

Chapter 6

Foraging behaviour: the effect of vegetation structure and invertebrate availability

“Our results suggest that availability of food for forest birds is a function of (i) the types and abundances of prey present, which vary among tree species, (ii) the foliage structure and characteristics of the tree, which influence prey detectability and accessibility, and (iii) the morphological and behavioural abilities of each bird species to perceive and capture those prey. Food availability therefore cannot be assessed by simply measuring prey abundance alone and must essentially be determined separately for each bird species.”

[Holmes & Schultz 1988]

Introduction

Studies of bird foraging behaviour in Australia have not addressed the question of whether species change their behaviour to deal with changes in their habitat caused by disturbances, such as grazing. However, some studies have shown that the foraging behaviour of insectivorous birds alters with changes in the abundance of invertebrates; either seasonally (Cameron 1985; Ford *et al.* 1990), or due to disturbances such as drought (Bell & Ford 1990). In the northern hemisphere, a number of studies have found that species change their foraging behaviour when they forage in different microhabitats (Robinson & Holmes 1984; Holmes & Schultz 1988), or in different vegetation types (Maurer & Whitmore 1981), but the response of each species differed. These studies indicate that species do respond to changes in vegetation structure and invertebrate availability, but these responses are species specific.

The disturbance to native vegetation caused by the grazing of domestic stock has the potential to affect the availability of food for birds in a number of ways. Grazing changes the structure and composition of the vegetation (Hobbs & Hopkins 1990; McIvor & Gardener 1990; Wilson 1990) and reduces the quantity and changes the structure of the

litter layer (King & Hutchinson 1983). Indirectly, it can influence the availability of food by increasing the nutrient levels of the soil and the vegetation (Hobbs & Hopkins 1990; Wilson 1990). This has been shown to affect the abundance of some invertebrate groups (Myers & Post 1981; Landsberg 1990). The effect of these grazing-induced disturbances on bird species would depend on the ability of the species to change its foraging behaviour to match the changes in the distribution and availability of its food resources.

This chapter describes the foraging behaviour of White-browed Babblers and how it is affected by vegetation structure, and the abundance and composition of invertebrates. The aim of this work was to assess how White-browed Babblers dealt with changes in their habitat which resulted from the disturbance caused by sheep grazing, and so determine if this disturbance represented a decline in habitat quality.

Methods

The foraging observations and sampling for invertebrates were conducted concurrently during two periods in 1996. The first sampling period was in March/April (Summer), which is at the end of the driest, hottest period of the year (see Chapter 2). The second was in August/September (Spring), which is at the end of the coolest, wettest period of the year. The first sampling period was during the non-breeding season of White-browed Babblers, while the second was during the breeding season.

I collected foraging observations over a period of three weeks for each sampling period. Foraging observations were made in the first 3-4 hours after sunrise and the last 2-3 hours before sunset. Foraging observations were not collected during the middle of the day as foraging activity was much lower at this time, especially in Summer. The invertebrate surveys were conducted at the same times of the day as the foraging observations.

Foraging Records

Each foraging record consisted of up to 10 successful or unsuccessful foraging attempts by an individual bird. Only one record was taken from each group encountered in any one day, but records were collected from the same groups on different days. Multiple foraging attempts were collected for each record, because this reduced the chances of biases resulting from obvious foraging behaviours.

The foraging method and substrate were recorded for each foraging attempt. I used the foraging methods described by Recher *et al.* (1985); glean, hang-glean, snatch, probe/prise, hover, pounce, hawk and taking nectar or seed. The ground substrates were divided into: 1) **litter**, either needle or broad/macro; 2) **annual weeds** (these occurred only during the Spring sampling period); 3) **debris**, logs and fallen branches; and 4) **other**, tussock grass clumps and termite mounds. Substrates in the vegetation were divided into: 1) **trunks**, 2) **branches** and 3) **foliage**.

When food resources were taken from a plant substrate, the plant was identified to species or genus. Each foraging record was allocated to one of the three vegetation types described in Chapter 5; *Allocasuarina* shrubland, mixed shrubland, or *Callitris* woodland.

Nestling Diet

During the breeding seasons of 1995 and 1996 observations on the behaviour of adults at nests enabled the collection of data on the items fed to nestlings (see Chapter 7). This analysis was done on 14 nests with nestlings, which were watched for a total of 150 hours. During these watches all visits to the nest were recorded and whenever possible food items delivered to the nestlings were identified.

Invertebrate Sampling

The invertebrate sampling was conducted by Noack (1996) in the same areas as the vegetation sampling (see Chapter 5). Samples were collected along the vegetation transects, or as close to the vegetation transects as possible. Invertebrates were sampled from three of the major substrates used by White-browed Babblers when foraging (*i.e.* litter, logs, and shrub canopies). During the Spring survey an additional substrate, weeds, was also sampled.

Litter samples were collected from 25 cm square quadrats. Four samples were taken along each vegetation transect traversing group home ranges (20 samples per home range). These samples were hand sorted for invertebrates, concentrating on those greater than 3 mm in size. The samples for the two periods were taken from the same locations, with the Spring quadrat being placed approximately 30 cm from the Summer quadrat.

Logs were sampled along the vegetation transects by selecting the nearest log to a randomly selected point. Ten logs were sampled in each habitat patch. Each log was broken up by hand into a large metal tray. Solid pieces of log were then beaten to dislodge invertebrates hiding in crevices. This sampling method collected invertebrates from the parts of each log that were accessible to White-browed Babblers. The diameter and length of each log was measured, so that each invertebrate sample could be standardised by the log volume.

Shrub canopies were sampled using a 1 m², white beating cloth, which was held 1 m above the ground under the foliage and branches. Approximately 1 m of the canopy above the cloth was struck a number of times to dislodge invertebrates. Ten shrubs were sampled in each habitat patch. A shrub species was sampled in a given patch, if it constituted greater than 10% of the canopy cover. The number of shrubs of each species was determined from their relative frequency in that habitat patch. All samples from the same shrub species were combined for each habitat patch.

During the Spring period annual weeds became abundant in some areas. Therefore, this substrate was sampled for invertebrates by sweep netting. Ten samples were collected from each habitat patch and were located randomly along transects in areas where annual weeds occurred. Each sample consisted of five sweeps of the net.

All invertebrates collected were preserved in 70% alcohol and later identified to Order or Class using a binocular microscope. The classification of insects used was that described in Naumann (1994). Where the abundance of an individual taxon was too numerous to count it was estimated to the nearest 50 individuals.

Data Analysis

Chi-square analysis (χ^2) was used to test the statistical significance of changes in foraging behaviour in different vegetation types, seasons, and grazing conditions. Where necessary categories were lumped to avoid cells with low expected values (Zar 1996). The patterns of change in foraging behaviour between grazed and ungrazed *Allocasuarina* and Mixed shrublands were very similar, so the data were combined for the analysis. Multiple foraging attempts were collected from the same group each time it was located. These

multiple attempts are not independent (Morrison 1984; Recher & Gebiski 1990), so only differences with statistical probabilities of less than 0.01 were considered significant.

The abundance of litter invertebrates in quadrat samples was tested to see if it followed a negative binomial distribution, using Chi-square analysis. The negative binomial distribution is described by the expansion of $(q-p)^{-k}$, where $p = \mu/k$ and $q = 1+p$ (μ is the mean and k is a constant determined for each distribution). The expected values for this analysis were determined from a negative binomial distribution, with parameters determined from the samples using the maximum-likelihood method (Elliott 1979). Differences between means for data with a negative binomial distribution were tested by comparing the 95% confidence limits of the mean estimates (\bar{y}). The mean estimates were determined using the method described by Elliott (1979) for small sample sizes with contagious distributions. The means were $\log(x+1)$ transformed for these analyses. Differences in the probability of an invertebrate being sampled in litter quadrats were tested using Chi-square analysis. Isoptera were removed from the analysis of litter samples, because the sampling technique inadequately represented the abundance and distribution of this taxon.

The Mann-Whitney U-test (U) was used to compare the mean abundance of log invertebrates between grazed and ungrazed sites (Zar 1996). The Wilcoxon paired-sample test (T) was used to test seasonal changes in the mean abundance of invertebrates in logs (Zar 1996).

Differences in the abundance of invertebrates in shrub canopies were not tested statistically, because samples from shrubs of the same species were combined for each habitat patch. Samples were combined into genera classes for comparisons of invertebrate abundance and composition. Samples of *Acacia* spp. were predominantly collected from *A. neurophylla*, those from *Allocasuarina* spp. were predominantly from *A. acutivalvis*, and those from *Eucalyptus* spp. were predominantly from *E. leptopoda*. No single *Melaleuca* spp. dominated these samples.

Results

Foraging Behaviour

White-browed Babblers foraged predominantly by probing (85% of observed foraging attempts). All other foraging attempts were gleans, except for a single snatch from the foliage during Spring. Two types of probing behaviour were observed. Prey were extracted from within substrates, such as leaf litter or the fissures of bark; or substrates were moved to reveal hidden prey. The latter behaviour often occurred within litter, but babblers also broke apart dead branches, fallen branches and logs. White-browed Babblers were also observed breaking into termite mounds. Most frequently this involved breaking into new construction on the sides of mounds or into the pavement mounds produced by some termite species.

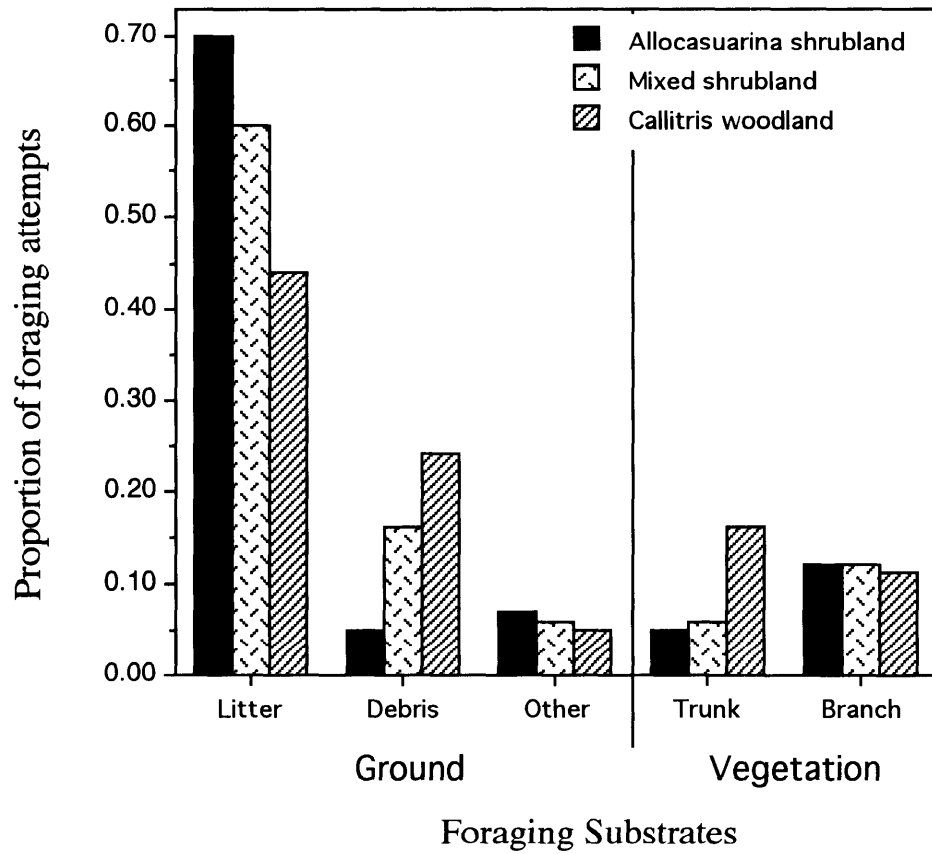
Substrate use

In Summer, White-browed Babblers did most of their foraging on the ground (Fig. 6.1a). The foraging patterns in *Allocasuarina* and Mixed shrubland were similar with the litter being the most commonly used substrate; whereas, in *Callitris* woodland ground debris and trunks were used more frequently than in shrublands ($\chi^2_{(8)} = 23.4$ $p = 0.003$).

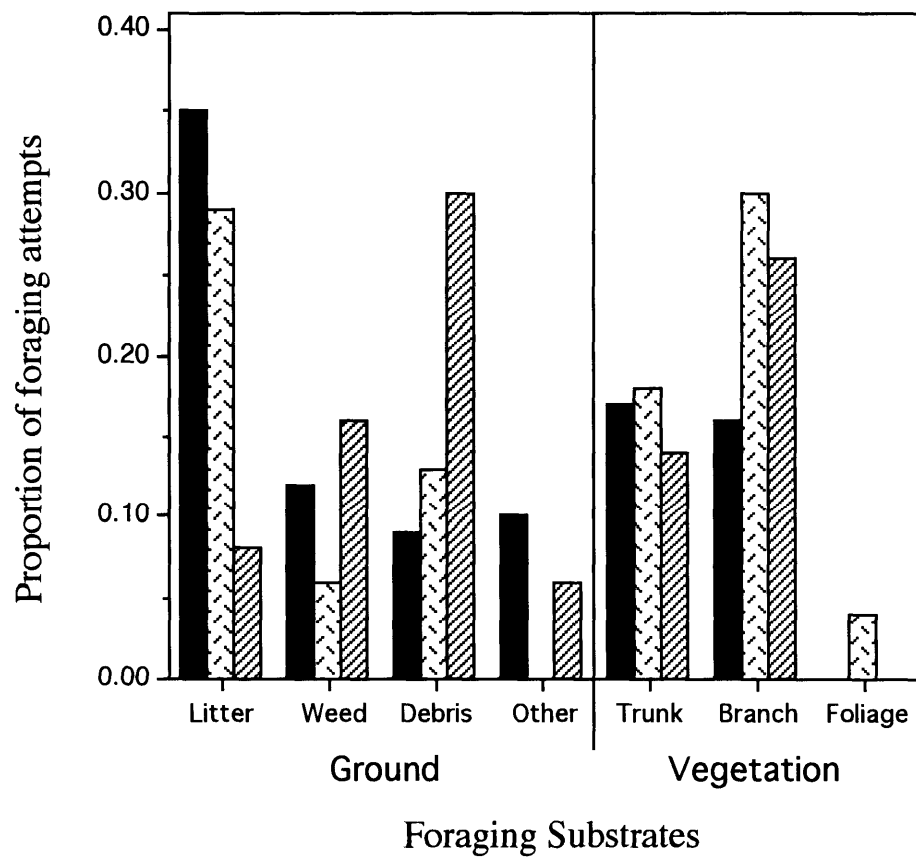
In Spring, White-browed Babblers foraged on a much wider range of substrates and the use of different substrates varied between vegetation types (Fig. 6.1b) ($\chi^2_{(10)} = 62.3$ $p = 0.0001$). In *Allocasuarina* and Mixed shrublands litter was still an important substrate, but in *Callitris* woodland ground debris became the most important ground substrate. The use of substrates in the vegetation increased in all vegetation types, but they were used less frequently in *Allocasuarina* shrubland.

Figure 6.1: The use of foraging substrates by White-browed Babblers in three vegetation types in a) Summer and b) Spring. *Allocasuarina* shrubland n = 114, 172; Mixed shrubland n = 266, 233; and *Callitris* woodland n = 55, 50.

a) Summer



b) Spring



Use of plant species

White-browed Babblers foraged on different plant species in Summer compared to Spring (Fig. 6.2) ($\chi^2_{(5)} = 63.1$ $p = 0.0001$). *Eucalyptus* spp. (mainly *E. leptopoda*) were frequently used during Summer, but were almost never used in Spring. *Acacia* spp. (mainly *A. neurophylla*) were rarely used in Summer, but they became the most frequently used plant genus in Spring. *Allocasuarina* spp. (*A. acutivalvis*, *A. campestris* and *A. corniculata*) were important substrates in both seasons.

The effect of grazing

In Summer, White-browed Babblers foraged predominantly in the litter in ungrazed shrubland, but used a wider diversity of substrates in grazed shrubland (Fig. 6.3a) ($\chi^2_{(4)} = 20.6$ $p = 0.0004$). The major change in grazed shrubland was the more frequent use of the vegetation (26% in grazed and 11% in ungrazed sites).

Although the litter was still an important foraging substrate in ungrazed shrubland during Spring, White-browed Babblers foraged more frequently in the vegetation (52% of foraging attempts) (Fig. 6.3b) ($\chi^2_{(6)} = 43.6$ $p = 0.0001$). In grazed sites babblers showed less of an increase in the use of the vegetation from Summer to Spring (Fig. 6.3). Instead the majority of their foraging was on the ground in the litter and weeds (51% of foraging attempts).

