983, Collins and Newland 1986). Thus, there has been a tendency for results to be biased in favor of obvious activities, such as insect hawking and foraging at exposed flowers, and birds that are particularly mobile. The purpose of this paper is to demonstrate that collection of data in this manner can conceal interand intraspecific differences in foraging behavior, which are revealed by extended observation, and the use of indirect evidence such as that provided by analysis of facial and fecal smears, for individual birds.

## METHODS

### STUDY AREAS

Investigations reported here were undertaken at three different sites in southwestern Australia and southern Africa. The African site was located at Betty's Bay, a narrow belt of coastal seepage fynbos (heath), approximately 90 km southeast of Cape Town (B. G. Collins 1983a, b). The two Australian sites occurred within the southwest botanical province of Western Australia. One of these was located in sclerophyllous jarrah forest, 9 km south of Jarrahdale (Collins 1985, Collins and Newland 1986), the other in proteaceous heathland at Fitzgerald River, approximately 25 km northeast of Bremer Bay (Collins et al., unpubl. ms).

The most abundant nectarivorous birds at Betty's Bay were Cape Sugarbirds (*Promerops cafer*) and Orange-breasted Sunbirds (*Nectarinia violacea*). Little Wattlebirds (*Anthochaera chrysoptera*), New Holland Honeyeaters (*Phylidonyris novaehollandiae*), and Western Spinebills (*Acanthorhynchus superciliosus*) were most frequently seen at Jarrahdale. With the exception of Little Wattlebirds, these honeyeaters were also common at Fitzgerald River, where White-cheeked Honeyeaters (*Phylidonyris nigra*), Brown Honeyeaters (*Lichmera indistincta*), and White-naped Honeyeaters (*Melithreptus lunatus*) also were observed.

### EXPERIMENTAL DESIGN

Data were gathered during the course of three independent projects. The most recent of these, at Jarrahdale and Fitzgerald River (1985–1987), involved some measurements that were not performed at Betty's Bay, where experimental work was conducted in 1982. In a few instances, the techniques used to obtain comparable information also were slightly different. Notwithstanding these variations, however, two of the major objectives of each study were to document inter- and intraspecific differences regarding the partitioning of available nectar by birds, and to identify possible reasons for the differences.

### PLANT DENSITY AND FLORAL ABUNDANCE

At each Australian study site, but not at Betty's Bay, plant densities and floral abundances were measured for species that had been identified previously as major nectar producers (Collins and Newland 1986; Collins et al., ms). Plants that had clearly defined and separate flowers (e.g., *Grevillea wilsonii* at Jarrahdale) had their flowers counted and treated independently. On plants with inflorescences comprising numerous flowers that were tightly packed together (e.g., *Dryandra sessilis* at Jarrahdale or *Banksia nutans* at Fitzgerald River), inflorescences were considered to be the floral units. For convenience, all such units will generally be referred to throughout the remainder of this paper as flowers.

Overall densities of major nectar-producing plant species were estimated, using a plotless, point-centered quarter method with at least 100 points located on a rectangular grid at 10 m centers (Mueller-Dombois and Ellenberg 1974). Only those plants that were judged likely to flower at some time during the year in which investigations occurred were included (for details, see Collins and Newland 1986). Numbers of flowers present were counted on at least 20 randomly chosen plants for each species, during July and/or September. Relative abundances of flowers belonging to different age-classes were scored for selected species (*D. sessilis, G. wilsonii*, and *Mimetes hirtus*) at Jarrahdale and Betty's Bay (for methodology, see B. G. Collins 1983b, 1985; Grey 1985).

### NECTAR AVAILABILITY AND PRODUCTION

Fresh flowers were chosen at random for major nectar-producing species on each of 2–3 successive days in July and/or September. These were sprayed with insecticide and "bagged" (i.e., protected from all nectarivores) with perforated fibreglass mesh at dusk. Insect adhesive was wiped around stems supporting the bags and flowers in order to prevent arthropods from reaching flowers via stems (Collins and Newland 1986). Twenty four hours later, the volumes and equivalent sucrose concentrations of nectar in at least 10 bagged flowers were recorded for each species, using techniques described by Collins et al. (1984) and Collins and Newland (1986). Similar measurements were made for separate sets of 10 unbagged flowers at dawn and dusk over the same period of time. The energy equivalent of each nectar sample was estimated as outlined by Collins and Briffa (1983), assuming that 1 mg sucrose yields 16.74 J. Daily (24 hour) nectar productions were calculated by subtracting mean dusk energy values for unbagged flowers from subsequent dusk values for bagged flowers.

In separate experiments at Jarrahdale, approximately 140 flowers, on which anthesis could be induced by a gentle touch to the style(s), were selected at random for each of the two major nectar-producing plant species (*D. sessilis* and *G. wilsonii*). Nectar was collected from subsamples of at least 10 flowers at dusk on day zero, and at dawn and dusk each subsequent day until nectar production ceased. Energy equivalents of samples were calculated as indicated above. Similar experiments were conducted at Betty's Bay, except that standing crops of nectar were measured for unbagged *M. hirtus* inflorescences classified as partly open (some flowers open), and fully-open (all flowers open), rather than for inflorescences whose ages were known more precisely (B. G. Collins 1983a, b). Corresponding data were not obtained for plants at Fitzgerald River.

### BIRD MORPHOMETRIC, TIME BUDGET AND ENERGY BUDGET DATA

Honeyeaters present at the Jarrahdale site were captured in mist nets during each of four successive days in July and September. Each bird was weighed using a top-loading electronic balance, color-banded, its bill (exposed culmen) length measured with micrometer calipers, then released. Nectarivores at the other sites were treated in similar fashion, except that honeyeaters at Fitzgerald River were not color-banded.

Time budget data were obtained throughout the day for nectarivores at Betty's Bay and Jarrahdale, using cumulative digital stopwatches. In each instance,

