THE IMPORTANCE OF MANNA, HONEYDEW AND LERP IN THE DIETS OF HONEYEATERS

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SUMMARY

PATON, D. C. 1980. **The importance of manna, honeydew and lerp in the diets of honeyeaters. Emu 80: 213-226.** Honeyeaters mainly collected manna, honeydew or lerp off the foliage and bark of eucalypts and not insects as has been previously reported. These carbohydrates were more abundant than insects and other invertebrates on the foliage or bark, offered energy rewards similar to those from nectar and were widespread, occurring in many habitats. Manna, honeydew and lerp have chemical compositions similar to nectar and were used as substitutes by many honeyeaters. Honeyeaters shifted feeding sites and showed seasonal movements with changes in the distribution and abundance of these resources and nectar. Manna, honeydew and lerp are important in the ecology of many honeyeaters.

INTRODUCTION

The Meliphagidae (honeyeaters) are one of Australia's dominant passerine families (Keast 1968a), with at least one representative in each habitat. Frequently more than ten species occur in an area (Keast 1968a; Ford and Paton 1977) and most ecological studies on honeyeaters have examined coexisting species (Keast 1968b; Keast and Condon 1968; Recher and Abbott 1970; Recher 1971, 1977; Ford 1976a; Ford and Paton 1976, 1977). Keast (1976) explained the success of the family by the ability of species, in the absence of potential competitors, to adapt themselves to many niches, from gleaning foliage and probing bark to feeding on nectar and fruit.

It has generally been assumed that honeyeaters take insects from foliage or bark and the genera *Melithreptus, Lichenostomus* and *Manorina*, which forage primarily on these substrates, have been classed as insectivorous (Keast 1968b, 1976; Ford and Paton 1976, 1977; Dow 1977). *Anthochaera, Phylidonyris* and *Acanthorhynchus* feed predominantly at flowers, collecting nectar, but also glean foliage, probe bark and catch insects by hawking (Keast 1976; Ford and Paton 1977). Their foliage-gleaning and bark-probing have also been interpreted as insectivory.

Honeyeaters, however, often feed on manna, honeydew or lerp from the foliage or bark of eucalypts (e.g. Darnell-Smith 1910; Tindale 1929; Hindwood 1932; Ryan 1951; Clark 1964; Swainson 1970) but the significance of this has been ignored. Manna is the sugary fluid that exudes from damaged plant material and later crystallizes. It consists of about sixty per cent sugar, sixteen per cent water (mainly water of crystallization), some ash and twenty per cent pectin and uronic acids. Sugars in the mannas from *Eucalyptus maculata, E. punctata* and *Angophora costata* are raffinose (65–80%) with some melibiose, sucrose, glucose, fructose and stachyose (Basden 1965). Those in manna from *E. viminalis* are also small polysaccharides and protein is less than 0.2 per cent of its weight (pers. obs.). Honeydew, the sugary secretions of nymphal stages of aphids, coccids and psyllids, consists of small polysaccharides, usually tri- to hepta-saccharides with some glucose, fructose or sucrose and has almost no protein (Basden 1966, 1968, 1970, 1972; pers. obs.). Lerp is the protective covering over many Australian psyllids and is mostly carbohydrate. Basden (1970) determined that the lerp of *Eucalyptolyma maidenii* was composed of dextrin, amylose and amylopectin, polymers of glucose of increasing complexity, and that the lerp of *Cardiaspina densitexta* was starch. Manna, honeydew and lerp are thus substitutes for nectar.

I show that manna, honeydew and lerp were often the major items taken from the foliage and bark by honeyeaters and discuss the implications of this.

STUDY SITES

I visited the Royal Botanic Garden's Annexe at Cranbourne, about forty kilometres south-east of Melbourne, about six days a month between September 1975 and March 1978. The habitat was a dense coastal heath, with scattered eucalypts, predominantly *E. viminalis.* The vegetation of the area has been described by Gullan (1978).

I visited Golton Vale, 265 kilometres west-northwest of Melbourne on the Western Highway between Stawell and Horsham, for six days about every two months from October 1976 to September 1978. The habitat was a dry sclerophyll forest of *E. obliqua*, with scattered clumps of *E. camaldulensis, E. melliodora* and *E. viminalis*. There was a low (< 1 m) dense heath layer of epacrids, mostly *Astroloma conostephioides*, and scattered bushes of *Callistemon macropunctatus, Xanthorrhoea australis, Banksia marginata, Grevillea aquifolium* and *Acacia* spp.

METHODS

I scored feeding by locating a bird and recording its first or next feeding action and recorded the site (air, leaves, bark [trunk or upper branches], flowers, low shrub or ground), species of plant and food item (when possible). I collected time-budgets on colour-banded birds for up to thirty minutes at intervals throughout the day, by recording the duration of each activity from a wristwatch to within five seconds. Activities were classed as sitting, preening, flying, types of foraging and aggression and, when the bird was out of sight or obscured, the time was classified as lost.

The rates at which birds fed on manna, honeydew, lerp or nectar (flowers) were timed with a stop-watch. Foraging consisted of sitting (visually searching for and handling food) and moving (mainly hopping through the foliage or along branches). The proportion of time spent in each by foraging New Holland Honeyeaters *Phylidonyris novaehollandiae* was determined by recording the two on different stop-watches. Costs of foraging were estimated by assuming that costs of sitting were about twice the daytime dark metabolic rate and those of non-flight movement about four times this rate (Wolf 1975; Wolf *et al.* 1975). Only one to three per cent of foraging was flight, which was assigned to non-flight movement. The daytime dark metabolic rate of New Holland Honeyeaters was 15.8 calories per gram-hour in the zone of thermoneutrality and the average weight was twenty grams (per. obs.). I calculated the rate of energy consumption below the thermoneutral zone, given a thermal conductance of 0.93 cal./g $\times$ hr $\times$ °C calculated from the equation of Herreid and Kessel (1967) and a body temperature of 42 °C. I assumed the lower critical temperature of the thermoneutral zone to be 25 °C (Herreid and Kessel 1967) and calculated the costs of foraging on manna and the honeydew of psyllids and eriococcids at an ambient temperature of 20, 12.5 and 15 °C respectively and those for birds collecting nectar at the average ambient temperature at peak of flowering for each plant species.

I estimated populations of honeyeaters at Cranbourne and Golton Vale by recording all honeyeaters seen or heard within fifty metres of either side of a marked transect line, while walking slowly along it. The transect was 1,800 metres at Cranbourne and 2,000 metres at Golton Vale. The censuses began about an hour after dawn and took about two hours.

At Cranbourne, manna exuded from leaves, petioles, buds and fruits of *E. viminalis*, damaged by insects, and formed white sugary blobs. I estimated its abundance on trees by scoring the manna on ten samples, each of about 100 leaves, with associated buds, fruits and petioles (equivalent to about 0.03 m^3 of canopy). For each sample, all manna was collected and all insects counted. I weighed samples of manna to the nearest 0.1 milligram and converted to units of energy (3.4 $\pm$ 0.1 [s.d.] calories for 1 mg of manna). I estimated the manna on each tree by estimating the size of the canopy in sampling units and multiplying this by the average quantity of manna found on the ten samples. Ten to twenty trees were examined each time.

Standing crops (kcal./ha) were estimated by multiplying the average quantity of manna (all samples) by the average canopy and the density of trees. Canopies of thirty-seven trees averaged 208 $\pm$ 167 units (range 40–1,000) and determinations on the same trees on different days had standard deviations of less than twenty per cent of the mean. *E. viminalis* were counted in nine hectares and averaged 66.2 trees per hectare.