Nestling Diet

A total of 1401 food items were delivered to nestlings in 150 hours of observation at 14 nests (Table 6.1). Fifty five percent of these food items could not be identified; because they were too small, or the bird entered the nest from an obscured position. Of the 636 items that could be identified the majority were invertebrate larvae (70% in 1995, 56% in 1996). Lepidopteran larvae were the most common larvae that could be identified. Spiders, beetles and moths were also common prey items. They each represented more than 10% of food items and were recorded at the majority of nests, in at least one year.

Figure 6.2: Foraging use of different shrub genera in Summer (n = 67) and Spring (n = 161).

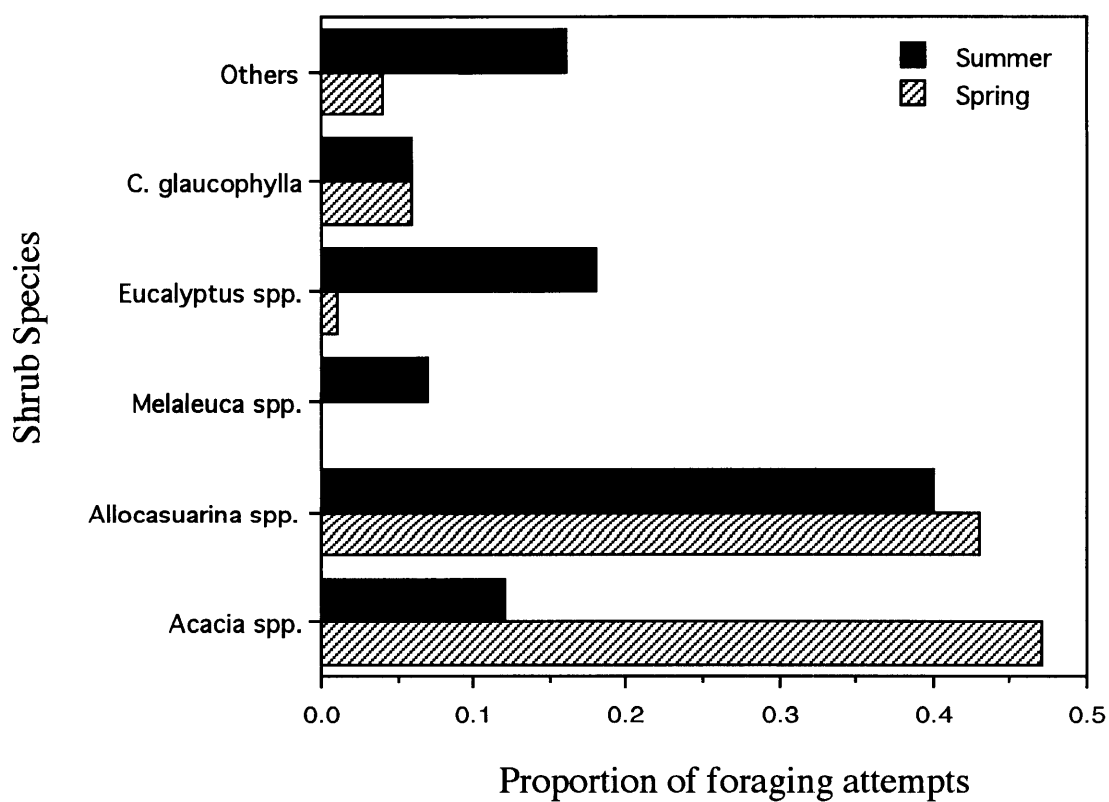
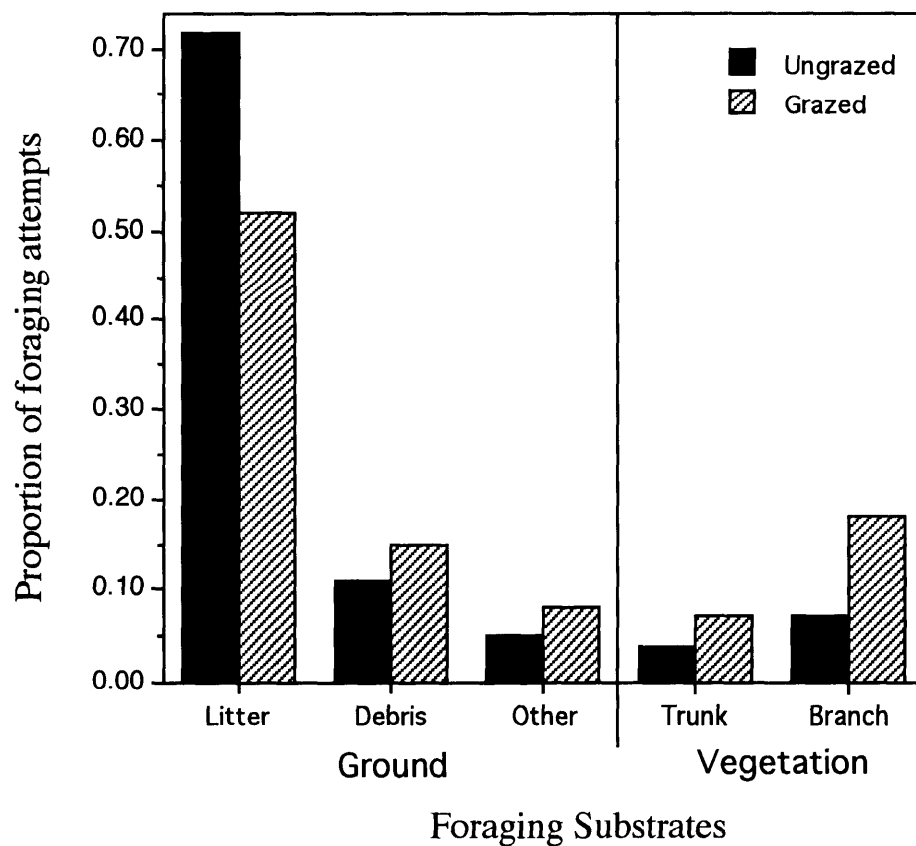


Figure 6.3: The use of foraging substrates in grazed and ungrazed shrublands in a) Summer and b) Spring. Grazed sites $n = 184, 176$ respectively; Ungrazed sites $n = 196, 229$ respectively.

a) Summer



b) Spring

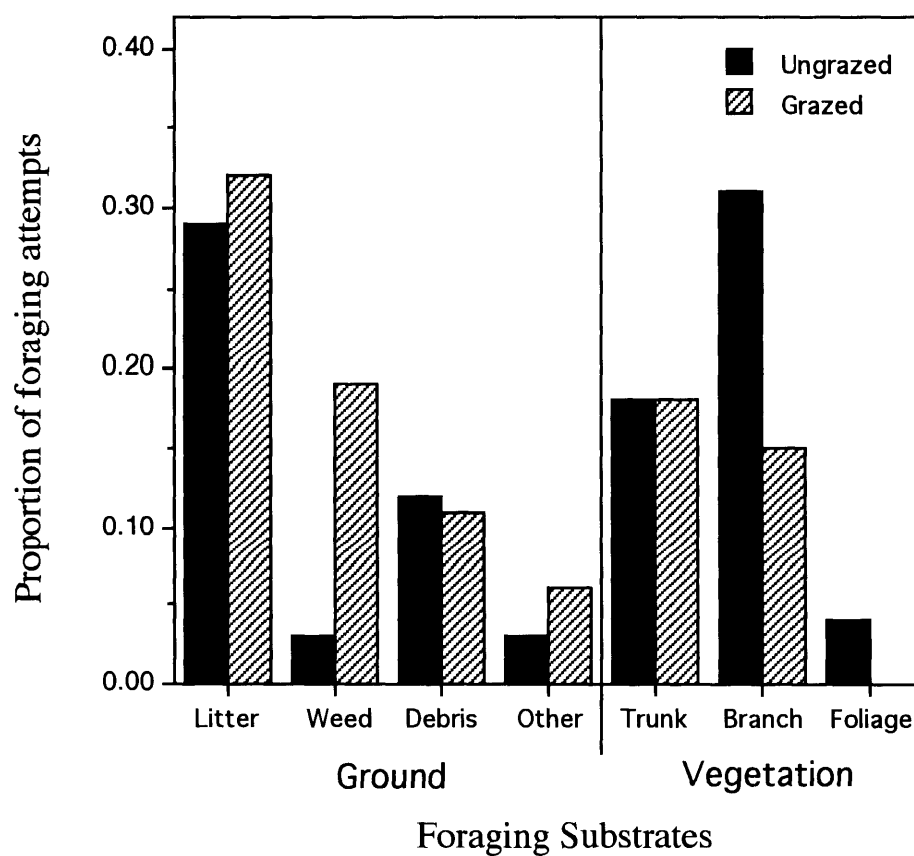


Table 6.1: Prey items delivered to nestling White-browed Babblers in 1995 (7 nests; 431 identifiable items) and 1996 (7 nests; 205 identifiable items).
* indicate taxa which represented less than 1% of total prey items.

Prey Items		1995		1996	
		# of nests	Percentage	# of nests	Percentage
Larvae	Lepidoptera	5	26	5	17
	Beetle	5	4	4	2
	Sawfly	-	-	1	2
	Unknown	7	41	6	36
Spiders		6	6	7	23
Beetles		5	12	1	2
Moths		5	5	6	12
Centipedes		3	2	2	2
Grasshoppers		1	*	-	-
Hymenoptera	Wasps	2	1	2	1
	Honey bees	1	1	-	-
	Formicidae	-	-	1	1
	Unknown	1	*	-	-
Cockroaches		1	*	-	-
Earwigs		-	-	1	1
Millipedes		-	-	1	1
Reptiles	Skinks/Geckoes	5	3	5	3

The most commonly observed spiders delivered to nestlings were from the families Lycosidae (Wolf Spiders) and Heteropodidae (Huntsman Spiders), which live on the ground and under bark (Main 1976). White-browed Babblers removed the legs of these spiders before feeding them to the nestlings. Moths fed to nestlings were mainly a single species, *Dasypodia selenophora*, which is the largest, common moth in the area (approximately 30-50 mm body length). I frequently found these moths during the day resting on branches in the canopy of shrubs. White-browed Babblers removed the wings of these moths before feeding them to nestlings.

Invertebrate Abundance

Litter invertebrates

The distribution of invertebrates in needle and broad leaved litter during Summer and Spring fitted a negative binomial distribution, suggesting they have a clumped distribution (Table 6.2). There were no significant differences in the mean number of invertebrates in needle and broad leaved litter, or between seasons. However, for both litter types the mean number of invertebrates was higher in Spring.

Table 6.2: The abundance of invertebrates in needle and broad leaved litter in Summer and Spring. n = number of samples. μ is the mean number of invertebrates per m^2 . The Chi-square analysis tested the fit between the data and a negative binomial distribution (***) indicates $p < 0.001$. \bar{y} is the estimated mean number of invertebrates per m^2 , based on the log transformed data. The 95% confidence limits are of \bar{y} . The difference in the estimates of \bar{y} are significant when there is no overlap between their confidence intervals.

Season	Litter Type	Negative Binomial Distribution				\bar{y}	Confidence Intervals	
		n	μ	k	Chi-square		-95%	+95%
Summer	Needle	77	13.3	0.131	7.05 ***	0.330	0.156	0.531
	Broad	60	9.3	0.213	2.02 ***	0.294	0.132	0.481
Spring	Needle	82	16.2	0.755	2.53 ***	0.641	0.431	0.872
	Broad	49	36.3	0.173	2.88 ***	0.793	0.373	1.342

A needle leaved litter sample collected in Spring was more likely to contain an invertebrate than one collected in Summer (Table 6.3). The same trend was found for broad leaved litter, but the difference was not significant. There were no significant differences in the probabilities of collecting an invertebrate between litter types.

Table 6.3: Differences in the probability of a needle or broad leaved litter sample containing an invertebrate in Summer and Spring. ^a represents significantly different probabilities (Chi-square test $p < 0.01$).

	Summer	Spring
Needle leaved Litter	0.23 ^a	0.48 ^a
Broad leaved Litter	0.25	0.38

Table 6.4: The relative proportions of invertebrate taxa collected in litter samples, during Summer and Spring. Only those taxa representing $\geq 1\%$ are shown. Needle and broad leaved litter samples were combined.

Taxon		Percentage	
Class	Order	Summer	Spring
Arachnida	Acarina	-	2
	Araneae	18	21
Diplopoda		1	-
Chilopoda		-	5
Collembola		-	2
Insecta	Thysanura	7	3
	Blattodea	-	1
	Embioptera	-	2
	Psocoptera	-	1
	Hemiptera	-	2
	Coleoptera	35	4
			26
	Diptera	1	11
	Lepidoptera	-	5
	Hymenoptera	36	14
			1

Formicidae, Carabid beetles and Araneae constituted 87% of the invertebrates found in all litter samples during Summer (Table 6.4). In Spring, there was a much higher diversity of invertebrate groups represented in litter samples. Coleopteran larvae, Araneae, Formicidae and Diptera were the most abundant groups, and represented 72% of the invertebrates collected.

Log invertebrates

There was an increase in the abundance of invertebrates in logs, from Summer ($43.1 \pm 8.7/\text{m}^3$) to Spring ($80.7 \pm 9.8/\text{m}^3$) ($T_{(19)} = 24$ $p < 0.01$). This was due to increased numbers of Araneae ($0.7/\text{m}^3$ to $4.3/\text{m}^3$) and Formicidae ($4.6/\text{m}^3$ to $17.5/\text{m}^3$), and a higher diversity of taxa in Spring.

Isoptera represented 80% of all invertebrates found in logs during Summer, and 57% during Spring (Table 6.5). These values were an unreliable estimate of the relative

abundance of this group, because Isoptera were generally too numerous to count and so their numbers were estimated to the nearest 50 individuals.

Table 6.5: The relative proportions of invertebrate taxa collected from logs, during Summer and Spring. There were very large numbers of Isoptera in log samples, so other taxa have been included if they represented at least 0.1% of the invertebrates collected. * indicate taxa which represent <0.1%.

Taxon		Percentage	
Class	Order	Summer	Spring
Arachnida	Scorpionida	-	0.2
	Pseudoscorpionida	0.1	0.1
	Acarina	0.1	0.5
	Araneae	2.1	5.7
Crustacea	Isopoda	-	1.7
Diplopoda		0.1	0.2
Chilopoda		*	1.9
Collembola		-	1.0
Insecta	Thysanura	3.1	2.7
	Blattodea	0.1	0.5
	Isoptera	80.1	56.8
	Hemiptera	0.2	0.7
	Coleoptera	0.6	1.0
			0.6
	Diptera	-	1.3
	Lepidoptera	-	1.1
	Hymenoptera Formicidae	13.3	23.2

Weed invertebrates

The weed invertebrate fauna was dominated by Diptera (38% of individuals), Hemiptera (18%), Collembola (15%), Coleoptera (9%) and Psocoptera (7%). The majority of invertebrates collected in weed samples were mobile flying insects, suggesting that mainly those taxa that had alighted on the weeds were collected.

Canopy invertebrates

The number of invertebrates collected from shrub canopies was higher in Spring than Summer (Table 6.6). The abundance of invertebrates in shrubs of different genera did not vary greatly in either season. In Summer, *Eucalyptus* spp. and *Melaleuca* spp. had the highest abundance of invertebrates, while in Spring *Eucalyptus* spp. had the lowest abundance. *Callitris glaucophylla* had much higher numbers of invertebrates per shrub than other genera in Spring, but this was based on a small sample size.

Table 6.6: The abundance of invertebrates (number of invertebrates/shrub) in the canopies of shrubs of different genera during Summer and Spring. n = the number of shrubs sampled.

Plant Species	Summer		Spring	
	n	#/shrub	n	#/shrub
<i>Acacia</i> spp.	13	2.3	13	10.4
<i>Allocasuarina</i> spp.	76	2.7	63	11.1
<i>Callitris glaucophylla</i>	5	3.4	3	19.7
<i>Eucalyptus</i> spp.	11	5.4	9	7.1
<i>Melaleuca</i> spp.	9	4.9	9	10.8

In Summer, Araneae (47% of invertebrates collected), Formicidae (24%) and Hemiptera (14%) were the most abundant invertebrate taxa. The relative numerical importance of these invertebrate taxa were similar between shrubs of different genera, with the exception of *Eucalyptus* spp., in which Formicidae dominated (45%) and Araneae were less abundant (10%).

In Spring, the observed increase in the abundance of invertebrates in the shrub canopy was due, in part, to the addition of Lepidopteran larvae (21% of invertebrates collected). Diptera also became a numerically important invertebrate taxon (17%), but this was mainly in *Melaleuca* spp.. Araneae were still a numerically dominant invertebrate taxon (25%) as were Formicidae (13%). The relative numerical importance of these invertebrate taxa were similar between shrubs of different genera, with the exception of *Eucalyptus* spp. (dominated by Formicidae, 36%) and *Melaleuca* spp. (dominated by Diptera, 34%).