TABLE 1. Densities and Floral Availability for Some Ornithophilous Plant Species at Study Sites in Southwestern Australia (Partly after Collins 1985, Collins et al., Unpubl. Ms)

| Location and plant species | Plant density (plants/ha) | Floral abundance (flowers/plant) | | | | Floral density (flowers/ha) |
|---|---|---|---|---|---|---|
| | | X̄ | SD | Range | N | |
| Jarrahdale (July) | | | | | | |
| *Adenanthos barbigera* | 553 | 2.2 | 1.1 | 0–10 | 30 | 1217 |
| *Calothamnus rupestris* | 12 | 0.0 | 0.0 | 0–0 | 30 | 0 |
| *Dryandra sessilis* | 243 | 6.9 | 4.2 | 0–27 | 30 | 1677 |
| *Grevillea wilsonii* | 314 | 2.2 | 0.9 | 0–11 | 30 | 691 |
| Jarrahdale (September) | | | | | | |
| *Adenanthos barbigera* | 553 | 4.2 | 1.8 | 0–17 | 30 | 2323 |
| *Calothamnus rupestris* | 12 | 115 | 201 | 0–815 | 30 | 1387 |
| *Dryandra sessilis* | 243 | 1.9 | 0.4 | 0–9 | 30 | 1191 |
| *Grevillea wilsonii* | 314 | 1.8 | 0.5 | 0–7 | 30 | 565 |
| Fitzgerald River (July) | | | | | | |
| *Banksia baueri* | 380 | 0.8 | 0.3 | 0–4 | 20 | 304 |
| *Banksia coccinea* | 180 | 0.7 | 0.2 | 0–3 | 20 | 126 |
| *Dryandra cuneata* | 230 | 4.1 | 1.9 | 0–12 | 20 | 943 |
| *Lambertia inermis* | 310 | 1.2 | 0.4 | 0–7 | 20 | 372 |

amounts of time allocated by a bird to foraging at flowers, gleaning of leaves and bark, hawking, perching ("resting"), hopping between perches and flying were recorded (Collins and Briffa 1983, Collins and Newland 1986). Where data were clearly associated with particular color-banded birds, and had been gathered over intervals of several hours, they were accumulated for the individuals concerned. In most cases, however, birds timed were either unbanded, or were seen only infrequently and for short periods of time. Data for all such birds were pooled according to species and type of activity, thus providing an "overall" indication of the manner in which time was allocated (Collins and Newland 1986). Air temperatures approximately 0.5 m above ground, within vegetation visited by nectarivores, were recorded each hour using shielded thermistors, thus making it possible to construct energy budgets for the birds (see B. G. Collins 1983a, Collins and Briffa 1983).

### Foraging Preferences

Frequencies with which nectarivores visited flowers on various plant species were recorded throughout the day, in conjunction with collection of general time budget data at Jarrahdale and Betty's Bay, and as a separate exercise at Fitzgerald River (Collins 1985). In cases where species had flowers at different ages that could be readily distinguished (e.g., *D. sessilis, G. wilsonii, M. hirtus*), visits to these flowers were scored separately (Collins 1985, Grey 1985).

Supplementary information concerning the types of plants visited was obtained by taking pollen smears from foreheads and throats of birds captured in mist nets and comparing these with type pollen smears from flowers nearby (Wooller et al. 1983, Collins and Newland 1986). Numbers of particular types of pollen grains present in each pair of smears from a given bird were summed and expressed as percentages of total grains counted.

### Dominance Hierarchies

The outcomes of agonistic encounters between conspecifics and different species while foraging for nectar were recorded opportunistically at Jarrahdale and Betty's Bay, but not at Fitzgerald River. As relatively few encounters occurred between color-banded birds of known age, virtually no data illustrating age-related differences in social status were obtained.

## RESULTS

### Plant Density and Floral Abundance

Nectar-producing species had patchy distributions that tended to overlap one another within all study sites except that at Betty's Bay, where the two principal species (*Mimetes hirtus* and *Erica perspicua*) occurred in fairly discrete, "pure" stands (B. G. Collins 1983b; Collins 1985; Collins et al., ms). Plant densities and numbers of flowers available per plant were not measured at Betty's Bay, although both parameters often differed considerably from species to species at the other two locations (flowers per plant: Jarrahdale [July] $F = 15.5$, $P < 0.001$, [September] $F = 328.1$, $P < 0.001$, Fitzgerald River $F = 11.7$, $P < 0.001$). Variability in floral abundance also was great for individual plants within a given species. Consequently, contributions that particular species or plants made to the total floral pool at a given site often were quite different (Table 1).

### Floral Morphology

All but three plant species involved in this study had gullet-shaped flowers (Table 2). In most cases, individual flowers were arranged in spikes,

TABLE 2. FLORAL MORPHOLOGY FOR MAJOR PLANTS VISITED BY NECTARIVOROUS BIRDS AT STUDY SITES IN SOUTHWESTERN AUSTRALIA AND SOUTHERN AFRICA. N = 30 FOR ALL MEASUREMENTS OF FLOWER DIAMETER AND STIGMA–NECTARY DISTANCE

| Location and plant species | Flower shape[a] | Flower diameter (mm)[b] | | Stigma–nectary distance (mm) | | Inflorescence type | Flowers/ inflorescence |
|---|---|---|---|---|---|---|---|
| | | $\bar{X}$ | SD | $\bar{X}$ | SD | | |
| Jarrahdale | | | | | | | |
| *Adenanthos barbigera* | gullet | 1.8 | 0.2 | 28.3 | 2.7 | solitary | 1 |
| *Calothamnus rupestris* | semi-tube | 5.1 | 1.9 | 35.5 | 3.1 | spike | 15–27 |
| *Dryandra sessilis* | gullet | 1.1 | 0.3 | 29.8 | 2.9 | capitulum | 70–90 |
| *Grevillea wilsonii* | gullet | 2.9 | 1.3 | 35.5 | 3.8 | raceme | 7–12 |
| Fitzgerald River | | | | | | | |
| *Banksia baueri* | gullet | 0.9 | 0.2 | 31.1 | 1.7 | spike | >5000 |
| *Banksia baxteri* | gullet | 0.9 | 0.1 | 29.5 | 2.1 | spike | 260–280 |
| *Banksia coccinea* | gullet | 1.0 | 0.2 | 24.6 | 1.9 | spike | 180–250 |
| *Banksia media* | gullet | 1.1 | 0.2 | 27.8 | 2.2 | spike | >5000 |
| *Dryandra cuneata* | gullet | 0.8 | 0.1 | 20.2 | 2.1 | capitulum | 30–50 |
| *Dryandra quercifolia* | gullet | 0.9 | 0.1 | 29.6 | 2.4 | capitulum | 40–70 |
| *Lambertia inermis* | tube | 4.9 | 1.1 | 31.5 | 3.3 | raceme | 7 |
| Betty's Bay | | | | | | | |
| *Erica perspicua* | tube | 2.8 | 0.7 | 19.8 | 2.4 | spike | 20–30 |
| *Mimetes hirtus* | gullet | 1.0 | 0.1 | 59.4 | 8.8 | capitulum | 8–11 |

[a] Gullet-shaped flowers are categorized by zygomorphic perianth tubes with one or more slits; semi-tubular flowers each comprise four fused staminal bundles which are separate from one another; the only flowers into which at least some of the birds present would have been able to insert their bills were those of *A. barbigera, C. rupestris, G. wilsonii, L. inermis* and *E. perspicua*.

[b] Diameters of individual flowers were measured 10 mm from their bases in all instances, using micrometer calipers.

capitula, or racemes, with more than 5000 small flowers present per inflorescence for species such as *Banksia baueri* and *B. media*. The only species with individual flowers into which bills of at least some nectarivores could be inserted were *Adenanthos barbigera, Calothamnus rupestris, Grevillea wilsonii, Lambertia inermis,* and *E. perspicua*. Birds visiting other species were obliged to use nectar that accumulated between the bases of flowers.

