

CHAPTER 6

GENERAL BREEDING BIOLOGY

6.1 Introduction

The reproductive parameters of a population are a set of co-adapted characteristics that reflect the ecological circumstances of the population (Lack 1968, Cody 1971). Such parameters may include the number of nesting attempts per season and lifetime, clutch size, incubation, care of nestlings, and reproductive success. There has been much progress toward an understanding of the factors which affect reproductive parameters in bird populations and of the adaptive significance of many life-history traits.

In co-operative breeding species a further dimension, the presence of supernumerary birds in breeding groups, may influence or complicate the reproductive parameters of the population. Brown (1978), for example, suggested that supernumerary birds may influence the behaviour patterns of reproductive investment (ie. the number of eggs laid or the rate of delivery of food to nestlings) and the fitness of individuals within the population.

An assessment of the degree to which helpers contribute to the production of offspring and the fitness of breeders is fundamental to any study of co-operative breeding. The adaptive significance of delayed dispersal and helping behaviour can be analysed by comparisons of

the lifetime reproductive^{output} of individuals within the population. In a number of studies the reproductive success of breeding birds was found to be enhanced in the presence of helpers (see refs. in Brown 1978, Emlen 1978, also Brown et al. 1982, Rabenold 1984, Reyer 1980, Woolfenden and Fitzpatrick 1984). Comparisons of the lifetime reproductive success of individuals may therefore allow an assessment to be made of the adaptive significance of delayed dispersal to helpers, and of the possible benefits of helping behaviour to breeding birds. There is sufficient variability in the social organisation of the Superb Fairy-wren, and the life-history of individuals, to allow such comparisons to be made.

In the present chapter some features of the breeding biology of Superb Fairy-wrens at Eastwood S.F. are described. The observations made are considered in relation to the ecology and social organisation of the species. Included is the presentation of data on the timing of reproductive events, the number and size of clutches laid per breeding season, the growth and development of nestlings, and brood parasitism. The influence of helpers, and certain habitat variables, on the reproductive output of breeding birds is tested. Some further influences on the reproductive success of fairy-wrens at Eastwood (ie. nest-site selection and the feeding of nestlings) are covered in more detail in Chapters 7 and 8.

6.2 Methods

An attempt was made to locate all fairy-wren nests at Eastwood State Forest in the period from September 1982 to February 1986. The progress of each nest was followed from the time of discovery through to fledging and the number of offspring recorded at each stage. Most nests were checked daily, or every second day, until nestlings were about 8 days old, and then again close to the estimated date of fledging. Nestlings were banded with numbered aluminium bands when 7 days old. Nests were left undisturbed in the latter stages of the nestling period because disturbance may lead to premature fledging.

Nestling age was recorded from the day of hatching (= day 0) if possible or estimated, in the early stages, from the degree of development (see this chapter). Nestlings that could be aged accurately were weighed and morphological measurements taken at various stages of development. Measurements were made of nestling weight, tarsus length, and length of the fourth primary feather (including shaft). Notes were also made of behavioural and morphological changes that occurred during nestling development.

Opportunistic sampling of some aspects of adult behaviour such as courtship, territorial disputes, agonistic interactions between group members, and the responses of adults to disturbance of the nest was made. The relationship between adult helpers and the offspring that they help to raise was determined from banding and genealogical analysis (see Chapter 3).

6.3 Results

Superb Fairy-wrens in the Eastwood population bred as monogamous pairs with from zero to five non-breeding adult helpers present in each group. The exact relationship between helpers and breeding birds could be established for 9 male and 2 female helpers (Chapter 3). In no cases were helpers known to be unrelated to both members of the breeding pair. Male helpers were either the offspring of both birds or, at least, the offspring of the breeding male, except in one case where the male helper was the younger (by at least one year) sibling of the breeding male. Both of the female helpers were found to be offspring of the breeding female but unrelated to the breeding male.

Within a breeding season, the offspring from a previous brood would also act as helpers at later nesting attempts. The contribution made by these immature helpers appears to be small (see Chapter 8) and they are not included further in discussions of helping behaviour (see also Rowley 1965, 1981).

The breeding season for fairy-wrens at Eastwood S.F. was defined as the months during which egg-laying was recorded. In general, the breeding season lasted from September to February (Fig. 6.1) although some variation in the length of the breeding season was noted between years (Table 6.1). The timing of the onset of egg-laying was correlated with the amount of rainfall recorded in the previous non-breeding season ($r = -0.96$, $p < 0.01$). The lateness of the last clutch was positively, but not

significantly, correlated with the rainfall recorded during the entire breeding season ($r = 0.65$, n.s.) and in the last three months of the usual breeding season ($r = 0.75$, n.s.). The interval between the start of the first and last clutches, a measure of the length of the breeding season, was significantly correlated with the rainfall recorded in the last three months of the breeding season ($r = 0.93$, $p < 0.05$).