At Golton Vale, the abundance of honeydew associated with psyllids under the bark of *E. viminalis* and eriococcids in or under the bark of *E. obliqua* was assessed. Honeydew was collected in capillary tubes (10 or 50 μl), the volume measured and the concentration of sugar measured with a hand refractometer compensated to 20 °C. I calculated the energy value of these secretions, assuming that honeydew was equivalent to sucrose and gave four calories of energy per milligram (Brody 1945; Hainsworth and Wolf 1976).

I estimated the abundance of honeydew by counting the number of psyllid nymphs under one metre sections of bark on upper branches of *E. viminalis* and measuring the honeydew associated with them. Different sections of bark were examined at dawn and dusk. I estimated the amount of honeydew taken by birds by covering bark with fine netting, which prevented birds from probing the bark but allowed ants access to the psyllids. Suitable sections of bark were covered at dawn and available honeydew measured at dusk and compared with uncovered sections examined at dawn and dusk. I also estimated the production of honeydew by sampling it from the same insects at dawn and dusk, keeping the insects covered.

The honeydew associated with eriococcids (Coccoidea) on the bark of *E. obliqua* was also measured at dawn and dusk. Nymphs were counted on 0.3 metre sections of bark on upper branches (not 1 m because the insects were so numerous).

No correction was made for different diameters of the sections of bark examined on *E. viminalis* and *E. obliqua*. *E. viminalis*, on average, had 47 $\pm$ 47 metres (range 9 – 161, 9 trees scored) of bark suitable for psyllids, and *E. obliqua* 86 $\pm$ 75 metres (range 4–300, 65 trees scored) of bark suitable for eriococcids. Standing crops of honeydew (kcal./ha) were estimated by multiplying the average amount of suitable bark by the density of trees (calculated from 200 random quadrats [5 $\times$ 5 m] in 20 hectares), the density of nymphs and the quantity of honeydew per nymph.

I compared estimates of standing crops of manna and honeydew with those of nectar, which were calculated from data on nectar rewards, densities of plants and number of flowers per plant. Densities of plants were based on 252 and 200 random quadrats (5 $\times$ 5 m) at Cranbourne and Golton Vale respectively. The numbers of flowers in samples of twenty to 500 plants (depending on the species of plant and its density) were counted at regular intervals through the flowering season for each of the species used by honeyeaters. Standing crops of nectar were measured at or just before dawn and at three- to four-hour intervals during the day till dusk. I took samples of forty to 100 flowers (or 5 to 10 inflorescences) from several plants each time and measured the volume of nectar in each flower with a 10-μl capillary tube and the concentration with a hand-refractometer compensated to 20 °C. I then calculated the energy content of the nectar by converting sugar concentrations to milligrams of sugar, taking into account the density of different sugar concentrations and assuming that one milligram of sucrose gave 4.0 calories.

RESULTS

Abundance of manna, honeydew and lerp at Cranbourne

Nectar and manna were the major carbohydrates available to honeyeaters at Cranbourne, though there was a little honeydew and lerp. Manna was available mostly during summer and autumn, when usually over fifty per cent of foliage samples from *E. viminalis* bore it (Fig. 1a). Each sample usually had more than one blob

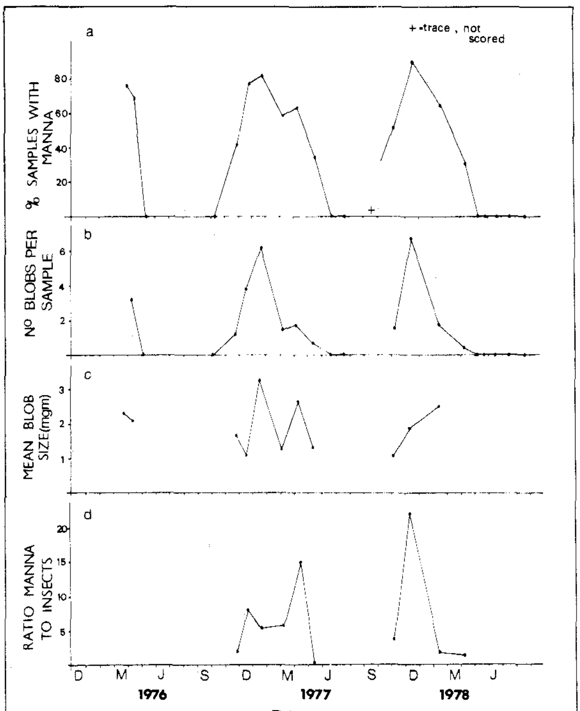

Figure 1. The seasonal abundance of manna and insects on the foliage of *Eucalyptus viminalis* at the Royal Botanic Garden's Annexe, Cranbourne. **a.** Percentage of sampling units (approx. 100 leaves) with manna. **b.** Mean number of blobs per sampling unit. **c.** Seasonal changes in mean blob size (mg). **d.** Ratio of blobs of manna to number of insects (and other invertebrates).

and even more than five blobs in mid-summer (Fig. 1b). Blobs weighed from 0.2 to 80 milligrams and the mean weight was 2.03 milligrams (2,687 blobs weighed, but not individually), equivalent to 6.9 calories. Mean weights for blobs collected on different days ranged from 1.01 to 3.30 milligrams (Fig. 1c).

Standing crops at midday were usually over seventy-five kilocalories per hectare from December to April, with peaks of over 500 kilocalories per hectare in mid-summer (Fig. 2). Standing crops of nectar at midday were usually less than ten kilocalories per hectare over this period (Fig. 2). Even standing crops of nectar at dawn, which were much higher than those at midday, were usually less than fifty kilocalories per hectare during summer and autumn and were also lower than the standing crop of manna. Less manna was measured on 5 March 1977, probably because there had been rain and strong winds during the week before sampling. Rain dissolves the manna and washes manna off the foliage; strong winds dislodge it (Basden 1965; pers. obs.). Manna was not recorded during sampling in winter but after several days of fine weather small amounts occurred.

Basden (1965) reported manna exuding at 1 to 2.5 milligrams (3–8 cal.) per site per day, which is similar to that of nectar from flowers of several plants (from 0.6 cal/flower/day in *Epacris impressa* to over 20 in *Eucalyptus leucoxylon*, pers. obs.).

Insects and other invertebrates occurred on the foliage of *E. viminalis* but blobs of manna outnumbered them by 2:1 and up to 21:1 during summer and autumn (Fig. 1d). The low ratio (0.35:1) on 19 May 1977 was due to

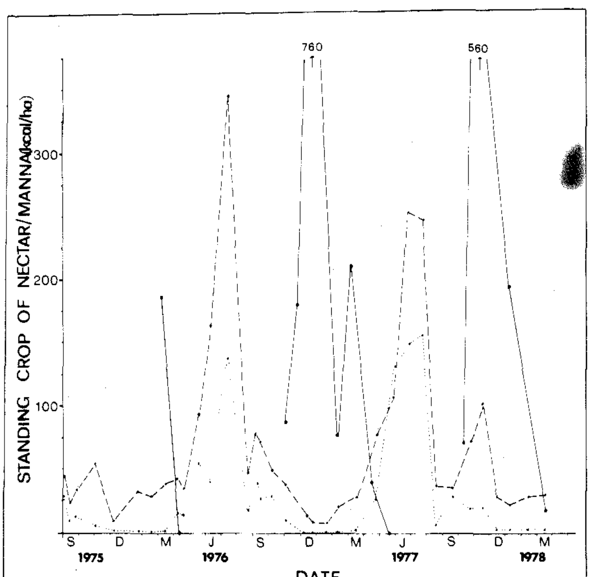

Figure 2. Seasonal changes in standing crops (kcal./ha) of nectar and manna at Cranbourne. ——— manna at midday; ----- nectar at dawn; ······ nectar at midday.

