THE ECOLOGY OF HONEYEATERS IN SOUTH AUSTRALIA

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I shall present this evening a summary of the work which has been carried out on honeyeaters in the Department of Zoology at Adelaide University over the past three years by myself, David Paton and Neville Forde.

The initial reason for my interest in honeyeaters was that I was interested in the ecological phenomenon of interspecific competition. Interspecific competition can be defined as the endeavour of two or more species to consume a common resource which is in short supply, or, if it is not in short supply, then nevertheless to harm each other in some other way, for example by aggression. This is an important concept in ecology, and has been extensively investigated theoretically, in plants and laboratory populations of invertebrates; but the importance of competition in natural populations of vertebrates is not understood well. The honeyeaters are a particularly suitable group for the study of competition, as there are frequently many species in one habitat, and they often use a series of common resources, i.e. nectar from a range of flower species. In addition this resource is relatively easy to measure and manipulate.

Although I was initially interested in competition, my approach has broadened considerably; and our studies in Adelaide have become more concerned with exploring the importance of honeyeaters in the community, that is the whole assemblage of living organisms and non-living entities in their environment. In any community the green plants capture the sun's energy and convert it into chemical energy, which is in turn consumed by animals. Honeyeaters consume a large amount of this energy in a very simple form from the plants, nectar, which is a solution of sugars. In return honeyeaters effect pollination in the plants they visit. They also consume many herbivorous insects, which feed on plants, and predatory insects which consume mostly herbivorous insects. As well as competing amongst themselves for these foods, they compete with a range of insects which feed on nectar and an array of insectivorous birds. Honeyeaters are themselves food for predatory birds, reptiles and mammals, and are parasitised by a range of micro-organisms. Thus by studying honeyeaters we can start to fill in a few pieces of the picture of a community in an Australian environment.

The 22 species of honeyeaters regularly found near Adelaide can be separated into two main groups; the short-beaked and the long-beaked honeyeaters. In a study of the feeding habits and food of these species in the sclerophyll forest and woodland habitats of the Mount Lofty Ranges, I have shown that the short-beaked species feed more on insects than nectar, and the long-beaked ones more on nectar than insects. The short-beaked species belong to the genera *Meliphaga* (or *Lichenostomus*) and *Melithreptus*. The Yellow-faced Honeyeater *Meliphaga chrysops* is a bird of the forests and neighbouring woodland, and takes a lot of insects by hawking and also by gleaning from leaves and bark, whereas the White-plumed Honeyeater *M. penicillata* is a bird of woodland, especially along red-gum creeks, and feeds by gleaning from leaves and bark, and by hawking. The White-naped Honeyeater *Melithreptus lunatus,* Brown-headed Honeyeater *M. brevirostris* and Black-chinned Honeyeater *M. gularis* all take small insects from both leaves and bark, and appear to occupy different habitats; tall forest, scrubby forest and drier woodland, and savannah woodland respectively. All of these five species will visit flowers, especially of *Eucalyptus,* when they are available.

On the other hand the long-beaked species appear to rely largely on nectar and move, at least locally, in search of flowering bushes and trees. The Yellow-winged Honeyeater *Phylidonyris novaehollandiae* visits a very broad array of flowers in forest, heath and woodland. The Crescent Honeyeater *P. pyrrhoptera* and Eastern Spinebill *Acanthorhynchus tenuirostris* live mostly in forest, and feed rather more selectively on flowers of mistletoe, heaths (*Astroloma* and *Epacris*) and *Correa,* as well as *Eucalyptus.* However these three species are frequently found in the same area feeding on the same species of flower. The Tawny-crowned Honeyeater *P. melanops* inhabits more heathy open areas, and feeds on flowers of low bushes such as *Adenanthos* and *Grevillea.* The Red Wattlebird *Anthochaera carunculata* inhabits woodland more than forest and feeds principally on *Eucalyptus* flowers. All of the long-beaked species take most of their insects by hawking, except for the Tawny-crowned which takes insects from low shrubs and the ground. Although these species spend nearly as long feeding on

insects as on nectar, we have calculated that when they are hawking they spend far more energy in capturing insects than they gain from them. On the other hand, they usually gain more energy from nectar than they use. Nectar is therefore the major source of energy. This is especially true in winter when demands are high, and insects are small and so would provide little energy. Insects are the major source of protein and other essentials. Neville Forde has been collecting information on the kinds of insects eaten by honeyeaters at different times of the year.

