

CHAPTER 6

FORAGING BEHAVIOUR AND DIET OF THE FUSCOUS HONEYEATER

6.1 INTRODUCTION

The foraging behaviour of insectivorous birds has often been studied, and is used to indicate the diet of a particular species. Sampling of the actual foods available has been done much less frequently (for example, Paton 1979, 1980, Noske 1982, 1985, Wykes 1982, 1985, Bell 1983a, 1985a, Woinarski 1984a, 1985a). Gut sampling by collection of stomachs or the less destructive stomach flushing and collection of faeces can be used to discover what the birds are actually eating (Calver and Wooller 1981). These methods are subject to some biases, with easily-digested materials being under-represented (see, for example, Woinarski 1984a, 1985a). A combination of time-budgeting the foraging behaviour of birds, gut-sampling (as done by Tullis *et al.* 1982) and sampling of the various substrates gives the most complete picture of a bird's diet. Ideally, all this sampling should take place concurrently, to try to reduce the biases associated with apparent differences in diet which may only be the result of varying availability of the foods.

Data have previously been collected at Eastwood on foraging behaviour (Ford *et al.* 1986) and diet, from stomach-flushing and faecal analysis (Ford, unpublished data). The present study did not attempt to collect more information on the same aspects, but tried to fill in the gaps, with concurrent bird-censusing (see Chapter 3), food sampling (see Chapter 4), the effects of exclusion of birds on their food supply (see Chapter 5) and the experimental manipulation of the abundance of food (see below). This work viewed the arthropods as food for birds and, in particular, concentrated on the behaviour and ecology of the Fuscous Honeyeater.

The aim of the food manipulation experiment was to determine if the Fuscous could respond to changed food abundance. Other studies have altered the abundance of food, usually in examining the responses of territorial birds (for example, Lyon *et al.* 1977, Pimm 1978, Ewald and Bransfield 1987, Carpenter 1987). These studies used nectarivorous birds, with few workers attempting to manipulate in the field the food of insectivorous species (Franzblau and Collins 1980, Ydenberg and Krebs 1987). Food supplementation has been done to test for birds' responses to predation (for example, Valone and Lima 1987) or to examine the effects on breeding (Smith *et al.* 1980, Davies and Lundberg 1985, Arcese and Smith 1988 etc.).

In this chapter, an attempt will be made to integrate the data from the studies on insect availability with the diet and foraging behaviour of the Fuscous Honeyeater. The specific questions to be examined are :-

1. What is the foraging behaviour of the Fuscous Honeyeater?
2. How does the diet of the Fuscous differ from the available insect distribution?
3. Can Fuscous respond behaviourally to changes in food abundance?

6.2 METHODS

The data on diet and foraging were collected by Ford and others, during 1981 to 1984 for the latter and late-1979 to 1981 for the former. Wild-caught birds had their stomachs sampled by flushing with warm water, and faeces were collected at the same time. Time-budgeting was used by Ford *et al.* (1986) to obtain data on foraging behaviour. Additional observations made during the present study were also used, and were obtained by following a bird and noting its activities onto a tape-recorder. When transcribing the tape, a stop watch was used to time the duration of activities. An individual bird was followed for as long as possible but as Fuscous Honeyeaters are very active, the total duration for observations on any bird was rarely more than five minutes.

Fuscous Honeyeaters forage mostly from eucalypt leaves (Ford *et al.* 1986 and present study), and so the arthropod sampling program concentrated on this substrate (see Chapter 4 for detailed methods and results). Arthropod abundance from the exclusion experiment (Chapter 5) was also used for comparison between tree types. The results from these two chapters were expressed as insects/100 leaves and, in the canopy sampling (Chapter 4), as dry weight biomass in mg/kg of foliage as well. Other data collected by Ford and Harrington (unpublished) during 1980 to 1982 were expressed as numbers of insects per sapling on stringybarks and *E. viminalis*, and those collected by Lowman (unpublished, see Chapter 5 for a brief description of the methods) from mid-1982 to mid-1983 were from sweep-net and standard beating tray samples on *E. viminalis* and *E. blakelyi* . The data were only for comparisons between tree types using the same sampling method.

Food manipulation experiments were conducted from 14/7/87 to 1/7/88. In these, six eucalypt saplings were selected and randomly assigned treatments of increased food, decreased food and control, with two saplings as replicates of each treatment per experiment. Food was increased by the addition of 'artificial lerps' that were made from icing-sugar mixture stuck onto the leaves by spraying with a saturated sugar solution. One hundred leaves were examined and the lumps of sugar counted to

give an estimate of 'lerp equivalents' for each tree. The increases in food were up to two orders of magnitude greater than on the control trees, with a mean for all experiments of 278.4 'lerp equivalents' per 100 leaves ($n=12$). The lumps of sugar varied in size, so this gives only an approximate idea of the magnitude of the increase. Food was decreased by spraying the leaves with a non-residual insecticide, which was then washed off by water. The saplings in this treatment were then closely examined and any other arthropods found were removed including attached bugs and lerps. This gave a treatment mean of approximately zero. The control saplings were sprayed with water alone, 100 leaves were examined and the number of arthropods on them were counted. Flying insects were removed by this treatment, but not other types and the mean number of insects was 5.9 insects per 100 leaves ($n=12$). The trees were watched for varying periods after treatment, and on the subsequent days during the later experiments due to a slow visit rate by the birds to the trees. Only visits by Fuscous Honeyeaters were counted and timed. The food-decreased and control trees were visited so infrequently that lengths of visits to saplings collected during the whole study were used.

6.3 RESULTS

Table 6.1 shows the different measures of insect abundance on the main tree types and the relative density of the different trees in Eastwood, and Table 6.2 shows the foraging preferences of the Fuscous. Fuscous Honeyeaters consistently preferred foraging on *E. viminalis* and avoided *E. caliginosa* (the stringybark), seen by comparing tree preferences to the relative densities of the trees (see Chapter 2 for detailed vegetation analysis). *E. melliodora* were sometimes preferred. *E. blakelyi* were always visited in about the frequency at which it occurred. Of the five available data sets on arthropod abundance, there were no significant differences between tree types (t-tests, $P>0.05$).

Visits to trees were found to be short in my time-budgeting with 75% of visits being less than 60 seconds in duration (see Table 6.2). Visits to stringybarks were just significantly longer (t-test, $n=81$, $P<0.05$) than those to *E. blakelyi*'s but there were no other differences (t-tests, $P>0.05$). Ford (unpublished data) found Fuscous to show an extreme preference for the *viminalis* in late-1985 to early 1986 although these observations were made in an area of Eastwood where *viminalis* predominated (Ford pers. comm.).

TABLE 6.1: The percentage of different eucalypt types in Eastwood, and abundance of arthropods on the different trees. Percentages from vegetation analysis (Chapter 2). In this, and all future captions in this chapter, GUMS combines *E. melliodora*, *E. viminalis* and *E. blakelyi* and OTHER includes *E. bridgesiana*, *Angophora floribunda*, unidentified eucalypts and *Acacia* spp. Abundance of arthropods are means from several studies. There are no significant differences between tree types of arthropods (t-tests, $P>0.05$), comparisons only between trees sampled by the same method. The units of abundance in the study of Ford and Harrington (unpublished data, collected 1980-1982) are numbers of arthropods per sapling, Lowman (unpublished data, collected 1982-1983) sampled by beats and sweeps (see Chapter 5 for more details on Lowman's methods) and the present study presents data as numbers of insects/100 leaves (for methods, see Chapter 5, data collected 1985-1986 and Chapter 4, data collected 1987-1988).

	TREE SPECIES				GUMS	OTHER
	<i>E.caliginosa</i>	<i>E.melliodora</i>	<i>E.blakelyi</i>	<i>E.viminalis</i>		
PERCENTAGE OF TREES	57.5	6.75	13.25	13.75	33.75	8.75
ARTHROPOD ABUNDANCE:						
Ford and Harrington	27.5			25.8		
Lowman - Beats			16.7	13.2		
- Sweeps			30.3	23.9		
Present Study (Ch. 4)	5.5	5.0	4.8	4.3		
Present Study (Ch. 5)	3.4	3.0	2.6	2.4		

TABLE 6.2: Foraging behaviour of the Fuscous Honeyeater. Tree species are as before. Foraging observations are from Ford *et al.* (1986, methods in article), data collected in 1981, 1982 and 1984 from the central part of the Forest. Ford (unpublished data, collected 1985-1986) and the present study (data collected 1984-1988) recorded foraging behaviour when observed, the former mostly in the south-west corner, and the latter in most areas. Percentages are of total observations, durations of a visit (in seconds) to an individual tree in the present study were timed by stop-watch. Durations of visits were compared by t-tests. The only significant difference ($P < 0.05$) is between visits to stringybarks (*E. caliginosa*) and *E. blakelyi*.

	TREE SPECIES					
	<i>E.caliginosa</i>	<i>E.melliodora</i>	<i>E.blakelyi</i>	<i>E.viminalis</i>	GUMS	OTHER
Ford <i>et al.</i> (1986)						
% OBSERVATIONS ON	45.6	18.7	14.4	15.7	48.8	5.6
Ford (unpublished data)						
% OBSERVATIONS ON	5.0	1.0	14.0	79.0	94.0	1.0
Present study						
% OBSERVATIONS ON	30.3	10.8	15.4	43.5	69.7	
DURATION OF VISIT	62.7	53.3	31.3	52.5	50.1	47.3
n	51	20	30	84	159	8
se	10.6	10.4	7.6	7.3	4.0	14.2

During the food manipulation experiment, the saplings with increased food were visited significantly more frequently and for longer (see Table 6.3, t-test for visit length, $n=21$, $P<0.05$, χ^2 for visit frequency, $P<0.005$) compared with the control, food-decreased and untreated trees.