The effects of grazing

The mean abundance of litter invertebrates in samples from grazed sites was higher than for samples from ungrazed sites in Summer and Spring, but these differences were not significant (Table 6.7). In ungrazed sites, there was a significant increase in the mean abundance of litter invertebrates between Summer and Spring. Although a similar trend was apparent for grazed sites it was not significant.

Table 6.7: The abundance of invertebrates in the leaf litter of grazed and ungrazed sites, in Summer and Spring. n = samples size. μ is the mean number of invertebrates per m^2 . The Chi-square analysis tested the fit between the data and a negative binomial distribution (***) indicates $p < 0.001$. \bar{y} is the estimated mean number of invertebrates per m^2 , based on the log transformed data. The 95% confidence limits are of \bar{y} . The difference in the estimates of \bar{y} are significant when there is no overlap between their confidence intervals.

Season	Litter Type	Negative Binomial Distribution				\bar{y}	Confidence Intervals	
		n	μ	k	Chi-square		-95%	+95%
Summer	Ungrazed	62	7.5	0.116	3.68 ***	0.192	0.059	0.340
	Grazed	75	14.9	0.196	5.27 ***	0.425	0.228	0.654
Spring	Ungrazed	78	17.9	0.525	4.05 ***	0.642	0.425	0.893
	Grazed	74	24.0	0.284	8.06 ***	0.686	0.414	1.010

A litter sample taken from an ungrazed site in Spring was more likely to contain an invertebrate than one collected in Summer (Table 6.8). Although the same trend was apparent in grazed sites it was not significant. There were no significant differences in the probabilities of an invertebrate being collected in a litter sample from grazed and ungrazed sites in either season.

In Summer, Formicidae (38% of individuals), adult Coleoptera (29%) and Araneae (23%) were numerically the most important invertebrate taxa in the litter of grazed sites. The same invertebrate taxa were important in the litter of ungrazed sites, but adult Coleoptera represented 52% of individuals found. In Spring, Coleopteran larvae were common in the litter of grazed sites, but were not as common in ungrazed sites (33% of individuals in grazed compared to 18% in ungrazed sites). Other important invertebrate

taxa in Spring for grazed and ungrazed sites were Araneae (23%, 20% respectively) and Formicidae (12%, 16% respectively).

Table 6.8: Differences in the probability of a litter sample, from grazed or ungrazed sites, containing an invertebrate in Summer and Spring. ^a represents significantly different probabilities (Chi-square test $p < 0.01$).

	Summer	Spring
Ungrazed Sites	0.18 ^a	0.46 ^a
Grazed Sites	0.29	0.42

The abundance of log invertebrates did not differ significantly between grazed and ungrazed sites in Summer or Spring (Table 6.9). The abundance of log invertebrates in grazed sites was significantly higher in Spring than Summer. Although the same trend was observed in ungrazed sites, it was not significant.

In Summer, Isoptera represented the majority of individuals found in logs of grazed (78%) and ungrazed (85%) sites. Formicidae constituted most of the remaining individuals found (16% in grazed and 9% in ungrazed sites).

Table 6.9: Differences in the mean # invertebrates/m³ of log, between grazed and ungrazed habitat, in Summer and Spring (Mean \pm S.E.). ^a represents significantly different probabilities (Wilcoxon paired-sample test $p < 0.01$).

	Summer	Spring
Ungrazed Sites	37.5 \pm 11.6	67.2 \pm 12.0
Grazed Sites	47.2 \pm 12.9 ^a	91.5 \pm 14.5 ^a

In Spring, Isoptera and Formicidae again constituted the majority of individuals found in logs of grazed (56% and 26% respectively) and ungrazed sites (59% and 19% respectively). Other common invertebrate taxa (Araneae, Chilopoda, Coleopteran and Lepidopteran larvae) made up similar proportions of the remaining invertebrates found in grazed and ungrazed sites (8% vs 11% respectively).

Discussion

The foraging behaviour of the White-browed Babbler could best be described as active searching for hidden prey. The majority of observed foraging attempts involved extracting prey from within substrates by probing. This foraging method also appears to be typical of White-browed Babblers in other parts of their range (Wooller & Calver 1981; Recher & Davis 1997; Brooker 1998).

Spatial and Temporal Changes in Substrate Use

In Summer, White-browed Babblers foraged mainly on the ground and there were only minor differences in substrate use between vegetation types. In *Callitris* woodland babblers showed the most distinctive differences in substrate use, mainly due to the lower than expected use of litter. This lower use of litter in *Callitris* woodlands corresponds to the very low litter volumes found for this vegetation type (see Chapter 5). *C. glaucophylla* produces poor litter, because the fine, needle-shaped leaves of this species become very brittle and break up once they have fallen from the tree. This appears to produce a litter which is a poor source of food for White-browed Babblers.

In Spring, adult White-browed Babblers forage not only for themselves, but also for nestlings and juveniles. Invertebrate larvae, especially those of Lepidoptera, are a major component of the diet of nestling babblers. This means that White-browed Babblers need to forage in substrates that will provide such prey. The frequency of use of some of the taxa of prey fed to nestlings (*i.e.* spiders, beetles and moths) differed between both years and nests. This suggests that there are spatial and temporal variations in the availability of these food resources, and/or there are differences in the abilities or tendencies of individual birds to forage on particular prey items. The first of these possibilities appears likely, given the foraging behaviour of babblers in different vegetation types at this time of the year. In Spring, there was a decrease in litter foraging and an increase in the amount of foraging in the vegetation in all vegetation types. However, the foraging patterns in the three vegetation types varied. In *Callitris* woodland the decline in foraging in the litter corresponded to an increase in the use of ground debris and to a lesser extent the branches of shrubs. Corresponding to this was a major increase in the abundance of log invertebrates, particularly Araneae, and the addition of taxa, such as Chilopoda, and the larvae of

Lepidoptera and Coleoptera. All four of these taxa were important components of nestling diets. In *Callitris* woodland it appears that White-browed Babblers are attracted to the abundant log substrate as well as the vegetation, due to the abundance of specific invertebrate taxa.

It is less clear why the pattern of foraging observed in *Allocasuarina* shrubland differed from that in Mixed shrubland. The vegetation in both shrublands showed increases in the abundance of invertebrates from Summer to Spring, yet in *Allocasuarina* shrubland there was only a small increase in the use of vegetation substrates, and litter remained the most important foraging substrate. One possible reason for these differences in foraging may be differences in the structure of the plant species within these shrublands. Holmes and Schultz (1988) proposed that the availability of prey was not simply a factor of their abundance, but was also influenced by vegetation structure and its effect on the detectability of prey. *Allocasuarina* shrubland is dominated by shrubs with smooth-barked branches and open canopies. When foraging in the vegetation, babblers tend to concentrate on probing into the bark of branches and trunks. Therefore, it is possible that the invertebrates living on *Allocasuarina* spp. are less detectable or available than those on other shrub species. This is supported by the disproportionately high level of foraging during Spring on *Acacia* spp., which have rough-barked branches. This was despite little difference in the abundance of invertebrates in these shrubs compared to other shrub genera. Mixed shrubland is characterised by its high diversity of plant species (see Chapter 5), which generally results in a greater diversity of microhabitats for invertebrates (Abbott 1976; Andersen 1986, Abensperg-Traun *et al.* 1996a). Therefore, it is possible that the canopy of Mixed shrublands contains a greater range of microhabitats from which White-browed Babblers can obtain food.

Another possible reason for differences in foraging behaviour between *Allocasuarina* and Mixed shrublands may be the abundance of litter invertebrates. There was no significant increase in the abundance of litter invertebrates from Summer to Spring in either vegetation type. However, this is probably an artifact of the sampling design, caused by the spatial distribution of invertebrates in this substrate. Invertebrates in the litter were found to have a strongly clumped distribution, and therefore many samples had no invertebrates. This results in a high variability in the abundance of invertebrates between

samples, and reduces the power of any statistical analysis. There was an increase in the likelihood of litter invertebrates being collected in Spring samples compared to Summer samples. Given the clumped distribution of invertebrates in this substrate, this is likely to be the result of an increase in the number of patches of invertebrates in an area, and/or an increase in the area covered by each patch of invertebrates. Whichever is the case, it is likely that the abundance of invertebrates increases from Summer to Spring, because the mean abundance of invertebrates per sample is equivalent between seasons. This relationship was found to be stronger in needle leaved litter than broad leaved litter. Since *Allocasuarina* shrubland is predominantly needle litter; whereas, Mixed shrubland is a mixture of litter types, *Allocasuarina* shrubland may have a greater availability of invertebrates during Spring.

The observed patchiness of invertebrates within the litter substrate creates a problem for assessing the habitat quality of babbler home ranges with respect to food resource, because substrates were the smallest patch scale measured. It appears that these substrates contain internal patchiness with respect to invertebrates which babblers are responding to. Therefore, the scale of invertebrate sampling in this study was too coarse to represent the true distribution of invertebrates (Kotliar & Wiens 1990). Despite this limitation in the invertebrate sampling, the observed spatial and temporal changes in the use of substrates by White-browed Babblers indicate that this species is able to respond to differences in food dispersion and availability by using different substrates. This suggests that White-browed Babblers should be able to alter their foraging behaviour in response to changes in the structure of their habitat, due to disturbances such as grazing by domestic stock.

The Effects of Grazing

Sheep grazing was found to reduce the cover and foliage density of the vegetation and the density of standing stems in the shrublands used by White-browed Babblers (Chapter 5). The level of grazing in these remnants had little effect on the ground layer, besides increasing the level of weed invasion (Chapter 5). The effect of these structural changes on the foraging behaviour of the White-browed Babbler differed between the seasons.

During Summer, White-browed Babblers foraged more frequently in the litter in ungrazed sites, despite a lack of significant differences in the quantities of this substrate or

the abundance of invertebrates that it supported. In arid shrublands, Isoptera were found to be a major component of the diet of White-browed Babblers during Summer (Brooker 1998). Frequent observations of babblers foraging on termites in this study, suggest that they may also be an important food item in this area. This taxon was not included in the analysis of litter invertebrates, because the sampling technique poorly represented their abundance. However, they did occur in very high abundance in the litter at certain times of the day, when conditions were appropriate (*i.e.* low temperatures and high humidity). Work in the Kellerberrin area has shown that the abundance of Isoptera declined in grazed sites (Abensperg-Traun *et al.* 1996b). Therefore, it is possible that the observed differences in foraging on the litter in grazed and ungrazed sites is a consequence of differences in the abundance of this taxon. This was supported by the higher use of ground substrates other than litter in grazed shrubland. Most of this foraging was on logs and termite mounds. The most abundant taxon found in log samples were Isoptera and they did not differ in abundance between grazed and ungrazed sites. This suggests that in grazed shrubland these substrates may provide a more reliable source of this important Summer food than the litter did.

In Spring, White-browed Babblers tended to forage on ground substrates in grazed shrubland and in the vegetation in ungrazed shrubland. The abundance of litter invertebrates did not differ between grazed and ungrazed sites during Spring, but invertebrate taxa which were frequently fed to nestlings (*i.e.* Coleopteran larvae and Araneae) were more common in grazed sites. In addition, grazed sites had a significantly higher abundance of log invertebrates and the cover of weeds, a major foraging substrate for babblers, was higher (see Chapter 5). Abensperg-Traun *et al.* (1996b) also found an increase in the abundance of some invertebrate taxa in grazed sites, and they attributed this to higher nutrient levels. The greater abundance of invertebrates, especially those used to feed nestlings, and the greater quantity of some ground substrates (*i.e.* weeds), is the likely reason why babblers forage more on the ground in grazed sites, during Spring.

Summary

White-browed Babblers eat a wide range of invertebrate taxa (Brooker 1998 and see Table 6.1). They also used a wide variety of substrates when foraging, and demonstrated a high degree of plasticity in their use of foraging substrates when vegetation structure or invertebrate abundance changed. Therefore, the small differences in vegetation structure caused by grazing in the study sites would likely have little effect on the ability of White-browed Babblers to obtain food. This is supported by the fact that no nestling deaths resulted from starvation (see Chapter 8). However, higher levels of grazing by domestic stock than those observed in the study sites may influence the food resources of White-browed Babblers.

Because of their foraging plasticity, the home ranges of babbler groups in the study sites which differed in their level of grazing disturbance were considered to be of similar quality with respect to the availability of food. However, the invertebrate sampling done in this study was at a larger scale of patchiness than babblers were responding to. Therefore, this sampling may have failed to record differences in invertebrate availability, resulting from grazing or different vegetation structure, which had adverse effects on babblers.

Chapter 7

The social structure of the White-browed Babbler

“I concluded that each nest was tenanted by one pair of birds, but the social instinct of this species is strong. Birds from more than one nest would assist in the building of a neighbour's home, and if not burdened by nesting cares would even help in feeding the young.”

[Chandler 1920]

Introduction

Cooperative breeding is a breeding system in which some individuals help to raise young that are not their own. Though all cooperative breeders have this common trait they differ widely in other aspects of their breeding behaviour (Brown 1978; Smith 1990).

Groups vary in size from a few individuals, such as in the Splendid Fairy-wren *Malurus splendens* (Russell & Rowley 1993a), through to colonial species with several hundred individuals (e.g. Noisy Miner *Manorina melanocephala*, Dow & Whitmore 1990). In some species there is only one breeding pair per group (e.g. Florida Scrub-jay *Aphelocoma coerulescens coerulescens*, Woolfenden & Fitzpatrick 1984), while in other species females may copulate with more than one male (e.g. Arabian Babbler *Turdoides squamiceps*, Lundy *et al.* 1998). Some species have more than one breeding female in each group (Brown 1978). These females can lay their eggs in the same nest (Joint nesting *sensu* Brown 1978) which has been found in the Groove-billed Ani *Crotophaga sulcirostris* (Koford *et al.* 1990), or each female can lay in a different nest (Plural breeding *sensu* Brown 1978), such as in the colonial Bell Miner *Manorina melanophrys* (Clarke 1988).

In some cooperative breeding species the mating tactics can vary greatly within a population. For example, individuals of the Common Babbler *Turdoides caudatus* were

found to have three different mating tactics in an area near New Delhi in northern India (Gaston 1978). These mating tactics ranged from a single pair per group, to a single male breeding with several females, to more than one breeding pair in a group. The mating tactic used by a group was related to the group's size and the density of individuals in the group's home range (Gaston 1978). In the White-browed Scrubwren *Sericornis frontalis* the mating tactics used varied depending on the relatedness of group members (Whittingham *et al.* 1997). When subordinate males were related to the breeding female they did not sire any young. If they were unrelated to the breeding female they attempted to sire young, but their probability of siring young was higher if they were also unrelated to the dominant male (Whittingham *et al.* 1997).

Chandler (1920) was probably the first to describe cooperative breeding in the genus *Pomatostomus* with his observations on the White-browed Babbler. He described what appear to be multiple pairs from the same social group nesting separately, but the group cooperated in building nests and feeding nestlings. Since Chandler's paper cooperative breeding has been found in two other species of this genus, the Grey-crowned Babbler *P. temporalis* (King 1975; Counsilman 1977, 1979; Brown *et al.* 1978) and Hall's Babbler *P. halli* (Balda & Brown 1977). Plural breeding has been recorded in the White-browed Babbler (Chandler 1920) and the Grey-crowned Babbler (Counsilman 1979). North (1984) also reported evidence of joint nesting in these two species.

Differences in the social structure of cooperatively breeding birds affect many aspects of their breeding biology and dispersal. So, an understanding of the social structure of these species is important to determining their population dynamics. This chapter describes aspects of the breeding behaviour of the White-browed Babbler in the Kellerberrin area and proposes a model for the social structure of this species. Aspects of the breeding system will be related to the demography of this species in Chapter 8 and the model of social structure will be used to interpret their dispersal behaviour in Chapter 9.

Methods

Nest Watches

Fifteen nests from 11 groups were watched in 1995 and 1996. More than one nest was watched in four groups. Three groups were watched in 1995 and 1996, and two

consecutive nests of the same group were watched in 1995. All of these nests were watched during the nestling period. Watches were also made at eight nests during the incubation period, but two of these nests were not watched during the nestling period as they were predated before the eggs hatched.

Nest watches were made from a hide, which consisted of a wool bale (70 cm x 70 cm x 140 cm high) supported on four fibreglass poles. The hides were placed 10-20 m from the nest. At this distance the birds at the nest were not disturbed and an observer using binoculars was able to identify them clearly.

Three to ten watches (an average of 6.4 ± 0.6 watches/nest) were made on each nest during the nestling period. Each watch was 100 minutes long. A total of 160 hours of observation were made on nests during the nestling stage. The age of nestlings varied between nests, but an attempt was made to watch nests when nestlings were from 6-13 days old. At this stage feeding activity was at its highest. Nest watches were made in the early morning or the late afternoon, because activity at the nest declined during the middle of the day. Watches started when the first bird returned to the nest after the observer had entered the hide. During each one minute period of a watch the observer recorded all activities in the nest shrub. For each visit to the nest the identity of the bird and its behaviour were recorded. If the bird fed the nestlings, the type of prey item was identified where possible. The size of prey items was allocated to one of three size classes based on a comparison with the length of the bird's bill. Small prey were smaller than the bird's bill, medium sized prey were approximately the same size, while large prey were larger than the bird's bill.