### AVAILABILITY OF NECTAR

Daily nectar production varied from one plant species to another at each site (Table 3, Jarrahdale [July] F = 37.4, $P < 0.001$, [September] F = 11.9, $P < 0.001$, Fitzgerald River F = 1482.1, $P < 0.001$). Those species with inflorescences comprising numerous, tightly packed, small flowers usually generated the most nectar, regardless of plant density. For instance, production by *Dryandra sessilis* at Jarrahdale in July and September averaged 1614.7 and 663.2 kJ/ha, respectively, compared with 22.8 and 8.5 kJ/ha for *G. wilsonii*. At Fitzgerald River, *B. baueri* produced 2397.0 kJ/ha in July, as opposed to 42.8 kJ/ha by *L. inermis* (estimates made by combining data in Tables 1 and 3). At each site, amounts of nectar produced by individual flowers of a given species also varied considerably.

In general, nectar availability (standing crop) at dawn differed among plant species in much the same way as nectar production (Table 3, Jarrahdale [July] F = 29.6, $P < 0.001$, Betty's Bay F = 50.96, $P < 0.001$), some individual flowers containing copious amounts of nectar and others virtually none. Nectar was lost from most flowers during the day, although percentages of dawn standing crops that remained at dusk often varied considerably from species to species. For instance, flowers of *A. barbigera, G. wilsonii,* and *E. perspicua* appeared to retain relatively more nectar than those of *D. sessilis* or *M. hirtus* (Table 3).

A large part of the variability in nectar availability for flowers chosen at random from species such as *D. sessilis, G. wilsonii,* and *M. hirtus* can be attributed to differences associated with floral age. For instance, dawn and dusk standing crops of nectar for all three species varied inversely with floral age, nectar production finally ceasing after approximately 7, 3, and 7 days, respectively (Table 4, at dawn: *D. sessilis* F = 337.3, $P < 0.001$, *G. wilsonii* F = 5.9, $P < 0.001$, *M. hirtus* F = 2.4, $P < 0.05$).

### MORPHOMETRIC AND TIME BUDGET DATA

At each study site, body masses and bill (exposed culmen) lengths of most nectarivore species differed from one another (Table 5, body mass: Jarrahdale [July] F = 1050.0, $P < 0.001$, [Sep-

TABLE 3. NECTAR PRODUCTION, AVAILABILITY AND DEPLETION FOR PLANT SPECIES VISITED BY HONEYEATERS, SUNBIRDS OR SUGARBIRDS (PARTLY AFTER B. G. COLLINS 1983A; COLLINS AND NEWLAND 1986, COLLINS ET AL., UNPUBL. MS)

| | Nectar production (kJ/24 hour/flower) | | | | Nectar availability at dawn (kJ/flower) | | | | Nectar remaining at dusk (%)[b] |
|---|---|---|---|---|---|---|---|---|---|
| Location and plant species | $\bar{X}$ | SD | Range | N | $\bar{X}$ | SD | Range | N | |
| Jarrahdale (July) | | | | | | | | | |
| *Adenanthos barbigera* | 0.028 | 0.013 | 0.005–0.037 | 30 | 0.017 | 0.009 | 0.000–0.029 | 30 | 42.6 |
| *Calothamnus rupestris* | | | | | | | | | |
| *Dryandra sessilis*[a] | 0.963 | 0.327 | 0.375–1.121 | 30 | 0.643 | 0.196 | 0.179–0.817 | 30 | 12.4 |
| *Grevillea wilsonii* | 0.033 | 0.018 | 0.017–0.048 | 30 | 0.022 | 0.008 | 0.005–0.031 | 30 | 46.7 |
| Jarrahdale (September) | | | | | | | | | |
| *Adenanthos barbigera* | 0.012 | 0.006 | 0.003–0.019 | 30 | | | | | |
| *Calothamnus rupestris* | 0.219 | 0.110 | 0.112–0.288 | 30 | | | | | |
| *Dryandra sessilis*[a] | 0.557 | 0.269 | 0.121–0.783 | 30 | | | | | |
| *Grevillea wilsonii* | 0.015 | 0.007 | 0.005–0.037 | 30 | | | | | |
| Fitzgerald River (July) | | | | | | | | | |
| *Banksia baueri*[a] | 7.885 | 3.919 | 3.899–12.174 | 10 | | | | | |
| *Banksia baxteri*[a] | 0.560 | 0.221 | 0.150–0.717 | 10 | | | | | |
| *Banksia coccinia*[a] | 0.125 | 0.071 | 0.009–0.184 | 10 | | | | | |
| *Banksia media*[a] | 15.350 | 8.023 | 4.632–18.151 | 10 | | | | | |
| *Dryandra cuneata*[a] | 0.500 | 0.113 | 0.105–0.788 | 20 | | | | | |
| *Dryandra quercifolia*[a] | 3.111 | 0.927 | 1.952–4.923 | 20 | | | | | |
| *Lambertia inermis* | 0.115 | 0.042 | 0.034–0.175 | 40 | | | | | |
| Betty's Bay (September) | | | | | | | | | |
| *Erica perspicua* | | | | | 0.003 | 0.001 | 0.000–0.006 | 100 | 54.0 |
| *Mimetes hirtus*[a] | | | | | 0.081 | 0.009 | 0.011–0.116 | 30 | 15.6 |

[a] Species with flowering units that are inflorescences comprising numerous small flowers; other species have widely-spaced flowers.

[b] Nectar present at dusk expressed as percentage of dawn nectar availability.

tember] F = 1398.7, P < 0.001, Fitzgerald River F = 407.1, P < 0.001, Betty's Bay F = 736.7, P < 0.001). For instance, Cape Sugarbirds were considerably larger than Orange-breasted Sunbirds at Betty's Bay, and both New Holland and White-cheeked Honeyeaters larger than other honeyeaters at Fitzgerald River. Intraspecific variability was often quite marked, males generally being larger than females, at least for those species where sexes could be readily distinguished (e.g., Western Spinebills, Cape Sugarbirds, Orange-breasted Sunbirds; body mass: t = 5.94, 4.65 and 3.04, respectively, for comparisons of males and females; P < 0.01). Body masses and bill lengths were recorded for all birds captured, although the only particular values provided in Table 5 are those for individual birds subsequently involved in extended time budget investigations.

At Jarrahdale, nectarivore body size varied inversely with amounts of time spent foraging, hopping, and flying (Table 6). For instance, relatively large Little Wattlebirds devoted much less time to these activities than either New Holland Honeyeaters, or Western Spinebills in July and September. Similar relationships possibly existed at Betty's Bay, although these are obscured by the fact that hopping and foraging were not measured as separate components of time budgets for either Cape Sugarbirds or Orange-breasted Sunbirds. Differences among time budgets of individual birds and sexes appear not to have been so pronounced as those among species, although male and female Western Spinebills, in particular, may have differed significantly in general activity patterns and foraging behavior.