Thus the short-beaked species partition their environment chiefly on the basis of habitat, while the long-beaked species overlap far more, yet differ slightly in their preferences for different flowers. The short-beaked genus *Meliphaga* was studied in more detail to see if this pattern of separation by habitat was repeated in the drier parts of South Australia.

On a broader scale the Yellow-faced Honeyeater is a bird of sclerophyll forest in the South-East, Mount Lofty Ranges and Southern Flinders Ranges, and the White-plumed Honeyeater is a bird of savanna woodland, and tall trees along creeks in more arid areas. The Purple-gaped Honeyeater *M. cratitia* lives almost exclusively in mallee-heath, dense usually low mallee with shrubs such as *Melaleuca uncinata,* in southern Eyre and Yorke Peninsulas, Kangaroo Island and the Murray Mallee. The Yellow-plumed Honeyeater *M. ornata* is a bird of drier more open mallee, often dominated by *E. gracilis* and *E. oleosa* with a semi-succulent or grassy understorey. The Singing Honeyeater *M. virescens* occurs in a range of open habitats: coastal heath, saltbush-bluebush shrubsteppe and *Acacia* woodland; but it also overlaps with the previous two species in mallee-heath and mallee. However it usually feeds lower down than these two species, in shrubs or near the ground. It also takes berries from plants such as the native cherry *Exocarpos,* or the saltbushes *Rhagodia* and *Enchylaena.* The White-eared Honeyeater *M. leucotis* proves to be the exception to the rule as it lives in a wide range of semi-arid habitats, and also in forest and woodland on Kangaroo Island and in the South-East. It differs markedly in feeding behaviour from the other species, as it feeds almost entirely on insects from bark, and rarely visits flowers.

Two other species, the Yellow-fronted *M. plumula* and Grey-headed Honeyeater *M. keartlandii,* live in rocky mallee-spinifex and arid woodland, but their detailed habitat requirements merit further study. The only

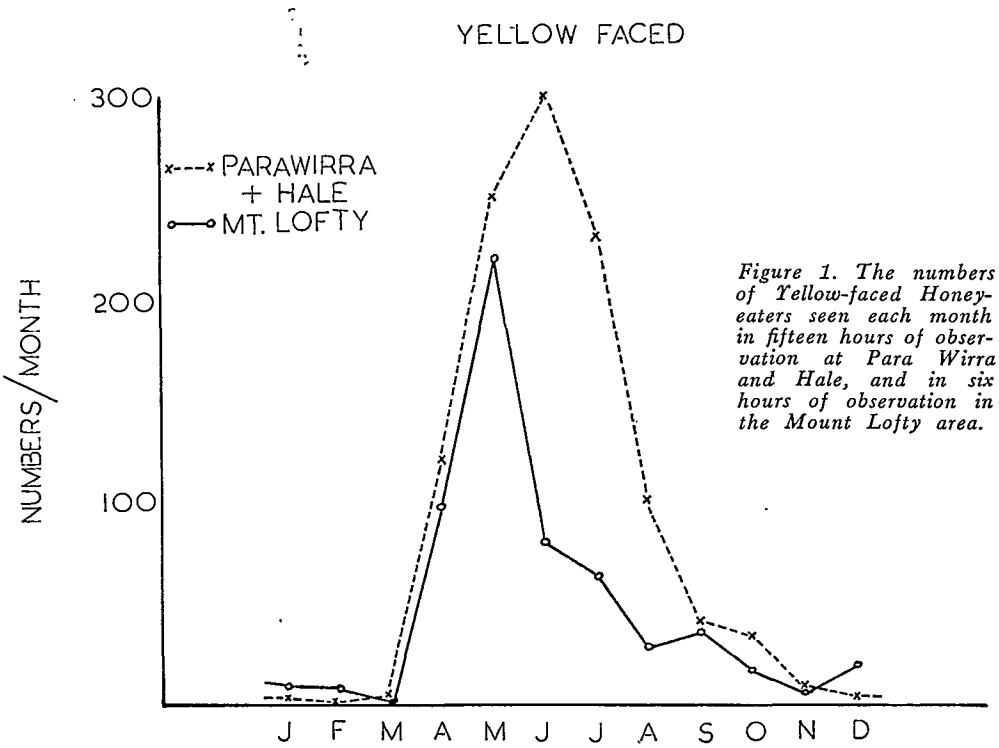

Figure 1. The numbers of Yellow-faced Honeyeaters seen each month in fifteen hours of observation at Para Wirra and Hale, and in six hours of observation in the Mount Lofty area.

species of this genus on Kangaroo Island are the White-eared and Purple-gaped Honeyeaters. The former is found only in woodland, but the latter occurs in all habitats including forest and woodland occupied by the Yellow-faced and White-plumed Honeyeaters on the mainland.