Mean lengths of arthropods and their percentage composition by number, from the canopy-level tree sampling (see Chapter 4) for all times combined (1987 to 1988), are shown in Table 6.4. Table 6.5 shows the results of the stomach and faeces sampling, by Ford and others during 1979 to 1981. Hemipterans seemed to be under-represented in the gut samples, probably due to their readily-digestible nature. Fuscous were frequently seen to be eating lerps, in particular, which would be completely dissolved in the stomach very quickly. The bugs were also the only arthropod order that was nearly the same size in the gut and on leaves, possibly indicating that they were taken as encountered, although lengths from the gut samples were only approximate. All other arthropod groups seemed to be larger in the diet than on leaves, indicating that larger sizes of insects were selected, but it could be also that the smaller sizes were more readily digested. Dipterans, coleopterans and hymenopterans occurred more frequently in the diet than would be expected from encounters on the leaves, although the former, being highly mobile, were likely to be missed when sampling the leaves. Spiders were under-represented in the Fuscous Honeyeaters' diet, and larvae seemed to be avoided, or the birds did not readily find them.

6.4 DISCUSSION

Considerable work has been done at Eastwood, with foraging data (Ford *et al.* 1986), insect-sampling (Lowman, and Ford and Harrington unpublished data), bird-censusing (Ford and Bell 1982, Ford *et al.* 1985) and stomach-flushing and faecal analysis (Ford, unpublished data) in addition to the present study. It has been found that although Fuscous Honeyeaters fed primarily by gleaning (64% of observations) arthropods off leaves (59% of observations, see Ford *et al.* 1986), they are a generalized forager, and have been seen feeding off most substrates, at most heights and on most plant species employing several methods. They never tore at substrates nor fed off shrubs other than *Acacia* spp. Consistent with their patterns of foraging, they took most arthropod prey that they encountered, although they avoided larvae (or could not locate them) and spiders. Most of the insects on leaves were small (mean size 3.8 mm) which makes it hard for an observer to identify the insects that were taken. Small insect size meant that most arthropods could be swallowed

TABLE 6.3: Results of food manipulation experiment (see text for detailed methods). FOOD INC are saplings on which food was increased, CONTROL are water-sprayed trees, OTHER includes visits to control saplings and saplings in the experiment area that were not treated in any way, but were included in the analysis due to other experimental saplings being visited very infrequently. All treatments were observed for the same time period. Food-decreased saplings were not visited during the experiment. Visit lengths were compared by t-test and were significantly longer to food-increased trees, compared to other treatments and untreated trees ($n=21$, $P<0.05$). Visits were also significantly more frequent to food-increased trees (χ^2 test, $n=21$, $P<0.005$).

	TREATMENT		
	FOOD INC	CONTROL	OTHER
DURATION OF VISITS	149.4	25.0	16.7
NUMBER OF VISITS		12	2
se	45.1	15.0	3.2

TABLE 6.4: Mean length (in mm) of arthropods and percentage composition (by number) from canopy sampling (see Chapter 4). n is sample size. OTHER mainly includes Thysanopterans, Blattodeans and Psocopterans.

GROUP	LENGTH	n	% COMPOSITION
ARACHNIDS	3.3	1208	25.7
HEMIPTERANS	2.3	1455	31.0
LARVAE	7.2	1056	22.5
COLEOPTERANS	3.4	491	10.5
HYMENOPTERANS	3.4	373	8.0
DIPTERANS	3.2	19	0.4
OTHERS	3.8	91	1.9
TOTAL	3.8	4693	100.0

TABLE 6.5: Diet of Fuscous Honeyeaters, from analysis of gut contents and faeces of 72 birds (Ford, unpublished data). Mean length (in mm) is estimated from comparison with samples of whole insects collected from Eastwood. Percentage composition is by number of arthropods counted. n is sample size.

GROUP	LENGTH	n	% COMPOSITION	n
ARACHNIDS	4.6	7	4.1	11
HEMIPTERANS	2.4	26	10.9	29
COLEOPTERANS	4.3	76	30.8	82
HYMENOPTERANS	5.1	79	38.0	101
DIPTERANS	4.1	13	4.9	13
EGG CASES	1.9	4	1.5	4
UNKNOWN INSECTS	7.7	3	1.9	5
CHITIN PIECES			6.8	18
STONES/DIRT			0.7	2
NOTHING			0.4	1
TOTAL	4.3	208	100.0	266

immediately, that is, that handling times were usually short. Fuscous were rarely seen to take larger arthropods such as larvae, and when they did so, processing the insect before swallowing took a much longer time. Because the Fuscous were common in most of the areas where foraging was observed in the present study (see Chapter 3), birds could not feed for long without some interference from other Fuscous, and long handling times meant an increasing likelihood of being interrupted (Barnard and Thompson 1985, and references therein). In one case, a Fuscous was seen to steal a larva from another Fuscous, after the bird that had caught the larva had spent a considerable time preparing the food item for swallowing.

Arthropods were usually in low numbers (abundances rarely exceeded 5 insects per 100 leaves) and were often significantly depleted by the birds (see Chapter 5). Foraging visits to individual trees were short, and the Fuscous moved and searched rapidly. Locally abundant patches of food would be detected and rapidly utilized, with a high frequency of visits of longer duration (from food experiment). This behaviour appears adapted to the usual distribution of food resources, with a small item size, rarely encountered insects, and few richer patches that may occur unpredictably in time and space. Such food resources might not be defensible, and so

must be utilized as quickly as possible. Ford (1989) has found that Fuscous spend between 46% (in spring) and 77% (in autumn) of their time foraging, suggesting that food is not abundant. Nectar, as a food source, was also generally sparse and ephemeral in Eastwood, as few eucalypts flowered well during this study (see Chapter 2) and mistletoe, though quite reliable, is not a very rich source of nectar (Paton 1986, Ford pers. comm. and my observations). There is some evidence that Fuscous have a high metabolic rate (Ambrose, pers. comm.) which might be a physiological adaptation to the necessity to search rapidly many leaves to obtain sufficient food. This suggests that the Fuscous may be closely adapted to exploit the observed distribution of food.

Since the tree types did not differ substantially in the abundance of arthropod food (see also Chapters 4 and 5), it is surprising that Fuscous showed such a pronounced preference for foraging in *E. viminalis*. The analyses of the distribution (Chapter 3) showed that Fuscous Honeyeaters were found least often in areas with many stringybarks. Stringybarks were found to have more larvae than other tree types (Chapter 4). Gums were found to have more 'sugary' lerps (Chapter 4 and 5) and Fuscous, like some other honeyeaters and small insectivores (Smith and Robertson 1978, Paton 1980, Woinarski 1984a and b, 1985a), seem to prefer lerps. For instance, Woinarski (1984a, 1985a) studied several species of acanthizids, including thornbills, pardalotes and gerygones. He compared diets from stomach samples and from foraging observations, and found that pardalotes were relatively inflexible in foraging behaviour but were specialized on a particular food type (lerps, the sugary covering to psyllids). Aggression from other species, particularly honeyeaters, often excluded pardalotes, especially, from areas of abundant food (Woinarski 1984a and b, 1985a, Loyn *et al.* 1983). In the present study, however, food was nearly always sparse (Chapter 5), and it is possible that the Fuscous cannot afford to be a specialist. Holmes and Robinson (1981), working in a Northern Hemisphere hardwoods forest, found bird species that were uncommon or in marginal habitat to have the strongest tree preferences. Many birds preferred the tree species with the most abundant insect fauna, although Holmes and Robinson thought that structural differences of the trees were also important. The trees in the present study are quite closely related and do not differ in structure very much, certainly not to the extent that conifers might be different from deciduous hardwoods.

Comparisons can be made between the foraging behaviour found in Eastwood (Ford *et al.* 1986) and at Bondi, on the southern tablelands of N.S.W. (Recher and Holmes 1985). Differences in foraging behaviour of some species of birds were found between the two sites, with widely dispersed species displaying some plasticity. The foraging guilds assembled by both studies were quite similar, but Recher and

Holmes (1985) lumped all honeyeaters together, although 4 of the 7 species were mostly gleaning insects off leaves. White-naped Honeyeaters were the most common honeyeaters at Bondi and very similar in foraging behaviour to those at Eastwood. Brown-headed Honeyeaters were found by Recher and Holmes to feed off bark substrates as much as foliage, but this species was quite specialized on foliage at Eastwood (Ford *et al.* 1986). Red Wattlebirds and Eastern Spinebills foraged less frequently at flowers at Eastwood, possibly reflecting the relatively poor availability of nectar sources here. Fuscous Honeyeaters were not found at Bondi, the role of generalized insectivorous honeyeater being taken by Yellow-faced Honeyeaters (which are present at Eastwood, but in low numbers, see Chapter 3). Fuscous Honeyeaters are probably generalized foragers over most of their range, and have been observed exploiting locally abundant nectar sources in Victoria (Wykes 1982).

Many species of honeyeaters have been found to respond numerically or behaviourally to changes in food abundance (Rooke 1979, Paton 1979, 1985, Wykes 1982, 1985, Ford 1983, Pyke 1985 but see 1983, McFarland 1985a, Collins and Newland 1986, etc.). The nature of these changes depended on the time scale of the variation in food levels, with birds found to change their diets, foraging behaviour, defence of resources, or to move into or out of areas. The relationships between food abundance and honeyeater behaviour and distribution will be explored more fully in Chapter 8.

In summary:-

1. The arthropod distribution on different tree types at Eastwood was compared with the foraging behaviour and diet of Fuscous Honeyeaters.
2. From time-budgeting, foraging visits to trees were usually short. Gums, especially *Eucalyptus viminalis*, seemed to be preferred foraging substrates.
3. Fuscous could detect increases in food abundance (from food manipulation experiment) and responded by visiting more often and for longer, relative to control trees.
4. It was found that, relative to the observed distribution of insects, Fuscous appear to take more bugs and fewer larvae and spiders from the leaves of eucalypts. This distribution of arthropods corresponds more closely to the types of insects found on gums.

CHAPTER 7

THE FUSCOUS HONEYEATER

7.1 INTRODUCTION

This chapter covers several aspects of the ecology and behaviour of the Fuscous Honeyeater, which have not previously been discussed. Firstly, the findings from banding studies at Eastwood and the yearly cycle of specific behaviours of Fuscous will be presented. Secondly, I will discuss the sociality of Fuscous Honeyeaters during breeding.