Copulation was rarely witnessed, possibly because it did not seem to be preceded by any elaborate rituals. The single instance of attempted copulation recorded outside the breeding season was performed by an immature male. Early in the breeding season males were occasionally observed chasing females. The male rapidly pursued the female throughout the territory, with both birds twisting and weaving through the foliage until coming to rest, after which the pair usually engaged in mutual preening. It is not known if copulation occurred after the chasing bouts, but it was not observed.

Agonistic interactions were occasionally observed between two males in the same group. One such interaction was observed in detail early in the 1983/84 breeding season. The two males were known to be siblings, with the dominant male (92733 M) being at least one year older than the subordinate male (18837 M). The subordinate male had been a helper in the previous breeding season to his older sibling. In September 1983 however, the younger male appeared to be courting and attempting to copulate with

the newly arrived dominant female (30824 F). The older male continually harrassed the younger male when he approached the female and several chases were observed. In the month after this encounter was recorded, the younger male left the group and paired with an immigrant female in a separate territory.

Nests were built in a minimum period of about 7 days after the initial strands of grass, bark-fibre and spider webs had been positioned in the substrate. A typical sequence of events was observed in the 1984/85 breeding season at the nest of group K. The dominant female was first seen carrying nest material on 27th November and the nest was found on the following day in a blackberry bramble about a quarter completed. From 0859h to 0929h a total of 10 visits to the nest-site were made by the female with nest material. The first egg was laid on 4th December, some 7 days after nest building had commenced. The dominant male (56448 M) often accompanied the female as she searched for nest material but did not participate in any of the nest-building.

A number of nests however, were not used for up to 14 days after construction, and many 'false starts' were made. In 1984 for example, the dominant female in group X started to build a nest in late August. On 28th August the nest was discovered in the early stages of construction; a basic shape was present, the thin walls of the nest contained dry grass stems and fine pieces of bark-fibre interwoven with spider's webs and a few feathers. By 7th September

however, nest construction had progressed little and the task seemed to have been abandoned. A second nest was subsequently located nearby and some of the materials seemed to have been taken from the previous nest. By 10th September the second nest was about three-quarters completed but no more construction was observed. On the 2nd October a third nest containing four eggs was discovered. It is possible that the discovery of nests in the early stages of construction by potential predators (or human observers) may lead to abandonment of the nest.

Nests were usually built among dense foliage, or in thickets, with the entrance facing the outer edge of the substrate. Most nests at Eastwood were built in blackberry brambles but nests were also found among woodpiles/fallen trees, at the base of small trees and on the ground in long grass (Table 6.2, see also Chapter 7). Only two nests were made among the foliage of live trees, one in an Exocarpus sp. 2m above the ground and the other in a eucalypt about 5m above the ground.

A new nest was built for each separate nesting attempt and no nest was ever found to have been used more than once.

Clutch size was typically three or four eggs with a mean clutch size of 3.35 eggs being recorded for the entire study period. However, mean clutch size in the 1982/83 breeding season was lower than that recorded in the remaining breeding seasons (Table 6.3). Fewer 4-egg, and more 3-egg, clutches were laid in the 1982/83 breeding

season relative to remaining breeding seasons (Chi-squared test on the proportion of 3-egg clutches, 1982/83 b.s. versus pooled data from remaining breeding seasons, $\chi^2 = 5.1$, $p < 0.05$).

Brood parasitism by cuckoos (Chrysococcyx sp.) was recorded in November (n = 3 nests), December (n = 5 nests) and January (n = 3 nests) and represented 22.4% of all nests recorded in these months. In total, 10.4% of all nests were subjected to brood parasitism compared with a rate of 3.4% at Gungahlin (Rowley 1965).

Incubation lasted about 14 days and all nestlings within a brood hatched on the same day. The breeding female was the only bird ever seen incubating the eggs. When disturbed while incubating, the breeding female flew quickly and quietly out of the nest into a nearby thicket or bramble where she began giving alarm calls. Hatching usually began early in the morning, close to sunrise, and often continued to mid-morning or occasionally into the afternoon. Newly hatched nestlings were naked, silent and their eyes were closed. If the nest was disturbed at this stage the nestlings would respond only by begging but at age 5 or 6 days weak alarm calls were usually given. By 9 days old the nestlings were fully feathered and would prematurely fledge if disturbed sufficiently at this stage of development. Nestlings normally left the nest after about 12 days, barely capable of flight.

When the nestlings were disturbed during banding and weighing operations the remaining group members would respond with alarm calls, often approaching and hopping agitatedly in the vicinity of the observer. On occasions, the distraction or 'rodent-run' display (Rowley 1962) was performed by one, or more, birds in the group. During the display the bird hunches over with its feathers fluffed, tail depressed, head extended and lowered, and wings held slightly out from the body. The bird then scurries along the ground in this posture for several seconds. The distraction display was not recorded when only eggs were present (n = 23 visits) or when nestlings were less than 5 days old (n = 14 visits). When nestlings were between 5 days old and fledging, distraction displays were performed by breeding females (8 out of 18 visits) and breeding males (6 out of 18 visits). When young fledglings (less than 7 days out of the nest) were approached, distraction displays were occasionally given by breeding females (6 out of 16 visits) but rarely by breeding males (once in 16 visits). Adult helpers and immatures from previous nests were not seen giving distraction displays (n = 14 visits to nests with adult helpers, n = 42 visits to nests with immatures).