Other behaviours, such as interactions among group members, interactions with other species and activities related to the maintenance of the nest, were also recorded. Nest maintenance activities included the removal of nestling faecal sacs and behaviours collectively described as the maintenance of nest structure (*e.g.* bringing new nest lining material, replacing lining material that had fallen from the nest, or general maintenance of the outside of the nest).

At some nests unbanded adults were present. These could be uniquely identified if only one occurred in a group and it was assumed group composition remained constant during the period of observation. Where more than one unbanded bird occurred in a group

their activities were combined into an 'unbanded' category. There were also occasions when birds could not be identified, because their colour bands were obscured or their arrival was missed. These observations were combined into an 'unknown' category.

Group Composition

I considered a group to be present in a given year if it occupied the area throughout the breeding season. The members of a group for a given year were defined as those individuals that remained in the group throughout most of the breeding season. This sometimes included birds that were never seen during nest watches.

The analysis of age, sex, and the origin of helpers was based on 9 of the 11 groups for which nest watches were made. Two newly established groups were excluded from this analysis, because no information was available about the members' ages or their origin. For those groups where nests were watched in both 1995 and 1996 the data from the 1996 nest were used, because it contained the most complete information. For the one group where two nests were watched in the same year the data from the first nest were used.

Some groups contained several females with brood patches, but only one female developed a complete brood patch. Nest watches showed that this female was the only bird to incubate the eggs, or brood nestlings. This enabled identification of breeding females in groups where nest watches were not made.

It was not possible to determine the breeding male in groups. Therefore, it was assumed that the male which contributed most to breeding activities was the breeding male and he is called the *Dominant Male*. This limited the identification of probable breeding males to those groups where nest watches were made. In these groups the dominant male was defined as the male which contributed most to the feeding of the nestlings (*i.e.* highest feeding effort). In some groups there were several males that had similar high levels of feeding effort. The dominant male was chosen from these males using other behaviours, such as escorting the breeding female to and from the nest and a greater association with the breeding female when she was away from the nest.

Analysis

The relative contribution made by each group member to the feeding of nestlings was measured using a modified version of the index of feeding effort presented by Piper (1994).

$$\text{FEEDING EFFORT} = (F_A \cdot n) / F_T$$

where F_A is the number of feeds delivered by bird A, n is the number of individuals in the group and F_T is the total number of feeds delivered by all group members. The higher the value of this index the greater the individual's contribution to feeding the nestlings. When the bird contributed feeds in equal proportion to the number of birds in the group this index equals one (*i.e.* it contributed 'its share' of the feeds).

This index of feeding effort was modified to account for differences in the biomass of prey items. This was done by weighting prey items based on their size; with small prey equal to 1, medium prey equal to 3 and large prey equal to 9. This coarse weighting system reflects the cubic relationship between prey length and biomass.

These biomass weightings were also used to compare the quality of prey delivered to nestlings by group members. This index of biomass was calculated as;

$$\text{BIOMASS INDEX} = \sum (P_i \cdot B_i)$$

where P_i is the proportion of prey items of size i delivered and B_i is the biomass weighting for prey size i . This index ranges from 1 to 9, with a value of one indicating that all prey items delivered by that bird were small and a value of nine indicating that all prey items delivered were large. Differences in the quality of prey items (Biomass index) were compared between the breeding female, the dominant male and the average value for helpers in each group. This was done using Friedman's test (χ^2_r), which is a nonparametric analysis of variance with a block (*i.e.* groups) design (Zar 1996).

To investigate the effect of the number of helpers on the feeding behaviour of the breeding female and the dominant male the proportion of the total feeding rate attributable to these birds was used. This was calculated using the feeding effort formula, but with $n = 3$. In effect this combines the contribution of all helpers in the group and makes the effort of the breeding female and the dominant male independent of group size. Linear regression

was used to compare this standardised feeding effort for breeding females and dominant males with the number of helpers in their groups.

The members of each group were ranked based on their feeding effort, with the highest receiving a rank of 1. The average rank of male and female helpers was calculated in this way for nine groups where helpers of both sexes were present. Differences in the average rank of male and female helpers in these groups was tested using the Wilcoxon paired-sample test (T).

All but one of the observed nesting attempts, including those for the same group in the same year or in consecutive years, were included in the analysis of feeding effort. This was because the composition of groups changed between the watched nesting attempts. So, the contribution made by the same bird at different nests was not expected to be the same. One nest was excluded from these analyses, because there were indications that the breeding male in this group had died before or during the incubation period.

Feeds by unknown birds were excluded from estimates of feeding effort. This was based on the assumption that failure to identify a bird was not related to its social position. For groups with multiple unbanded birds each unbanded bird was allocated an equal proportion of the feeds observed for all the unbanded birds in that group. This enabled an accurate estimate of the feeding effort of banded birds in the group, but not of the unbanded birds.

Results

Group Composition

In 1994, 1995 and 1996 the distribution of group sizes changed slightly, as shown by the decline in the median and modal group size (Table 7.1). However, there was no significant difference in average group size between the three years ($F_{(2,73)} = 1.61$ $p = 0.207$).

Groups consisting solely of a breeding pair were rare. In 1994 there were no pairs, in 1995 there were two (7% of all groups), and in 1996 there were four (14% of all groups). Only one pair persisted for more than one year.

Table 7.1: Changes in the size of groups in the Kellerberrin area. Mean is presented as mean \pm S.E.

	1994	1995	1996
Number of Groups	21	27	28
Mean Group Size	6.9 \pm 0.6	6.2 \pm 0.5	5.4 \pm 0.5
Range	3-13	2-12	2-13
Modal Group Size	6	4	4
Median Group Size	6	6	4.5

The sex ratio in the study area ranged from 1.2:1 males to females in 1994 (n = 109) and 1996 (n = 121) to 1.4:1 males to females in 1995 (n = 121). The proportion of individuals whose sex was unknown ranged from 24% to 28%. Therefore, it is possible that the real sex ratio may have been quite different. However, the sex ratio calculated for 1996 using only those groups in which all birds were of known sex was similar to that of the whole population (1.4:1 males to females, n = 78).

Breeding female

In 1995 the breeding female could be determined for 20 groups. Of these groups 13 (65%) had the same breeding female as in 1994, two (10%) had new breeding females and five (25%) were newly formed groups. The two new breeding females had joined their new group just before the start of the breeding season and both had been the breeding female in their previous group. It was not known what happened to the breeding females they replaced.

In 1996 the breeding female could be determined for 19 groups; seven (37%) of which had the same breeding female as in the previous two years, one (5%) had the same as in 1995, four (21%) had new breeding females, and seven groups (37%) were newly formed. Two of the new breeding females joined their new group in 1995 and had a partial brood patch during that breeding season. The other two new breeding females arrived in their new groups, from their natal group, just before the start of the 1996 breeding season. The two

groups these new breeding females joined had no other female members. In all four cases where a group had a new breeding female the 1995 breeding female had disappeared.

Of the 20 known breeding females in 1995 eighteen (90%) were 2+ years old and the other two (10%) were 1+ years old. Of the nineteen 1996 breeding females seven (37%) were 3+ years old, three (16%) were 2+ years old, two (11%) were two years old, and seven (37%) were 1+ years old.

Dominant male

For the seven nests watched in 1995, six of the dominant males were 2+ years old (caught as adults during 1994). The seventh dominant male was 1+ years old.

For the seven nests watched in 1996, five of the dominant males were recorded in their group as adults during 1994 and one joined his group in 1995. All of these males were 3+ years old. The seventh dominant male was in a new group and was first caught during 1996 (1+ years old). Therefore, there was no evidence that one year old males attained breeding status.

Nests from consecutive years (1995 and 1996), were watched in two groups and in both cases the first (*i.e.* dominant male) and second ranked males switched positions between the nests watched. All four males were 2+ years old in 1995. In one of these groups the breeding female had changed, but in the other the breeding female was the same.

For one group two consecutive nests were watched in 1995. At the first nest two males (both 2+ years old) were almost identical in behaviour, so it was not possible to determine which was the dominant male. At the second nest one of these males maintained his dominant position while the other showed a marked decline in effort, but was still the second ranked male in the group.

Helpers

A total of 62 helpers occurred in nine groups, 14 (23%) were one year old and 48 (77%) were 2+ years old (Table 7.2). Thirty five (56%) of the helpers were males, 18 (29%) were females and the sex was unknown for nine (15%) birds. If the sex ratio in these groups is the same as for the whole population, then the majority of the birds whose sex was unknown were females.

Table 7.2: The origin and age structure of male and female helpers in groups where nest watches were made during 1995 and 1996. The category unknown origin includes all birds which were adults when they were first caught in the group during 1994.

	Born in Group	Unknown Origin	Born outside Group
1 year old			
Male	6	-	1
Female	4	-	0
Unknown Sex	3	-	0
2+ years old			
Males	4	18	6
Females	0	3	11
Unknown Sex	0	4	2

At least 50% of the 14 one year old helpers were males (Table 7.2). Thirteen one year old helpers were helping in their natal group. A male, one year old helper joined a new group in November after his natal group had broken up. He helped at a late nest (December) in this new group.

Only four adult helpers were known to have been born in the group they helped in and all were males (Table 7.2). At least 40% of adult helpers were born in another group. This number is probably underestimated, because some of the birds first caught in 1994 (*i.e.* their origin was unknown) could have come from other groups. The majority of adult helpers were males ($\geq 58\%$), but the majority of adult helpers which were known to have come from other groups were females ($\geq 58\%$).

Nest Construction and Maintenance

Three nests were watched while being built (approximately one hour for each nest). In each case the breeding female was the major contributor to nest construction. The degree of help by the dominant male varied at the three nests. At one the dominant male shared the work of nest construction with the breeding female. At another nest he contributed some assistance, while in the third case the breeding female built the nest alone. Helpers did not contribute to the construction of the breeding nest. However, in one case a helper did

deliver material to the breeding female and the dominant male, which they then incorporated into the nest. The identity of this helper was not known. In the nest constructed solely by the breeding female the other three members of the group (all males) followed her on trips in search of nest material, but did not assist her.

The breeding female and the dominant male contributed equally to the task of removing nestling faecal sacs from the nest (Table 7.3). They contributed considerably more to this activity than did helpers. Among helpers, males contributed approximately twice the effort per bird compared to female helpers and did so in more nests.

Table 7.3: The contribution of group members to nest maintenance in 14 nests. The number of nests indicates the number where that category of group members were observed contributing. The calculation of the number of observations/bird for each activity was based on the number of birds in that category for the total number of nests where the activity was observed (indicated in parentheses).

Activity	Breeding Female	Dominant Male	Helpers	
			Male	Female
Removal of Faecal Sacs				
Number of Nests (14)	11	13	7	3
Number of Observations/Bird	2.6	2.7	0.6	0.3
Nest Structure Maintenance				
Number of Nests (10)	5	5	7	1
Number of Observations/Bird	1.2	0.7	0.3	0.1

The breeding female contributed more to the maintenance of nest structure than the dominant male (Table 7.3). When considered on a per bird basis the dominant male contributed approximately twice that of male helpers. In turn, male helpers contributed more than female helpers. The helpers that contributed to both nestling faecal sac removal and the maintenance of nest structure tended to be the highest ranked helpers in the group.

The incubating female was regularly observed being fed by group members, but mostly when she was off the nest. Since this activity was not quantified when the female

was off the nest, analysis of the contributions made by group members was not possible. At seven of the eight nests watched during the incubation stage the incubating female was fed by one or more members of her group. At four of these nests the dominant male was observed feeding the female. The majority of helpers that fed the incubating female were males (5 of 6 birds).

Feeding Effort

There were significant differences in the average feeding rate of the dominant male (1.1 ± 0.1 feeds/chick/hour), the breeding female (0.8 ± 0.1 feeds/chick/hour) and the rate per helper (0.5 ± 0.1 feeds/chick/hour) in each group ($\chi^2_{(3,14)} = 23.891$ $p = 0.001$). The quality (based on size) of the prey fed to nestlings by the dominant male and the breeding female (biomass index of 3.6 ± 0.4 and 3.5 ± 0.2 , respectively) did not differ significantly, but were significantly higher than that delivered by helpers (biomass index 2.6 ± 0.3) ($\chi^2_{(3,14)} = 9.00$ $p = 0.011$). Helpers rarely fed nestlings large prey items and 55% of the prey items they delivered were small (Fig. 7.1).

The feeding effort (standardised) of dominant males declined as the number of helpers in the group increased ($F_{(1,12)} = 10.442$ $p = 0.007$; Adjusted $R^2 = 0.42$) (Fig. 7.2). A similar relationship was found for breeding females ($F_{(1,12)} = 16.198$ $p = 0.002$; Adjusted $R^2 = 0.54$). Although the decline in the feeding effort of dominant males was greater (slope of regression was -0.097 ± 0.03) than that for breeding females (slope of regression was -0.058 ± 0.01) the difference was not significant ($t_{(24)} = 0.024$ $p > 0.5$).

Within the same group, male helpers (average rank 4.6 ± 0.5) generally had greater feeding efforts than female helpers (average rank 7.0 ± 0.5) ($T_{(9)} = 0$ $p = 0.012$). The majority of helpers that had a feeding effort ≥ 1.0 were males (89%), while the reverse was true for those with feeding efforts < 0.1 (29% males) ($\chi^2_{(2)} = 13.12$ $p = 0.008$) (Fig 7.3).

Three of the five males with low feeding efforts (< 0.1) were known to be the sons of the current breeding female. Four of the males with low feeding efforts disappeared from their group during or just after the breeding season, while the fate of the fifth male was unknown.

Figure 7.1: The size of prey items fed to nestlings by breeding females (n = 270), dominant males (n = 383), and helpers (n = 699).

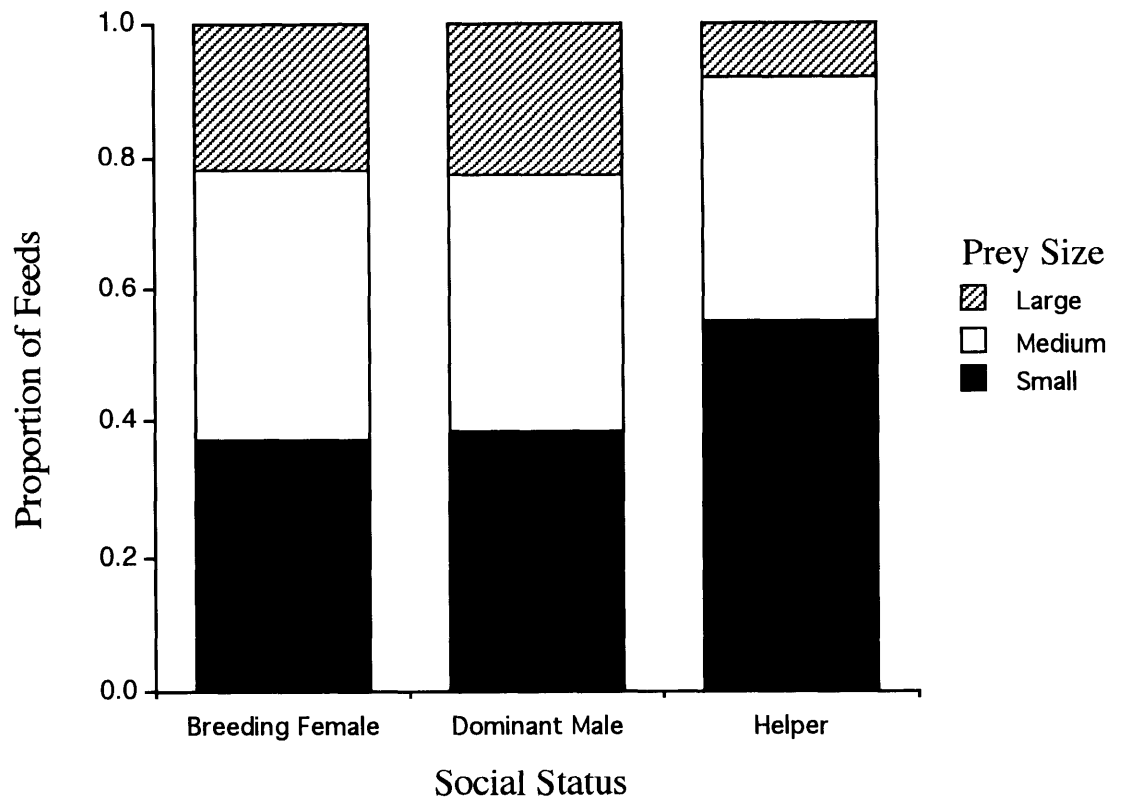


Figure 7.2: Relationship between the the number of helpers in a group and the feeding effort of a) the dominant male and b) the breeding female. The solid line represents the line of best fit.