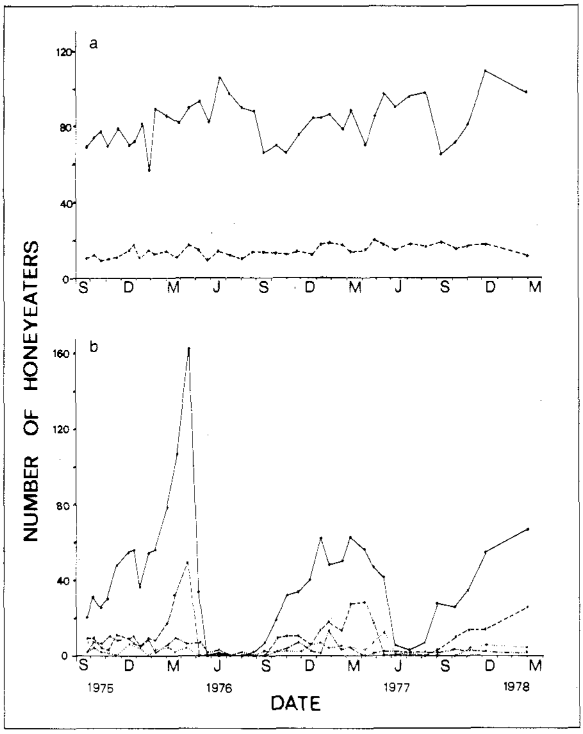

Figure 3. Counts of honeyeaters at Cranbourne. Number of birds counted on 1,800 metres of transect. **a.** New Holland (———) and White-eared (-----) Honeyeaters. **b.** White-naped (———), Yellow-faced (-----), Brown-headed (······) and White-plumed (-··-··-··) Honeyeaters.

many minute Diptera about two millimetres long (93% of insects). These would offer less than two calories of energy (Bryant 1973) and not be as rewarding as manna, which averaged 1.35 milligrams (4.6 cal.) on this day. They were easily disturbed and so probably were not available to leaf-gleaning honeyeaters. Ants, small Diptera and Hymenoptera were usually over half of the insects on the foliage and insects likely to induce production of manna (e.g. Coleoptera, Hemiptera, larvae of Lepidoptera and Hymenoptera) were not common and estimated at less than fifty per tree. Probably many phytophagous insects fed at night and left the foliage during the day to avoid predation.

Birds feeding on manna at Cranbourne

Fourteen species were seen feeding on manna but most data were collected on New Holland Honeyeaters, which were resident throughout the year (Fig. 3). New Holland Honeyeaters fed primarily on nectar but, when there was little nectar during summer (Fig. 2), they used manna. Figure 4 shows the proportion of monthly feeding observations that were collecting manna. During January and February the birds became almost entirely leaf-gleaners.

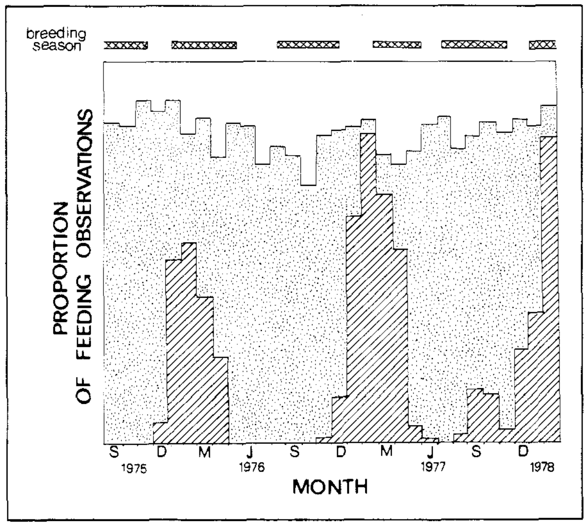

Figure 4. Monthly feeding observations for New Holland Honeyeaters at Cranbourne. The figure shows the proportion of feeding observations collecting nectar (stippled), manna (hatched) or insects (blank). Total number of observations, 10,848.

My observations of feeding were often biased towards conspicuous feeding activities. I collected 51,800 seconds of time-budget on New Holland Honeyeaters in January and February. Fifty-six per cent of this was spent feeding, of which ninety-five per cent was collecting manna, three per cent nectar and two per cent hawking insects. New Holland Honeyeaters collected 9.1 blobs of manna per minute (860 blobs timed) or about sixty-three calories per minute (9.1×6.9). They spent seventy-one per cent of feeding time sitting and costs of foraging on manna were estimated at about eighteen calories per minute. Thus the birds would have had a net energy gain of about forty-five calories per minute, which compares favourably with net gains from collecting nectar during the afternoon (Table I). In fourteen hours of daylight New Holland Honeyeaters would feed for 470 minutes and collect about twenty-eight kilocalories of manna. I estimated the daily energy requirements of these birds from the complete time-budget to be about twenty kilocalories per day; so the birds ought to meet their requirements easily when feeding on manna. The higher intake might have been expected because some of the birds had begun breeding in February and presumably needed additional energy for this. Manna was also taken during the breeding season (Fig. 4) and blobs were given to the young.

New Holland Honeyeaters often defended one to four trees for several weeks and excluded conspecifics and other species from the foliage, particularly Spotted *Pardalotus punctatus* and Striated *P. striatus* Pardalotes, White-naped *Melithreptus lunatus*, Brown-headed *M. brevirostris* and Yellow-faced *Lichenostomus chrysops* Honeyeaters.

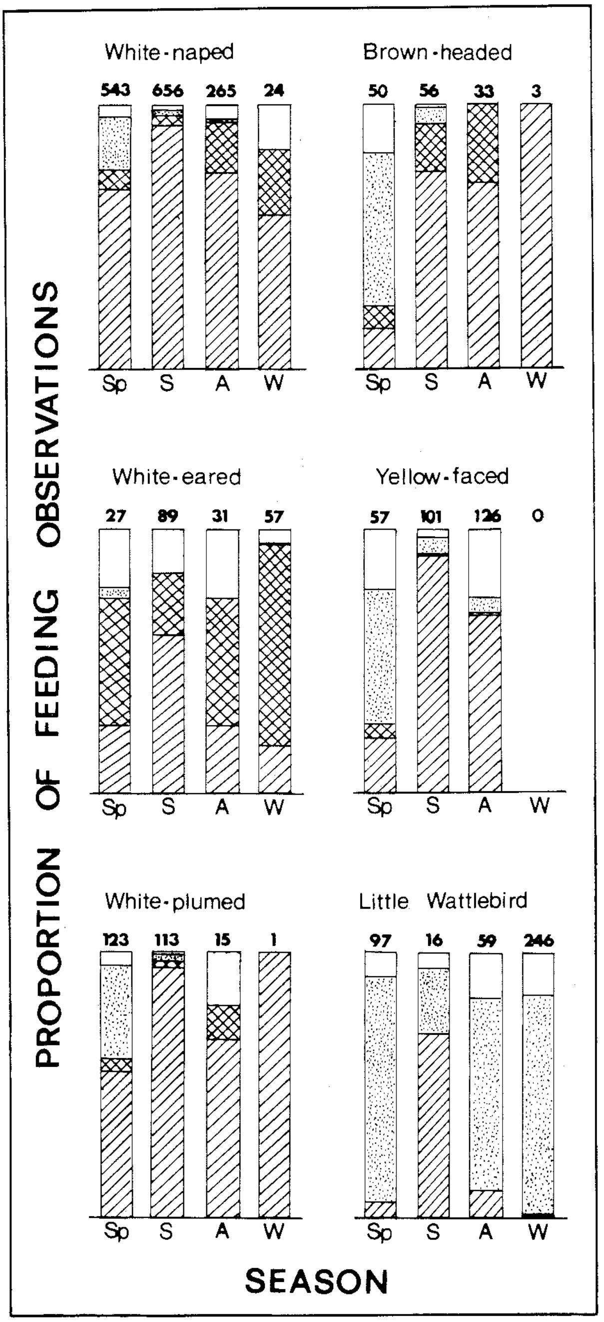

Figure 5. Seasonal feeding observations for six species of honeyeater at Cranbourne. **Hatched,** on *E. viminalis* foliage (manna); **cross-hatched,** on *E. viminalis* bark (honeydew); **stippled,** on nectar; **blank,** other feeding, including hawking and collecting insects off bushes.