Three measures of nestling growth were made; weight (Fig. 6.2), tarsus length (Fig. 6.3), and length of the fourth primary feather (Fig. 6.4). A logistic growth-curve was fitted to the weight data using the graphical

method of Ricklefs (1967). Growth parameters were then calculated for the equation:

$$W_t = \frac{A}{1 - e^{-k(t-t_1)}}$$

where W = weight at age t , t = the point of inflection of the curve (estimated at 3.5 days), A = the asymptote of the growth curve (estimated at 8.5 grams), and k is the growth constant (0.55). When fledged, nestlings weigh about 8.5g or about 93% of adult female weight (A.f.w. = $9.1 \pm 0.6g$, $n = 19$) or about 89% of adult male weight (A.m.w. = $9.5 \pm 0.5g$, $n = 37$).

Cuckoo (probably Chrysococcyx basalis) nestlings hatched before fairy-wren nestlings and ejected the remaining fairy-wren eggs from the nest. One nest that was found to contain two cuckoo eggs was abandoned by the hosts. Although the nestling period of cuckoos (about 16 days) exceeded that of fairy-wrens, there was only a short period of post-fledging dependence. Data for nestling growth rates indicated that by day 7 after hatching, cuckoo nestlings were about 1.7 times the weight of an average fairy-wren nestling or about 60% of the weight of an average brood of 3 fairy-wren nestlings.

Most breeding groups made more than one nest attempt per breeding season. Inter-year variation in the number of nest attempts per season (Table 6.4) again emphasises the low reproductive effort in the 1982/83 breeding season.

After the nestlings from one nest had fledged, a new clutch was started from 6 to 58 days later (mean = 29 days, n = 20 nests). Table 6.5 shows the inter-clutch intervals (the time from the laying of the first egg of nest N to the laying of the first egg of nest N + 1) recorded for successive breeding attempts by the same breeding pairs. New clutches were started sooner after unsuccessful nests than for nests which resulted in dependent fledglings ($t = 8.04$ $p < 0.001$, $n = 39$). Following successful nest attempts, pairs with adult helpers were able to start new clutches sooner than were simple pairs ($t = 2.55$, $p < 0.05$, $n = 23$).

Reproductive output at various stages of nesting and inter-year variation in reproductive success are summarised in Table 6.6. Included are data collected by H.A. Ford on six fairy-wren groups at Eastwood in the 1981/82 breeding season.

The number of fledglings produced per breeding pair varied for each breeding season in a manner consistent with the differences in rainfall recorded. A significant regression equation was obtained for the relationship between the number of fledglings produced per breeding season by each pair (FLEDS) and the rainfall (RAIN) recorded in the previous non-breeding season months (March to August, rainfall in mm) ($FLEDS = -0.14 + 0.01 RAIN$; $r = 0.91$, $p < 0.05$, $n = 5$ seasons) although there was no significant correlation between FLEDS and the rainfall recorded within the breeding season (September to February, rainfall in mm, $r = 0.08$, n.s., $n = 5$ seasons).

The reproductive success of simple pairs was similar to that of pairs with adult helpers (Tables 6.7, 6.8). Pairs with helpers and simple pairs hatched a similar number of nestlings per egg laid ($\chi^2 = 3.42$, n.s.) and a similar number of these nestlings fledged ($\chi^2 = 1.57$, n.s.). The proportion of nests which were successful (ie. those that produced at least one fairy-wren fledgling) did not differ between pairs with helpers and simple pairs ($\chi^2 = 0.00$, n.s.). A comparison of pairs with, and without, helpers in only the 'good' rainfall years again did not produce significant differences in the mean number of fledglings per breeding pair ($t = 0.52$, n.s.).

Habitat variables measured in the 1983/84 breeding season, when few pairs had helpers, were tested for correlation with reproductive success in that season (Table 6.9). The area of brambles per territory (BAREA) was the only variable to be measured which was significantly correlated with the number of fledglings produced per breeding pair, per season (FLEDS). Combining the data for four breeding seasons (1982/83 to 1985/86), a significant correlation was found between bramble area per territory (BAREA) and the number of fledglings produced per season (FLEDS) by pairs without helpers ($r = 0.58$, $p < 0.001$, $n = 33$ pairs).

An analysis of covariance (Table 6.10) was used to test for the effects of adult helpers on reproductive success, using BAREA as a covariate. No significant effect of helpers on reproductive success was found after

simultaneously controlling for the area of brambles present (BAREA) and the effects of inter-year variability in rainfall (YEAR).