7.2 BANDING AND BEHAVIOUR

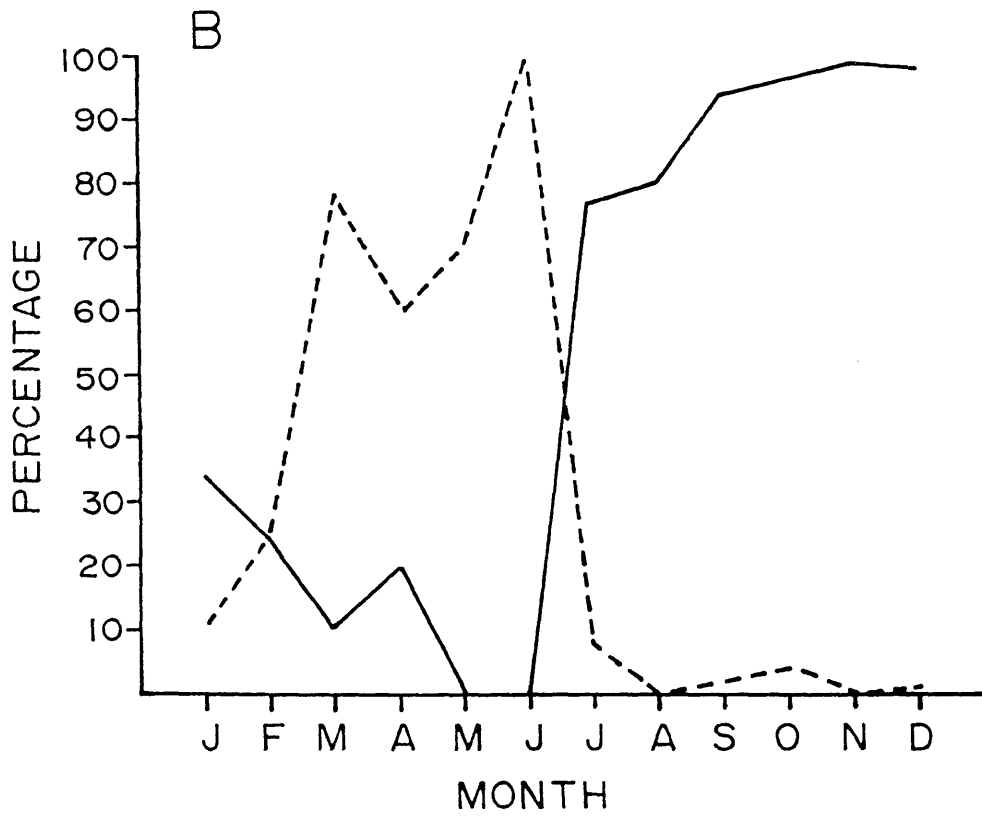
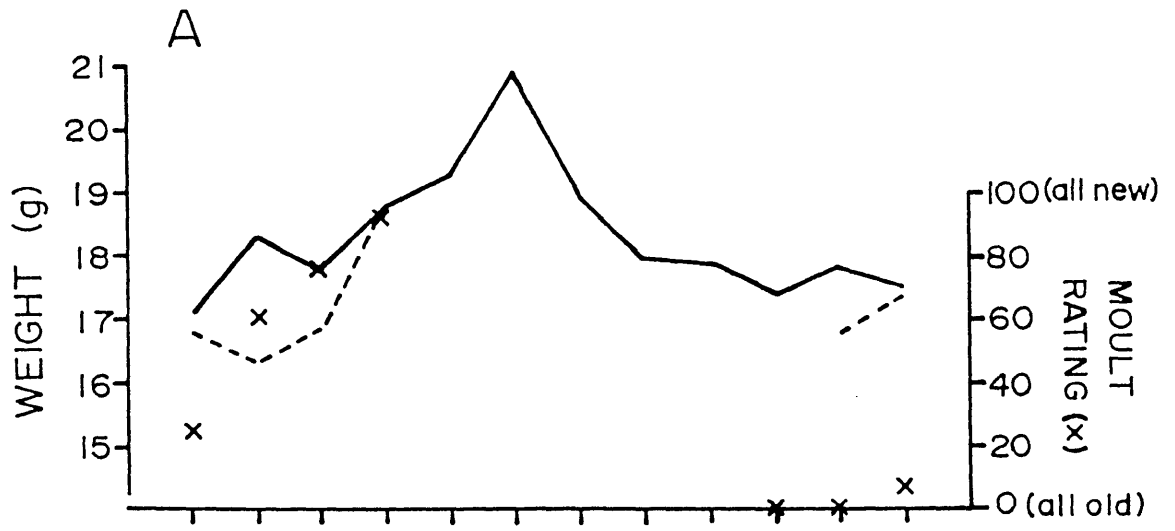
The mist-netting and banding of many species of birds by several people including Ford and myself, has continued at Eastwood since 1979. The data presented here concern only the Fuscous. Most banding effort was concentrated during the summer months (see Table 7.1) and in the area near the large dam in the south-west of the Forest (see Figure 2.1). Fuscous that were retrapped or able to be sexed or suspected to be from a known nest, were usually colour-banded to permit individual identification.

Previously, it has been found that adult Fuscous Honeyeaters changed the colour of their soft facial parts, specifically the gape and eye-ring, from black in the breeding season to yellow in the non-breeding season (see Chapter 1 and Dow 1973, 1975b, Lane 1974 and Morris 1974). During this study, the change in gape and eye-ring colour was also noted with very few known adults retaining yellow soft parts in the breeding season (see Figure 7.1). The breeding status of these birds was unknown. Weights and measurements of Fuscous taken during banding at Eastwood State Forest are shown in Table 7.1. Males were generally larger in wing size and total head length, and were heavier than females (t-tests, $P < 0.001$), although considerable overlap occurred. Birds weighed the most in winter, and generally declined in weight throughout the breeding season (Figure 7.1). Juveniles were captured from November through to April, when they became indistinguishable from the adults. Moulting of primaries (for method of rating moult, see The Australian Bird Bander's Manual Lowe 1989) took place from December and was completed by May (Figure 7.1), although individual birds presumably completed their moult in a

TABLE 7.1: Numbers of Fuscous Honeyeaters caught, including re-trapped birds, and mean weights (in g) and measurements (in mm). Measurements are wing length (WL), taken from carpal joint to tip of longest primary feather of the right wing, and total head length (THL), taken from back of head to beak tip. Birds were sexed by nesting behaviour (both sexes) or the presence of a brood patch (females). Unknown birds (UNK) are adults, but of unknown sex. Juveniles (JUV) were detected by plumage (lack of worn feathers, presence of downy feathers or lack of moult). Samples sizes differ because not all measurements were taken on every bird. Data on Victorian birds (VIC) for several sites and birds of unknown sex from Rogers *et al.* 1986.

MONTH	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
NO.													
ADULTS	48	18	14	5	10	1	7	15	62	82	79	109	450
NO.													
JUV	8	6	5	5	0	0	0	0	0	0	12	17	53
BIRD	WEIGHT			WL			THL						
	n	mean	sd	n	mean	sd	n	mean	sd				
MALES	38	18.4	0.90	25	82.1	1.96	19	33.7	0.69				
FEMALES	60	16.9	1.37	48	77.2	2.04	41	32.5	0.91				
JUV	48	16.9	1.35	20	76.1	2.69	22	32.8	1.13				
UNK	344	18.2	1.37	152	79.0	3.56	153	33.5	1.02				
VIC				203	82.2	3.24	243	33.6	0.99				
				EASTWOOD			VICTORIA						
NO. NEW BIRDS				373			475						
NO. RETRAPS				103			14						
PERCENTAGE				21.6			2.9						

FIGURE 7.1: A. Mean weights of Fuscous Honeyeaters. Solid line indicates weight of adults, and broken line is weight of juveniles (not trapped before November, and merge with adult population in May. Graph includes moult rating (crosses), where 0 means all primary feathers are old and 100 indicates that moulting of primaries is complete (all new feathers). B. Percentage of trapped adult birds that had black gapes and eye-rings (solid line) and yellow gapes and eye-rings (broken line). Birds were transitional with blackish-yellow soft face parts between these states.