TABLE I

Net energy gains for New Holland Honeyeaters collecting nectar.
Calculations made at peak of flowering, by using average levels of nectar, average rates of feeding (flowers/min.) and assuming 95% extraction of nectar from flowers and 100% assimilation.

Plant species	Net energy gains (cal./min.) Dawn	Afternoon
Amyema pendulum	171	41
Astroloma conostephioides	262	243
Banksia marginata	313	20
Callistemon macropunctatus	208	12
Epacris impressa	36	15
Eucalyptus leucoxylon	558	38
E. melliodora	112	–
E. obliqua	107	6
Grevillea aquifolium	339	67

White-naped, Brown-headed, Yellow-faced, White-plumed *L. penicillatus* and White-eared *L. leucotis* Honeyeaters frequently foraged among the foliage of *E. viminalis* during summer and autumn (Fig. 5). Over ninety-five and up to one hundred per cent of items taken from the foliage by each species was manna and birds, caught in mistnets, often had small amounts of manna on their bills. Pardalotes also frequently fed on manna and White-naped and Brown-headed Honeyeaters gave manna to their nestlings.

White-naped, Yellow-faced, Brown-headed and White-plumed Honeyeaters left the Annexe during April and May when manna decreased (Fig. 3); so, little feeding by these species was seen during winter (Fig. 5). The birds returned from about September and in early spring, when manna was less abundant, these species often fed on the nectar of *Amyema pendulum* (Fig. 5). A few White-naped Honeyeaters remained during winter 1977 when small amounts of manna and lerp occurred on *E. viminalis.* White-eared Honeyeaters remained in about the same numbers throughout the year (Fig. 3) and in winter fed mainly on the secretions of psyllids under the bark of *E. viminalis* (Fig. 5).

Abundance of carbohydrates at Golton Vale

Nectar and the honeydew of psyllids (Psyllidae, Psylloidea) under the bark of *E. viminalis* and of scale insects (Eriococcidae, Coccoidea) on the bark of *E. obliqua* were important sources of carbohydrates for honeyeaters at Golton Vale. The psyllids occurred where bark was folding back or split and were distributed mainly on the outer branches. The scale insects were concentrated in transitional areas between the rough bark of the trunk and major branches and the smooth bark of the smaller limbs. Both insects appeared more common where the outer branches forked.

It was difficult to be certain of items being taken by honeyeaters probing the bark of *E. viminalis* but their feeding behaviour was consistent with collecting honeydew. They foraged only on upper branches where bark was beginning to peel or split, probing under bark and often spending five to ten seconds and sometimes over thirty seconds at one site without withdrawing the bill. Feeding birds were sometimes displaced by others, which continued to feed in the same manner at the same site. In over 1,000 minutes of observing New Holland Honeyeaters feeding on *E. viminalis*, on only two occasions was an insect seen to be taken. Nymphs also excreted a white floccular material, which was not sweet-tasting, and this occasionally stuck to the bill of the birds, indicating that they were feeding near the psyllids. The energetic value of this material was not assessed but the birds usually wiped it off their bills before probing again and large patches of it remained under the bark even where nymphs were scarce.

Psyllid nymphs were most abundant in winter (Table II). Nymphs were mainly small in July, increasing in size through August until October when most were large and many had pupated or been parasitized. A few occurred during summer. Most nymphs had produced small droplets of honeydew and, in areas where several nymphs had congregated (up to 24), pools of honeydew (often over 50 μl and up to 300 μl) had formed and begun to ooze out of cracks. Refractive indices of this fluid indicated sugar concentrations of from forty-three to eighty-four per cent and droplets were often the consistency of honey. In October some droplets had crystallized.

In July and August 1977 I sampled honeydew (cal./nymph) at dawn and dusk and compared these to measurements from nymphs that had been protected with fine netting during the day. The quantity of honeydew at uncovered nymphs was greater at dawn than dusk and that from protected nymphs was higher than both (Table III), indicating that honeyeaters were harvesting honeydew and that honeydew was being produced during the day. These data could not be tested statistically. However, in July, significantly fewer nymphs had honeydew at dusk (40 of 50) compared to dawn (103 of 107) ($\chi_1^2 = 11.09$, $p < 0.001$), but those covered with netting all had honeydew (71 of 71, Table III). In August, the number of nymphs with honeydew did not change significantly during the day (142 of 161 and 91 of 106) but significantly more of the covered nymphs had honeydew (111 of 111, $\chi_1^2 = 16.87$, $p < 0.001$, Table III). Large variations in the number of nymphs per metre made it difficult to assess whether the birds were also taking these. Differences in numbers under bark examined at dawn and dusk and those covered with netting were not significant ($F = 3.2$, d.f. 2, 15 and $F = 0.8$, d.f. 2, 21, Table III). That the number of nymphs did not change between July and August (Table II), when there was little recruitment, suggests the birds were not taking the nymphs and supports observations on their feeding behaviour.

The standing crop at dawn peaked at about fourteen kilocalories per tree or twenty-eight kilocalories per hectare in August. *E. viminalis* was clumped in a small area of about two hectares and in this area the standing crop would have been about 280 kilocalories per hectare at dawn in August. However not all the honeydew would be available to the birds as some droplets would be inaccessible.

In July and August 1977 I tried to measure the rate of excretion of honeydew by resampling the same insects at dawn and dusk. I was not very successful because many nymphs, once disturbed, moved away from the covered area and those that remained may have been interrupted, though they continued to feed and excrete honeydew. In July seven nymphs produced on average 2.7 calories each between 08:00 and 17:00 and two nymphs 3.3 calories between 17:00 and 08:00. In August

TABLE II

Seasonal abundance of psyllids and other invertebrates under the bark of *Eucalyptus viminalis* at Golton Vale.

Date	No. nymphs/m Mean ± s.d. (n)	Range	No. other inverts/m Mean ± s.d.	Range
Feb. 77	2.1 ± 0.8 (20)			
May 77	0 (5)			
Jul. 77	12.7 ± 9.8 (18)	1–44	1.4 ± 2.8	0–11
Aug. 77	15.7 ± 8.4 (24)	1–32	3.4 ± 3.5	0–11
Oct. 77	2.8 ± 2.6 (18)	0–9	3.8 ± 4.8	0–15
Sep. 78	6.6 ± 5.4 (10)	0–16	5.3 ± 5.9	0–16

TABLE III

Abundance of honeydew from the nymphs of psyllids (Psyllidae) living under the bark of *E. viminalis* and the effect of birds on honeydew.

	Uncovered bark		Covered* bark
	Dawn	Dusk	Dusk
July 77			
Nymphs/m	10.7 ± 6.5 (10)†	10.0 ± 6.7 (5)	23.7 ± 17.7 (3)
H'dew cal./nymph	11.4	9.5	24.7
% nymphs with h'dew	96.3	80.0	100
August 77			
Nymphs/m	16.1 ± 8.7 (10)	13.1 ± 8.9 (8)	18.5 ± 7.7 (6)
H'dew cal./nymph	19.1	14.7	23.6
% nymphs with h'dew	88.2	85.7	100

* covered with fine netting from dawn to dusk.
† mean ± s.d. (n).