## ENERGY BUDGETS AND FORAGING EFFICIENCIES

At each of the study sites, estimated energy expenditure and requirements vary between different nectarivore species (Table 5). In general, values are greatest for the largest and most active birds. Limited evidence also suggests that expenditures and needs are greater for males than females of a given species, principally because of differences in their body masses.

The efficiencies with which birds extract nectar from flowers can be calculated using data provided in Tables 4 and 5. Extraction efficiency varies according to the species of nectarivore or plant involved, nectar availability and the distances between flowers that are visited. Efficiency is greatest for small birds that visit productive flowers which are close together (Table 7).

## FORAGING PREFERENCES

Data (Table 8) have been pooled for individual species of nectarivores, yet reveal some striking differences with regard to types of plant whose flowers were visited by them. For instance, Little Wattlebirds at Jarrahdale visited virtually no flowers other than those of *D. sessilis* in July and *C. rupestris* in September. In contrast, the smaller Western Spinebills supplemented nectar from these species with that from *A. barbigera* and *G. wilsonii.* At Betty's Bay, Cape Sugarbirds relied upon *M. hirtus* flowers; yet, Orange-breasted Sunbirds visited both *M. hirtus* and *E. perspicua.* The situation at Fitzgerald River was more variable. Most honeyeaters at that location appeared to favor *Dryandra cuneata* and *L. inermis,* although two of the smaller species, Brown Honeyeaters and Western Spinebills, visited *Banksia baueri* more frequently than did the larger honeyeaters. Intermediate-sized White-naped Honeyeaters were particularly interesting in that they did not appear to visit *B. baueri* at all, and foraged rarely at *L. inermis,* yet visited *Banksia coccinia,* which is a relatively poor source of nectar.

Analysis of pollen smears provided evidence that generally supported direct observations of the type outlined above (Table 9), although pollen from plant species found only outside the study site was often present in smears obtained at Fitzgerald River (e.g., pollen from *B. media* and *Dryandra quercifolia*). The White-naped Honeyeaters, whose observed foraging preferences at that site differed so markedly from those of other species, had an average of only 14% of the total pollen grains counted that were from plant species listed in Table 9. Marked intraspecific variations in the incidence of pollen types occurred for all nectarivore species. Quite often, particular types were absent from some individual birds of a given species, but present on others (e.g., *G. wilsonii* pollen present on some New Holland Honeyeaters at Jarrahdale, but not on others).

Honeyeaters studied at Jarrahdale, and Cape Sugarbirds at Betty's Bay, all demonstrated clear preferences for flowers of particular ages (Table 10). Invariably, highest preferences were shown for younger flowers that produced the most nectar, although the three Jarrahdale species differed from one another in that they sometimes foraged at flowers whose ages spanned varying ranges (e.g., when visiting *D. sessilis,* Little Wattlebirds visited day 1–2 and day 3–4 flowers only, whereas New Holland Honeyeaters also used day 5–6 flowers).

TABLE 4. AVAILABILITY OF NECTAR AT DAWN AND DUSK ON SUCCESSIVE DAYS DURING THE FLORAL DEVELOPMENT OF UNBAGGED *DRYANDRA SESSILIS, GREVILLEA WILSONII* AND *MIMETES HIRTUS* (PARTLY AFTER B. G. COLLINS 1983A, B). N DENOTES NUMBERS OF FLOWERS TESTED. HORIZONTAL LINES INDICATE RANGES OF FLORAL AGES SPANNED WHEN CALCULATING NECTAR AVAILABILITY FOR *M. HIRTUS*

| Plant species and time of year | | Nectar availability (kJ/flower) at dawn on day | | | | | | | Nectar availability (kJ/flower) at dusk on day | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| *Dryandra sessilis* | X̄ | 0.603 | 0.540 | 0.284 | 0.060 | 0.034 | 0.007 | 0.005 | 0.065 | 0.040 | 0.018 | 0.012 | 0.007 | 0.004 | 0.004 |
| (July, N = 10) | SD | 0.031 | 0.028 | 0.029 | 0.018 | 0.009 | 0.006 | 0.003 | 0.010 | 0.013 | 0.008 | 0.007 | 0.004 | 0.004 | 0.003 |
| *Grevillea wilsonii* | X̄ | 0.030 | 0.026 | 0.011 | | | | | 0.016 | 0.013 | 0.004 | | | | |
| (July, N = 10) | SD | 0.011 | 0.013 | 0.007 | | | | | 0.007 | 0.006 | 0.004 | | | | |
| *Mimetes hirtus* | X̄ | | 0.119 | | | | 0.021 | | | 0.021 | | | | 0.003 | |
| (September, N = 10) | SD | | 0.125 | | | | 0.039 | | | 0.024 | | | | 0.009 | |

TABLE 5. MORPHOMETRIC DATA FOR NECTARIVOROUS BIRDS CAPTURED AT STUDY SITES. MEASUREMENTS FOR COLOR-BANDED INDIVIDUALS ARE PROVIDED IF EXTENDED TIME BUDGET DATA WERE OBTAINED FOR THESE BIRDS