Before leaving the short-beaked species I should like to mention two species which are apparently migratory in South Australia. The Yellow-faced and White-naped Honeyeaters are almost absent from the Para Wirra area (northern Mount Lofty Ranges) from October to March, and are scarce in the Mount Lofty area. (See Figs. 1 and 2.) Their numbers increase very markedly in April and reach a peak in May near Mount Lofty, and in June at Para Wirra, and fall gradually thereafter. Numbers of most species of honeyeaters appear to increase in autumn, partly owing to greater activity by the birds; but the Yellow-faced Honeyeater changes almost overnight from a scarce bird to the second most abundant species of bird at Para Wirra. I do not know where these species go during the summer; but as they are almost restricted to sclerophyll forest the most likely area is the South-East and western Victoria. Both species are large-scale migrants along the east coast of Australia. More extensive banding of birds of all species in the Mount Lofty Ranges would in time provide very interesting information on the movements of these and other species. In the autumn of 1976 the arrival of Yellow-faced and White-naped Honeyeaters was more noticeable than in previous years, as they were seen in reasonable numbers in the suburbs of Adelaide, the far northern Mount Lofty Ranges and even in the Murray Mallee. The most likely reason for this was that the Mount Lofty Ranges were very dry, with little flowering except for *E. odorata* on the lower slopes. Out-of-season flowering, and a range of exotic plants in the Adelaide area, could well have been very important to the survival of these and other species of honeyeaters during this time.

For the rest of the talk I shall discuss the interactions between plants, the nectar they produce and their pollination systems, and honeyeaters, especially their use of nectar as a resource. First of all I shall start by running through some of the plants which are important to birds in South Australia.

The most important genus is *Eucalyptus,* at least one species of which has been seen to be visited by all the species of honeyeaters, three species of lorikeets, silvereyes and pardalotes. The most important species in the Mount Lofty Ranges are *E. leucoxylon,* the South Australian

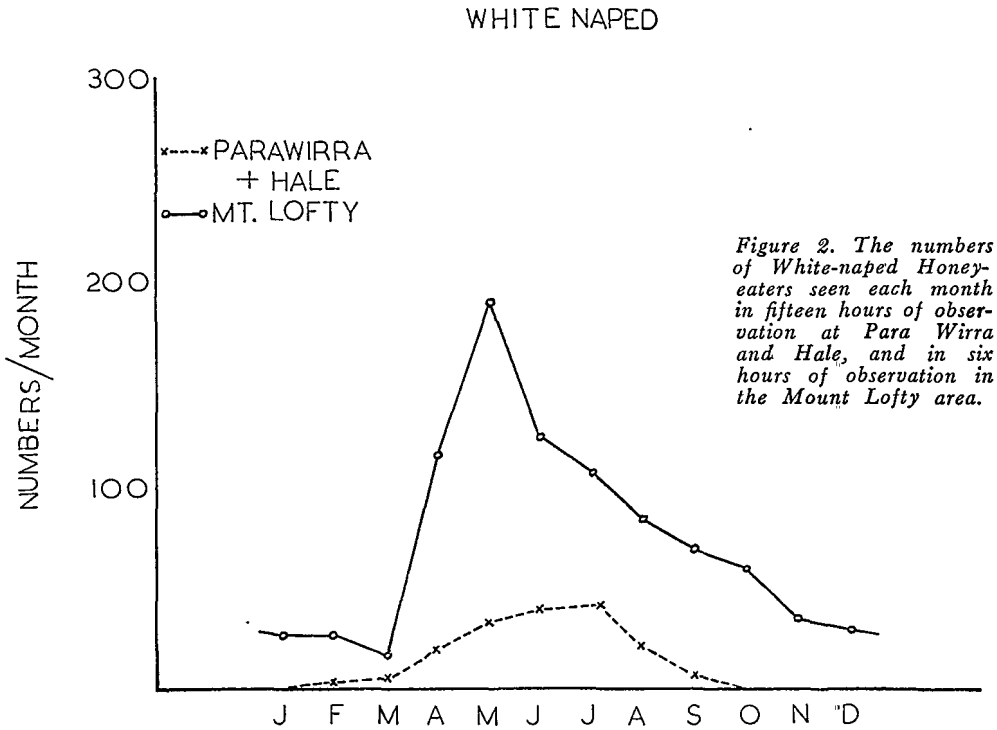

Figure 2. The numbers of White-naped Honeyeaters seen each month in fifteen hours of observation at Para Wirra and Hale, and in six hours of observation in the Mount Lofty area.