TABLE IV

Abundance of honeydew from eriococcids living on *E. obliqua* bark, measured in May 1977 at Golton Vale.

	Dawn	Dusk
No. eriococcids/0.3 m bark	33.8 ± 27.7 (5)*	40.8 ± 27.8 (5)
% eriococcids with > 1μl honeydew	14.2	2.5
Mean volume (μl) of honeydew for eriococcids with > 1μl	2.2 ± 2.0	1.4 ± 0.6
Total calories of honeydew† per metre of bark	189	107

* mean ± s.d. (n).
† calculated assuming 0.25μl of honeydew for all eriococcids with < 1μl and multiplied by average number eriococcids per metre (123).

fifteen nymphs produced on average 6.8 calories each between 07:00 and 19:00.

Other invertebrates were less common than psyllids under the bark (Table II). Most were small sugar ants or small flying insects that also fed on honeydew. They seemed to have no major effect on the availability of honeydew (Table III).

It was easier to assess food being gathered by honeyeaters on the bark of *E. obliqua* because secretions were often on the surface and birds could be seen licking them off the upper branches as well as probing under suitable bark. Honeyeaters usually fed methodically, licking most of the surface of the bark and sometimes spending several minutes in the same area as they worked slowly along a limb. Honeyeaters were never observed feeding on the rough bark of the trunk.

Many eriococcids were exposed on the surface of the bark and available to birds. However I could dislodge them only with difficulty and their tests tasted bitter; so they were probably inedible. No birds were seen collecting them or their coats.

Honeydew from these insects was available throughout the year but prominent only in May 1977, December 1977 and May 1978, when upper branches were sticky to touch. I measured the secretions in May 1977. Concentrations averaged seventy-seven per cent and volumes ranged up to eight microlitres. Most insects had a small amount of honeydew but it was difficult to collect in capillary tubes because of the high concentration of sugars and the small volumes and because droplets generally diffused, forming a thin sticky layer on the bark. At dawn 14.2 per cent (24 of 169) of the scale insects had at least one microlitre (mean 2.21 ± 2.04, 24) of honeydew but at dusk only 2.5 per cent (5 of 204) had volumes above one microlitre (1.40 ± 0.55, 5), the difference being significant. All

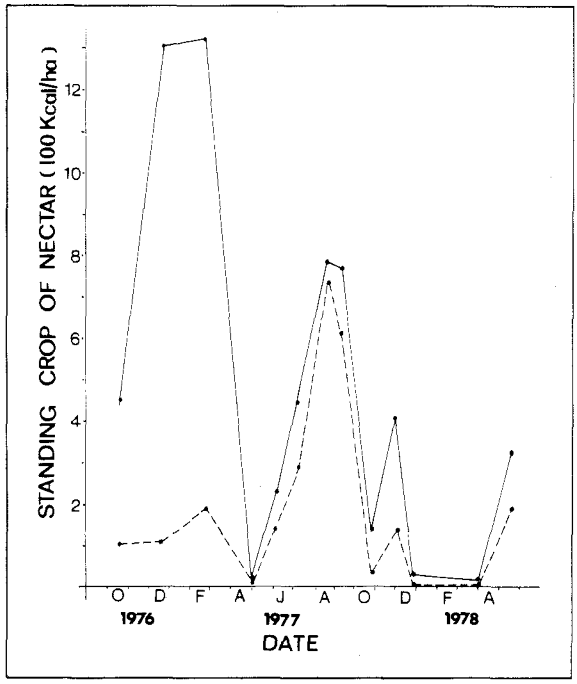

Figure 6. Standing crops (kcal./ha) of nectar at Golton Vale at dawn (________) and at midday (-----).

other nymphs had trace amounts estimated to be about 0.25 microlitres each. Table IV sets out the abundance of these insects and their secretions. The standing crop at dawn, if one assumes 0.25 microlitres for all other nymphs, would be about 2,340 kilocalories per hectare. If those with less than one microlitre of honeydew are excluded, the standing crop at dawn would still be about 1,485 kilocalories per hectare. Figure 6 plots the standing crops of nectar for Golton Vale. The abundance of eriococcid honeydew in May 1977 compares to the most abundant levels of nectar. In May and December 1977 when nectar was scarce, honeydew was a major source of carbohydrate. In March 1978, there was little carbohydrate, either nectar or honeydew, on the site and many honeyeaters had moved into adjacent areas to feed on the nectar of *E. leucoxylon* (Fig. 7), though they still used the study area for shelter.

Birds feeding on honeydew of psyllids and eriococcids at Golton Vale

Figure 8 shows that as much as forty per cent of monthly feeding observations for New Holland Honeyeaters were collecting honeydew. Pooled time-budgets for New Holland Honeyeaters at these times gave similar results (Table V). The results, however, obscure the importance of these secretions to some individuals. In July most birds had either breeding or individual feeding territories. Some had territories round flowers of *Astroloma conostephioides* with no *E. viminalis* and no

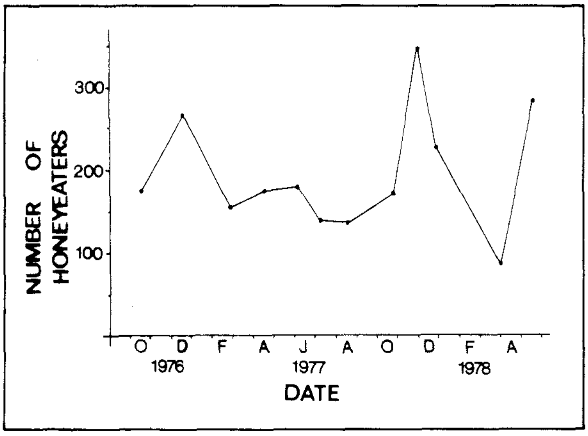

Figure 7. Number of honeyeaters counted on 2,000 metres of transect at Golton Vale.

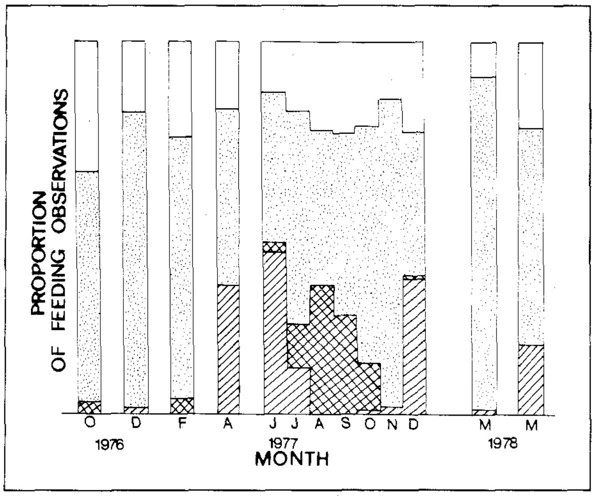

Figure 8. Monthly feeding observations for New Holland Honeyeaters at Golton Vale, showing the proportion of feeding observations collecting nectar (**stippled**), honeydew (**hatched**, *E. obliqua* bark; **cross-hatched**, *E. viminalis* bark) or insects (**blank**). Total number of observations, 5,160.

access to honeydew but others spent as much as eighty per cent of feeding time collecting honeydew. Most bred from July to October and the secretions remained an important component of the diet.