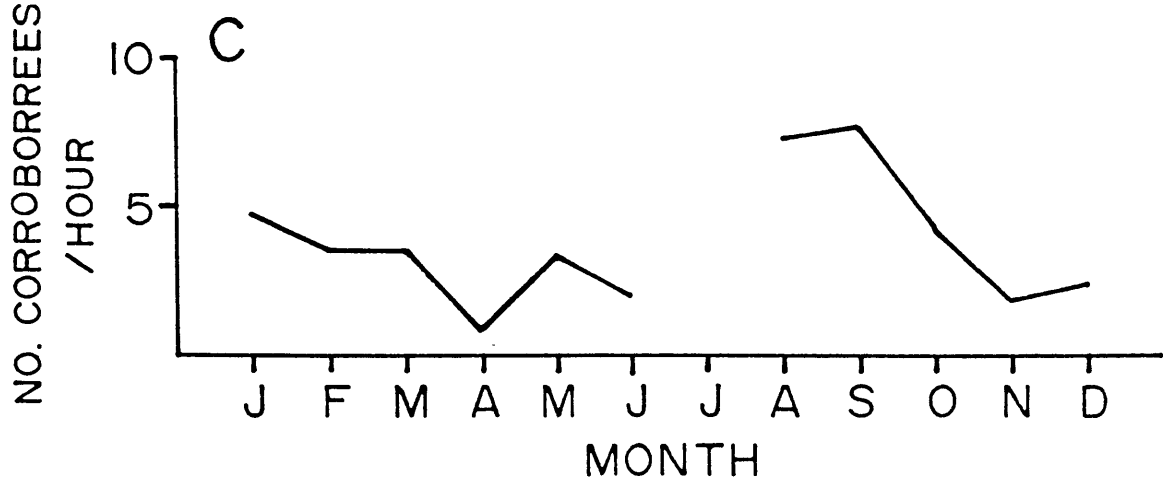
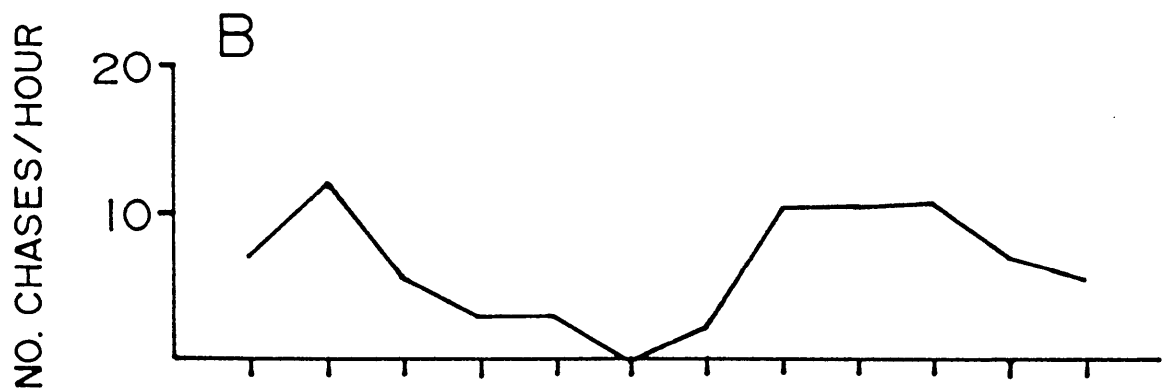
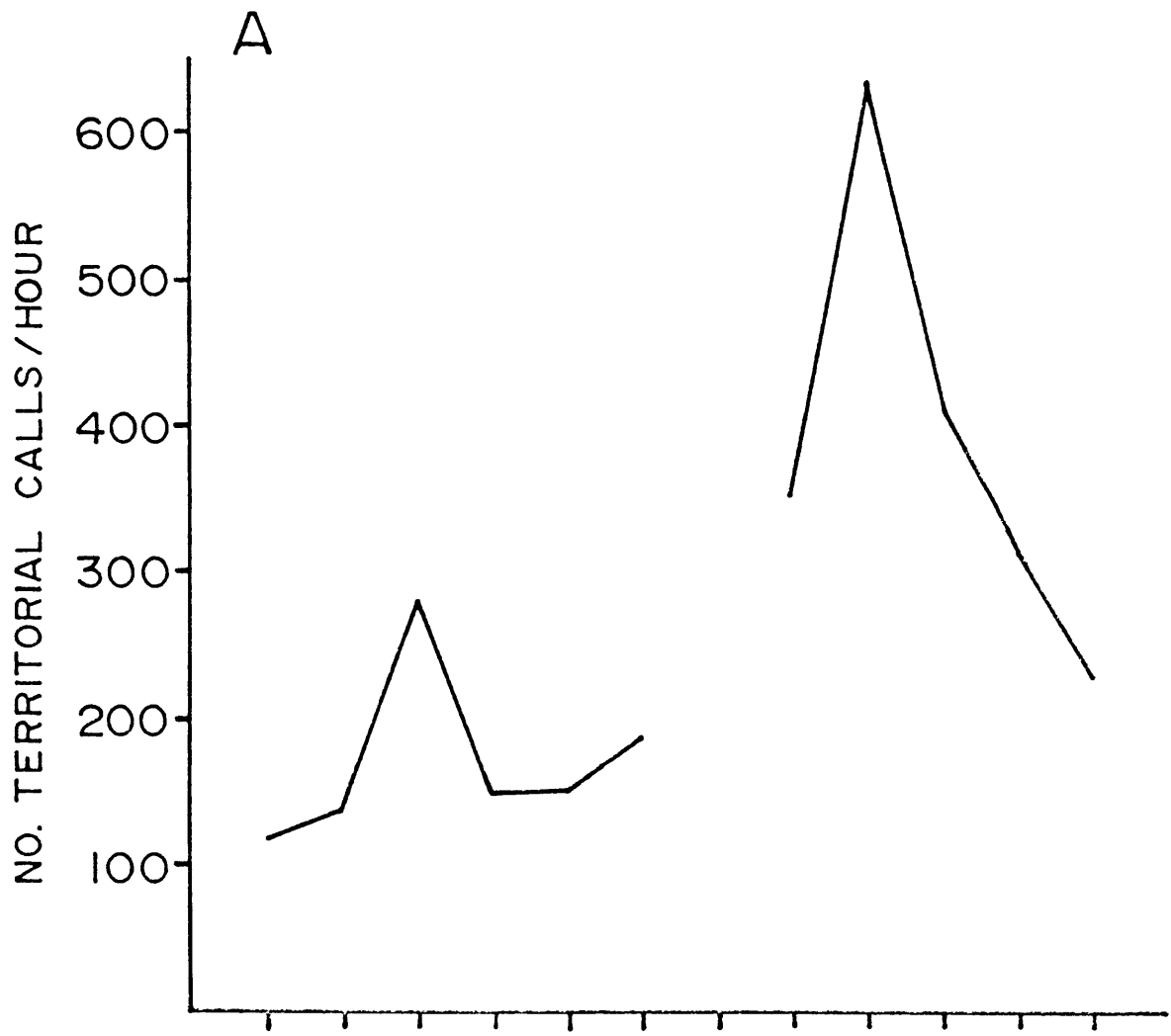
shorter time than this. The percentage of retrapped birds was quite high (21.6%, see Table 7.1), confirming the sedentary nature of birds at Eastwood. This can be compared to birds banded in Victoria (see Table 7.1, data from Rogers *et al.* 1986) where the retrapping rate was very low (2.9%, although depends on trapping effort).

Fuscous Honeyeaters show a variety of behaviours that have been described in other honeyeaters. Corroborrees are meetings of 2 or more birds that call repeatedly and may gape and move their wings. These were first described by Cameron (1970) in Noisy Miners (*Manorina melanocephala*, see also Dow 1975a) and have also been found to occur in New Holland Honeyeaters (*Phylidonyris novaehollandiae*, Paton 1979, Rooke 1979, Pyke and O'Connor 1989), White-cheeked Honeyeaters (*P. nigra*, Pyke and O'Connor 1989), Yellow-tufted Honeyeaters (*Lichenostomus melanops*, Wakefield 1958, Wykes 1982), Yellow-tinted Honeyeaters (*L. flavescens*, Immelmann 1961) and Yellow-plumed Honeyeaters (*L. ornatus*, Rooke 1979). In the present study, Fuscous Honeyeaters were seen to perform corroborrees. The mean number of birds involved in a corroborree at Eastwood was 4.9 ($n=97$, s.d. 2.07, range 3 to 20 birds) and the birds were together for 14.9 seconds on average ($n=37$, s.d. 11.00, range 5 to over 60 seconds).

Rooke (1979), working on New Holland Honeyeaters, found corroborrees to be performed most frequently in late winter when birds were establishing breeding ranges. Corroborrees occurred most commonly throughout the breeding season in Paton's study (1979). In the present study, the frequency of corroborrees, territorial calls (see later) and chases, as detected during censusing (see Chapter 3) and from casual observations, varied throughout the year, with all forms of interaction being most common in the spring and early summer breeding season (from August to January, see Figure 7.2 and Section 7.3).

Rooke (1979) observed birds in the field and performed removal experiments from aviaries, and suggested that corroborrees were gatherings of mostly known birds, and served as a way to learn to recognize their neighbours and so to reduce intra-specific aggression. The behaviour observed in this study, and by Pyke and O'Connor (1989) do not contradict this suggestion. Corroborrees were often observed during my study to start from, or end in, a chase. Where the corroborrees originated from chases, it is possible that an intruder was detected and chased before it was recognized, and where the corroborree ended in a chase the bird(s) were strangers. Few Fuscous were individually banded, and corroborrees were short and the birds highly active, so it was hard to determine the identities of participating birds. However, frequent observations of birds coming into a corroborree from some distance around without being chased and of several instances of co-operative chasing (that is, a bird being chased into a Fuscous territory from an adjacent one, the original

FIGURE 7.2: Seasonal occurrence of Fuscous Honeyeater behaviours, from general observations and during bird censusing. A. Territorial calls per hour. B. Chases per hour for chases between Fuscous only. C. Corroborrees per hour of Fuscous, see text for explanation.



chaser stopping and the chase being taken over by one of the pair in that territory, with the initial aggressor not being chased) suggested there was a distinction between known birds and strangers.

The Fuscous Honeyeater has a wide repertoire of calls, most of which are associated with particular activities or stimuli. The corroborrees described above have a specific call, a high twittering. A call that is a rolling chitter, described in Slater *et al.* (1986) as 'arig arig a taw taw' (with a variable number of latter elements), has a territorial or 'personal space' connotation. A high pitched, rapidly repeated fluting is a specific alarm call for raptors (similar to, but higher pitched and faster than the Noisy Miner raptor alarm call, Dow 1975a). A call intermediate between those for alarm and corroborrees was often given during chases, when caught in a mist net, or when birds such as butcherbirds or currawongs were close to nests and probably indicated distress. While feeding, it was quite usual for birds to give a soft chip call, possibly having a contact or location function. Nestlings and recent fledglings gave a begging call.

7.3 BREEDING BIOLOGY

7.3.1 Introduction

Much study has concentrated on the mating systems of birds, with most birds found to breed as monogamous pairs (see Oring 1982 for review). Australian birds, however, show a high incidence of co-operative breeding (Dow 1980, Ford *et al.* 1988), with birds other than the parents helping at the nest. Fuscous Honeyeaters display some characteristics that are similar to honeyeaters that are co-operative breeders, for instance, they occur in dense and highly active groups, will chase intruders from territories and mob predators co-operatively and give group displays like corroborrees (see previous section). These behaviours have been found in Noisy Miners (*Manorina melanocephala*, Dow 1978) and Bell Miners (*M. melanophrys*, Clarke 1984a) which are well-known co-operatively breeding species.

Miners will co-operatively defend an area which forms a group territory (Dow 1977b, Smith and Robertson 1978, Loyn *et al.* 1983). This group territory is used for all feeding and breeding. Territoriality has been found quite frequently amongst birds (Lack 1968), but territories are more usually defended by a single bird or a pair. Territories can be defended for varying amounts of time ranging from a few days, or even hours (Gass 1978, Carpenter 1978, McFarland 1986d etc.), to all year. In the non-breeding season, territories are used mostly for feeding purposes

(Ford 1979, Wittenberger 1981, Davies and Houston 1983, McFarland 1985a), but can be also necessary to retain a breeding location or a mate (Lack 1968, Wittenberger 1981, Scott 1984 etc.). During the breeding season, territories may be held to attract a mate (see references in Wittenberger 1981), protect a nest site and/or to provide a feeding area.