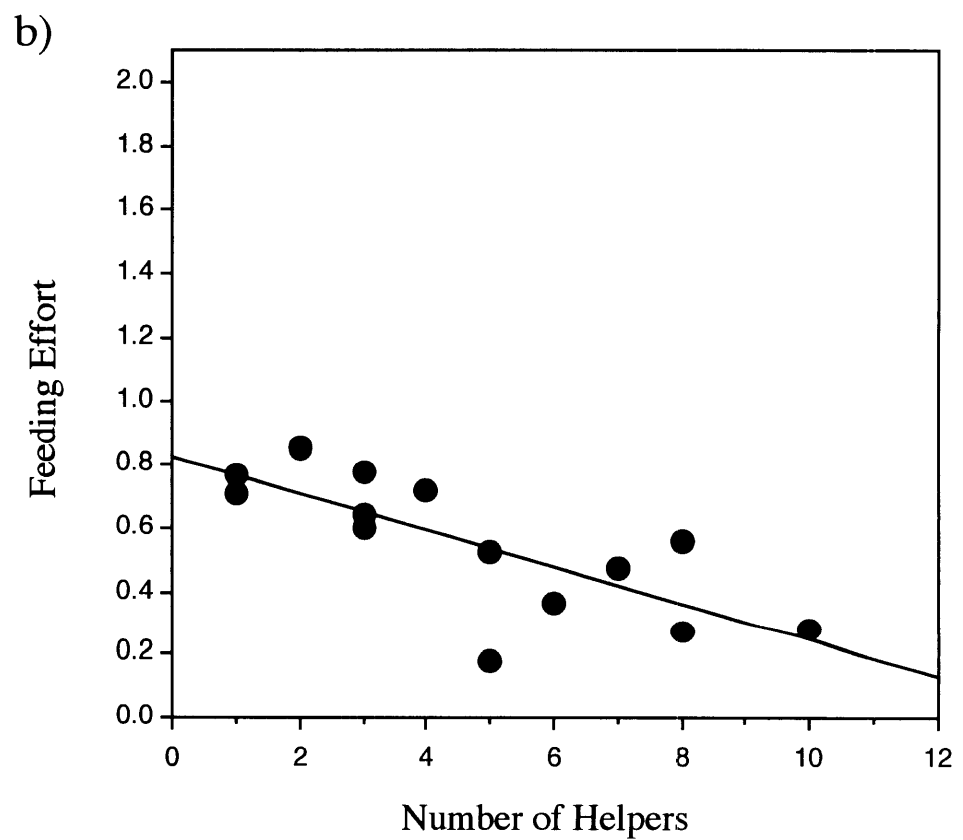
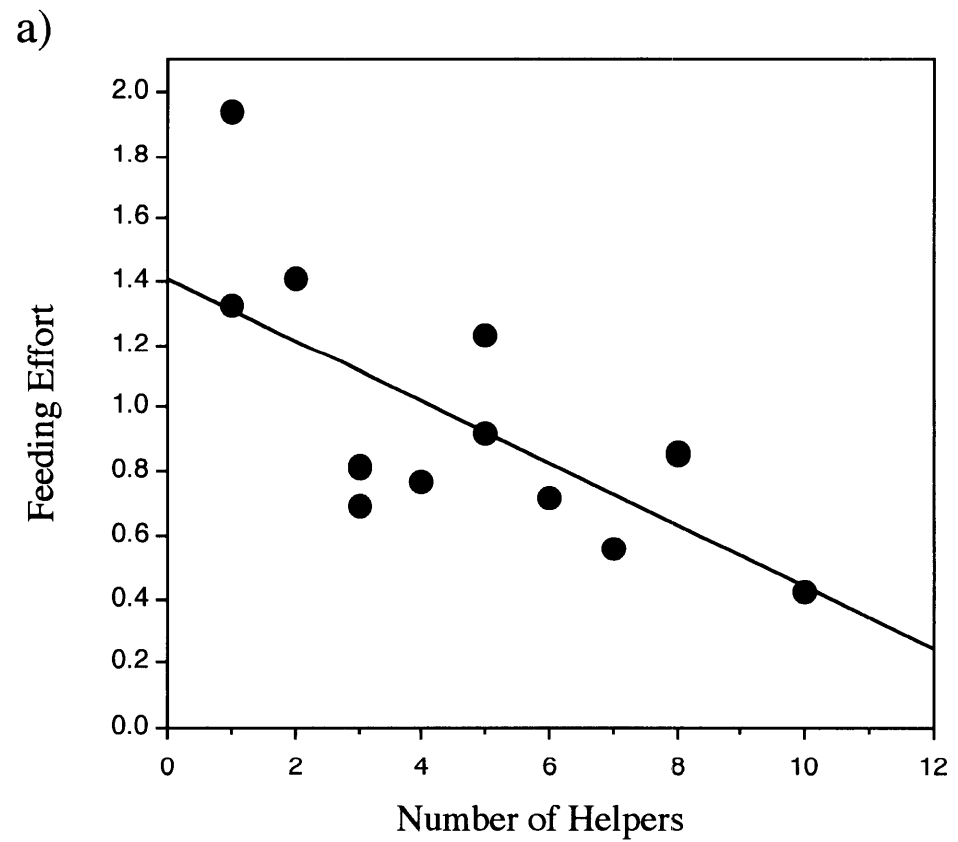
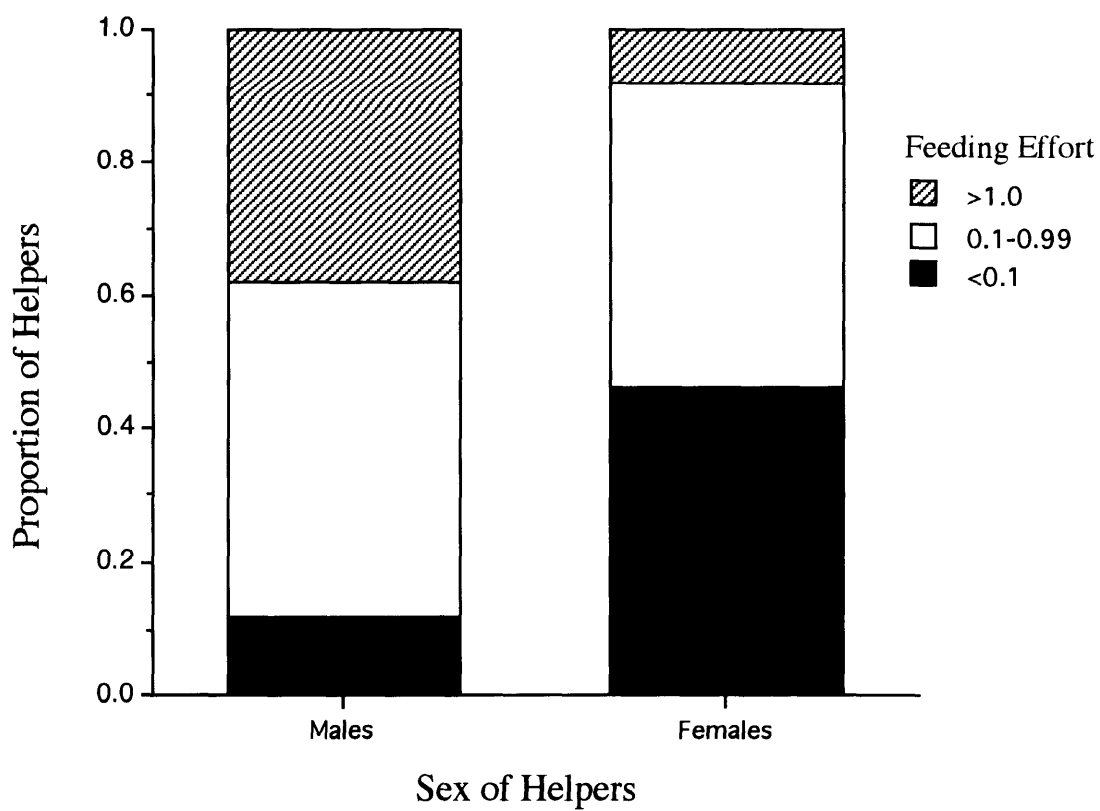


Figure 7.3: The relative proportions of male and female helpers that gave different levels of help when feeding nestlings.



Aggressive Interactions between Group Members

Eight sets of aggressive interactions near the nest were observed in four groups. Five of these interactions involved aggression by the breeding female toward a female helper. The other three interactions were by a dominant male toward a female helper, by a high ranking male toward a female helper, and between two high ranking males.

In three groups the breeding female was observed chasing a female helper who attempted to approach the active nest. In one of these groups the breeding female was seen chasing two different female helpers. On most occasions the female helpers involved in these interactions were carrying food when they approached the nest. These aggressive acts denied the female helpers access to the active nest, so they did not help in feeding the nestlings or the level of their help was reduced. In three of the four cases the females subjected to this aggression had a partial brood patch. The exception was a one year old female who was denied access to the nest of her mother when the nestlings were young, but was later allowed to feed them.

All four female helpers who were denied access to the active nest became breeding females in the next breeding season. In two of these cases the helper replaced the breeding female who had been aggressive toward them in the previous year. Both of these previous breeding females disappeared during the non-breeding period. One of the other female helpers formed a new group by group budding (see Chapter 9) and the fourth (the one year old bird) dispersed to another group.

The other aggressive interaction between a breeding female and a female helper occurred in a group of four birds in 1995. In this group the female helper was a major contributor to feeding the nestlings. The only known male in the group contributed little to feeding the nestlings and an unbanded bird was never seen at the nest. There was evidence that the dominant male in this group may have died when the nest was at the incubation stage. The interaction occurred one evening when the breeding female entered the nest, apparently to brood the nestlings for the night. The female helper attempted to join her in the nest. The breeding female responded by forcing the female helper from the nest. This resulted in a vigorous physical fight between the two birds which lasted for 13 minutes. On several occasions the two birds separated and the breeding female attempted to return to the nest, but she was prevented from doing so by the female helper. The fight ended when

the breeding female successfully returned to the nest and the female helper did not follow her. There was no obvious effect of this interaction on the feeding activity at the nest in subsequent days. The female helper continued to feed the nestlings at the same rate. She remained with the group in 1996 and helped the same breeding female. There was no evidence that the female helper had laid eggs in this nest as it had contained only two eggs.

The two interactions seen between males and female helpers were in the same group. One involved the same one year old female helper who was denied access to the nest by the breeding female. In this case the dominant male was seen chasing this female helper when the nestlings were young, but later allowed her to feed the nestlings. The other interaction was between a one year old male, who was a major contributor to feeding the nestlings (second ranked male), and a one year old female, who was probably his sister. This interaction was only seen once and this female later assisted in feeding the nestlings.

The only interactions seen between males occurred between two males who were both behaving as if they were the dominant male. They contributed equally to feeding the nestlings and both were seen escorting the breeding female to and from the nest. The interactions between these two males involved one chasing the other when they approached the active nest. Both initiated these aggressions and the outcome of these chases was always unclear. At a second nest in the same year one of these males showed clear dominant male behaviour. The other male became the second ranked male in the group.

Discussion

In the Kellerberrin area the White-browed Babbler generally lives in groups. These consist of a breeding pair and from one to 11 helpers, though most groups have two to four helpers. Breeding pairs with no helpers occurred in 1995 and 1996, but only one of these pairs persisted for more than one year. The rest were either groups declining after the loss of their breeding female, or pairs attempting to establish new groups by group budding (see Chapter 9).

The sex ratio in the study area was slightly male-biased, which is often found in cooperative breeding birds (Reyer 1980; Clarke & Heathcote 1990; Rowley & Russell 1990; Noske 1991). The majority of White-browed Babbler helpers that dispersed to join

new groups were females. Therefore, it is possible that this male-bias was a consequence of higher mortality in females as a result of this dispersal (Clarke & Heathcote 1990; Noske 1991).

Since it is not possible to age babblers beyond six months old and this study covers only three years, it was difficult to determine at what age birds obtain breeding positions. However, the available evidence suggests that females may obtain opportunities to breed at 2 years, while for males it appeared to be later. This tendency for females to breed earlier than males was also found in the Splendid Fairy-wren, where females had a median age at first breeding of 1 year compared to 2 years for males (Russell & Rowley 1993b). Counsilman (1977) found a tendency for an earlier age of first breeding in female Grey-crowned Babblers. He found only 16% of breeding males were less than 3-4 years old, but the proportion was slightly higher (22%) for breeding females.

Competition for Breeding Positions

Evidence of competition for breeding positions was found for both sexes. However, the breeding status of males appears to be less permanent than that of females. No breeding female was replaced unless she disappeared from the study area, which suggests that she had died. In contrast, the dominant male was observed changing from year to year and even within the same year without the death of the previous dominant male.

For females, competition during the nesting period involved the breeding female denying other females access to the nest. This behaviour has also been found in the Sittella *Daphoenositta chrysoptera* and in this species always involved females who were unrelated to the breeding female (Noske 1998). In White-browed Babblers the majority (but not all) of females denied access to the nest were probably unrelated to the breeding female and all became breeding females in the next year. Joint nesting was found in babbler groups (see Chapter 8) and is a likely cause of the breeding female's aggression to other potential breeding females. However, I never found a case of joint nesting where both clutches of eggs hatched, so this behaviour appears to rarely provide real breeding opportunities to female helpers.

The observations of dominant males changing between nesting attempts regardless of whether the breeding female changed suggests that competition for the male breeding

position occurs. This competition should occur in the pre-laying period when females are seeking copulations from males. Breeding pairs were not observed intensely during this period, but dominant males were found escorting breeding females to and from the nest in the early stages of nesting. This behaviour is probably a form of mate guarding similar to that observed in other cooperatively breeding birds (Zahavi 1989; Ligon & Ligon 1990; Rabenold 1990).

The only aggressive interactions seen between males were between two males who both behaved as if they were the dominant male. This suggests that both may have copulated with the breeding female prior to that particular breeding attempt. At the next nest of the same year one of these males was clearly dominant. These observations suggest that males attempt to monopolise the breeding female, but this monopoly may not be complete.

Stacey (1982) developed a model which predicted female promiscuity if this increased the number of males which helped raise her young. Promiscuity was only expected if helpers increased the chance of young surviving. This was found to be the case in White-browed Babblers (Chapter 8) and so promiscuous behaviour by the breeding female is not unexpected. Males on the other hand should try to monopolise the breeding female (*i.e.* employ mate guarding) when male helpers are related to the dominant male and their chances of gaining a breeding position elsewhere are low (Stacey 1982). If male helpers are unrelated to the dominant male Stacey's model predicts that the dominant male would relax his monopoly of the female if this increases the chance of the male helpers remaining in the group. This model has been supported by genetic studies of reproductive success in the White-browed Scrubwren and the Arabian Babbler, where the only subordinate males which produced young were unrelated to the dominant male (Whittingham *et al.* 1997; Lundy *et al.* 1998).

Contribution by Helpers

Generally helpers were not involved in the construction of breeding nests, though they did contribute to the maintenance of the nest. The main contribution made by helpers to breeding attempts was the feeding of nestlings and the defence of nests and fledglings (see Chapter 8 for a discussion of the value of helpers in defence). Male helpers generally

made greater contributions than female helpers. However, the level of help by individuals of both sexes varied greatly.

Work on other cooperative breeding birds has found that the level of effort was often correlated with the degree of relatedness between the helper and the young that received their help (Reyer 1984; Emlen & Wregge 1988; Davies 1990). Piper (1994) found no correlation between relatedness and effort in the Stripe-backed Wren *Campylorhynchus nuchalis*, but he also found that the helpers were generally related to the young they helped. It is likely that for White-browed Babbler groups the relatedness of helpers to the nestlings they fed varied greatly, because a high proportion of group members were born in another group. This may explain some of the observed variation in the effort of helpers.

Part of the variation in the level of feeding effort by helpers was the result of aggressive behaviour by higher ranked birds. Some females were denied access to the nest by the breeding female and high ranked males. This prevented them from helping, or reduced the level of their help. In some cases these females were closely related to the nestlings they attempted to feed, because they were the daughters of the breeding female. Several of the males which did not help to feed nestlings (Feeding Effort <0.1) were the sons of the breeding female. The lack of any contribution by these males appeared to be related more to their likelihood of disappearing from the group during the breeding season. It is likely that these males were dispersing (see Chapter 9) and their small contribution probably reflected the limited time they spent within the group during the breeding attempt.

The Effect of Helpers on the Effort of the Breeding Pair

One question frequently asked in studies of cooperatively breeding birds is whether the presence of helpers increases the fitness of the breeding pair (Clarke 1995). The effect of helpers on breeding success is discussed in Chapter 8, where I show that helpers do increase the reproductive output of the breeding pair. However, this was more likely to be the result of reductions in the predation of nests and juveniles, than due to an increase in the provisioning of nestlings. Helpers can also contribute indirectly to the fitness of the breeding pair by reducing the costs of each reproductive attempt (Brown *et al.* 1978; Tidemann 1986). This may result in an increase in the likelihood of multiple nesting

attempts in a season, and/or an increase in the survival of the breeding female (Russell & Rowley 1988).