Table 6.11 shows nesting attempts classified according to nest-site substrate. Pairs with helpers were no more successful in bramble nest-sites than were simple pairs ($\chi^2 = 0.19$, n.s.) and were no more successful in total ($\chi^2 = 0.00$, n.s.). This is despite the observation that pairs with helpers nested more frequently in bramble nest-sites than did simple pairs (pairs with helpers = 92.1% bramble nests, simple pairs = 64.7% bramble nests; $\chi^2 = 9.03$, $p < 0.01$) and nests in brambles were more often successful ($\chi^2 = 5.10$, $p < 0.05$) than nests in other substrate types.

In order to control for some of the effects of high levels of nest predation (see Chapter 7) on the reproductive output of breeding pairs, only nests which were successful were compared. No effect of helpers on the number of fledglings, or independent fledglings, produced per nesting attempt was detected (all comparisons between means were n.s.). Overall, pairs with helpers did not produce more fledglings per season from successful nests (mean = 3.92 fledglings per pair) than did simple pairs (mean = 4.20 fledglings per pair, $t = 0.47$, n.s.).

The effect of prior experience on breeding success was calculated for data from the 1983/84, 1984/85 and 1985/86 breeding seasons combined. A bird was defined as being 'inexperienced' if it had not previously been recorded as part of a breeding pair. All first-year birds

and birds which had previously been helpers (but not breeders) were therefore counted as 'inexperienced'. Table 6.12 summarises the reproductive success of breeding pairs in which both, one or neither of the partners had previous breeding experience. Although a trend can be seen for inexperienced pairs to be less successful, there was no significant difference in the number of fledglings per season (Kruskal-Wallis test, $H = 1.35$, n.s.). The trend may be due to the fact that a higher proportion (41.3%) of nests built by inexperienced pairs were not built in brambles compared to pairs where one (29.6%), or both (23.3%) partners were experienced. Overall, inexperienced pairs (usually first-year males with newly arrived females) were more likely (5 out of 13) to occupy poor quality territories (ie. those with 10sqm or less brambles present) than were pairs where one (2 out of 11), or both (1 out of 9) partners were experienced.

A total of seven breeding groups (1983/84 to 1985/86 inclusive) contained an experienced breeding male together with an inexperienced breeding female. Four of these groups also contained at least one adult helper (all helpers were first-year males). Although the data are few, there did not appear to be any greater reproductive success for inexperienced females with helpers (0, 0, 7 and 7 fledglings per pair per breeding season) compared to inexperienced females without helpers (0, 4 and 8 fledglings per pair per breeding season).

6.4 Discussion

The start and cessation of egg-laying, and the length of the period between the first and last clutches of the season, were influenced by rainfall. In the extremely dry 1982/83 breeding season, for example, egg laying was restricted to the period between October and January. Similarly, an early end to egg-laying in the 1984/85 breeding season coincided with a dry summer. At Gungahlin, the beginning and end of breeding seasons were also affected by the weather conditions. A drought in 1957, for example, delayed egg laying by one month and inhibited egg laying in later months. In contrast, good rainfall stimulated both early egg laying and a lengthening of the breeding season into January. At Armidale, summer rains are more prevalent and egg-laying usually continued until February.

In addition to the timing of the breeding seasons, rainfall at Eastwood State Forest also seemed to influence clutch size. In the dry year of 1982, clutch sizes were smaller, on average, than other years, with a high proportion of 1, 2 or 3 egg clutches. In addition, 5 groups present in the 1982/83 breeding season did not attempt to breed at all. In general, good rainfall prior to the breeding season stimulated an early start to egg-laying and higher reproductive success for fairy-wrens.

The separation of the influence of helpers, from that of territory quality, on the reproductive success of breeding groups is often difficult (Lack 1968, Zahavi 1974,

1976, Brown 1978, Emlen 1978). A number of studies have attempted to control for environmental variables using multivariate statistical procedures, although some problems are inherent in this approach (Woolfenden and Fitzpatrick 1984). Furthermore, the evidence from these studies has not been consistent between species. In some studies for example the presence of helpers and territory quality may both be important factors contributing to reproductive success (Lewis 1981, Zack and Ligon 1985b) but in other studies variation in territory quality may be less important than the presence of helpers (Rabenold 1984, Hunter 1985). The influence of helpers on the reproductive success of breeding birds can be most readily identified in colonial-nesting species (eg. Reyer 1980, Emlen 1981) or when the effects of territory quality are controlled by experimental manipulation of group sizes (Brown 1982). In addition, the mechanism by which helpers increase reproductive output is, with a few exceptions, rarely understood. In some species helpers may increase the amount of food delivered to nestlings (Reyer 1980, Emlen 1981, Hunter 1985), help in such a way that the rate of nest-predation is reduced (Woolfenden and Fitzpatrick 1984, Austad and Rabenold 1985) or reduce the relative amount of energy expenditure by parents, allowing extra clutches to be laid per season (Rowley 1965, Woolfenden and Fitzpatrick 1984).