A cost and benefit approach is usually taken when evaluating the evolution and contemporary occurrence of territoriality. Territoriality results when a resource that may be limited is economically defensible, that is, that the benefits of access are greater than the costs of defense (Brown 1964, Pulliam and Millikan 1982, Davies and Houston 1984). Food is the resource that is most often defended, and whether a bird is territorial or not depends on the distribution of the food and the number of other birds trying to gain access to it. Costs of defence increase with the dispersion of the food, that is, large areas are more difficult to defend than small areas, and with intruder pressure. Costs may exceed the benefits when food is sparse and evenly dispersed, or when food is very abundant and/or intruder pressure is high. Hence most territorial behaviour, at least theoretically, should occur at intermediate food densities. Many studies have examined such territorial behaviour (Feinsinger 1976, Wolf *et al.* 1976, Carpenter and MacMillen 1976, Davies 1976, Paton 1979, Davies and Houston 1981, Hixon *et al.* 1983, McFarland 1985a, 1986d etc.). Dominance hierarchies may also affect a bird's access to resources (Rooke 1979, references in Pulliam and Millikan 1982) and the resulting distribution and behaviour of individuals may be quite similar to that of territoriality. These are not conflicting patterns of social organization, though, and may form a continuum of defensive behaviours.

A similar cost and benefit approach has been taken in the study of coloniality, but this behaviour has received much less attention, presumably because it is less easy to quantify. Few hypotheses have been proposed to explain the origins of coloniality (Horn 1968, Ward and Zahavi 1973). Benefits of this social system have been thought to be enhanced detection and defence against predators, increased foraging efficiency from information transfer, increased access to mates and increased opportunities to disrupt the mating and nesting of competitors. Costs are thought to be attraction of predators, increased intraspecific competition for food, more competition for mates and a higher frequency of aggressive and disruptive behaviour from neighbours and possibly greater spread of parasites and disease. There is some evidence to support the existence of these factors, particularly the relative benefits of reduced predation and costs of increased competition for food (see reviews by Wittenberger 1981 and Wittenberger and Hunt 1985, and references therein). Some instances of coloniality seem to originate from the distribution of necessary resources (Orians 1961, Crook 1964, Lack 1967, 1968, etc.) and it is difficult to know

whether many of the proposed advantages of coloniality arose secondarily to reduce the costs of the increased clumping of the birds, or whether these behaviours already existed in the community.

The specific questions to be answered in this part of the study, then, are :-

1. What is the mating system of the Fuscous Honeyeater?
2. What are the various factors that affect reproductive success in this species?
3. What is the social organization of this bird during the breeding season?

7.3.2 Methods

From early August and throughout the breeding season, regular searches were made for nests. Since there were probably several hundred Fuscous Honeyeaters in Eastwood (see Chapter 3) and the nests were found opportunistically, a small proportion of the existing nests were actually located for study, and most searching effort was concentrated in the high density Fuscous area, in the south-west corner of the Forest (see Chapter 3). When found, the location, height, substrate, and stage of the nest was recorded. Mist-netting and banding was done irregularly throughout the study, so in some areas there were a number of colour-banded birds (see Section 7.2). This permitted identification of individuals at some nests.

Nests were watched from a distance of 10 to 20 m through a pair of 7 x 50 binoculars. Fuscous Honeyeaters are not shy, and observations from this distance did not appear to disturb them. Nest watches ranged from a few minutes for checking of nest stage up to two hours. Fuscous were found to be fairly rapid visitors to the nest, so nest watches of 30 minutes duration were the most common. Most nests were followed through to completion or failure, but nests that were easy to observe by being low or unobscured by vegetation were watched more frequently. While a nest was being watched, all visits were recorded as to duration and the identity (where possible) of the visitor. Visits were often short or the bird was not banded, so it was not always possible to establish the bird's identity. At the same time, particularly in later seasons, interactions such as chases or corroborrees and the presence of birds of any species in the area were recorded, along with other incidental behaviours.

The breeding season was taken to be that period in which there were known active nests. At the end of each season, the location of nests was plotted on maps of Eastwood and distances between all nests were calculated. Where possible, nestlings were banded before fledging, but mostly nests were too high for this (see results). A few nests were collected after the young had fledged or the nest was abandoned, and were measured. Some additional data were obtained from the RAOU (Royal Australasian Ornithologists Union) Nest Record Scheme.

Weather was noted throughout the season, as storms were found to affect nesting success, and rainfall, temperature and wind speeds obtained for the study period (see Chapter 2).

7.3.3 Results

Data were obtained for four breeding seasons, from 1984/85 to 1987/88. A total of over 200 hours were spent on nest watches, with 97.4 hours in 1984/85, 39 hours in 1985/86, 43.8 hours in 1986/87 and 21.2 hours in 1987/88. Thirty nests were found in 1984/85, in two of which the outcome was unknown. Thirty-seven nests were detected in 1985/86, 40 in 1986/87 and 22 in the final season, and a result could be inferred for all of these. Plate 7.1 shows a nest with eggs, Plate 7.2 a nest with 5-day old nestlings and Plate 7.3 a recent fledgling of the Fuscous Honeyeater.

The length of the breeding season varied between years (Table 7.2) and ranged from late-August to late-January. In 1986/87, which was a dry year, the breeding season started a month late and finished earlier than the previous two years. The peak of breeding activity for all years was during October and November. The average height of nests was 11.4m over the four seasons, with a range of 0.8m to 30m. Nests were usually located in the outer leaves of eucalypt branches, suspended from horizontal or vertical leafy twigs by several attachment points (mean 4.6, n=7), and were cup nests constructed mostly of grass and bark held together by cobwebs and lichen. Nests were found most often in smooth-barked gum trees (*E. viminalis* and *blakelyi*), but this was probably a consequence of the distribution of nesting activity and where most search effort was concentrated. More nests were found north of the big dam in the south-western corner of the Forest in 1984/85 and 1985/86 (where there were mixed stringybarks and gums), and south of this dam in 1986/87 (there were no stringybarks in this area). Nests were rather dispersed in 1987/88, many being where there were mixed stringybarks and boxes.

Table 7.3 shows the losses during nesting, and the reproductive success. Overall, 28.2% of nests reared some young, however, in the dry season 1986/87, reproductive success was much lower (7.5%). In the first and last seasons, most losses occurred during the nestling stage. In 1985/86, many nests were abandoned during the construction stage, and in 1986/87 losses were highest during incubation. Nests started later in the season were more successful than those started in the first half of the season, even though about 75% of nests were commenced in the earlier half.

The mean distance between consecutive nests of known birds was 9.8m (n=40, s.d. 5.95). The distance to known adjacent nests (not necessarily

PLATE 7.1: Nest of Fuscous with three eggs.

PLATE 7.2: Nest of Fuscous with approximately 5-day old nestlings.

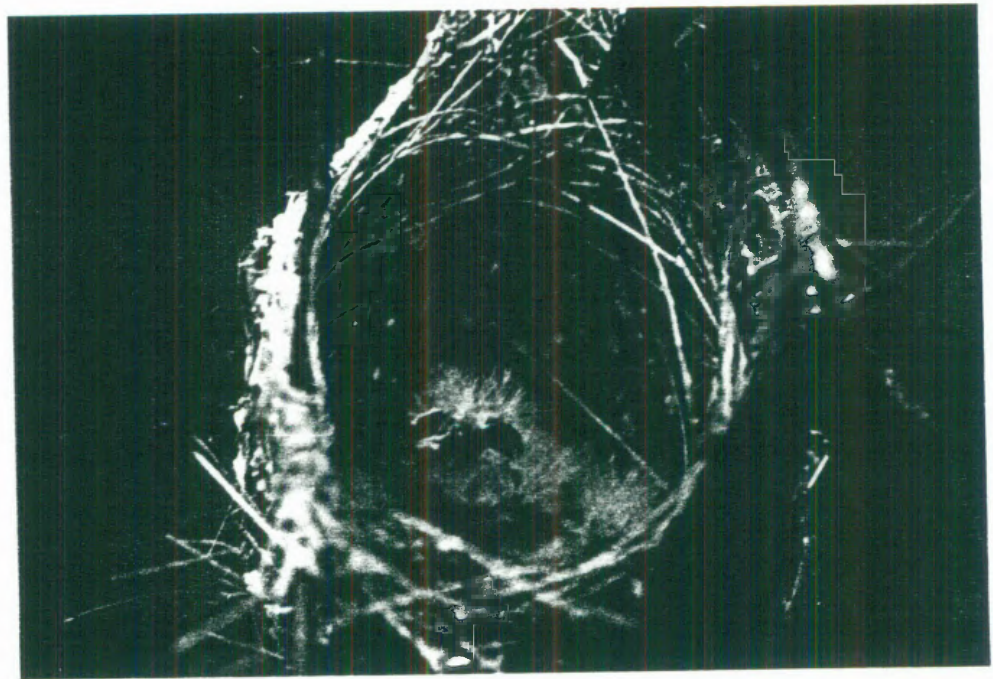


PLATE 7.3: Recently fledged Fuscous chick.

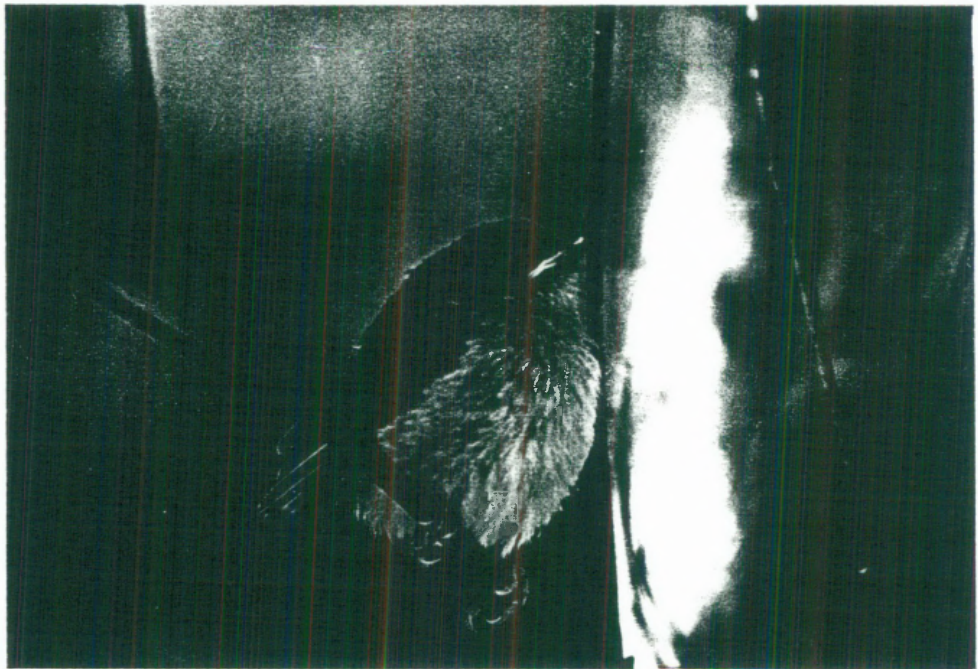


TABLE 7.2: Nest heights, tree type used for nesting and season length of breeding Fuscous Honeyeaters. Percentage use of the tree types *Eucalyptus viminalis* and *E. blakelyi* is combined for the seasons 1984/85 and 1985/86 and the mean.