| Location and bird species | Banding code[a] | Approx. age (years) | N | Mass (g) | | | Exposed culmen length (mm) | | | Photoperiod duration (hours) | Daytime energy expenditure (kJ)[b] | Daytime energy requirement (kJ)[c] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | X̄ | SD | Range | X̄ | SD | Range | | | |
| Jarrahdale (July) | | | | | | | | | | | | |
| Little Wattlebird (unsexed) | overall | | 9 | 61.8 | 3.1 | 51.9–67.3 | 29.6 | 1.2 | 27.8–32.0 | 10.1 | 74.0 | 147.8 |
| | LG/R | >1 | 1 | 67.3 | | | 32.0 | | | | 76.2 | 156.6 |
| | MA/R | <1 | 1 | 59.3 | | | 28.7 | | | | 67.6 | 138.4 |
| New Holland Honeyeater (unsexed) | overall | | 53 | 20.6 | 1.3 | 15.5–23.5 | 21.3 | 1.0 | 19.2–23.7 | 10.1 | 39.7 | 72.8 |
| | R/Y | >1 | 1 | 20.7 | | | 20.6 | | | | 39.3 | 72.5 |
| | R/MA | <1 | 1 | 15.5 | | | 19.7 | | | | 27.6 | 52.5 |
| Western Spinebill (male) | overall | | 7 | 11.8 | 0.9 | 10.5–14.0 | 23.7 | 1.2 | 21.9–25.9 | 10.1 | 21.4 | 44.5 |
| Western Spinebill (female) | overall | | 4 | 9.5 | 0.8 | 8.3–10.7 | 19.5 | 1.0 | 18.8–20.6 | 10.1 | 21.9 | 40.5 |
| Jarrahdale (September) | | | | | | | | | | | | |
| Little Wattlebird (unsexed) | overall | | 3 | 69.1 | 2.1 | 66.4–70.1 | 32.7 | 2.7 | 30.1–34.9 | 11.5 | 119.7 | 187.0 |
| New Holland Honeyeater (unsexed) | overall | | 35 | 20.1 | 0.9 | 16.2–24.4 | 22.2 | 0.8 | 20.1–24.4 | 11.5 | 48.9 | 75.2 |
| Western Spinebill (male) | overall | | 11 | 10.7 | 0.4 | 10.0–11.2 | 22.3 | 0.9 | 21.0–23.9 | 11.5 | 30.8 | 47.9 |
| Western Spinebill (female) | overall | | 3 | 9.5 | 0.6 | 9.0–10.4 | 19.2 | 0.1 | 19.1–19.4 | 11.5 | 29.6 | 44.8 |
| Fitzgerald River (July) | | | | | | | | | | | | |
| White-cheeked Honeyeater | overall | | 17 | 19.1 | 0.9 | 17.9–20.7 | | | | | | |
| White-naped Honeyeater | overall | | 7 | 12.8 | 0.7 | 11.6–13.2 | | | | | | |
| Brown Honeyeater | overall | | 7 | 10.3 | 0.6 | 9.4–11.1 | | | | | | |
| Western Spinebill (male) | overall | | 5 | 11.5 | 0.7 | 10.2–11.9 | 22.9 | 0.9 | 20.6–24.4 | | | |
| Western Spinebill (female) | overall | | 2 | 9.6 | 0.1 | 9.4–9.8 | 20.3 | 1.0 | 19.3–21.3 | | | |
| Betty's Bay (September) | | | | | | | | | | | | |
| Cape Sugarbird (male) | overall | | 8 | 42.6 | 1.9 | 38.9–43.7 | 29.8 | 0.5 | 28.4–30.3 | | | |
| | Y/W | | >1 | 1 | 41.8 | | 29.3 | | | 12.6 | 84.9 | 138.5 |
| Cape Sugarbird (female) | overall | | 5 | 39.5 | 1.8 | 36.2–40.5 | 28.2 | 0.3 | 27.7–28.9 | | | |
| | R/Y | >1 | 1 | 40.5 | | | 28.5 | | | 12.6 | 79.1 | 129.9 |
| Orange-breasted Sunbird (male) | overall | | 10 | 9.9 | 0.3 | 9.5–10.6 | 21.9 | 0.2 | 21.6–22.7 | 12.6 | 33.8 | 52.6 |
| Orange-breasted Sunbird (female) | overall | | 4 | 9.4 | 0.4 | 8.9–9.9 | 21.1 | 0.3 | 20.6–21.8 | | | |

[a] "Overall" denotes data pooled for several birds; where individual birds have been studied, the code denotes the colors of bands used on left/right legs.

[b] Daytime energy expenditures were calculated using data from Tables 5 and 6, and the methodologies outlined by B. G. Collins (1983a), Collins and Briffa (1983) and Collins and Newland (1986); the equations used for honeyeaters were appropriately scaled versions of those empirically-derived for 10 g Brown Honeyeaters (Collins and Briffa 1983, Collins and Newland 1986).

[c] Daytime energy reuqirements were calculated by adding daytime expenditures to predicted overnight expenditures that had been divided by 0.875 to allow for 12.5% loss of energy when excess carbohydrate ingested during the day was stored as lipid (B. G. Collins 1983a, Collins and Briffa 1983, Collins and Newland 1986).

TABLE 6. ENVIRONMENTAL TEMPERATURES AND TIME BUDGETS FOR NECTARIVOROUS BIRDS AT STUDY SITES (PARTLY AFTER B. G. COLLINS 1983A). MORPHOMETRIC MEASUREMENTS FOR THESE AND OTHER BIRDS ARE PROVIDED IN TABLE 5, AS ARE DEFINITIONS OF BANDING CODES. HORIZONTAL LINES AND BRACKETS DENOTE RANGE OF ACTIVITIES INCLUDED IN TIME-BUDGET DATA FOR BETTY'S BAY

| | | | | Percentage of total time devoted | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Location and bird species | Banding code | Approx. age (years) | Total observ. time (s) | Perching (resting) | Probing flowers | Gleaning | Forward flight | Hopping | Hawking | Mean day/night temp (°C) |
| Jarrahdale (July) | | | | | | | | | | |
| Little Wattlebird (unsexed) | overall | | 16,491 | 76.6 | 15.7 | 0.5 | 4.6 | 2.4 | 0.2 | 11.5/8.2 |
| | LG/R | >1 | 4188 | 74.0 | 19.7 | 0.0 | 4.2 | 2.1 | 0.0 | |
| | MA/R | <1 | 3241 | 82.0 | 10.9 | 0.7 | 3.3 | 2.7 | 0.4 | |
| New Holland Honeyeater (unsexed) | overall | | 15,095 | 54.7 | 30.4 | 0.6 | 8.3 | 4.8 | 1.2 | 11.5/8.2 |
| | R/Y | >1 | 2879 | 63.7 | 22.4 | 0.0 | 11.2 | 2.7 | 0.0 | |
| | R/MA | <1 | 3325 | 63.5 | 24.1 | 0.2 | 5.1 | 5.2 | 0.2 | |
| Western Spinebill (male) | overall | | 2564 | 45.9 | 43.8 | 0.0 | 3.4 | 6.9 | 0.0 | 11.5/8.2 |
| Western Spinebill (female) | overall | | 2103 | 54.4 | 27.2 | 1.0 | 4.9 | 12.5 | 0.0 | 11.5/8.2 |
| Jarrahdale (September) | | | | | | | | | | |
| Little Wattlebird (unsexed) | overall | | 4369 | 80.3 | 7.6 | 0.2 | 5.6 | 5.3 | 1.0 | 13.5/9.2 |
| New Holland Honeyeater (unsexed) | overall | | 14,117 | 51.1 | 30.3 | 0.5 | 6.6 | 11.0 | 0.5 | 13.5/9.2 |
| Western Spinebill (male) | overall | | 1413 | 59.8 | 17.9 | 0.5 | 14.3 | 7.0 | 0.5 | 13.5/9.2 |
| Western Spinebill (female) | overall | | 1869 | 31.5 | 43.0 | 0.1 | 8.3 | 17.1 | 0.0 | 13.5/9.2 |
| Betty's Bay (September) | | | | | | | | | | |
| Cape Sugarbird (male) | Y/W | >1 | 3600 | —— | 94.8 | —— | —— | 5.2 | —— | 17.7/12.5 |
| Cape Sugarbird (female) | R/Y | >1 | 28,400 | —— | 98.4 | —— | —— | 1.6 | —— | 17.2/13.3 |
| Orange-breasted Sunbird (male) | overall | | 3800 | —— | 89.0 | —— | —— | 11.0 | —— | 17.7/12.5 |
| Orange-breasted Sunbird (female) | overall | | | | | | | | | |

## DOMINANCE HIERARCHIES

Clearly defined interspecific hierarchies were identified at both study sites where detailed observations of agonistic interactions were recorded (Jarrahdale and Betty's Bay). In each case, larger species (e.g., Little Wattlebirds, Cape Sugarbirds) were consistent winners against smaller species (e.g., Western Spinebills, Orange-breasted Sunbirds) (Table 11). Intraspecific hierarchies were also apparent, with males usually winning out against females. Insufficient data were available to test the hypothesis that the winners of intraspecific encounters are determined on the basis of body size or age.