New Holland Honeyeaters averaged 13.6 probes per minute (430 timed) and spent about seventy-four per cent of the feeding time sitting, when feeding on the bark of *E. viminalis* in July and August. If each probe reached a new blob of honeydew, the birds could have collected 129 to 260 calories per minute, which gives net gains of 106 to 237 calories per minute after the costs of feeding (23 cal./min.) have been deducted. However some of the probes would have been unsuccessful and net gains would have been lower. I indirectly estimated gains of this feeding from estimates of total time spent probing bark by territorial birds, the amount of suitable bark in each territory and the abundance of honeydew from Table III. Table VI sets out the calculations, which show that birds spent about one and a half minutes probing in each metre of bark each day and averaged net gains of about sixty calories per minute. With such intense feeding the birds would have quickly reduced the number of psyllids if they were taking them.

The territorial New Holland Honeyeaters attacked all birds except Red Wattlebirds *Anthochaera carunculata* that settled near *E. viminalis* bark, likely to house psyllid secretions. New Holland Honeyeaters drove Red Wattlebirds away with difficulty but interfered with their feeding. They also had difficulty in driving off flocks of Brown-headed Honeyeaters, which swamped their territories. Table VII shows sites where aggression started, between July and October, when psyllid secretions were available. Nearly all aggression was associated with a source of carbohydrate. Honeyeaters, even conspecifics,

TABLE V

Time-budgets for New Holland Honeyeaters feeding on honeydew at Golton Vale.

Date	Observation time* (sec.)	% day feeding	% of feeding time collecting: Honeydew† *E. viminalis* bark	Honeydew† *E. obliqua* bark	Nectar	Insects
May 77	23,318	86.8		30.0	68.0	2.0
Jul. 77	72,906	59.4	44.0		54.0	2.0
Aug. 77	107,961	33.7	58.0		32.6	9.4
Sep. 77	99,881	46.9	32.5		51.7	15.8
Dec. 77	51,421	33.2		34.8	62.7	2.5

* excludes time classified as lost.
† birds feeding on *E. viminalis* bark collecting psyllid secretions.
birds feeding on *E. obliqua* bark collecting eriococcid secretions.

TABLE VI

Indirect estimate of net energy gains for New Holland Honeyeaters feeding on psyllid secretions at Golton Vale.

Date	Territory*	No. nymphs	Sec./day feeding on bark	Probes per day	Probes per psyllid per day	Honeydew taken		Energy gain (cal./min.)	
						cal./nymph /day	cal./ probe	gross	net
July 77	1	3,975	42,417	9,615	2.42	15	6.20	84	61
July 77	2	1,562	17,008	3,855	2.47	15	6.07	83	60
TOTAL OR MEAN		5,537	59,425	13,470	2.43	15	6.17	84	61
Aug. 77	1	4,914	17,521	3,971	0.81	7	8.64	118	95
Aug. 77	2	1,932	15,982	3,623	1.88	7	3.72	51	28
TOTAL OR MEAN		6,846	33,503	7,594	1.11	7	6.31	86	63

* 1 = 313 metres of bark; 2 = 123 metres.

TABLE VII

Frequency of aggressive acts by New Holland Honeyeaters at Golton Vale between July and October. New Holland Honeyeaters averaged 2.24 aggressive acts per hour over this period and spent on average 6.7 seconds per encounter.

Species attacked	Where aggression initiated					Total
	E. vim. bark	*E. vim.* foliage	*E. obl.* bark	Nectar	Other†	
Competitors						
(Honeyeaters)						
New Holland	76		4	125	36	241
Tawny-crowned	2			3		5
White-plumed	36		2		2	40
Fuscous	6					6
Black-chinned	2		1			3
Brown-headed	62		3	1	1	67
Red Wattlebird	1*			1*		2
Prob. competitors						
Crested Shrike-tit	2					2
Varied Sittella	2					2
White-thr. T'creeper	5		2			7
Spotted Pardalote		4				4
Striated Pardalote		13				13
Weebill	1	5		2		8
Non-competitors						
Golden Whistler				7		7
E. Yellow Robin	1					1
Hooded Robin	1			1		2
Jacky Winter	1					1
Ch-rump. Hylacola				1		1
Superb Fairy-wren				3		3
Grey Fantail					3	3
Horsf. B-Cuckoo					2	2
Total	198	22	12	144	44	420

* interfering with feeding but not excluding.
† birds attacked as they flew over, perched or approached nest or female.

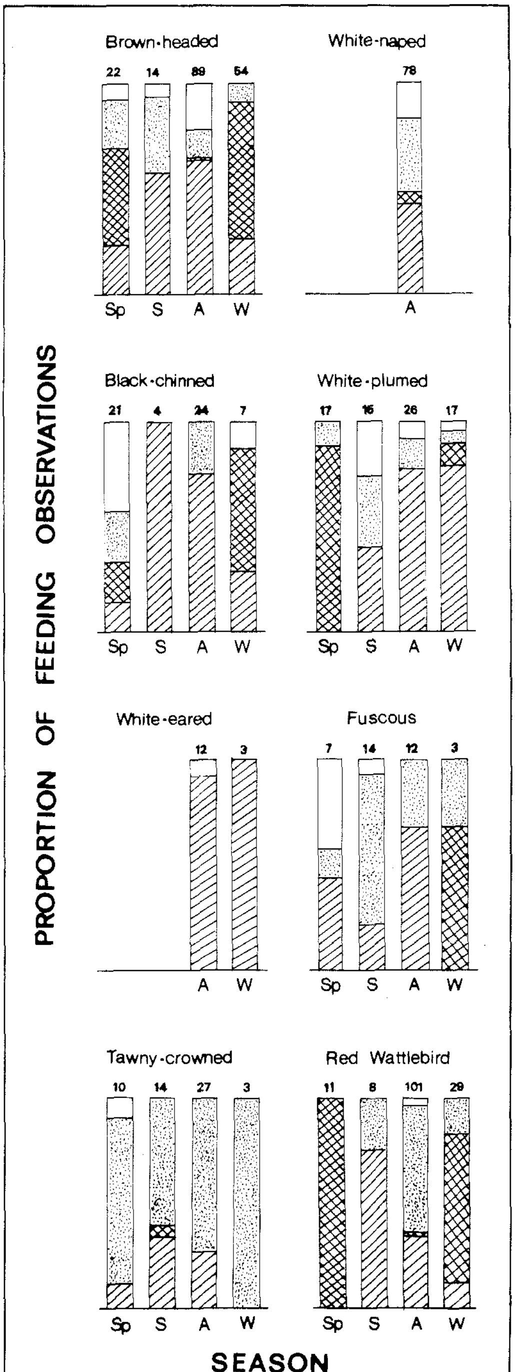

Figure 9. Seasonal feeding observations for eight species of honeyeater at Golton Vale. **Hatched,** on *E. obliqua* bark (honeydew); **cross-hatched,** on *E. viminalis* bark (honeydew); **stippled,** on nectar; **blank,** other feeding, including on foliage and hawking insects.

that did not land on suitable bark were not always chased. Birds that rarely landed on bark or in flowering bushes were rarely attacked. For example, both Hooded Robins *Melanodryas cucullata* and Superb Fairy-wrens *Malurus cyaneus* nested in shrubs under the canopies of *E. viminalis*, where New Holland Honeyeaters were defending territories but were rarely chased (Table VII). They appeared to avoid the flowering bushes and bark being defended by the honeyeaters. White-throated Treecreepers *Climacteris leucophaea*, Varied Sittellas *Daphoenositta chrysoptera* and Crested Shrike-tits *Falcunculus frontatus* tried to feed on the bark of *E. viminalis* but were promptly driven away. These species possibly took honeydew and psyllids and aggression towards them may have been doubly advantageous, particularly against Shrike-tits, which also destroy suitable habitat for nymphs by ripping off bark.