For Superb Fairy-wrens at Eastwood, no evidence could be found to support the hypothesis that helpers

increase the reproductive success of breeding pairs. No enhancement of the reproductive success of pairs with helpers could be detected after the effects of inter-year variation (YEAR) and territory quality (BAREA) were controlled by analysis of covariance. In addition, pairs with helpers were no more successful on average than simple pairs in nests built in the most favoured substrate type (brambles) and neither did they produce more fledglings from successful nests.

No effect of prior breeding experience on the number of fledglings produced per season could be detected. A slight trend for inexperienced pairs to be less successful than pairs where one, or both, partners had prior breeding experience could be accounted for by differences in territory quality. Inexperienced pairs were generally first-year males with newly arrived females and, in at least four cases (out of 13), they were males that had left their natal group and attempted to breed in nearby, marginal, habitat. Many inexperienced pairs (5 out of 13) attempted to breed in territories with 10sqm (or less) of brambles present, and few were found in high quality (greater than 100sqm of brambles) territories.

In Splendid Fairy-wrens (M. splendens), naive females (those without prior breeding experience) were found to be more successful when helpers were present, than when they were not (Rowley 1981). A similar, though non-significant trend was reported for naive males.

I suggest that one of the main reasons for the influence of BAREA, as well as the lack of influence of helpers, on the reproductive success of breeding pairs, is due to the high rates of nest-predation in the Eastwood population. Much of the evidence presented in this, and other chapters, can be used to support the hypothesis that nest predation is a major selective factor influencing the breeding biology of the Superb Fairy-wren. In Chapter 7, the loss of nest contents to predators was estimated to be very high (up to 51% of all nests may be lost, or abandoned, because of predators) but nest success varied with factors such as substrate type and degree of nest concealment. In particular, nests placed in blackberry brambles were considerably more successful than nests in other sites and well concealed nests were more likely to be successful than less well concealed nests. These results suggest that fairy-wrens at Eastwood select nest-sites so as to minimise their losses from predators.

Nestling behaviour and growth strategies in Superb Fairy-wrens also seem to be influenced by nest-predation. When nestlings are about 9 days, or older, they may fledge prematurely if sufficiently disturbed. The nestlings make a quick exit from the nest and seek shelter in nearby shrubs, grass tussocks, or other form of cover. Such behaviour might be advantageous if the nest is discovered by a predator late in the nestling stage. Normally however, nestlings fledged at about 12 days of age, at a weight considerably less than that of the adults.

Nestling development continued after fledging and a period of fledgling dependence was noted. Newly fledged nestlings were barely capable of flight and remained hidden in dense foliage where they were fed by the parents and any helpers present. In many other species however, nestlings exceed the weight of the adults prior to fledging and thereafter lose weight during the post-fledgling period (O'Connor 1978). Cody (1971) suggested that weight at fledging was correlated with the degree of post-fledging care among the alcids and that this might be a general trend for birds. Grey-crowned Babbler nestlings also fledge below adult weight (Dow and Gill 1934) and have extensive post-fledging care. In addition both the Superb Fairy-wren and Grey-crowned Babblers are co-operative breeders and therefore have helpers which might share the feeding of dependent fledglings with the parents.

Parents react in an agitated manner when the nest is disturbed and, particularly in the latter stages of the nestling period, may approach and scold the observer, or other bird species which approach the nest. Disturbance of older nestlings may also result in the performance of a distraction display by the parents (Rowley 1962, 1965). The distraction display was most frequently observed in the latter stages of nestling development (ie. between the ages of 6 days and fledging), but rarely observed when young nestlings (less than 6 days), eggs, or even fledglings were approached.

Table 6.13 shows that reproductive success in the Eastwood population was comparable with that of fairy-wrens at Gungahlin. Similarly, mean clutch-size did not differ significantly between the two populations and the proportion of eggs that eventually produced independent fledglings was also similar.

Rowley (1965) suggested that the feeding of dependent fledglings by helpers may result in increased reproductive success for the parent birds. The breeding female, relieved of some of the responsibility of caring for dependent fledglings, may therefore be able to re-direct her efforts to starting a new clutch. As a consequence, it might be predicted that inter-clutch intervals for pairs with helpers would be shorter than for those pairs without helpers. In the present study a significant shortening of inter-clutch intervals between successful nests could be attributed to the presence of helpers. The difference in the inter-clutch intervals for pairs with, or without, helpers may result in a time saving which would be enough for an extra clutch to be produced within the breeding season. In the present study however, pairs with helpers did not tend to produce more successful clutches, or fledglings, per season than simple pairs. Perhaps the ability to produce more clutches per season is important in populations that do not experience the same level of nest predation as the Eastwood population. The presence of helpers may be advantageous for example in populations where nestling starvation, rather than nest predation, is

the major cause of reproductive losses. The evidence from the present study however, suggests that the maintenance of delayed dispersal and helping behaviour in fairy-wrens is not dependent on there being any reproductive advantage to breeding pairs with helpers.

Table 6.1 Variation in the start, finish and length of breeding season and its relationship to variation in rainfall.