	1984/85	1985/86	1986/87	1987/88	MEAN
NO. OF NESTS	30	37	40	22	129
NEST HEIGHT (m)	9.9	13.4	11.9	10.3	11.4
Range	1-20	1-30	2-28	0.8-30	
PERCENT USE OF:					
<i>E. viminalis</i>	63.3	67.6	70.0	27.3	64.2
<i>E. blakelyi</i>			15.0	13.6	
<i>E. caliginosa</i>	23.3	29.7	12.5	22.7	22.1
<i>E. melliodora</i>	13.4	0	0	31.8	11.3
Other	0	2.7	2.5	4.6	2.4
SEASON LENGTH:					
Date first nest found	24/8	13/9	26/9	25/8	
Date last nest finished	2/2	20/1	12/1	4/1	
No. days	163	129	108	133	133.25

	1984/85	1985/86	1986/87	1987/88	MEAN
NO. NESTS INITIATED IN:					
August	1	0	0	3	1.00
September	6	3	3	5	4.25
October	8	19	9	5	10.25
November	9	9	25	1	11.00
December	1	5	3	8	4.25
January	3	1	0	0	1.00

TABLE 7.3: Reproductive success, defined as the number of nests initiated that fledged at least one young. The outcome of two nests in the 1984/85 season could not be determined, and these nests are omitted. Nests were counted as starting in the first half of the season if they were initiated before the mid-point date of the season, else they were started in the latter half. Close nests were a mean distance apart of 27.3m (n = 128) and distant nests were, on average, 87.3m apart (n = 44). See text for further details.

NESTS:	1984/85		1985/86		1986/87		1987/88		TOTAL MEAN	
	NO.	%	NO.	%	NO.	%	NO.	%	NO.	%
Abandoned during:										
Construction	3	10.7	11	29.7	4	10.0	3	13.6	21	16.0
Incubation	3	10.7	7	19.0	18	45.0	2	9.1	30	21.0
Feeding (<8 days)	4	14.3	4	10.8	8	20.0	0	0	16	11.2
Feeding (>8 days)	7	25.0	3	8.1	7	17.5	8	36.4	25	21.8
Feeding (unknown)	2	7.1	0	0	0	0	0	0	0	0
Fledged	9	32.2	12	32.4	3	7.5	9	40.9	33	28.2
Total	28	100.0	37	100.0	40	100.0	22	100.0	127	100.0

NESTS:	1984/85	1985/86	1986/87	1987/88	TOTAL MEAN
PERCENTAGE OF NESTS SUCCESSFUL:					
Started first half	23.8	23.3	3.4	28.6	19.8
Started second half	66.7	71.4	18.2	75.0	57.8
Close nests	36.8	40.0	6.3	50.0	30.3
Distant nests	12.5	0	12.5	25.0	11.1

simultaneously occupied) was, on average, 52.5m (n=132, s.d. 46.17) overall. Nests could be grouped according to whether they occurred in the high nest density area (located near the large dam in the south-west of Eastwood), or whether they had few close nests. These approximately corresponded to areas of many Fuscous (see Chapter 3) and areas of few Fuscous respectively. In the high nest density area, the mean distance to the nearest known nests was 27.6m (n=128, s.d. 20.39), and the mean distance to nearest known nest in the low density areas was 87.3m (n=44, s.d. 62.05). Nests that were close to other Fuscous nests, that is, were in the high density Fuscous area, were significantly more successful (t-test on all seasons combined, n=126, P<0.05) than nests that occurred in low density Fuscous areas.

Table 7.4 presents data obtained from the RAOU Nest Record Scheme, for the period 1965 to 1983 and from most areas of the Fuscous distribution (Victoria to southern QLD). The average height of nests was lower, most likely because it is easier to check the contents of low nests, but the range was similar. There were slightly more nests in non-eucalypts, again probably reflecting the availability of substrates (there are very few evergreen shrubs in Eastwood), but eucalypts were still used for 90% of nests. Overall nest success was similar, with most losses occurring during the construction stage, rather than later as found in most seasons of my study. Fuscous are sensitive to disturbance whilst the nest is being built (personal observation), and it is possible that the inspection of the nests caused them to be abandoned.

I found no evidence that Fuscous bred co-operatively, with recognized parents accounting for most of the visits. A few examples of nest visits by non-parents were seen. These were either visits by young of earlier broods who inspected the nest (seen only twice, and nest was at construction and incubation stages, so they were not feeding) or by other birds stealing nesting material. These birds were chased by the parents if detected. Two cases of feeding of fledglings by birds other than the parents were seen and in both cases could be attributed to misplaced parenting. On the first occasion, the non-parent birds were unknown and were chased by the parents. In the second case, the fledglings were perched midway between two nests (from one of which they had fledged), and the non-parent male from the other (abandoned) nest fed the young. This male had lost young of the same age a few days previously. His mate was building a new nest and did not approach the fledglings. The birds involved nested in adjoining areas for several years (O/M and O/B, see following paragraph).

Selected case histories are shown in Figure 7.3. These Fuscous were colour-banded and followed over several seasons. Two male Fuscous, banded orange over mauve on the left leg (known hereafter as O/M) and orange over black on the left leg (O/B), banded on 27/9/84, were both males that nested in adjoining areas probably

FIGURE 7.3: Selected case histories of banded Fuscous Honeyeaters. Year (Y) and month (M) given, where S is September, O is October, N is November, D is December and J is January. Line gaps indicate a new month or between breeding seasons. Birds are male Y/W (yellow over white on left leg) and female O/B(r) (orange over black on right leg, initially UB unbanded), male O/B (orange over black on left leg) and male O/M (orange over mauve on left leg). UB denotes unbanded females, * denotes successful nest, build is construction stage (done by female), incub is when female is incubating eggs, feed indicates that banded bird is feeding at a nest, A means nest is abandoned, FL are fledged young from a nest, juv are older, same season juveniles, area is within 40m of a tree that has been previously used by that bird for nesting (nest may not be active).

Y	M	Y/W, O/B(r)	O/B	O/M
1984	S		UB feed at nest	
		Y/W banded	O/B banded	O/M banded
	O		*Nest fledged 2	UB build nest O/M feed at nest
			O/B feed FL	
			UB build nest	
	N	UB build nest		Nest A, predation by currawong
		Y/W feed at nest Nest A	Nest A, egg infertile O/B retrapped	
	D	O/B(r) banded		
1985	J			O/M seen in area
			O/B seen in area	
	S	Y/W seen in area	O/B seen in area	O/M seen in area
	O	O/B(r) build nest	UB incub	O/M seen in area UB build nest

Y	M	Y/W,O/B(r)	O/B	O/M
			O/B seen in area	
		Y/W retrapped	O/B feed at nest	
		Nest A during incub	Nest A	Nest A during incub
	N	O/B(r) build nest	UB build nest	UB build nest
		O/B(r) & Y/W feed at nest		O/M feed at nest
			O/B feed at nest	
	D	*Nest fledged 2		*Nest fledged >=1
			*Nest fledged 3	
				UB build nest
			O/B retrapped	
		O/B(r) incub nest	UB build nest	
		O/B(r) & Y/W feed at nest		
1986	J		O/B feed at nest	Nest A
		Nest A		
			*Nest fledged 2	O/M in area, feed juv
	S	O/B(r) build nest		
		O O/B(r) & Y/W feed at nest		
		Nest A		
		O/B(r) build nest		
	N		O/B seen in area	
			UB incub	UB build nest
		Y/W seen in area		
			Nest A	Nest A
		O/B(r) & Y/W feed at nest		
		Nest A		
		O/B(r) build nest		O/M seen in area
	D	Nest A		
				O/M seen in area

Y	M	Y/W,O/B(r)	O/B	O/M
1987	J			O/M seen in area

O/B(r) & Y/W not seen
this season

O		O/B seen in area UB build nest	O/M seen in area
---	--	-----------------------------------	------------------

N		O/B feed at nest *Nest fledged 2	
---	--	-------------------------------------	--

D		O/B feed 2 FL UB build nest O/B feed at nest	
---	--	--	--

1988	J	*Nest fledged 2	
			O/B feed 2 FL & 1 juv

throughout all four seasons. Their nests were located about 80 to 100 m NNW of the big dam. Their females were unbanded (more males were banded than females as the males were more easily captured). Male, yellow over white on the left leg (Y/W), was banded on 28/9/84 and was followed for three seasons. He was generally detected in the area 30 to 40 m north of the dam. His mate was orange over black on the right leg (O/B(r)). She was banded on 5/12/84 and may have been the unbanded bird that was mated to Y/W in the season 1984/85. Certainly, they nested together in the following two seasons.

Over the four breeding seasons, O/M made 5 known nesting attempts, of which one was successful. He was last seen on 27/10/87 in his area. O/B was much more successful, with 5 nests fledging out of 8 known attempts over the four years. Y/W and O/B(r) were not seen in the 1987/88 season, but in the three earlier seasons, they made 7 known attempts at nesting, of which one was successful.