Blue Gum, *E. cosmophylla,* Cup Gum, *E. fasciculosa,* Pink Gum, and *E. odorata,* Peppermint Gum. Several of the mallees such as *E. incrassata* are also visited frequently by birds; and many of the introduced species grown in Adelaide are also popular. The flowers are open and cup-shaped with a ring of stamens, and the nectar is easily accessible to birds and insects. Any of these visitors are likely to brush against the stamens and stigma and bring about pollination.

The heaths, *Epacris impressa* from the forest, *Astroloma conostephioides* from more scrubby forests and heaths, and *Brachyloma ericoides* from drier heaths, are visited by birds. *Astroloma* provides one of the most important sources of nectar in winter in the Para Wirra area. The flowers are tubular with the stamens inside the tube, and the pollen is sticky, adhering to the beaks of visiting birds. The mistletoes *Amyema* spp. and *Lysiana exocarpi* are frequently visited by birds in summer, and *Correa* is another popular tubular flower in late summer and autumn. The stamens of *Correa* protrude beyond the corolla, and deposit pollen on the forehead, face and throat of visiting birds. Several species of *Grevillea* and *Adenanthos* are frequently visited by birds, and here the mechanism of pollination is very precise: the style is long and curved and the protostigma deposits pollen on the forehead of a bird, and then becomes receptive to pollen from another flower.

In the more arid parts of South Australia the most important flowers, in addition to *Eucalyptus,* are the Eremophilas, for instance *Eremophila oppositifolia* and *E. maculata,* the Spotted Emu Bush. In wet years the latter flowers very prolifically in a few localities, and each flower produces a large amount of nectar: in fact we have estimated that the smaller honeyeaters could gain their daily energy requirements in about ten minutes of feeding on these flowers. *Brachyzema,* a member of the pea family is also visited by birds, as is the Sturt's Desert Pea *Clianthus formosus* (see Mack, *S.A. Orn. 26,* 90) although we have not seen birds feeding on it. An exotic, the Tobacco Bush *Nicotiana glauca* has spread through disturbed semi-arid habitats and is also visited by birds, and may be an important source of nectar in summer. It is perhaps one of the few introductions which could have had a positive effect on wildlife in Australia, and for this reason should be tolerated.

A different group of plants visited by birds are those with brush-like inflorescences. In these the stamens of many flowers at one time brush against the feathers of the head and underside of birds. The Scarlet Bottlebrush *Callistemon* is popular, especially with the Yellow-winged Honeyeater. The Banksias *B. ornata* and *B. marginata* are visited by a wide range of species, including the Little Wattlebird whose distribution is closely linked with the Banksias. The extreme example of a brush inflorescence is shown by *Xanthorrhoea,* the Yacca, Blackboy or Grasstree, which has a flowering spike up to a metre in length, with as many as 2,000 individual flowers.

Although it is well known that birds visit these flowers for nectar there has been until recently very little information on pollination by birds in Australia. This subject has been pioneered in Adelaide by David Paton, who has collected and identified pollen from about 500 birds, most of them honeyeaters. The pollen can be dusted from the beak and feathers with a mascara brush. His results show that birds carry pollen, frequently in very large amounts, from the flowers they visit. He has also carried out experiments with stuffed birds and shown that, when they are probed into a series of flowers of one species they almost always deposit pollen on the stigmata of these flowers. Another interesting finding relating to pollen and birds was made by Neville Forde, who discovered that the droppings of honeyeaters and lorikeets frequently contain large amounts of pollen. He has not discovered yet whether the contents have been digested: the outer shell is indigestible, but it is possible that the pollen grains germinate inside the bird as they are mixed with the nectar. Pollen could be a supplementary source of protein for honeyeaters and other birds.