## DISCUSSION

Casual observation of vegetation within plant communities that support nectar-feeding birds usually reveals striking variations in abundance and distribution of different species, although this patchiness has only occasionally been quantified by people interested in resource partitioning (e.g., Wolf et al. 1976, Feinsinger 1978, Collins 1985, Wykes 1985). Data presented in this paper indicate that most nectar-producing species at Jarrahdale and Fitzgerald River have patchy distributions, and are generally supported by independent results for the same areas obtained by Wykes (1985) and Newby (unpubl. data). A similar level of diversity does not occur within the small *Mimetes hirtus-Erica perspicua* community at Betty's Bay, although Boucher (1978) has demonstrated that many additional species occur in adjacent habitats.

For any given plant species, numbers of flowers present on individual plants at a particular time of year also can be quite variable (e.g., Feinsinger 1978, Paton and Ford 1983, Collins 1985, Collins and Newland 1986). Some plants have no flowers, others have many. As a result, differences in flower counts combine with patchy distributions of the plants themselves to present an uneven floral environment to potential visitors.

The contribution that a particular plant species makes to the total nectar pool is clearly related to plant density, floral abundance and the amount of nectar that each flower produces (e.g., Pyke 1983, Collins et al. 1984, Collins and Newland 1986, Paton 1986). We found that standing crops of nectar in flowers that have not been visited by honeyeaters for a considerable time can be quite variable (see also Feinsinger 1978, Carpenter 1983, Gill and Wolf 1977). Genetic and environmental factors are involved (e.g., Cruden

TABLE 7. Foraging Efficiencies for Honeyeaters, Sugarbirds and Sunbirds Visiting Flowers at Jarrahdale or Betty's Bay

| Location and plant species | Age of flower/ time of day | Standing crop energy (J/flower)[a] | Nectarivore species[b] | Foraging efficiency (J)[c] | | |
|---|---|---|---|---|---|---|
| | | | | A | B | C |
| Jarrahdale (July) | | | | | | |
| *Dryandra sessilis* | Day 1/dawn | 603 | *A.s.* | 597 | 593 | 590 |
| | | | *P.n.* | 594 | 587 | 581 |
| | | | *A.c.* | 589 | 568 | 548 |
| | Day 4/dawn | 60 | *A.s.* | 54 | 50 | 47 |
| | | | *P.n.* | 51 | 44 | 38 |
| | | | *A.c.* | 46 | 25 | 5 |
| *Grevillea wilsonii* | Day 1/dawn | 30 | *A.s.* | 27 | 24 | 24 |
| | | | *P.n.* | 26 (?) | 19 (?) | 16 (?) |
| | | | *A.c.* | 21 (?) | 1 (?) | −20 (?) |
| | Day 3/dawn | 11 | *A.s.* | 8 | 5 | 1 |
| | | | *P.n.* | 7 (?) | 0 (?) | −7 (?) |
| | | | *A.c.* | 2 (?) | −18 (?) | −39 (?) |
| Betty's Bay (September) | | | | | | |
| *Mimetes hirtus* | Partly-open/dawn | 119 | *N.v.* | | | |
| | | | *P.c.* | 107 | 99 | 91 |
| | Fully-open/dawn | 21 | *N.v.* | | | |
| | | | *P.c.* | 3 | −5 | −12 |

[a] Nectar standing crops have been taken from Table 4.

[b] *A.s.*, *P.n.*, *A.c.*, *N.v.* and *P.c.* denote Western Spinebills, New Holland Honeyeaters, Little Wattlebirds, Orange-breasted Sunbirds and Cape Sugarbirds, respectively.

[c] Foraging efficiency is the difference between energy intake, assuming 100% ingestion of available nectar when a flower is visited by a bird, and the energy expended in flying to the flower 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: *D. sessilis* (*A.s.* 15.3, *P.n.* 12.5 and *A.c.* 6.7 s); *G. wilsonii* (*A.s.* 4.1, *P.n.* 3.3(?) and *A.c.* 1.8(?) s); *M. hirtus* (*P.c.* male 13.9 and *P.c.* female 24.7 s, *N.v.* no data); (?) denotes that extraction times and calculations involving these are estimates, since these birds were not observed visiting such flowers.

et al. 1983), although the ages of flowers are especially significant (this study, see also Gill and Wolf 1977, Grey 1985). For example, *Dryandra sessilis* flowers whose ages range from 1 to 7 days would be expected to have more variable standing crops than a sample of uniform age.

Patchiness of the floral and nectar environments presents nectarivores with a diversity of foraging options. For instance, the most abundant and uniformly distributed plant species at Jarrahdale is *Adenanthos barbigera*; yet, each plant usually bears relatively few flowers, most of which produce small amounts of nectar. In contrast, *Calothamnus rupestris* and *D. sessilis* are less abundant, and often more widely spaced; yet, each has such large numbers of flowers per plant or produces such quantities of nectar per flower that its overall contribution to the nectar pool is much greater. How do nectarivores forage under these conditions? If nectar is harvested selectively, is the choice based on plant density, floral abundance per plant, flower morphology, amount of nectar present per flower, or some combination of these parameters? Even if preferential foraging does occur, variations in size and behavior suggest that species and individual birds may partition nectar resources in different ways.

According to optimal foraging theory (e.g., Pyke et al. 1977, Pyke 1984), nectarivorous birds should maximize their net rates of energy acquisition. This might be achieved by adopting a foraging strategy that maximized energy intake, perhaps by selecting plant species offering the greatest nectar rewards per plant and/or flower, although there would be some energetic sacrifices if the plants were widely spaced (Table 7). Alternatively, birds might select species with the greatest plant and floral densities, at least within certain parts of the habitat. In this situation, the energetic cost of moving between flowers would be minimized, although energy intake would not necessarily be at the highest possible level. Of course, birds could opt for a combination of both strategies (e.g., Gill and Wolf 1977; B. G. Collins 1983a, b; Paton and Ford 1983; Collins 1985; Grey 1985; Collins and Rebelo 1987). For instance, Little Wattlebirds and New Holland Honeyeaters at Jarrahdale foraged selectively at *C. rupestris* or *D. sessilis* flowers, when these were available, but also preferred the densest patches of either species, and individual plants with the most flowers (Collins 1985, Grey 1985). This allowed them to increase their foraging efficiency and satisfy their energy requirements).