Birds made between one and five known attempts at nesting per season, with three to four probably being typical. With the exception of late in the season (mid-December or January), renesting occurred whether or not the previous attempt had been successful. After fledging young, birds generally delayed renesting for 3 to 4 weeks, whereas if the previous nest failed or only fledged one, construction of the new nest could begin in a few days. Building of a nest took, on average, 5.3 days ($n=46$, s.d. 1.82, range 3 to 11) and was done by the female. Clutch size averaged 2.4 eggs ($n=15$, s.d. 0.63) with a range of one to three eggs which were laid on consecutive days. Incubation was also done entirely by the female and commenced immediately after laying. The eggs hatched, on average, 14.9 days ($n=32$, s.d. 1.76, range 11 to 18) after the start of incubation. All nest maintenance and brooding of the young during the nestling period was done by the female. The young fledged about 15.7 days ($n=18$, s.d. 2.20, range 12 to 19) after hatching, and were totally dependent on their parents for food for about a further week. After this, they fed themselves increasingly and were probably completely independent four to six weeks after fledging, although late in the season they could follow their parents for up to 2 months.

Visits to the nest were rare by males until the feeding stage (see Table 7.5). During the nestling period, the young were brooded by the female for the first 5 to 6 days after hatching. Both parents fed the nestlings, with the female visiting much more in the first third of the nestling period, and thereafter males visited almost as frequently as females (Table 7.5). Visiting rates peaked in the final third of the nestling period, with a combined rate of 26 visits per hour. Some nests could have received up to 60 visits per hour. For the female, visits were longest during

TABLE 7.4: Data from RAOU Nest Record Scheme. Nests from locations in Victoria to southern Queensland.

MEAN HEIGHT OF NESTS (m)	4.8	
Range	0.5-25	
USE OF TREE TYPES:	NO.	%
Gums	15	20.5
Boxes	12	16.4
Stringybarks (& other rough-barked spp.)	12	16.4
Total Eucalypts (including unknown spp.)	66	90.4
Other (introduced shrubs)	7	9.6
Total	73	100.0
NEST SUCCESS:	NO.	%
Abandoned during Construction	11	40.8
Incubation	4	14.8
Feeding	3	11.1
Fledged at least 1 young	9	33.3
Total	27	100.0
AVERAGE CLUTCH SIZE (n=27):	2.2	

TABLE 7.5: Attendance at the nest by female (F) and male (M) Fuscous Honeyeaters. First column (R) in any season is the mean rate of visits (in number per hour), the second column (D) within a season is the mean duration of those visits (in seconds) and the third column (%) is the percentage of time (per hour) that the bird was at the nest, calculated by multiplying rate by duration and expressing as a percentage. Sample sizes (n) and standard errors (se) are given for rates and durations. Means and figures are approximate where sample sizes are small. The feeding period was about 15 days, so the first third is day of hatch to 5 days, the second third is for nestlings 5 to 10 days old, and the final third is from 10 days to fledging of the young. All data are per nest, that is, visits to individual nestlings or fledglings were not distinguished.

SEX	1984/85			1985/86			1986/87			1987/88			MEAN		
	R	D	%	R	D	%	R	D	%	R	D	%	R	D	%
STAGE OF NEST CONSTRUCTION															
F	17.0	23.3	11.0	18.4	24.9	12.7	16.2	23.6	10.6	12.4	37.8	13.0	16.0	27.4	12.2
n	16	139		9	28		19	71		5	14				
se	2.1	3.0		3.0	4.7		1.9	2.6		3.3	10.9				
M	0.04	5.0	<0.01	1.0	3.8	0.1	2.4	6.3	0.4	3.8	13.3	1.4	1.8	7.1	0.4
n	1	1		1	4		19	7		5	3				
se					0.8		0.9	3.0		2.8	8.3				
INCUBATION															
F	5.6	313.0	48.7	7.0	231.6	45.0	7.0	237.4	46.2	6.9	443.4	85.0	6.6	306.4	56.2
n	64	196		6	6		31	40		11	28				

		1984/85			1985/86			1986/87			1987/88			MEAN		
SEX		R	D	%	R	D	%	R	D	%	R	D	%	R	D	%
STAGE OF NEST																
	se	0.3	17.7		0.8	57.7		0.4	25.3		0.8	84.6				
	M	0.04	3.5	<0.01	0.5	7.8	0.1	0.2	1.5	<0.01	0.6	7.3	0.1	0.3	5.0	0.04
	n	1	2		1	5		33	2		11	6				
	se		1.5			2.2		0.1	0.5		0.4	1.9				
FEEDING NESTLINGS																
1/3	F	9.9	191.1	52.6	13.4	82.7	30.8	12.8	96.3	34.2	7.9	297.1	52.0	11.0	166.8	51.0
	n	16	125		10	51		10	32		4	16				
	se	0.5	19.2		1.6	7.1		1.8	11.2		0.7	64.7				
	M	4.4	7.3	0.9	11.7	7.0	2.3	6.3	11.1	1.9	4.3	18.5	2.2	6.7	11.0	2.0
	n	16	73		9	48		10	21		4	11				
	se	0.8	0.7		1.6	0.5		1.2	1.2		1.7	5.4				
2/3	F	20.8	23.8	13.7	12.9	68.1	24.4	12.2	24.0	8.1	7.4	16.9	3.5	13.3	33.2	12.3
	n	13	168		2	27		9	27		3	17				
	se	2.0	6.3		5.8	18.1		0.9	7.3		2.7	4.4				

		1984/85			1985/86			1986/87			1987/88			MEAN		
SEX		R	D	%	R	D	%	R	D	%	R	D	%	R	D	%
STAGE OF NEST																
	M	13.5	5.8	2.2	15.5	5.7	2.5	8.9	8.1	2.0	4.3	10.1	1.2	10.6	7.4	2.2
	n	13	99		2	23		9	19		3	7				
	se	1.7	0.3		0.5	0.3		1.4	0.9		1.2	1.5				
3/3	F	13.1	25.5	9.3	14.6	7.9	3.2	15.0	16.1	6.7	12.7	29.2	10.3	13.9	19.7	7.6
	n	9	96		1	15		1	7		6	20				
	se	2.7	7.4			1.4			2.4		2.7	10.1				
	M	12.9	4.9	1.8	9.7	5.9	1.6	15.0	16.0	6.7	10.2	4.3	1.2	12.0	7.8	2.6
	n	9	101		1	12		1	5		6	15				
	se	2.6	0.2			0.7			4.3		2.3	0.5				
POST-FLEDGING																
	F & M	51.7	3.0	4.4							14.0					
	n	15	330								2					
	se	56.5	0.1								2.0					

incubation, lasting about 300 seconds, and shortest during late feeding when they were less than 20 seconds. The male's longest visits were during early feeding (11 seconds on average). Females were always more attentive at the nest than males (see Table 7.5).

The females also spent more time close to the nest than males (see Table 7.6), with up to 29% of time being spent less than 10m from the nest, excluding the nest visits. This figure occurred during the laying phase and may be high due to a small sample size. Apart from this, the female was close to the nest most during the nestling stage (18.3% of total time), while the male spent more time near the nest during the incubation stage (12.8% of total time). The female always concentrated her activities nearer to the nest than the male, who probably used the 10 to 20m area more than that within 10m of the nest, especially as birds were less likely to be detected in the more distant zones. The time spent near the nest was probably a gross underestimate, due to birds not being identified while I was watching.

The area around the nest was defended, and both the male and the female chased intruding Fuscous about equally (see Table 7.7). Intrusion rates were highest when the nest had just been abandoned and, during incubation, although differences were not great. This probably reflected the low activity and hence visibility of the parent birds during these stages, with high activity by the parents having a deterrent effect on potential intruders, who were more likely to be detected and chased. This was supported by the percentage of intruders that were chased, which was highest close to the nest at most stages but especially during feeding of the nestlings, when parents were attentive at the nest and also very actively visiting the nest. Within 10m of the nest, most interactions were chases (91.7%, see Table 7.7). As distance from the nest increased, more corroborrees took place, supporting the idea that corroborrees were encounters between neighbouring birds who were treated less aggressively than strangers (see Section 7.2). Only 25 to 51.5% of intruders were chased when close to the nest. However, many of those birds that were not attacked could have been unidentified parents, particularly the males which did not visit the nest as often (Table 7.5) thus preventing confirmation of their identity. Other birds that were not chased and known not to be the parents were birds from adjacent nests (which could be as close as 10m) or juveniles from previous nests. Juveniles generally seemed to be tolerated more by adults, whether or not they were related. A limited amount of data from mapping of known birds suggested that birds ranged over at least 600m² (n=9, s.d. 284) in the nest area, with females covering a smaller area than males and that males overlapped in range with other males and females about equally (mean overlap around 46% (n=6, s.d. 14), but females overlapped more with their mates (about 75%, n=2, s.d. 20.5).

TABLE 7.6: Mean percentage of time that Fuscous Honeyeaters are near their nest. Females and males are known parents at their nest, unknown birds may be parents that were not identified or were unchased intruders. Distance is distance from nest, first column for any stage is mean amount of time in that zone, second column is sample size. Empty cells indicates no data for that distance.

BIRD	DISTANCE	STAGE OF NEST							
		Construction		Laying		Incubation		Feeding	
Female	<10m	15.4	18	29.0	5	14.4	44	18.3	22
	10-20m	12.3	9	14.3	3	9.0	21	6.5	9
	>20m	16.5	2			17.5	2	1.6	1
Male	<10m	9.8	10	11.1	4	12.8	26	8.3	18
	10-20m	8.2	5	1.7	1	9.6	5	8.0	8
	>20m								
Unknown	<10m	26.8	3	6.1	1	2.7	3	19.9	2
	10-20m	3.6	4	2.8	1	2.3	2	28.3	1
	>20m	11.0	2			1.3	1	2.8	1

TABLE 7.7: Intrusion rates by Fuscous into the nest area, and percentage of these intrusions that are interacted with by parent birds (includes chases and corroborrees). Distances are from the nest, n indicates sample size.