Breeding season	Rainfall in non-breeding season (mm)	Mean start of first clutch ¹	Rainfall in breeding season (mm)	Rainfall in Dec, Jan, Feb (mm)	Mean start of last clutch ¹	Mean inter-clutch interval (days)
		mean (S.E.)			mean (S.E.)	mean (S.E.)
1981/82	247.1	62.0 (10.9)	445.6	230.0	116 (15.0)	58 (20.2)
1982/83	122.6	70.1 (4.7)	327.4	185.2	118 (6.8)	56 (6.6)
1983/84	404.8	38.2 (6.6)	700.2	453.8	126 (6.7)	88 (10.6)
1984/85	297.8	50.9 (8.9)	375.2	182.6	107 (3.9)	66 (8.0)
1985/86	318.2	44.2 (6.3)	357.2	178.4	99 (8.4)	61 (12.4)

1. Number of days after 31st August.

Table 6.2 Nest-sites used by fairy-wrens, data from
1981/82 to 1985/86 breeding seasons.

Type of nest substrate	N of nests
Blackberry brambles	106
Woodpiles or fallen trees	32
Long-grass	
(i) base of sapling	12
(ii) other	6
Foliage of living trees	2 ^a
Rose bush	1

a. Eucalyptus sp., Exocarpus sp.

Table 6.3

Inter-year variation in clutch size.

Breeding season	Number of clutches					Mean clutch size
	C1	C2	C3	C4	(1) ¹	
1982/83	2	3	16	2	1	2.78
1983/84	1	0	18	18	7	3.43
1984/85	0	0	4	7	2	3.64
1985/86	0	1	7	17	1	3.64
Total	3	4	45	44	11	3.35

1. Nest parasitised by cuckoo, not included in calculation of mean clutch sizes.

Table 6.4 The number of nesting attempts made by breeding pairs each season.

Breeding	Number of nests per breeding pair					mean	
	0	1	2	3	4		5
1982/83	5	5	8	2	0	0	1.35
1983/84	0	1	3	4	6	2	3.31
1984/85	0	1	3	4	1	0	2.56
1985/86	0	0	2	3	5	2	3.58
Total	5	7	16	13	12	4	2.52

Table 6.5

Inter-clutch intervals (the number of days between the first egg of nest N and the first egg of nest N + 1, where N and N + 1 are successive nests).

Category	N successful				N not successful			
	mean	S.D.	N	range	mean	S.D.	N	range
A: Simple pairs	57.2	11.6	18	37-81	23.3	14.3	21	10-66
B: Groups with adult helpers	42.4	10.9	5	30-54	58.0	5.3	3	52-62

Table 6.6 Inter-year variation in reproductive success

Year	N of nests	Eggs laid	Eggs hatched	% hatched	Nestlings fledged	% fledged	Fledglings per nest	Number of successful nests	%
1981/82	15	33	23	69.7	10	43.5	0.67	4	26.7
1982/83	27	65	48	73.8	22	45.8	0.81	10	37.0
1983/84	53	156	94	60.3	61	64.9	1.15	23	43.4
1984/85	23	56	39	69.6	28	71.8	1.22	8	34.8
1985/86	43	121	70	57.9	44	62.9	1.02	15	34.9
Total	161	431	274	63.6	165	60.2	1.02	60	37.3

Table 6.7

Comparison of reproductive success
(number of fledglings per pair, per
season for A: simple pairs, and B:
groups with adult helpers).

Breeding	Category	Fledglings per pair		N	t	sig. of t
		mean	S.D.			
1981/82	A:	1.50	1.00	4	0.35	n.s.
	B:	2.00	2.83	2		
1982/83	A:	1.50	1.31	8	-0.80	n.s.
	B:	1.00	1.41	12		
1983/84	A:	3.43	2.14	14	1.32	n.s.
	B:	5.50	0.71	2		
1984/85	A:	4.20	2.17	5	-1.71	n.s.
	B:	1.75	2.06	4		
1985/86	A:	3.00	2.50	9	1.63	n.s.
	B:	5.67	2.31	3		
All years	A:	2.80	2.19	40	0.85	n.s.
	B:	2.30	2.38	23		

Table 6.8 Comparison of reproductive variables for simple pairs and groups with adult helpers, all data from 1981/82 to 1985/86 breeding seasons combined.

	Number of nests	Eggs laid	Eggs N laid	Eggs hatched N (% of eggs laid)	Nestlings N (% of nestlings)	Fledglings per nest	% of nests successful
A: Simple pairs	111	302	189	(62.6)	117 (61.9)	1.05	38.7
B: Groups with helpers	50	127	92	(72.4)	49 (53.3)	0.98	34.0
Total	161	429	281	(65.3)	166 (59.1)	1.03	37.3

Table 6.9 Relationship between habitat variables and reproductive success (number of fledglings per pair) in the 1983/84 breeding season.

Variable ¹	Correlation Coefficient (r)	sig. of r
TAREA	-0.03	n.s.
BAREA	0.54	p<0.05
NTREE01	-0.02	n.s.
NTREE02	-0.10	n.s.
PWOOD	0.08	n.s.
CCOVER	-0.23	n.s.