Energy expenditures and requirements of larg-

TABLE 8. RELATIVE FREQUENCIES OF VISITS BY NECTARIVOROUS BIRDS TO FLOWERS ON PLANT SPECIES AT STUDY SITES. FIGURES IN PARENTHESES DENOTE RELATIVE ABUNDANCES OF PLANTS VISITED; 5.1% OF THE TOTAL PLANTS PRESENT AT JARRAHDALE BELONGED TO OTHER SPECIES (PARTLY AFTER COLLINS 1985)

| Location and bird species | Total visits to flowers | Percentage frequency of visits | | | | |
|---|---|---|---|---|---|---|
| Jarrahdale (July) | | *Adenanthos barbigera* (27.7) | *Calothamnus rupestris* (0.7) | *Dryandra sessilis* (16.6) | *Grevillea wilsonii* (18.1) | *Dryandra nivea* (31.8) |
| Little Wattlebird | 40 | | | 100.0 | | |
| New Holland Honeyeater | 411 | | | 99.3 | 0.5 | 0.2 |
| Western Spinebill | 43 | 37.2 | | 32.6 | 23.2 | 7.0 |
| Jarrahdale (September) | | | | | | |
| Little Wattlebird | 16 | | 100.0 | | | |
| New Holland Honeyeater | 222 | | 64.0 | 36.0 | | |
| Western Spinebill | 171 | 24.6 | 38.0 | 26.9 | 10.5 | |
| Fitzgerald River (July) | | *Banksia baueri* (34.5) | *Banksia coccinia* (16.4) | *Dryandra cuneata* (20.9) | *Lambertia inermis* (28.2) | |
| New Holland Honeyeater | 115 | 7.0 | 6.1 | 56.5 | 30.4 | |
| White-cheeked Honeyeater | 107 | 3.7 | 2.7 | 50.6 | 43.0 | |
| White-naped Honeyeater | 15 | 0.0 | 20.0 | 73.3 | 6.7 | |
| Brown Honeyeater | 38 | 23.7 | 2.6 | 26.3 | 47.4 | |
| Western Spinebill | 29 | 17.2 | 3.5 | 27.6 | 51.7 | |
| Betty's Bay (September) | | *Erica perspicua* (?) | *Mimetes hirtus* (?) | | | |
| Cape Sugarbird | 511 | 0.0 | 100.0 | | | |
| Orange-breasted Sunbird | 372 | 17.5 | 82.5 | | | |

er species, and bigger birds within these, are greater than those for smaller birds, all other things being similar (Table 5). For this reason, one might expect larger birds to be more discerning than others in their choice of nectar resources. As this paper indicates, Little Wattlebirds and New Holland Honeyeaters used young flowers of *C. rupestris* and *D. sessilis* almost exclusively at Jarrahdale, whereas the smaller Western Spinebills also made frequent visits to older flowers of the same species and to flowers of generally less-rewarding plants such as *Grevillea wilsonii* and *A. barbigera* (Table 8). Similarly, Cape Sugarbirds at Betty's Bay preferred partly open inflorescences of *M. hirtus,* and ignored *E. perspicua,* whereas Orange-breasted Sunbirds made considerable use of *E. perspicua.*

Perhaps the most obvious way in which nectar resource partitioning by different species is effected is by the establishment of dominance hierarchies (e.g., Ford and Paton 1982, Craig 1985, Newland and Wooller 1985), and at all three sites studied here larger species often displaced smaller birds from the most rewarding sources of nectar. Differential use of available resources is reflected in the time and energy budgets, larger nectarivores being able to devote less effort to foraging and more to "resting," thereby reducing their energy requirements.

Resource partitioning also occurs because bill lengths and breadths of the birds, and floral morphologies for the plants, are sometimes incompatible. For example, the tubular or gullet-shaped flowers of plants such as *E. perspicua, G. wilsonii* and *A. barbigera* clearly could not be probed by Cape Sugarbirds or Little Wattlebirds, both of which have relatively broad bills (Paton and Collins, unpubl. ms); yet, nectar should have been easily harvested by narrow-billed Orange-breasted Sunbirds or Western Spinebills. We found that the percentage depletion of dawn standing crops of nectar at Betty's Bay and Jarrahdale was not only greatest for plant species which were most productive, but also for those whose nectar was accessible to a wide range of nectarivores (e.g., *D. sessilis, M. hirtus*).

Little is known regarding intraspecific partitioning of nectar resources within bird communities. Rufous Hummingbirds (*Selasphorus rufus*) appear to adjust the sizes of their breeding territories daily (Carpenter et al. 1983, Gass and Lertzman 1980), in a manner that is influenced by their sex and age (Gass 1978, 1979). J. L. Craig (1985) provided some evidence that in-

TABLE 9. RELATIVE OCCURRENCE OF POLLEN GRAINS IN SMEARS TAKEN FROM THE FOREHEADS AND THROATS OF NECTARIVOROUS BIRDS (PARTLY AFTER B. G. COLLINS 1983A). MEANS AND RANGES ARE GIVEN FOR EACH PLANT AND NECTARIVORE SPECIES