In this study it was not possible to compare the absolute feeding rates between groups, because nest watches for each group were made at different stages of nestling development. As found in other species, feeding rates for older nestlings appeared to be higher (Brown *et al.* 1978; Tidemann 1986). However, it was possible to compare the relative contributions of birds between groups. This showed that an increase in the number of helpers resulted in a reduction in the level of feeding effort by the breeding female and the dominant male. This effect of helpers was generally greater on the dominant male. One factor which can complicate this relationship is a correlation between the quality of the habitat with respect to food availability and group size (Brown *et al.* 1978). However, this correlation did not appear to be very strong in the Kellerberrin landscape (see Chapter 9).

These data suggest that helpers may reduce the effort required by the breeding pair to feed their nestlings. However, this benefit may come at the cost of increased competition for breeding opportunities. This cost appears to be greatest for the breeding male, because he may lose his position when the next breeding attempt is made, or he may suffer cuckoldry from helpers. So, it is not surprising that his effort declines more with an increase in the number of helpers. For the system to remain stable any increase in the potential for competition must be offset by an increase in benefits. This was also found in the Pied Kingfisher *Ceryle rudis* where secondary helpers were males that were unrelated to the breeding pair and so were potential competitors (Reyer 1986). These secondary helpers were only accepted by the breeding male in areas of low habitat quality, where they increased breeding success by increasing the rate of food delivered to the young (Reyer 1980, 1986).

Social Structure

I propose a model for White-browed Babbler groups in which members occupy one of three social positions; breeding bird, primary helper and secondary helper. Secondary helpers are defined as those that provide virtually no assistance to the feeding of nestlings (<0.1 feeding effort), but may help in group defence and other social activities. This distinction between primary and secondary helpers is an arbitrary division of what is

essentially a continuum of helping effort. However, the division aids in defining groups of individuals which may respond differently with respect to behaviours, such as dispersal and competition for breeding status.

Wiley and Rabenold (1984) proposed a model of social structure in cooperatively breeding birds, based on the idea that birds queue for breeding positions (from now on referred to as the Queuing model). They proposed that queuing for breeding positions is a stable strategy, because there are direct and indirect benefits in delaying breeding when group size increases reproductive success. The indirect benefits come from an increase in indirect fitness through helping to raise closely related young. Direct benefits arise from an increased chance of gaining a breeding position (through inheritance) with a group of established helpers.

One requirement of the Queuing model is that a strategy to prevent cheating (*i.e.* taking breeding positions without waiting in the queue) must be operating. Wiley and Rabenold (1984) identified four possible conditions which might prevent cheating: 1) age-dependent changes in the advantages of delaying reproduction, 2) risks of losing rank as a result of losing contests, 3) enforcement of position in the queue by individuals at the front of the queue who have the most to lose from cheats and 4) mutualistic interactions among acquainted individuals. They argued that the fourth condition was the most likely possibility in Striped-backed Wrens. Helpers in that species differed in age and so all could gain the benefits of reproduction in a large group if they waited in the queue. However, if one individual cheated then all individuals should cheat and so the benefits would be lost. Under this condition the only individuals which should compete for a breeding position are those of the same age (Wiley & Rabenold 1984).

The observations for the helping and dispersal behaviour of male White-browed Babblers are consistent with the Queuing model. Most males were primary helpers and the presence of helpers increases reproductive success (Chapter 8). Male secondary helpers were not common and their designation as such appeared to be related more to their absence from the group than to their unwillingness to help. Under these conditions the model predicts that males should remain in their natal group and queue for a chance to breed there. Generally male babblers do remain in their natal group, but some male dispersal occurs. This is consistent with the Queuing model if these males obtain a higher

position in the queue of their new group and so shorten the time they are likely to have to wait for a breeding position. Small groups should accept such helpers, because they increase the size of the group and so improve their reproductive success (see Chapter 9).

I believe that mutualistic interactions between group members appear to be the most likely candidate for maintaining the queuing system in White-browed Babblers. However, it is not known if the advantages of delaying reproduction in babblers changes with age, so this condition is also possible. The other two possibilities proposed by Wiley and Rabenold (1984) are not consistent with the observations in babblers. If enforcement of positions in the queue occurred then aggression should be directed by high ranked males toward low ranked males. Aggressive interactions between male babblers did occur, but they were restricted to high ranked individuals within groups. The observed competition for breeding positions by high ranked male babblers did not appear to result in the losing male losing his position in the queue.

Females do not appear to inherit the breeding position in their natal group. It is likely that this is to avoid inbreeding (see Chapter 9). Therefore, the Queuing model does not relate directly to female social structure. Some females remained in their natal group for their first breeding season and served as primary helpers (see Fig. 9.9). Since one year old females were only observed helping their mothers, it is not clear what role these females would take if their mother was replaced by another breeding female.

It appears likely that all females eventually disperse from their natal group and join other groups, sometimes as helpers. Female secondary helpers may be a consequence of these birds being denied access to the nest by the breeding female, who is attempting to prevent them from laying in her nest. However, it is also possible that some of these female helpers make small contributions, because they gain fewer or no indirect benefits from helping to raise unrelated young (Brown 1978).

Chapter 8

The demography of the White-browed Babbler

“The implications for management of the reproductive strategy shown by Australian passerines are clear. Most species are not capable of a rapid reproductive effort to re-establish a devastated local population after a major disaster or to recolonize an area from which the population has been eliminated. Furthermore, most populations will contain a large proportion of older experienced breeders that are not only more efficient per nesting attempt, but are also more likely to repeat nest; they are the high producers amongst a low-producing species.”

[Rowley & Russell 1991]

Introduction

Australian passerines are characterised as having long breeding seasons; small clutches, but with multiple broods; low productivity (<4 young per year); and high adult survival (Rowley & Russell 1991). This means that variation in production is generally the result of differences in nest success and the number of breeding attempts. In cooperative breeding species reproductive success can also be influenced by the number of helpers in a group (Reyer 1980; Brown *et al.* 1982; Emlen & Wregge 1988; Boland *et al.* 1997).

Nest predation is one of the most important factors determining the success of nests (Martin 1988; Rowley & Russell 1997). So not surprisingly habitat characteristics that influence the frequency of nest predation have been used to describe breeding habitat quality (Nias 1986; Brooker & Rowley 1995). The quality of the breeding habitat of species can be affected by disturbances such as fire (Brooker & Rowley 1991; Russell & Rowley 1998) or grazing (Brooker 1998) which change the structure of the vegetation. Breeding habitat quality can also be affected by landscape fragmentation (Yahner & Scott 1988; Donovan *et al.* 1997; Hartley & Hunter 1998). In landscapes fragmented by clearing,

nest predation has been found to be higher near the edge of remnant vegetation than near the centre of such remnants, or in smaller patches compared to large patches (Brittingham & Temple 1983; Wilcove 1985; Angelstam 1986; Gibbs 1991). Although there are some inconsistencies in the findings of these studies, Paton (1994) argued that the body of evidence supports the pattern of higher nest predation at edges.

This chapter describes the demography of the White-browed Babbler in the Kellerberrin area. It quantifies breeding habitat quality with respect to habitat structure and landscape configuration, and describes the effect group size has on productivity within habitat of similar quality.

Methods

From 1994 to 1996 all group home ranges were searched regularly for active breeding nests. In 1994 searching did not start until late July, which was found to be after breeding had begun. Consequently, in 1995 and 1996 nest searching started in June and continued until the end of December.

I did not have a regular pattern of visits to nests. Nests with eggs were visited more regularly than those with nestlings, so that the date of hatching could be determined. However, some nests in 1995 and 1996 were monitored from a hide and visited frequently for this purpose, while others were visited less frequently. All nests were visited 10-12 days after the eggs hatched to band the nestlings, and then again when the nestlings were 16-17 days old (expected fledging date). The purpose of the latter visit was to assess whether the nest had been successful. If the nest was empty, success was determined from evidence of nest damage consistent with predation, and the presence or absence of the fledglings with the group.

The start of the breeding season was defined as the month when the first eggs were laid. The laying date for each nest was estimated using a 20 day incubation period. This incubation period was based on the maximum incubation periods for the nests found (see results). The breeding season was considered to extend from the month when the first clutch was laid to the month when the last clutch was laid.

Productivity Estimates

A total of 64 nests were found during this study. Not all of these nests could be used for each productivity estimate, because they were found at different stages of development and the outcomes of the various stages of some nests were not certain (*e.g.* the hatching success of eggs in a nest found predated before all of the eggs had hatched is unknown). Due to the small number of nests found each year, breeding data from all three years were combined for productivity estimates. Therefore, these estimates represent average yearly production.

Clutch size was defined as the number of eggs per nest and was determined from nests found at the incubation stage. Nests predated or abandoned during incubation were only included if the female had incubated the same number of eggs for at least one week.

Hatchability was defined as the percentage of eggs that survived to the time of hatching and produced a chick (Koenig 1982). I excluded deserted eggs, or those predated before the full clutch had hatched.

Nestling Survival was defined as the percentage of nestlings that fledged, from successful nests. Using only successful nests makes this variable independent of nest predation.

Nest Production was defined as the number of fledglings produced per nest. This measure was estimated from all nests where the outcome was known.

Breeding Success was defined as the number of fledglings produced per egg laid (Rowley & Russell 1991). This measure of success was calculated from all nests used to determine clutch size.

Group Productivity was defined as the average number of fledglings produced by a group in one breeding season. This measure was based on fledglings from observed nests and fledglings observed with a group when a nest had not been found. This parameter probably under-estimates real group productivity, because some groups were not searched for juveniles for up to one month after their juveniles had fledged. Given the high mortality for young in the first few months, some of the juveniles in these groups may have died before the groups were searched.

Nest Predation

Nest predation rates were estimated from all nests where the outcome was known except those found late in the nestling stage and those abandoned during the incubation stage. Nests found late were excluded, because nest survival estimates may have been biased by the small number of days these nests were monitored.

Nest Survival was defined as the probability that a nest would persist for the full term of its development. Since nests found at a later stage are more likely to succeed, the stage at which a nest is found may bias estimates of nest survival (Mayfield 1961). To overcome this, nest survival was estimated using the formal calculations of the Mayfield method described by Johnson (1979). This method calculates daily survival rates (s) for nests, using a maximum log likelihood function, based on the number of nest failures and the total number of days nests were exposed to risk. The period of exposure to risk for predated nests was not known, because nests were not visited every day. Therefore, the exposure time was estimated as the number of days the nest was active, plus half of the interval between the last visit the nest was active and the visit when it was found to be predated (Johnson 1979). The calculations derived by Johnson (1979) enhance Mayfield's method, because they provide a method for estimating the standard error of the survival estimates and so these estimates can be compared statistically.

Estimates of nest survival were made from 45 nests. Daily survival rates (DSR) for the incubation period (s_i) and the nestling period (s_n) were calculated from these nests. There was no difference between these rates ($s_i = 0.971 \pm 0.009$, $s_n = 0.970 \pm 0.009$: CONTRAST $\chi^2_{(1)} = 0.006$ $p = 0.937$). Therefore, the nest survival rate was calculated as s^t , where s is the daily survival rate of the combined incubation and nestling periods, and t is the duration of the incubation and nestling periods (37 days). Approximate 95% confidence intervals were estimated as $s \pm 2$ standard errors.

Survival Estimates

Juvenile Survival Rate was defined as the probability that a fledgling would survive to the beginning of the next breeding season (1 year old). It was determined only from fledglings banded in the nest or in the first 1-3 days after fledging. Juveniles banded later than this were not considered, as mortality appeared to be high in the first few weeks

after fledging. Juveniles were considered to be independent at 6 months, so the survival rate from independence to 1 year old was also estimated. Juvenile survival rate was estimated for each clutch found, because the survival chances of clutch members were considered to be correlated. The juveniles from groups which disappeared from the study area were not included in estimates of juvenile survival.

Adult Survival Rate was defined as the probability that an adult would be found in the study area from the beginning of one breeding season to the beginning of the next. Adult survival rate was estimated separately for breeding females and for all other banded adults that were known to be two or more years old. Adults of this age appeared to be more likely to remain in the same group compared to younger birds (see Chapter 9). So, using only these adults reduced errors in the estimate caused by birds that dispersed to groups outside the study area.

Recruitment

Juveniles produced by a group in one year that were still present in the group at the start of the next breeding season were considered to have recruited into that group. This was possible, because babblers did not disperse before the start of their first breeding season (Chapter 9). This estimate of recruitment was averaged for each group over the years of the study that group was monitored.

The production of potential breeders was calculated as the number of recruits multiplied by the adult survival rate over two years. This assumes that birds breed at three years of age (see Chapter 7) and that there is no net loss or gain of individuals from groups due to dispersal. Home ranges were classified as *sources* if the production of potential breeders was greater than the mortality of breeders, while in *sinks* the production of potential breeders were equal to or less than the mortality of breeders (Breininger *et al.* 1998).

Data Analysis

Comparisons of daily survival rates for nests, and juvenile survival rates, were made using the computer program CONTRAST, which uses the Chi-square statistic described by Sauer and Williams (1989). This analysis provides a framework for testing hypotheses

similar to an Analysis of Variance. For some of these analyses *a posteriori* hypotheses were tested. These multiple contrasts of the same survival rate data require an adjustment to the significance level, so the Bonferroni adjustment (α/m , where α is the significance level, and m is the number of contrasts made) was used (Sauer & Williams 1989). The purpose of these analyses was to identify factors which might be influencing nest survival and juvenile survival. Since the sample sizes for both survival rates were small the power of these analyses was low. Therefore, I considered it important to reduce the level of Type II errors (*i.e.* the probability of accepting H_0 when it is in fact false). I did this by using a less conservative significance level ($\alpha = 0.1$).

Three variables (group size, home range configuration, and foliage density) were investigated as possible influences on daily survival rates for nests, and juvenile survival rates. Group size was the average number of birds considered to be a member of the group in each year it was monitored (see Chapter 7 for definition of group membership). Groups were classed as small (2-6 birds), or large (7-13 birds). The configuration of a home range was classified as *linear* if the habitat it occupied was less than 100 m wide. Otherwise it was classified as a *patch*. Home ranges which contained both patch and linear components were classified depending on the configuration of the home range around the nest. Foliage density was the mean density, in the densest height category, for each home range (see Chapter 5). Foliage density was arbitrarily classed as low (foliage density ≤ 0.70), or high (foliage density > 0.70).

Results

The incubation period for White-browed Babblers was difficult to determine, because few nests were found before eggs were laid. It was estimated to be 20 days, based on three nests where eggs were incubated for 20 days and one nest where eggs were incubated for 19 days. In addition, the eggs in two nests, which were found with the eggs already laid, were incubated for 17 days. Nestlings fledged at 16-17 days old, although in one nest nestlings did not fledge until 19 days old. In three nests nestlings fledged prematurely (14-15 days), because the nest was disturbed.

Breeding Season

The major egg laying period for White-browed Babblers at Kellerberrin was from July to September (Fig. 8.1a). There appeared to be an abrupt start to the breeding season. No nests with eggs were found in June, despite considerable searching effort. The earliest estimated laying dates were the 10th of July in 1995 and the 9th of July in 1996. The peak of egg laying for the first nests of groups was earlier in 1995 (July-August) than in 1996 (August-September) (Fig. 8.1a). Egg laying continued through to at least November and occasionally nests must have started in December, because recently fledged juveniles were found in a group in early February 1997. Most attempts after September were second or third nesting attempts for the group.

Groups with experienced breeding females started nesting earlier than those with inexperienced breeding females, or newly formed groups (Fig 8.1b). One newly formed group did not attempt to breed until November, but most started in August or September.

Productivity

The majority of clutches (83%) consisted of either 2 or 3 eggs (Table 8.1). The other clutches were a clutch of 1 egg, four clutches of 4 eggs, one clutch of 6 eggs and one clutch of 7 eggs. Three of the clutches of 4 eggs produced two chicks and two of these clutches contained two infertile eggs (the other was not checked). The fourth clutch of 4 eggs was taken by a predator before hatching. The clutch with 6 eggs produced four nestlings (the other two eggs were found broken in the nest). The clutch of 7 eggs produced three nestlings and contained four infertile eggs. It is likely that clutches of four or more eggs are the result of two or more females laying in the same nest (joint nesting *sensu* Brown 1978). This is supported by the observation of two birds simultaneously incubating the clutch of 7 eggs. These putative cases of joint nesting represented 15% of nests for which clutch size was determined.

Hatchability was low for White-browed Babblers in the Kellerberrin area (Table 8.1). The estimate of hatchability for putative cases of joint nesting was 52% ($n = 25$). If the eggs from joint nesting are removed from the total sample, hatchability increases to 84%. No nestlings died of starvation during this study. The only nestling deaths found were the result of nest predation.