New Holland Honeyeaters occasionally collected lerp from the foliage of *E. viminalis* and aggression shown to pardalotes and weebills may have been associated with this food.

New Holland Honeyeaters averaged 18.5 probes per minute (130 timed) under loose bark of *E. obliqua* but often the almost continuous licking could not be separated into probes and that rate is probably a minimum. At dawn there are about 1.5 calories per scale insect and the birds ought to collect about twenty-five to thirty calories per minute but possibly not much more. Costs of foraging were estimated at about twenty calories per minute (78% sitting). The large amount of time spent feeding in May 1977 indicated that rewards were not particularly high (Table V) but they were probably sufficient to satisfy the birds. Birds caught in May 1977, May 1978 and December 1977 were in good condition and had good reserves of fat and generally weighed more than at other times. Fifteen individuals, caught twice in a few days in May 1977, had maintained their weight. Energy gains may have been higher in some areas, because Red Wattlebirds also fed on these secretions and defended parts of trees and their costs are much higher than those of New Holland Honeyeaters. New Holland Honeyeaters were also aggressive over parts of *E. obliqua* bark, chasing all birds that landed nearby. However they were not seen to defend a defined section for any length of time, though they often fed in the same area for several consecutive days.

Twelve other species of honeyeater also fed on secretions of psyllids and eriococcids at Golton Vale (Table VIII). Feeding observations of eight are given in Figure 9. Most fed from the bark of *E. viminalis* and *E. obliqua* and concentrated on *E. obliqua* during summer and autumn and on *E. viminalis* during winter and spring, the periods when eriococcid and psyllid secretions were available.

Some details of changes in feeding behaviour are lost in the seasonal presentation. For example, Red Wattlebirds fed predominantly on eriococcid secretions in May 1977 and most of the feeding on nectar occurred in

TABLE VIII
Availability of manna, honeydew and lerp in areas of South Australia and Victoria, with birds seen feeding on them.

Locality	Date*	*Eucalyptus*	Food (site)†	Species‡
Vic.				
Cranbourne	SA	*viminalis*	m (f)	NH, TC, RW, LW, WE, YF, WP, ES, WN, BH, ST, BT, SpP, StP
Cranbourne	W	*viminalis*	ph (b)	NH, WE, LW
Golton V.	SA	*obliqua*	eh (b)	NH, TC, WF, C, RW, WP, WE, YT, F, YF, BH, WN, BC
Golton V.	WSp	*viminalis*	ph (b)	NH, TC, RW, WP, BH, BC
Golton V.	Sp	*viminalis*	pl (l)	NH, StP
Golton V.	Sp	*obliqua*	m (f)	NH
Stawell	Y	*camaldulensis*	pl (l)	WP, NM
Churchill NP	Y	*ovata*	pl (l)	BM
Churchill NP	Y	sp	pl (l)	NM
Monash Univ.	A	*maculata*	m (f)	
Monash Univ.	Y	spp	pl, ph (l)	WP, RW
Hampton Pk	Sep 78	*radiata*	psh (b)	WP
SA				
Flinders Ch.	May 78	*cladocalyx*	ch (b)	PG, C, NH, WE
Flinders Ch.	May 78	*diversifolia*	ph, psh (b)	PG
Seal Bay	May 78	spp	ph, psh (b)	PG
Scott CP	Dec 77	*huberiana*	m (f)	
Scott CP	Dec 77	*baxteri*	ph, oe (b)	
Scott CP	Dec 77	*odorata*	ph (b)	
Inman V.	Dec 77	*obliqua*	ch, ph (b)	
Bonython CP	Dec 77	*obliqua*	ch (b)	NH, C
Mt Lofty	Jan 78	*obliqua*	op (b)	
Mt Lofty	Jan 78	*baxteri*	pl, ph (f)	
Mt Lofty	Jan 78	*baxteri*	ph (b)	
R. Torrens	Y	*camaldulensis*	pl (l)	WP, NM

* Sp = spring, S = summer, A = autumn, W = winter, Y = all year.
† m = manna, ph = psyllid honeydew, eh = eriococcid honeydew, pl = psyllid lerp, psh = pseudococcid honeydew, ch = coccoidea honeydew, oe = old eriococcids, op = old psyllids; (f) = foliage, (b) = bark, (l) = leaves.
‡ Species recorded feeding: NH = New Holland, TC = Tawny-crowned *Phylidonyris melanops*, C = Crescent, WF = White-fronted *P. albifrons*, LW = Little Wattlebird, RW = Red Wattlebird, ES = Eastern Spinebill *Acanthorhynchus tenuirostris*, WE = White-eared, PG = Purple-gaped, WP = White-plumed, F = Fuscous, YF = Yellow-faced, YT = Yellow-tufted, BH = Brown-headed, BC = Black-chinned *Melithreptus gularis*, WN = White-naped, NM = Noisy Miner, BM = Bell Miner, StP = Striated Pardalote, SpP = Spotted Pardalote, ST = Striated Thornbill *Acanthiza lineata*, BT = Brown Thornbill *A. pusilla*. Scientifiic names for other birds in text.

March and May 1978, when *E. leucoxylon* was flowering. In May 1977 one Red Wattlebird was territorial. The bird defended about 120 metres of bark (about half of a large *E. obliqua*) until late morning, chasing away all other honeyeaters. After about midday it no longer chased other honeyeaters and allowed as many as four New Holland Honeyeaters to feed without aggression. The Wattlebird left the area in the early afternoon and fed on other trees nearby, returning occasionally to the original tree. The same thing occurred for five days and presumably involved the same bird. On 5 June, a Red Wattlebird was using the same area and defending it in the morning. I obtained 150 minutes of time-budget on the Wattlebird in May 1977. It fed only on honeydew and spent seventy-one per cent of the time feeding.

Additional observations

I visited many localities in South Australia and Victoria and found honeydew, manna and lerp widespread (Table VIII). In all areas I found honeydew, manna or lerp within ten minutes of searching for them and often saw birds collect them.

At Flinders Chase National Park, Kangaroo Island, a variety of homopteran secretions were being taken by Purple-gaped *Lichenostomus cratitius*, New Holland, White-eared and Crescent *Phylidonyris pyrrhoptera* Honeyeaters. Several marked Purple-gaped Honeyeaters had fixed feeding areas, where they remained for at least several days. They spent 87.6 per cent of their time feeding, of which 99.7 per cent was collecting honeydew of coccids (Coccoidea) living under the bark of *E. cladocalyx* (7,905 seconds of time-budget). New Holland Honeyeaters also used and defended these resources in the morning.

At Churchill National Park, Victoria, Bell Miners *Manorina melanophrys* collected lerp off the foliage of *E. ovata* at a rate of thirty-nine lerps per minute (100 timed). The psyllid nymph living under the lerp was not always taken. On surfaces of leaves examined after Bell Miners had taken lerps, seventy-seven per cent (23 of 30) of the nymphs were left behind (although some naked nymphs may already have been present). Nymphs were small and in the samples that I measured the dry weight of the lerp was as much as thirty times that of the nymph; so Bell Miners were not missing much, though the nymph may be a valuable source of protein. Presumably the naked nymph survives and produces another lerp.