1. Variables explained in Chapter 4.

Table 6.10

Analysis of covariance table for effects
on annual reproductive output (number of
fledglings) per breeding pair.

Source of variation ¹	SS	df	F	sig. of F
Covariate				
BAREA	30.7	1	9.8	p < 0.01
Main effects				
YEAR	87.5	3	9.4	p < 0.01
GSIZE	0.0	1	0.0	n.s.
2-way Interactions				
YEAR x GSIZE	38.9	3	4.2	p < 0.05
Explained	153.7	8	6.2	p < 0.01
Residual	142.8	46		

1. Variables explained in text.

Table 6.11 Nest success of simple pairs, and groups with adult helpers, according to nest substrate type.

Nest substrate	Number of nests successful	Total nests	Percentage successful
A: Blackberry brambles			
Groups with adult helpers	14	36	38.9
Simple pairs	30	66	45.5
All groups or pairs	44	102	43.1
B: Others ¹			
Groups with adult helpers	0	3	0.0
Simple pairs	8	35	22.9
All groups with pairs	8	38	21.1

1. Nests in woodpiles, fallen trees, long-grass, living trees (see also Chapter 7.)

Table 6.12

Variation in reproductive success between pairs
with different levels of prior breeding experience.

	Fledglings per nest	⁹ Fledglings per season	Number of pairs
Neither partner experienced	0.30	2.85	13
One partner experienced	1.56	3.82	11
Both partners experienced	1.10	3.89	9

Table 6.13 Comparison of reproductive variables from Eastwood and Gungahlin populations of Superb Fairy-wrens.

Reproductive variable	Location of population	
	Eastwood S.F.	Gungahlin
Mean clutch size	3.35	3.37
Proportion of eggs that hatched	0.65	0.66
Proportion of nestlings that fledge	0.60	0.82
Proportion of fledglings that reach independence	0.82	0.53
Proportion of eggs that produce independent fledglings	0.32	0.29

Fig. 6.1 The number of clutches started in each month.
Data combined from five breeding seasons (1981/82 to 1985/86).