Figure 8.1: The estimated month when the first egg was laid in the first nests of each group for **a)** three years (1994 $n=13$, 1995 $n=15$, and 1996 $n=23$) and **b)** for experienced females ($n=19$), inexperienced females ($n=9$) and for newly formed groups ($n=7$).

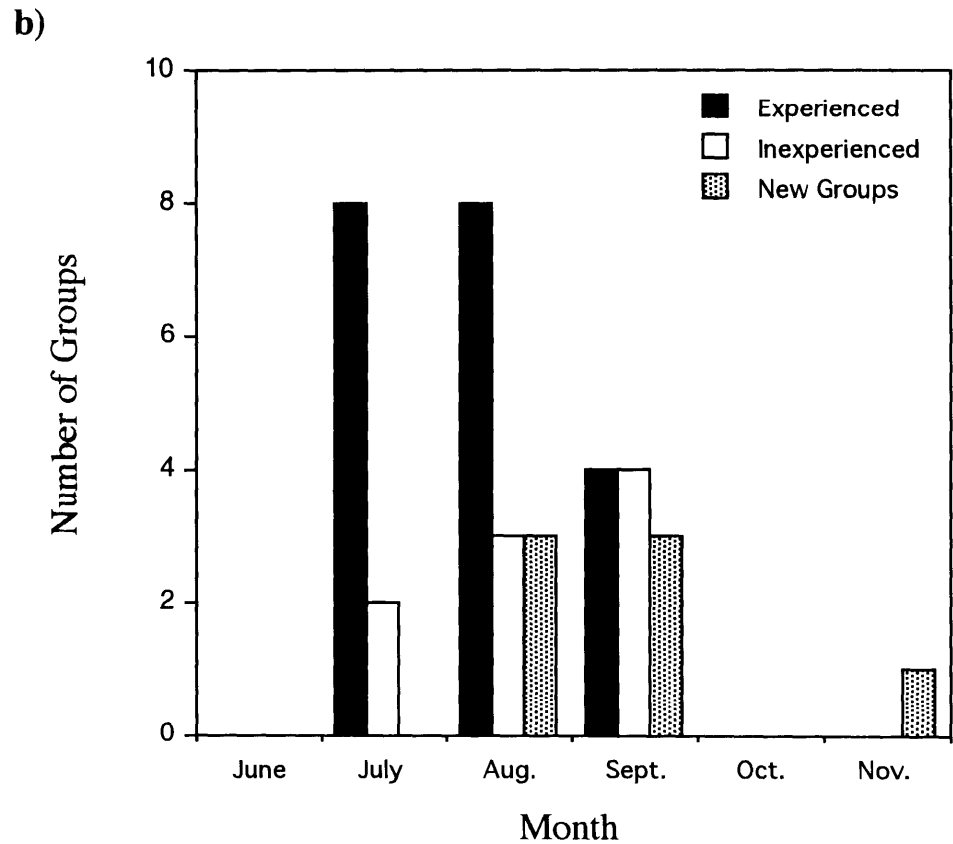
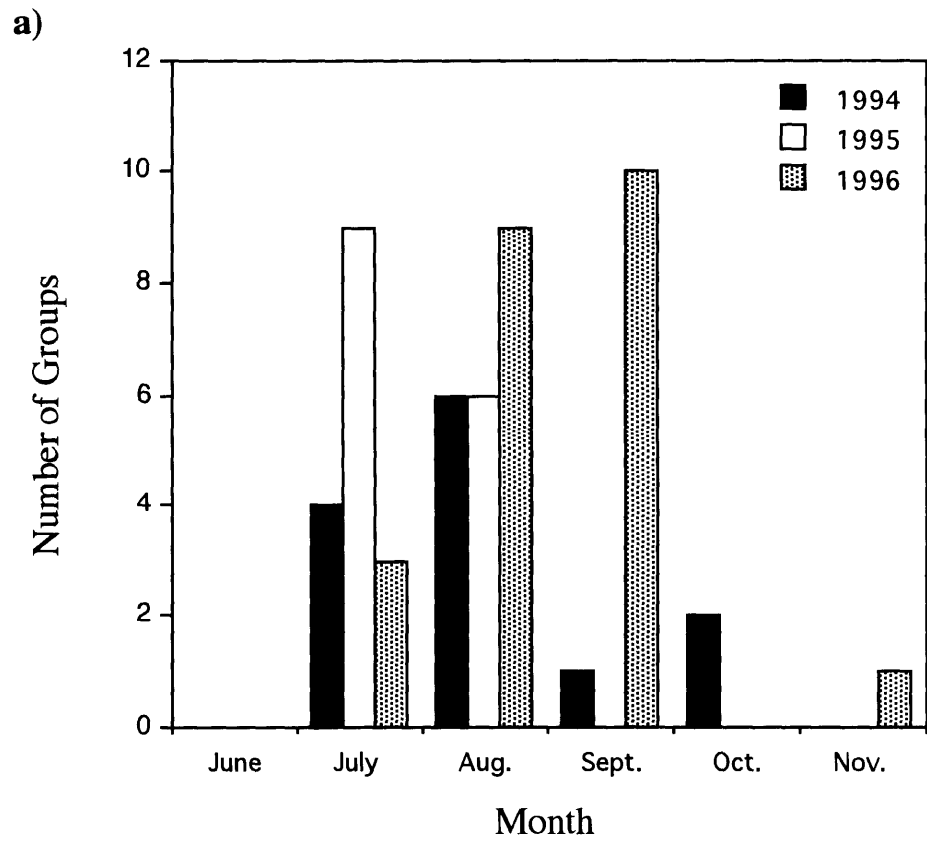


Table 8.1: Nest production parameters for White-browed Babblers in the Kellerberrin area. n equals the sample size for each parameter.

Clutch Size (n = 40) Mean \pm S.E.	2.9 \pm 0.2
Median	3.0
Hatchability (n = 87)	75%
Nestling Survival (n = 66)	100%
Breeding Success (n = 114)	44%
Nest Production (n = 63)	1.1 \pm 0.2

The average number of broods per year could not be determined precisely in this study, because not all nests were found. However, group production was estimated at 1.6 ± 0.2 fledglings/group and nest production was estimated at 1.1 ± 0.2 fledglings/nest. So, to obtain the estimated group production each group would have to make on average 1.5 breeding attempts per year.

On 11 occasions between 1994 and 1996 a group made a second nesting attempt after the first nest had failed, or the fledglings from the first attempt had disappeared soon after fledging. Three groups made second attempts after their first nest had been successful, and two of these groups successfully fledged their second brood. One group made three successful attempts in a single year.

There was no relationship between group size and the likelihood of additional nesting attempts after a successful attempt. The group making three attempts contained six birds while the three groups making two attempts contained four, six and 11 birds.

Group productivity in small groups (2-6 birds) occupying linear home ranges was 0.7 ± 0.3 fledglings/group (n = 10), while those occupying patches produced more than twice the number of fledglings per group (1.8 ± 0.3 fledglings/group, n = 12). For large groups (7-13 birds), group productivity was similar for those occupying linear home ranges (2.7 ± 0.0 fledglings/group, n = 2) and patches (2.1 ± 0.4 fledglings/group, n = 6). The small sample size for large groups occupying linear home ranges prevented a complete statistical

analysis. However, the difference in productivity of small groups occupying home ranges with different configurations was significant ($t_{(20)} = 2.71$ $p = 0.014$).

Effect of breeding experience on productivity

Group productivity in 1996 was significantly higher for groups with experienced breeding females than for those with inexperienced breeding females ($t_{(13)} = 2.45$ $p = 0.029$) (Table 8.2). The same trend in group productivity between experienced and inexperienced breeding females was found in 1995, but the difference was not significant ($t_{(14)} = 0.87$ $p = 0.402$).

Table 8.2: Differences in group productivity (mean \pm S.E.) for groups with inexperienced (1st year of breeding) and experienced (\geq 2nd year of breeding) breeding females.

	1995		1996	
	Inexperienced	Experienced	Inexperienced	Experienced
Number of groups	6	10	8	7
Mean # fledglings/group	1.7 ± 0.3	2.4 ± 0.6	0.4 ± 0.3	1.6 ± 0.4
Mean Group Size	4.8 ± 0.7	6.6 ± 0.9	6.5 ± 1.0	6.6 ± 1.2

There was no significant difference in group size between groups with experienced or inexperienced breeding females in 1995 ($t_{(14)} = 1.37$ $p = 0.137$), or 1996 ($t_{(13)} = 0.05$ $p = 0.964$) (Table 8.2).

Nest Predation

Nest survival for White-browed Babblers in the Kellerberrin area averaged 33% (95% confidence intervals were 20% to 52%). Twenty four of the 45 nests analysed were predated and in all but one case the total nest contents were taken. The exception was a nest attacked when the nestlings were almost due to fledge. One of the two nestlings in this nest survived by fledging prematurely. Another nest was attacked when the nestlings were

almost due to fledge, but both nestlings survived, so it was not considered a nest predation for estimates of nest survival.

Table 8.3: The effect of home range configuration and group size on nest survival. * The number of groups represented by the nests are indicated in parentheses. DSR is the daily survival rate of nests.

Configuration	Linear Home Ranges		Patch Home Ranges	
Group Size	2-6 Birds	7-13 Birds	2-6 Birds	7-13 Birds
# of Nests *	16 (11)	6(2)	11 (7)	12 (8)
Exposure (days)	211	146	216	274
# of Predations	14	2	4	4
DSR \pm S.E.	0.934 \pm 0.017	0.986 \pm 0.010	0.981 \pm 0.009	0.985 \pm 0.007
Nest Success	0.08	0.60	0.50	0.58
95% CI	0.02, 0.30	0.29, 1.00	0.25, 0.99	0.34, 1.00

Differences in group size and home range configuration resulted in significant differences in the daily survival rates of nests (CONTRAST $\chi^2_{(3)} = 8.20$ $p = 0.042$) (Table 8.3). The daily survival rates of nests produced by small groups were significantly lower than those produced by large groups (CONTRAST $\chi^2_{(1)} = 6.04$ $p = 0.014$). Significantly lower daily survival rates for nests produced by groups occupying linear home ranges compared to those of groups occupying patch home ranges were also found (CONTRAST $\chi^2_{(1)} = 4.08$ $p = 0.044$). The significance level used for the tests of the effect of group size and home range configuration were adjusted to 0.05, using the Bonferroni method ($\alpha = 0.1$, $m = 2$, see methods).

The major difference in the daily survival rate of nests was the very low success of small groups occupying linear home ranges. Only two of 16 nests produced by these groups survived to produce fledglings (Table 8.3).

Types of predation

Twenty seven nests showed evidence of disturbance consistent with an attempt by a predator to take their contents. Two of these nests contained eggs which had been abandoned by their group prior to the predation event. They were included in this analysis as they showed the same pattern of disturbance as predations of active nests.

Table 8.4: Types of nest predation observed on White-browed Babbler nests, in the Kellerberrin study area. * This predation event was observed from a hide. It was performed by a Grey butcherbird.

	Method 1	Method 2	Method 3
Description	Access via nest entrance. Lining material removed.	Access via hole in roof. Lining material removed.	Nest broken open on one side or from the top. Lining material removed.
Possible Predator	Medium birds (e.g. Grey butcherbird, Grey shrike-thrush)	Large birds (e.g. Raven)	Feral cats
1995			
Eggs	4	2	0
Nestlings	1*	1	2
1996			
Eggs	1	7	0
Nestlings	0	6	3
Total Nests	6	16	5
% of Nests	22	59	19

Three types of nest disturbance associated with nest predation were observed. The differences between these disturbance patterns suggest they were caused by different predators (Table 8.4). Predators which gained access via the entrance (method 1) must have been birds of babbler size or smaller, because the entrance to babbler nests are small and difficult to enlarge. Access by predators via the roof (method 2) has been attributed to large bird predators, such as the Australian Raven *Corvus coronoides* (Rowley & Russell 1997). These birds are too large to access the nest via the entrance and enter via the roof, because

it is the thinnest part of the dome. The breaking open of a nest found in method 3, suggests that these predations are by large predators. Feral cats are likely candidates for these predation events, because other large predators, such as Varanid lizards, are probably just as likely to predate eggs as nestlings.

Medium sized birds (method 1) took mainly eggs (83%). I observed the only predation event of this type to occur in the nestling stage. The predator in this case was a Grey Butcherbird *Cracticus torquatus*. It entered the nest via the entrance, removed one nestling, and left the nest completely undisturbed. When I returned the next morning the final nestling had disappeared and the lining of the nest had been removed via the nest entrance.

Large bird predators (method 2) took eggs (56%) and nestlings (44%), while large predators, such as feral cats (method 3), took only nestlings. On two occasions nestlings fledged prematurely possibly due to an attack by a feral cat (based on the damage to the nest). In one case both nestlings survived, while in the other only one of the two nestlings survived.

On three occasions a series of nests were disturbed on the same day, and the disturbances were consistent with a large bird predator (method 2). In all of these cases the nests were close together, and were in the same linear strips of vegetation, or were in small patches and connected linear strips of vegetation. In all of these cases old nests were also disturbed. This suggests that each of these events was the result of a single predator which had developed a search image for White-browed Babbler nests, because old nests, despite being common, are rarely disturbed in this way.

Juvenile and Adult Survival

Thirty nine percent of juveniles banded from 1994 to 1996 survived to the beginning of the next breeding season (1 year old). The juvenile survival rate was low in the first 6 months after fledging (50%), but increased between independence (6 months old) to 1 year old (75%).

Differences in the juvenile survival rate between small and large groups occupying home ranges with high and low foliage densities were significant (CONTRAST $\chi^2_{(3)} = 9.83$ $p = 0.020$) (Table 8.5). Groups occupying home ranges with high foliage density had

significantly higher juvenile survival rates than those occupying home ranges with low foliage density (CONTRAST $\chi^2_{(1)} = 3.92$ $p = 0.048$). Although juvenile survival rates were higher for large groups than small groups this difference was not significant (CONTRAST $\chi^2_{(1)} = 0.68$ $p = 0.411$) (Table 8.5).

Table 8.5: The effect of group size and foliage density on the juvenile survival rate. n = the number of clutches. Juvenile survival rates shown as mean \pm S.E.

Foliage Density	Groups of 2- 6 birds	Groups of 7-13 birds
Low (≤ 0.70)	$n = 12$ 0.19 ± 0.09	$n = 6$ 0.28 ± 0.18
High (> 0.70)	$n = 5$ 0.47 ± 0.23	$n = 8$ 0.65 ± 0.13

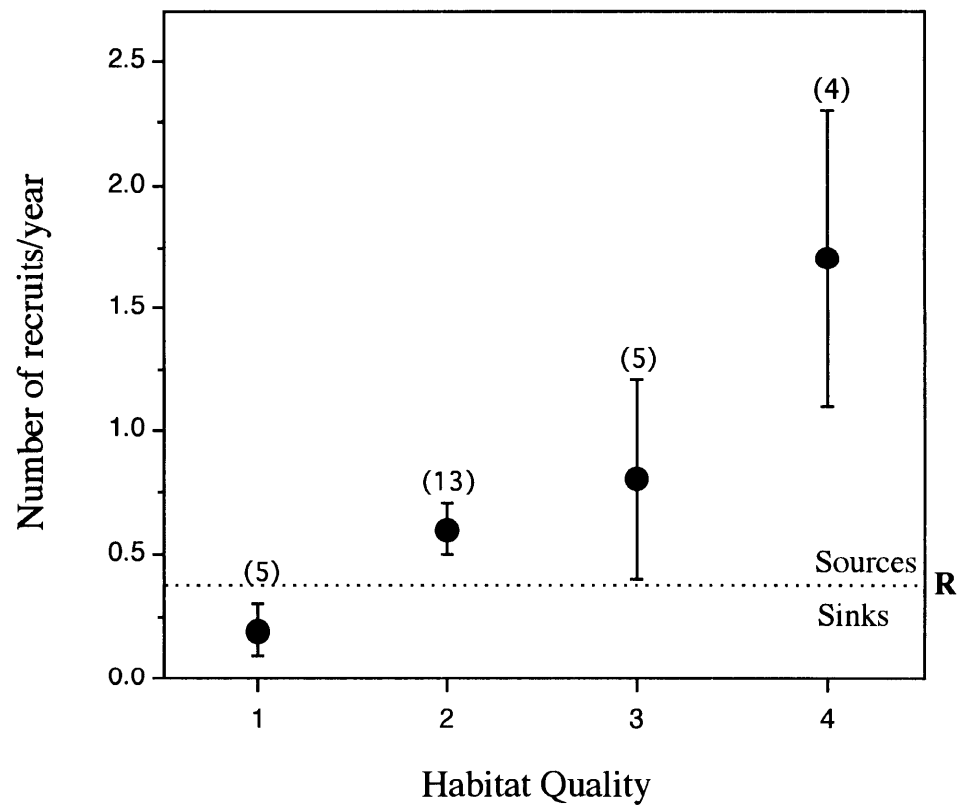
Seventy eight percent of adults (≥ 2 years old) caught in one breeding season were still alive at the beginning on the next breeding season ($n = 68$). A similar survival rate (80%) was found for breeding females ($n = 25$) ($\chi^2_{(1)} = 0.01$ $p = 0.944$).