| Location and bird species | Sex | N | Percentage frequency of pollen[a] | | | | |
|---|---|---|---|---|---|---|---|
| Jarrahdale (July) | | | *Adenanthos barbigera* | *Calothamnus rupestris* | *Dryandra sessilis* | *Grevillea wilsonii* | *Dryandra nivea* |
| Little Wattlebird | Mixed | 4 | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 |
| New Holland Honeyeater | Mixed | 24 | 0.0 | 0.0 | 95.8 91.4–100.0 | 4.2 0–7.3 | 0.0 |
| Western Spinebill | Male | 15 | 1.2 0–3.1 | 0.0 | 83.6 79.1–92.7 | 3.1 0–8.1 | 12.1 0–15.8 |
| Western Spinebill | Female | 3 | 2.5 0–3.8 | 0.0 | 85.4 85.4–89.6 | 3.8 0–5.1 | 8.3 0–16.2 |
| Jarrahdale (September) | | | | | | | |
| Little Wattlebird | Mixed | 3 | 0.0 | 54.0 36.5–79.3 | 46.0 33.2–58.4 | 0.0 | 0.0 |
| New Holland Honeyeater | Mixed | 14 | 1.0 0–4.2 | 51.0 32.7–78.8 | 43.0 29.2–61.5 | 5.0 0–11.1 | 0.0 |
| Western Spinebill | Male | 5 | 3.1 0–6.2 | 47.2 29.3–58.6 | 48.5 22.5–57.7 | 1.2 0–4.2 | 0.0 |
| Western Spinebill | Female | 0 | | | | | |
| Fitzgerald River (July)[b] | | | *Banksia baueri* | *Banksia coccinia* | *Banksia media* | *Dryandra cuneata* | *Dryandra quercifolia* |
| New Holland Honeyeater | Mixed | 7 | 8.0 0.0–17.0 | 1.0 0–0.7 | 26.0 0–31.0 | 47.0 0–67.6 | 9.0 0–19.4 |
| White-cheeked Honeyeater | Mixed | 7 | 1.0 0.0–20.0 | 1.0 0–20.0 | 28.0 0–39.3 | 31.0 0–57.0 | 30.0 0–53.9 |
| White-naped Honeyeater | Mixed | 7 | 0.0 | 1.0 0–1.3 | 1.0 0–3.7 | 11.0 0–17.8 | 1.0 0–7.1 |
| Brown Honeyeater | Mixed | 7 | 14.0 0.0–36.6 | 0.0 | 2.0 0–18.3 | 54.0 0–97.2 | 11.0 0–49.3 |
| Western Spinebill | Male | 5 | 23.0 0.0–29.8 | 0.0 | 31.0 0–42.6 | 31.0 0–58.2 | 8.0 0–17.2 |
| Western Spinebill | Female | 2 | 17.0 11.0–23.0 | 0.0 | 22.3 17.6–27.0 | 21.0 0–42.0 | 7.0 0–14.0 |
| Betty's Bay (September) | | | *Erica perspicua* | *Mimetes hiruts* | | | |
| Cape Sugarbird | Male | 5 | 0.0 | 100.0 | | | |
| Cape Sugarbird | Female | 3 | 0.0 | 100.0 | | | |
| Orange-breasted Sunbird | Male | 7 | 27.7 13.6–42.6 | 72.3 39.6–82.1 | | | |
| Orange-breasted Sunbird | Female | 1 | 85.7 | 14.3 | | | |

[a] Pollen counts from head and throat of each bird pooled before calculation of percentages.

[b] In cases where frequencies do not add to 100.0, birds also foraged at other plants.

TABLE 10. PREFERENTIAL FORAGING BY HONEYEATERS OR SUGARBIRDS AT FLOWERS OF DIFFERENT AGES (PARTLY AFTER B. G. COLLINS 1983A, 1985)

| Plant species and time of year[a] | Age of flowers (days) | Relative abundance of flowers (%) | Foraging preference (%)[b] | | | |
|---|---|---|---|---|---|---|
| | | | *A.c.* | *P.n.* | *A.s.* | *P.c.* |
| *Dryandra sessilis* (July, N = 150) | 1–2 | 29.4 | 76 | 68 | 56 | |
| | 3–4 | 39.5 | 24 | 28 | 39 | |
| | 5–6 | 21.3 | 0 | 3 | 5 | |
| | 7–? | 9.8 | 0 | 0 | 0 | |
| *Grevillea wilsonii* (July, N = 152) | 1–2 | 53.9 | | | 100 | |
| | 3–? | 46.1 | | | 0 | |
| *Mimetes hirtus* (September, N = ?) | 1–4 | 17.1 | | | | 99 |
| | 5–? | 82.9 | | | | 1 |

[a] N denotes the number of plants observed for a total time of at least 36,000 s.

[b] *A.c.*, *P.n.* and *A.s.* made 91, 208 and 38 visits, respectively, to *D. sessilis*; *A.s.* made 30 visits to *G. wilsonii*; *P.c.* made 408 visits to *M. hirtus*. The letters *A.c.*, *P.n.*, *A.s.* and *P.c.* denote Little Wattlebirds, New Holland Honeyeaters, Western Spinebills, and Cape Sugarbirds, respectively.

dividual New Zealand honeyeaters partition available nectar, with larger, male birds usually dominating the richest sources. We also found that foraging activity and nectar use by some sunbirds, sugarbirds and Australian honeyeaters varied individually.

Since intraspecific dominance hierarchies exist in honeyeater (Craig 1985, Newland and Wooller 1985) and sunbird-sugarbird (Wooller 1982) communities, there is no obvious reason why larger, dominant birds should not use more rewarding flowers, and spend less time foraging, than subordinates. Although we found this to be true for the larger color-banded New Holland Honeyeaters at Jarrahdale, it was not the case for Little Wattlebirds. Data for Western Spinebills were variable, with males spending less time than females foraging for nectar in July, but more time in September. This discrepancy could have arisen because of the particular (unknown) sizes and positions of individuals sampled in the intraspecific dominance hierarchies at those times.

TABLE 11. OUTCOMES OF AGGRESSIVE INTERACTIONS BETWEEN HONEYEATERS AT JARRAHDALE, AND BETWEEN SUNBIRDS AND SUGARBIRDS AT BETTY'S BAY. FIGURES DENOTE EITHER TOTAL NUMBERS OF INTERACTIONS OR NUMBERS OF WINS/LOSSES

| Winning species | Losing species | | | |
|---|---|---|---|---|
| Jarrahdale | *A.c.* | *P.n.* | *A.s.* ♂ | *A.s.* ♀ |
| Little Wattlebird (*A.c.*) | 5 | 25/0 | 15/0 | 10/0 |
| New Holland Honeyeater (*P.n.*) | | 52 | 31/0 | 10/0 |
| Western Spinebill (*A.s.* ♂) | | | 9 | 11/2 |
| Western Spinebill (*A.s.* ♀) | | | | 0 |
| Betty's Bay | *P.c.* ♂ | *P.c.* ♀ | *N.v.* ♂ | *N.v.* ♀ |
| Cape Sugarbird (*P.c.* ♂) | 4 | 2/0 | 45/0 | 30/0 |
| Cape Sugarbird (*P.c.* ♀) | | 0 | 15/0 | 12/0 |
| Orange-breasted Sunbird (*N.v.* ♂) | | | 3 | 21/5 |
| Orange-breasted Sunbird (*N.v.* ♀) | | | | 0 |

No direct observational data on intraspecific differences in the types of flowers visited by color-banded honeyeaters, sunbirds, or sugarbirds are available, although smears taken from foreheads and throats of these and other non-banded birds suggest that preferential foraging occurs. However, interpretation of smear data is complicated by the fact that the proportions of various pollen grains present will be biased by the sequence in which plant species are visited and the amounts of pollen that they produce. Sex-related differences were especially obvious at two sites. For instance, all female Western Spinebills at Fitzgerald River carried *Banksia baueri* and *B. media* pollen, but some males did not. At Betty's Bay, male Orange-breasted Sunbirds bore significantly more *M. hirtus* and less *E. perspicua* pollen than conspecific females.

At best, the evidence currently available merely suggests that intraspecific partitioning of nectar resources occurs. It will only be possible to test this hypothesis satisfactorily if quantitative data are obtained using a variety of techniques, over extended periods of time, for large numbers of individual birds of known age, sex, and social status.

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