DISCUSSION

Estimates of abundance of manna at Cranbourne and honeydew at Golton Vale are comparable with other figures. Cribb and Cribb (1975) reported that aborigines collected eighteen to twenty-three kilograms of lerp per day in some areas along the Murray and Darling Rivers and, if the harvest extended over six weeks, which it often did, the aborigines became quite fat. They listed eleven plants (seven eucalypts) that supplied useful amounts of manna, honeydew or lerp to the aborigines and reported that Tasmanian aborigines made holes in the bark of *E. gunnii* and collected sugary sap that ran out of the wound. White settlers copied the aborigines and made pint-sized notches, which filled daily for several days. In Europe, honeydew is abundant and is exploited primarily by insects (Esau 1961). Much of the honey produced in Europe (up to 70%) is derived from honeydew and Zoebelein (1954) calculated that ants collected 200 to 250 grams of honeydew per day off single pine trees. Esau gives several examples where levels were sufficiently high to be exploited by man. In other countries, birds are reported feeding on similar carbohydrates. Reichholf and Reichholf (1973) found hummingbirds feeding on the honeydew of coccids under the thin bark of *Mimosa bracaatinga* in Brazil and defending single trees or groups of trees. Hummingbirds also fed on the honeydew of Coccoidea in Villavicencio, Columbia (Koster and Stoewesand 1973). Acorn Woodpeckers *Melanerpes formicivorus* drilled holes in live oak trees *Quercus* sp in California and fed on the sap that oozed out (MacRoberts 1970). Other woodpeckers, hummingbirds and the Plain Titmouse *Parus inornatus* also tried to feed on the sap but were chased away by the Acorn Woodpeckers.

My observations have concentrated on manna and honeydew but lerp is equally important and frequently taken by honeyeaters. Lea and Gray (1936) listed ten species of honeyeater that had been feeding on lerp and Ryan (1951) reported many White-naped, Purple-gaped, Brown-headed and White-plumed Honeyeaters feeding on lerp near Bendigo. B. Wykes (pers. comm.) found that over eighty per cent of the food collected by Bell Miners at Yellingbo, Victoria, was lerp from *Glycaspis* on *E. ovata* and that in other areas of Victoria Fuscous *Lichenostomus fuscus*, White-plumed, Yellow-plumed *L. ornatus* and Yellow-tufted *L. melanops* Honeyeaters collected lerp as well as feeding on honeydew or manna. Many other birds, pardalotes, lorikeets, parrots and treecreepers, may feed on these secretions but careful field observations will be required to assess the importance of manna and honeydew because these, like nectar, will be quickly absorbed and not detected in stomachs. Manna, honeydew and lerp are clearly important to honeyeaters.

Psyllids, coccids and aphids are widespread in Australia and found on most species of *Eucalyptus* (Moore 1975, 1978; Table VIII), as well as many native plants (CSIRO 1970; pers. obs.). Honeyeaters not only fed on secretions on eucalypts but also fed on the honeydew of aphids living on *Callitris* (N. Forde pers. comm.) and Ford (1976b) observed Brown Honeyeaters *Lichmera indistincta* feeding on sweet sap oozing from the green unripe fruits of Corkwood *Hakea divaricata*, which was possibly the honeydew of a gall-forming homopteran. Red Wattlebirds, Crescent and New Holland Honeyeaters also fed on exuding sap from the bark of *Acacia pycnantha* (H. Ford pers. comm.).

Many insects, particularly ants, exploit honeydew and manna in Australia (CSIRO 1970; Mobbs *et al.* 1978; pers. obs.) and two mammals, the Yellow-bellied *Petaurus australis* and Sugar *P. breviceps* Glider, gouge channels in the bark of eucalypts and feed on the sap that oozes out (Wakefield 1970; A. Smith pers. comm.).

Manna, honeydew and lerp not only share chemical compositions with nectar but are also renewed at specific sites and at similar rates to nectar and are clearly substitutes for nectar in the diets of honeyeaters. They were more abundant than insects and other invertebrates on the foliage or bark, offered energy gains of the same order as those from nectar and were widely distributed. That honeyeaters fed on them is hardly surprising. However no honeyeaters fed entirely on them and all caught a few insects, which probably supplied protein that was absent in these secretions and nectar.

At Cranbourne and Golton Vale, many species of honeyeaters fed on the same resources (Table VIII) and appeared to affect the abundance of honeydew during the day (Table III and IV) and nectar (Figs. 2 and 6), suggesting that food was a limiting factor and that the birds were competing for it (Ford 1979). The aggression shown by Red Wattlebirds and New Holland Honeyeaters has obvious advantages in protecting and guaranteeing their food supply. Red and Little Wattlebirds *Anthochaera chrysoptera* and New Holland Honeyeaters frequently defended richer sources of nectar and forced conspecifics and smaller species to feed elsewhere on poorer more scattered resources. The larger honeyeaters were presumably also defending the richer sources of manna and honeydew, forcing the other species to use poorer sites.

Noisy Miners *Manorina melanocephala* and Bell Miners are very aggressive and monopolize areas often for many years (Dow 1977, 1978; McCulloch and Noelker 1971; Smith and Robertson 1978). They, almost certainly, monopolize rich sources of carbohydrates. Bell Miners are often found in, and move in groups to, areas where the trees are heavily infested with psyllids (McCulloch and Noelker 1971; B. Wykes pers. comm.) and the areas where I have observed Noisy Miners have had many psyllids. The high densities often reported for these two species (Dow 1978; Smith and Robertson 1978) and their continued occupation of small areas are more easily understood if the birds are using a renewable and abundant source of carbohydrate.

The long breeding seasons of many honeyeaters, including the *Phylidonyris, Melithreptus, Lichenostomus* and *Manorina* are probably related to the availability and abundance of these secretions, nectar or both. Psyllids and coccids may have one or several lifecycles during a year, which may be separate or overlapping (White 1971); so, the availability of honeydew may be seasonal, as at Golton Vale, or continuous. An example of the latter would be the lerps of *Glycaspis* living on *E. ovata*, which are abundant throughout the year (B. Wykes pers. comm.; pers. obs.). Sources of carbohydrate often supply good intakes of energy at times other than in spring (e.g. manna in summer and autumn at Cranbourne, nectar and honeydew in winter at Golton Vale). Honeyeaters by collecting energy from these carbohydrates will be freed from the restraints placed on insectivorous birds, as regards energy, and should be capable of breeding at times when insects are not freely available, such as autumn and winter, and of occupying habitats when insects are scarce.

Keast (1976) states that the *Melithreptus* and *Meliphaga* (*Lichenostomus*) are predominantly insectivorous and have become adapted to similar niches used by the insectivorous bark-probing *Parus* and the foliage-gleaning sylviid warblers and timaliids of Africa. However, these honeyeaters, though they feed in similar sites to their African counterparts, do not feed on the same foods, unless investigation shows that the African birds concentrate on sugary secretions. My observations show that these honeyeaters are rarely, if ever, entirely insectivorous and the adaptive radiation in feeding ecology shown by the Meliphagidae is probably not as great as Keast suggests.

The success and dominance of the family as a whole, particularly the genera *Lichenostomus, Melithreptus* and *Manorina*, is possibly related to the success of phytophagous insects and the abundance of associated sugary secretions. Possibly the honeyeaters have radiated along with these eucalypt-eating insects and the eucalypts and with the nectar-producing plants, rather than diversifying and acquiring unoccupied niches. Many species show remarkable versatility in feeding, foraging in many places (foliage, bark, flowers), which is probably another factor in their success. For example, New Holland Honeyeaters, which visit many flowers (Ford and Paton 1977; Paton and Ford 1977), almost entirely gleaned foliage at Cranbourne and probed bark at Golton Vale at times when manna or honeydew were available and nectar was scarce. *Lichenostomus* and *Melithreptus* mainly gleaned foliage at Cranbourne but probed bark at Golton Vale and White-eared Honeyeaters, which feed mainly on bark (Ford and Paton 1976), gleaned foliage at Cranbourne during the summer. The long brush-tipped tongue of the Meliphagidae may have evolved to exploit these sugary fluids, as well as nectar.

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