Recruitment

Home ranges were ranked from one to four depending on their configuration and foliage density. Linear home ranges with low foliage density were considered the lowest quality (Habitat Quality 1), patch home ranges with low foliage density were ranked 2, linear home ranges with high foliage density were ranked 3 and patch home ranges with high foliage density were considered the best quality (HQ 4).

The mean recruitment rate for groups in the Kellerberrin area was 0.7 ± 0.2 birds per year. There was a significant increase in the recruitment rate for groups with better quality home ranges ($F_{(3,23)} = 4.07$ $p = 0.019$) (Fig. 8.2).

Figure 8.2: The recruitment rate of White-browed Babbler groups in habitats of differing breeding quality. The numbers in parentheses represent sample sizes. R represents the level of recruitment required to replace the loss of breeders due to mortality.



Given a breeder mortality rate of 0.20 (1 - Breeding female survival) and an annual survival rate of 0.78 for potential breeders in the group, an average of 0.33 recruits would need to be produced to maintain equilibrium (*i.e.* breeder mortality equals potential breeder production). Therefore, groups which recruited more than 0.33 birds/year were considered to be in *source* habitat and those below this value were considered *sinks*. The average recruitment rates for groups in home ranges with habitat quality of 1 was 0.2 ± 0.1 birds/year and so this habitat was considered a *sink*. Groups in home ranges with habitat quality greater than 1 had average recruitment rates above 0.33 birds/year (Fig. 8.2) and so these habitats were considered *sources*.

Discussion

White-browed Babblers have a five to six month breeding season in the Kellerberrin area, which is typical for sedentary Australian passerines (average 5.5 months, Yom-Tov 1987). However, the experience of the breeding female and whether the group was new or established influenced the start of breeding in babblers. Groups that formed over the previous Summer did not start nesting until August or September and one group commenced as late as November. These data must be treated with caution as I may have missed earlier unsuccessful attempts by these groups. However, the behaviour of these groups suggested that this was not so. When groups start nesting their aggressive response to intruders, such as myself, increases. When nests of new groups were found it generally coincided with an increase in the group's aggressive behaviour. Some established groups moved during the Summer, but returned to their original home range for the next breeding season (see Chapter 9). These groups also appeared to delay nesting, but these delays were much shorter.

Productivity

The clutch size of the White-browed Babbler in the Kellerberrin area is similar to that of other Australian passerines (Yom-Tov 1987; Rowley & Russell 1991). Hatchability, the percentage of eggs that hatch in successful nests, is rarely reported in Australian breeding studies. Rowley and Russell (1997) estimated hatchability at 97% for the Splendid Fairy-wren *Mahurus splendens*, but this declined to 88% after a major wildfire. Estimates of

hatchability in other species of fairy-wren are also high (*M. elegans* 94%, *M. leucopterus* 97%; Rowley & Russell 1997). The hatchability of Thick-billed Grasswren eggs was estimated at 84% for 36 nests on Peron Peninsula (Brooker 1998). Williams (1979) reported a hatching success of 84% for the White-fronted Chat *Epthianura albifrons*, but he included nest desertions in this estimate. Data for White-browed Babblers collected from Peron Peninsula, an extensive area of uncleared vegetation in northern Western Australia, estimated hatchability to be 100% (11 nests, with 30 eggs) (Brooker 1998). This suggests that hatchability for babblers in the Kellerberrin area was low for this species.

The low hatchability estimate found in this study was due, in part, to instances of joint nesting. Hatchability for cases of joint nesting was very low (52%) and in the majority of these cases appeared to be due to one clutch of eggs being infertile. If cases of joint nesting are removed the estimate of hatchability is higher (84%), but it is still low compared to that found for babblers on Peron Peninsula.

Koenig (1982) estimated hatchability for 113 species of bird in the northern hemisphere and found it averaged 91%. He found that social organisation influenced hatchability, with cooperative breeders having lower average hatchability (83%) than non-cooperative species (91%). Koenig's work on the cooperatively breeding Acorn Woodpecker *Melanerpes formicivorus* found that groups with only one breeding female had higher hatchability (88%) than groups which had multiple breeding females (79%) (Koenig 1982). He suggested that this decline in hatchability was due to a reduced probability of fertilisation due to increased competition for mates and/or intrasexual competition during egg laying. In the Arabian Babbler joint nesting occurred when new females joined a group and competed with the existing breeding female (Zahavi 1990). In these cases eggs were broken and sometimes removed from the nest by the competing females. The result of these interactions was that multiple clutches fledge no more young than those produced by a single female despite containing more eggs (Zahavi 1990). It is possible that social disruption, similar to that found in the Acorn Woodpecker and the Arabian Babbler, may be the cause of the low hatching success observed in the current study. This is supported by the fact that many of the groups with low hatchability (8 of 11 groups) showed evidence of joint nesting or aggressive interactions between the breeding female and other females in the group (see Chapter 7).

The drop in hatchability found in the Splendid Fairy-wren after a major wildfire (Rowley & Russell 1997) suggests that major habitat disturbance may affect breeding patterns. This may explain the much higher estimate of hatchability for White-browed Babblers on Peron Peninsula compared to Kellerberrin, because Peron Peninsula has not suffered the major disturbance of land clearing and habitat fragmentation that has occurred at Kellerberrin. These disturbances may play a part in reducing hatchability by increasing the level of social disruption within and between groups. Eight of the 11 groups with low hatchability at Kellerberrin were in small habitat patches which supported only one or two groups, and the number of groups in a habitat patch affected social interactions (see Chapter 10).

The low hatchability at Kellerberrin compared to Peron Peninsula appears to cost groups little in production. The productivity of White-browed Babbler nests at Kellerberrin (1.1 fledglings/nest) was slightly higher than that on Peron Peninsula (0.8 fledglings/nest) (Brooker 1998). This is because nest predation was the most important determinant of the number of fledglings produced. On average 66% of nests failed to fledge young, because of nest predation. This was similar to the rate found for this species on Peron Peninsula (64%) (Brooker 1998).

The experience of the breeding female has been found to affect the number of fledglings/nest and the number of fledglings/year (measures of productivity) in the Splendid Fairy-wren (Russell & Rowley 1988). Such information is difficult to obtain requiring long term studies of known individuals. However, the data for the White-browed Babbler in 1996, though limited, showed that group productivity was higher for experienced than for inexperienced females. In that year, group size was similar between females of different experience and therefore did not confound the observed result. In 1995, the productivity of experienced and inexperienced females was not significantly different, although the same trend was observed. These results suggest that breeding experience probably increases the productivity of babbler groups. The correlation between lower productivity in 1996 and the greater difference in group productivity between females with different experience suggests that experienced females may be able to cope with bad breeding conditions better than inexperienced females. However, these data do not consider differences in breeding

habitat quality which could affect both within year and between year differences in productivity.

Multiple Nesting Attempts

As with many Australian passerines White-browed Babblers are capable of making more than one nesting attempt each year (Yom-Tov 1987). The probability of renesting a second or third time appeared to be higher if the previous attempt had failed, or the fledglings of the previous attempt were predated early. This is the general pattern found in Australian passerines (Rowley 1965, 1978; Yom-Tov 1987; Clarke 1988).

Russell and Rowley (1988) found that the likelihood of renesting by the Splendid Fairy-wren after a successful nesting attempt was higher for experienced breeding females and for larger groups. Larger groups were more capable of renesting, because the helpers could care for the juveniles of the earlier attempt. Helpers caring for dependent young while the female renested also occurred in this study. However, renesting after a success was rare, with only three females observed making the attempt. One group produced three successful broods in 1994 and two in 1995 which indicates that multiple, successful nesting attempts are achievable in the Kellerberrin habitat. So, it is not clear why this was such a rare event. One possibility is that only those groups which start breeding early have the opportunity to renest after a success (Russell & Rowley 1988). For White-browed Babblers in the Kellerberrin area an early start to breeding appears to be restricted to groups with experienced breeding females. In addition, the movement of groups during the Summer (see Chapter 9) also results in a slight delay in nesting.

Survival Rates

Sedentary and migratory Australian passerines generally have high adult survival rates (Rowley & Russell 1991, Yom-Tov *et al.* 1992; Bridges 1994; Ford 1998), and the White-browed Babbler is no exception to this pattern. The average yearly survival rate of 78% is substantially higher than the 66% recorded for this species by Yom-Tov *et al.* (1992). However, they acknowledged that their estimates were probably underestimates, because they were based on the recapture of banded birds. White-browed Babblers are also long lived birds. One bird in this study was first banded as an adult in 1985 and was 10+

years old when last seen. A female was found breeding in 1994 (7+ years old) in the same group where she was first caught in 1987. Birds of this age are not unusual among Australian passerines (Rowley & Russell 1991).

The survival of juvenile White-browed Babblers (39%) is similar to that found for two species of fairy-wren (*M. splendens* 34%, *M. elegans* 41%) which have strong natal philopatry (Rowley & Russell 1991). These juvenile survival rates are substantially higher than that for the Bell Miner *Manorina melanophrys* (7%) (Clarke & Heathcote 1990). For the Bell Miner, two periods during the first year are the most critical to their survival. The first is the period from fledging to gaining independence. The second is the dispersal period which occurs just prior to the next breeding season (Clarke & Heathcote 1990). The period from fledging to independence is also the most critical stage for the White-browed Babbler, with most of the mortality occurring during this first six months. However, the survival rate of babblers from independence to one year is high (75%). This appears to be because babblers do not disperse in their first year (Chapter 9).

The Quality of Breeding Habitat

The probability of a White-browed Babbler nest being taken by a predator is influenced by group size and the configuration of the group's home range. The biggest difference in nest survival was between small groups (2-6 birds) occupying linear home ranges, which rarely produced a successful nest, and all other groups. One possible reason for this pattern of nest survival is that these small groups may not be able to defend their nests as effectively in linear vegetation. Groups with linear home ranges are forced to forage further from the nest to obtain their food and this would reduce their vigilance for predators approaching the nest. This is the predicted outcome from Central Place Theory. This theory is generally used with respect to foraging behaviour (Andersson 1981; Recher *et al.* 1987), but can also be applied to nest defence (also see Chapter 9). The failure of groups to detect and defend the nest from predators would be most important against smaller predators (*e.g.* medium sized birds) which the babblers could deter. Defence against large predators (*e.g.* large birds and feral cats) would be less effective, so a lack of vigilance may not affect the level of predation by these predators. These expectations are supported by the patterns of nest predation for small groups. Predations by medium sized birds

(method 1) all occurred in linear vegetation, whereas predations by larger predators (methods 2 & 3) were divided almost equally between linear and patch home ranges (8 and 6 respectively).

Another possible cause of higher nest predation rates in linear vegetation is the increased probability of nest predators finding nests in linear strips. The three cases of multiple nests being predated on the same day were all associated with linear vegetation. These predations suggest that a predator which successfully predated a nest may acquire a search image for babbler nests and be more successful at finding others. The linear nature of the vegetation would direct these predators to other nests. In patches; however, the predator could move in any direction from a predated nest, and therefore would be less likely to find the nests of adjacent groups.

These patterns of predation could also be the result of a much higher density of predators in linear strips. This relationship between predator densities and landscape modification were demonstrated by Donovan *et al.* (1997) for forest birds in the USA. Potential predators, such as the Australian Raven, are common components of the bird fauna in road verge vegetation (linear strips) in the Kellerberrin area (Cale 1990). However, White-browed Babbler habitat patches in the study areas are small and have similar bird communities to road verges.

A lower nest survival does not necessarily result in lower group productivity, because groups renest after failure. However, renesting opportunities are limited by the length of the breeding season, and for small groups in linear vegetation nest survival was very low. Therefore, it might be expected that some of these small groups will fail to produce fledglings despite multiple nesting attempts. The estimates of group productivity support this expectation. Small groups in linear vegetation produced only about one half the number of fledglings per year as those living in patches. Large groups had similar productivity in linear vegetation and patches. This indicates that nest predation is a major determinant of production by groups.

The production of young is only the first step to reproductive success. The second is that juveniles must survive to contribute to the group in the next breeding season. Many juveniles die in the first year and the majority of these die in the first few months after they leave the nest. Predation is the most likely cause of mortality. Food does not appear

to be a problem given that no nestlings died from starvation. Inclement weather, such as thunderstorms, may cause some mortality, but these are not a common enough event to cause more than a small proportion of deaths. During the first few months after fledging juvenile babblers were not very mobile, being poor fliers, and they depended on the group to protect them from predators.

The group defended juveniles by giving an alarm call when a threat was perceived. Juveniles responded to this alarm by moving into the densest vegetation in their immediate vicinity and remaining silent and stationary. While the threat remained the adults in the group hid the presence of the juveniles by calling frequently and moving rapidly through the vegetation around the potential predator. I found, when searching for juveniles, that this technique was effective at hiding the exact location of the juveniles, especially when the group was large.

Based on this method of predator defence it would be expected that the density of the foliage and the size of the group might affect the survival chances of juveniles. The data from this study support this expectation. The strongest influence on juvenile survival rate was foliage density, but large groups tended to have higher levels of juvenile survival than small groups in home ranges with similar foliage density.

The differences in the daily survival rate of nests and the survival rate of juveniles within different home range configurations, vegetation densities, and group sizes are based on small sample sizes. Therefore, strong statistical inferences from these data are impossible. However, given this limitation the observed effects of habitat configuration on nest survival and foliage density on juvenile survival suggest that there are differences in the quality of the breeding habitat of individual groups. Differences in breeding habitat quality were also found in the other two species of babbler that have been studied (*i.e.* Grey-crowned Babbler and Hall's Babbler), and in both species vegetation structure was an important characteristic (Brown & Balda 1977; Brown & Brown 1981). Group size also influenced nest and to a lesser extent juvenile survival. In part, this is because group size is affected by habitat quality (see Chapter 9). However, small groups do occur in better quality habitat and occasionally large groups occur in lower quality habitat. In these cases group size can influence reproductive success.

The data from this study suggest that good breeding habitat for White-browed Babblers in the Kellerberrin area is a patch of vegetation with high foliage density. The poorest quality breeding habitat is a linear strip supporting vegetation with a low foliage density. The average recruitment rate for groups with different quality home ranges showed a significant increase as habitat quality increased (Fig. 8.2). The recruitment pattern found in this study indicates that a few high quality home ranges were responsible for a disproportionately high number of the individuals recruited into these populations.

The estimated recruitment rates and survival rates for babblers indicate that all but the poorest quality habitat (HQ 1) in the Kellerberrin area is source habitat for White-browed Babblers. This source habitat represents 81% of the home ranges assessed. This is a very different distribution of source-sink habitat to that found in the Florida Scrub-Jay *Aphelocoma coerulescens* where only 28% of the area was considered source habitat (Breininger *et al.* 1998). The estimates of source and sink habitat used here are crude and they do not take into account differences in group size. Small groups (2-6 birds) occupying home ranges of habitat quality 2 or 3 have average recruitment rates of 0.3 ± 0.1 birds/year which is below the threshold for source habitat. This means that 56% of groups in the study sites are producing insufficient recruits to compensate for breeder mortality. For cooperative breeding species where group size influences reproductive success assessment of habitat quality alone is not sufficient to determine the source-sink threshold, because intermediate quality habitat may be sufficient for reproduction only when groups are large. In Chapter 9 I show that there is a tendency for male babblers to disperse to small groups. This dispersal pattern may maintain groups in more marginal habitat by maintaining reasonable group sizes.

Summary

The demography of the White-browed Babbler in the Kellerberrin area is typical of Australian passerines. They can be characterised as having low fecundity and low nest success, but have multiple nesting attempts that result in a moderate annual production of juveniles per group and high adult survival. The only aspect of their productivity that appeared to be lower than expected was hatchability, but this parameter is not well

documented in Australian passerines. Low hatchability also appeared to have little effect on productivity when it was considered over a whole breeding season.

Reproductive success was affected by home range configuration and the foliage density of the vegetation in these home ranges. In combination these two variables described the breeding quality of the habitat, but reproductive success was also influenced by group size and the experience of the breeding female. Recruitment was on average less than one bird per group, but was offset by high adult survival. The observed recruitment rates were sufficient to maintain an equilibrium between breeder mortality and the production of potential breeders in all but the poorest quality habitat or where groups were small. Only a small number of groups consistently produced large numbers of recruits. These are the high producers in a low producing population referred to by Rowley and Russell (1991) and are probably the key to the persistence of these populations.