STAGE OF NEST	NO. INTRUSIONS/HOUR			% INTERACTED WITH		
	<10m	10-20m	>20m	<10m	10-20m	>20m
CONSTRUCTION	3.9	3.2	1.6	35.0	27.3	17.4
n	20	20	20	20	22	23
LAYING	3.3	8.2	0.8	25.0	38.5	10.0
n	11	11	11	12	13	11
INCUBATION	4.6	4.3	0.9	41.4	36.1	16.7
n	56	56	56	58	61	54
FEEDING	4.4	2.6	0.6	51.5	32.4	9.1
n	32	32	32	33	34	33
ABANDONED	13.0	9.0	3.4	43.6	42.9	23.1
n	13	13	13	16	14	13
PERCENTAGE OF INTERACTIONS THAT WERE:						
	CHASES			91.7	80.8	54.5
	n			35	42	12
	CORROBORREES			8.3	19.2	45.5
	n			5	10	10

Total intrusion rates by species other than Fuscous Honeyeaters were at about the same frequency as those by Fuscous (7.0 per hour, see Table 7.8). Most of these were by Dusky Woodswallows and Willie Wagtails, which were rarely chased by the Fuscous. Other species that were rarely or never chased were Eastern Rosellas, Crested Shrike-tits and treecreepers. Kookaburras, currawongs and Red Wattlebirds were always chased, the former two, and possibly the latter, being nest predators. Most other species that occurred in the Fuscous area (see also Chapter 3) were chased to some extent. The percentage that were chased seems to be higher further away from the nest, this was because the presence of most species was usually only noted at these distances when involved in interactions with Fuscous.

7.3.4 Discussion

Reproductive success varied from year to year and was most obviously related to weather, particularly rainfall. 1986 was a very dry and windy year (see Chapter 2) and nesting success was very low. The greatest losses, relative to the other years, occurred during incubation and it is possible that food was short (see Chapters 4 and 5) necessitating longer absences by the female, thus exposing the eggs to a higher potential risk of cooling, being tossed out by the wind (Fuscous nests are exposed to the wind as they are at the ends of branches and usually built quite high), and predation. There was, however, little evidence that parents were less attentive at the nest in this year (see Table 7.5). Storms, especially when there were several over a few days, or a prolonged wet spell also affected reproductive success particularly recently hatched young, with many nests being abandoned after a few wet days, presumably because of the death of the nestlings.

There was a difference in reproductive success between early nests and late nests, with nests recorded in the latter half of the season being more likely to fledge young (Table 7.3). There were no great differences in the abundance of food between early and late in the season (see Chapters 4 and 5). There could be, however, large differences in the windiness of the weather, perhaps causing eggs to be tossed out or more easily cooled (see Chapter 2). The weather was warmer later in the season, and this probably meant that nestlings had a lower energy demand, thus requiring less food and brooding, and the longer days permitted more time for foraging by the adults.

The enhanced reproductive success of nests that were close to other nests compared with isolated nests suggests there were some benefits from grouped nests. There were no differences in the density of avian predators between the low and high

TABLE 7.8: Intrusion rates of other species of birds and percentage chased or mobbed by Fuscous. Intrusions that were not chased were likely to be overlooked, so these represent minimums. Distances are from the nest and distances over 20m could be very close to an adjacent Fuscous nest. Gaps mean no intrusions were seen, n is sample size. See Appendix 2 for scientific names.

SPECIES	NO. INTRUSIONS/HOUR			% CHASED		
	<10m	10-20m	>20m	<10m	10-20m	>20m
Eastern Rosella	15.5	1.1	1.5	0	0	0
n	1	1	1	3	1	1
Crested Shrike-tit	4.5	3.6		0	0	
n	2	3		2	3	
Brown Treecreeper	4.1	3.6		0	0	
n	1	1		1	1	
Dollarbird		10.5			0	
n		2			2	
Striated Pardalote		4.6			0	
n		1			1	
Restless Flycatcher		3.9			0	
n		2			2	
White-throated Treecreeper		3.0			0	
n		1			1	
Dusky Woodswallow	5.8	3.7	2.9	2.9	0	100.0
n	22	3	1	34	4	1
Willie Wagtail	5.7	0.5		20.0	0	
n	8	1		10	1	
Superb Fairy-wren	6.4	4.1		0	33.3	
n	1	2		1	3	
Grey Shrike-thrush	4.5	3.7	4.1	37.5	40.0	0
n	7	5	3	8	5	4
Black-faced Cuckoo-shrike	4.3	3.1	1.9	37.5	0	75.0
n	7	5	4	8	5	4
Eastern Yellow Robin	4.0			50.0		
n	2			2		

		NO. INTRUSIONS/HOUR			% CHASED		
		<10m	10-20m	>20m	<10m	10-20m	>20m
Noisy Friarbird		4.0	6.4	1.8	0	33.3	100.0
	n	1	3	1	1	3	1
Red Wattlebird		2.0		1.5	100.0		100.0
	n	1		2	1		3
Laughing Kookaburra		5.0	6.1	3.6	0	100.0	100.0
	n	1	2	1	1	2	1
Pied Currawong			2.1	4.1		100.0	100.0
	n		1	1		1	1
Sacred Kingfisher			0.7	1.3		100.0	0
	n		1	1		1	1
Mean total		7.0	5.4	3.3	12.9	28.2	53.3
	n	41	27	11	70	39	15

density Fuscous nests (see Chapter 3), nor were there major differences in the types of trees present, although the areas of many Fuscous, and therefore many nests, tended to have more *E. viminalis* and significantly fewer stringybarks. There were many more leaf-gleaning insectivores in the high density Fuscous areas, despite the fact that there were fewer other leaf-gleaning insectivores that were potential competitors for food with the Fuscous. Food was in short supply in most seasons (see Chapter 5) so competition might be expected to occur. This higher density of competitors for food would be a cost of the grouped nesting, although partially offset by the reduction in numbers of other species. The benefits of high density nesting were probably those associated with earlier detection of predators because more birds could be vigilant and more effective mobbing by groups of Fuscous. These tend to decrease the costs of defence against predators for the individual. Grouping of nests has been found to increase reproductive success in Fieldfares (*Turdus pilaris*, Andersson and Wiklund 1978, Slagsvold 1980), gulls (Kruuk 1964) and other species (Krebs 1971, Goransson *et al.* 1975). Costs to the Fuscous of decreasing the number of competitors and defending the nest area may be reduced by co-operative chasing and by the recognition of neighbours. It is not known if costs of interference from other Fuscous (stealing nest material was observed, cuckolding of males could have occurred) were higher for close-nesting birds than for isolated pairs. There may be other benefits in increased foraging efficiency because the birds do not have to look around or interrupt their feeding as much. This possibly permits increased expenditure of energy by more rapid foraging for themselves and more rapid visiting rates and hence better provisioning and attention to the young. These latter changes would, however, be adaptive, requiring that Fuscous have to nest semi-colonially over some time. It is unknown whether the Fuscous population consists of individuals that always nest in groups and others that always nest singly, but this is thought highly unlikely.

Visiting rates by the Fuscous were high, compared with those found for other species (Noske 1982, Bell 1983a, Bridges pers. comm. etc.) and were comparable to those found for miners (Swainson 1970, Dow 1977a, Smith and Robertson 1978) although the latter species were co-operative breeders, that is there could be up to 12 birds attending the nest, whereas in Fuscous there were only two. Rates were probably high out of necessity, because food items were small (see Chapters 4 and 5). Clarke (1988) and Dow (1977a) suggested that the small size of food items was responsible for the rapid visiting rates of miners. A foraging bird trying to pick off small insects from leaves is likely to have its efficiency of prey capture quickly diminished by the necessity of holding a beakful of food. Furthermore, each delivery

of food to the young birds will be only a small amount and, to satisfy nestling or fledgling hunger, many visits will be necessary.

The Fuscous foraged to a limited extent in the area of their nest (personal observation) with some data suggesting that females foraged about 15% of total time in the nest area, males about 6% (from time-bugeting, Fuscous forage for 45-80% of time, Ford, Huddy and Bell in press, see Table 7.6 for amount of time in nest area). They also defended the area (see Tables 7.7 and 7.8). The areas can probably, therefore, be regarded as territories, although not exclusive ones. Interspecific aggression by the Fuscous was not indiscriminate, with nest predators and potential competitors (species in the same feeding guild) being preferentially chased (see Chapter 3 and Table 7.8). Intraspecific intrusion rates were also quite high (Table 7.7) although similar intrusion rates have been found for other honeyeaters (Dow 1978, Rooke 1979, McFarland 1986a and d, Paton 1986). With the limited feeding possible on a territory this size and the high rates of intrusion, it might be expected that small territories would not be economic, and that costs of defence might be reduced by the Fuscous if they nested further apart. However, if they did so, nest success would be lower (see Table 7.3). It is suggested, therefore, that the observed spacing of nests represents a compromise between a pairs' costs of defence and amount of food available in the nest area, and the enhanced reproductive success of close nesting.

Reproductive success for the Fuscous was comparable with that found in other species in the area (Noske 1982, Bell 1983a, Nias 1987, Bridges pers. comm.) and in Australia generally (see Woinarski 1985b, Ford 1989). Adverse weather seemed to be the greatest cause of nest failure in this population of Fuscous Honeyeaters, however, their semi-colonial nesting and observed instances of predation suggested that predation levels could be quite high. The losses due to starvation or disease were unknown.

In summary :-

1. Fuscous Honeyeaters occur along the south-eastern ranges and are locally common. At Eastwood State Forest, the population was sedentary and birds were smaller in size than Victorian birds. Males were generally larger than females, but the sexes overlapped.
2. Fuscous Honeyeaters showed several behaviours previously described for some other honeyeaters such as chases and corroborrees. The incidence of these, and territorial calls varied throughout the year and were most common during the breeding season.

3. The breeding behaviour of the Fuscous was studied over 4 seasons. Over 200 hours was spent watching 129 nests. Around 28% of nests successfully fledged young, with success varying from 8% to 41% in different years. Weather, particularly drought, appeared to affect reproductive success most. Nests that were close together were more successful than isolated nests.

4. No evidence of co-operative breeding was found. The female did all construction of the nest, incubation of eggs and brooding of young. The male helped feed the young. Visiting rates were high relative to other monogamous birds, and were comparable with the rates found in the co-operative miners.

5. The nest area was defended intra- and interspecifically and both parents chased intruders. Territories enabled birds, particularly the female, to forage to a limited extent in the nest area. Other species were reduced in abundance, probably because of Fuscous aggression, and this may have decreased competition for food. The advantages of grouped nests were thought to be more effective detection and mobbing of predators, reduction of costs of defence through co-operative chasing and perhaps greater foraging efficiency.