I collected information on the availability of nectar throughout the year in two main areas, Para Wirra and Hale National Parks, and Braendler's Scrub, Monarto, which are sclerophyll forest — woodland and mallee heath habitats respectively. I also gained additional data from a few other places in the Mount Lofty Ranges and Murray Mallee. The intensity of flowering of each important plant was estimated superficially on a scale of 0-5. Samples of about 50 flowers were collected in the early morning and late afternoon from the most abundant species. Some of the bushes, or branches of a tree, were covered with chicken wire to exclude birds, and insect-netting to exclude birds and insects. Samples of flowers were also collected morning and evening from these covered plants. The volume of nectar in each flower and the sugar concentration for each sample were measured and converted into energetic terms (the number of calories per

flower). If nectar was produced or reabsorbed through the day this would be shown by changes in the net-covered flowers. The amount of nectar taken by insects could be calculated from differences between net-covered and wire-covered flowers, and that taken by birds from differences between wire-covered and uncovered flowers.

There were always some plants in flower in most areas throughout the year, but they were more abundant in winter and spring. The amounts of nectar available in the morning were highest in spring in all areas, dropped through the summer and rose again in winter. In autumn 1975, after rain in March, nectar was abundant by early May; whereas in autumn 1976, which was dry, nectar was scarce until late June. Nectar probably accumulates in the flower from day to day, unless it is taken; so that the reason for the low level of nectar in the early morning in summer could be either that little is being produced, or that most has been taken by birds or insects. On some days in summer and early autumn, over 90% of the nectar was taken by mid-morning. In winter and spring usually only an insignificant proportion of nectar was taken during the day. It was hard to separate the effects of the insects from those of the birds, because birds fed very rapidly in the first few hours of the day in summer, while insects started feeding later and reached their greatest activity around the middle of the day. Insects probably took what the birds left, and this included the nectar from flowers covered by chicken-wire from which the birds were excluded. Thus although the results indicated that most of the nectar was taken by insects, the real story is much more complex.

So, to summarise the relationship between honeyeaters and this important resource, nectar:— (1) different species of honeyeater frequently overlap in habitat and in the species of flower they visit, at least in the year I studied them; (2) nectar is superabundant in winter and spring but scarce in summer; and (3) the birds are probably forced to feed on the same species during summer, and, as a large proportion of the nectar is taken, they are therefore likely to undergo strong interspecific competition for their major source of energy.

Some theoretical ecologists believe that high levels of overlap in the use of scarce resources such as food should prevent the coexistence of species. One species should be more efficient overall than the others and so should exterminate them. Probably the reason why so many honeyeaters can coexist in one area and use the same species of flower is that the intensity of flowering varies greatly by locality and from year to year, and also that birds move around, particularly during the summer. In addition the smaller species are more efficient than the larger ones as they require less energy; but the larger species could aggressively exclude the smaller ones from the most concentrated and rich sources of nectar. Thus the system is a dynamic one, with no single species favoured for long enough or in a large enough area to become dominant. The numbers of all species vary greatly through the year and from year to year, at least locally and perhaps over a wider area. Details of movements and population changes for all of these species are scanty at present, and need to be collected over a period of many years.

In conclusion, the short-beaked honeyeaters are mainly insectivorous and are separated from their congeners by habitat. They breed mostly in spring and early summer when insects are perhaps at their most abundant. The long-beaked honeyeaters are mostly nectarivorous, but take insects for protein and other essentials. They overlap in habitat and in the flowers they visit, and compete for nectar when it is scarce in summer and autumn. They breed in late winter and early spring when nectar is most abundant, and in some years also in autumn. Our studies at Adelaide University over the last three years have allowed us to construct a superficial picture of the comparative ecology of honeyeaters in South Australia; but many more longer term studies are necessary to see if this picture is a realistic and accurate one.

List of papers which present more substantial data on our studies on honeyeaters.

H. A. Ford and D. C. Paton, 1976. The value of insects and nectar to honeyeaters. Emu, 76, 83-84.
D. C. Paton and H. A. Ford, 1977. Pollination by birds of native plants in South Australia. Emu, 77, 73-85.
H. A. Ford and D. C. Paton, 1976. Resource partioning and competition in honeyeaters of the genus Meliphaga. Aust. J. Ecol. 1, 281-287.
H. A. Ford and N. Forde, 1976. Birds as possible pollinators of Acacia. Aust. J. Bot. 24, 793-5.
H. A. Ford. The honeyeaters of Kangaroo Island, 1976. S.A. Orn. 27:134-8.
In preparation:
H. A. Ford and D. C. Paton. The comparative ecology of ten species of honeyeaters in South Australia.
H.A. Ford. Competition for resources in South Australian honeyeaters.
H. A. Ford. The Black Honeyeater in South Australia.
H. A. Ford. The timing of moult and breeding in South Australian honeyeaters.

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