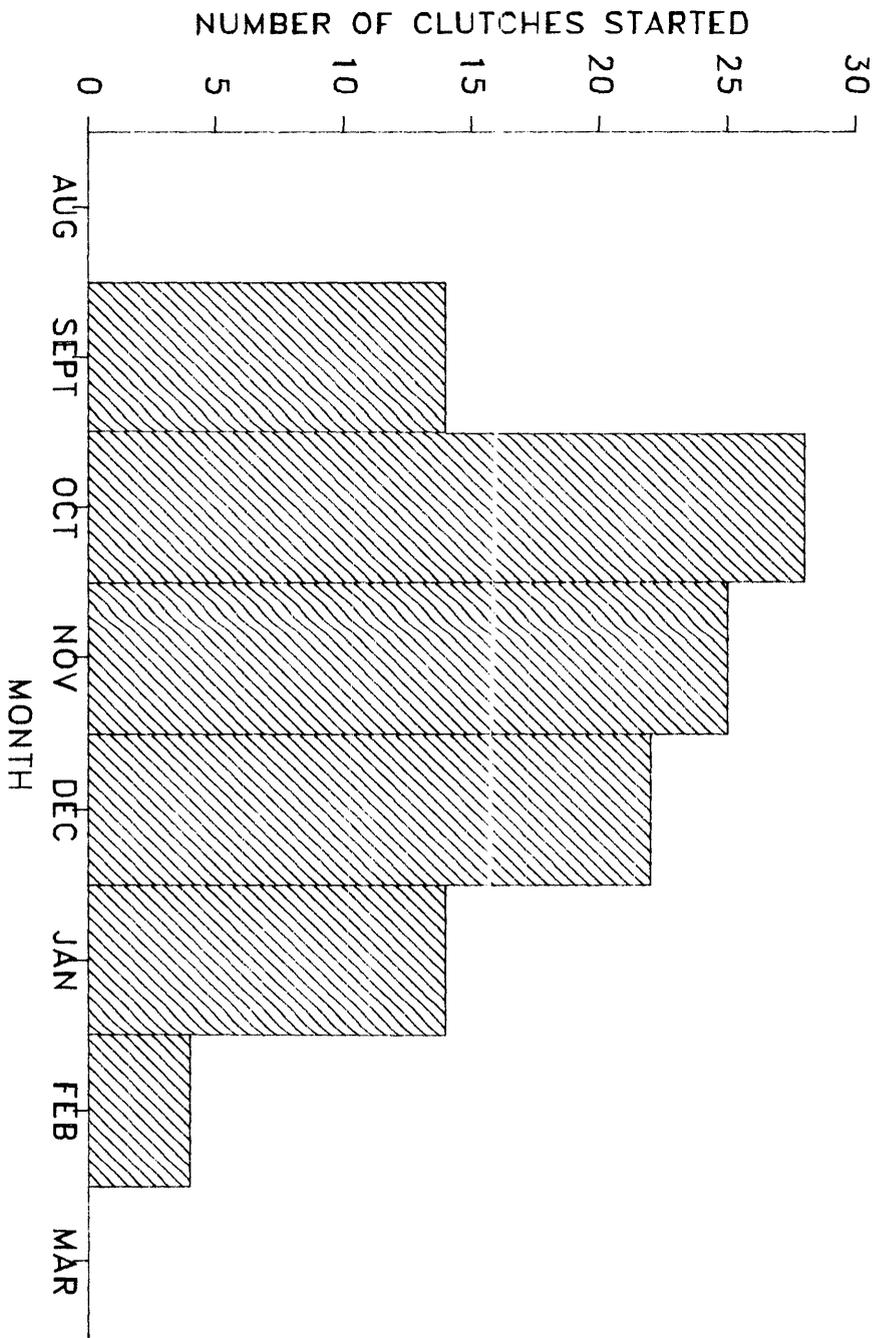


Fig. 6.2 The relationship between nestling weight (grams) and age (days after hatching).

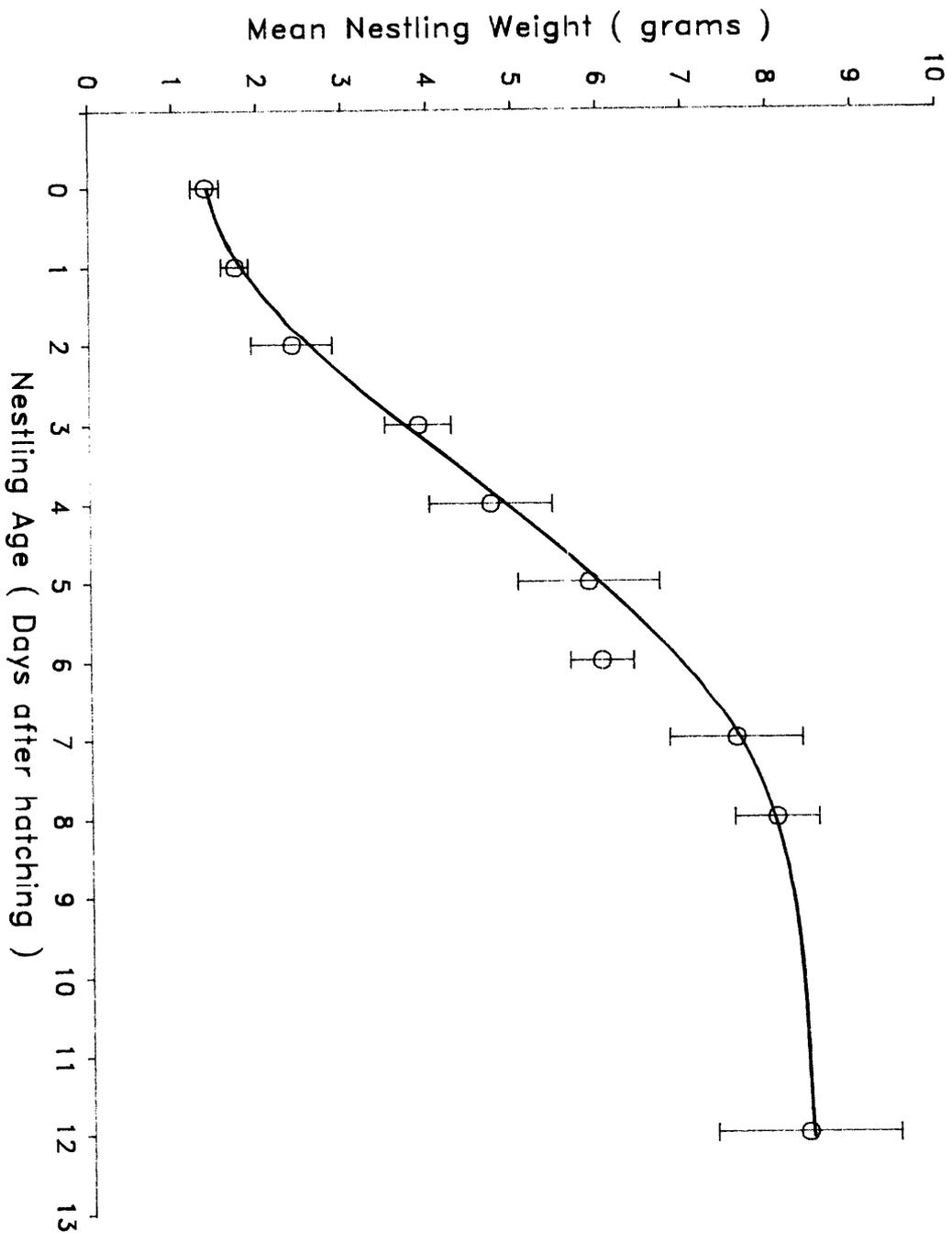


Fig. 6.3 The relationship between tarsus length of nestlings and age.

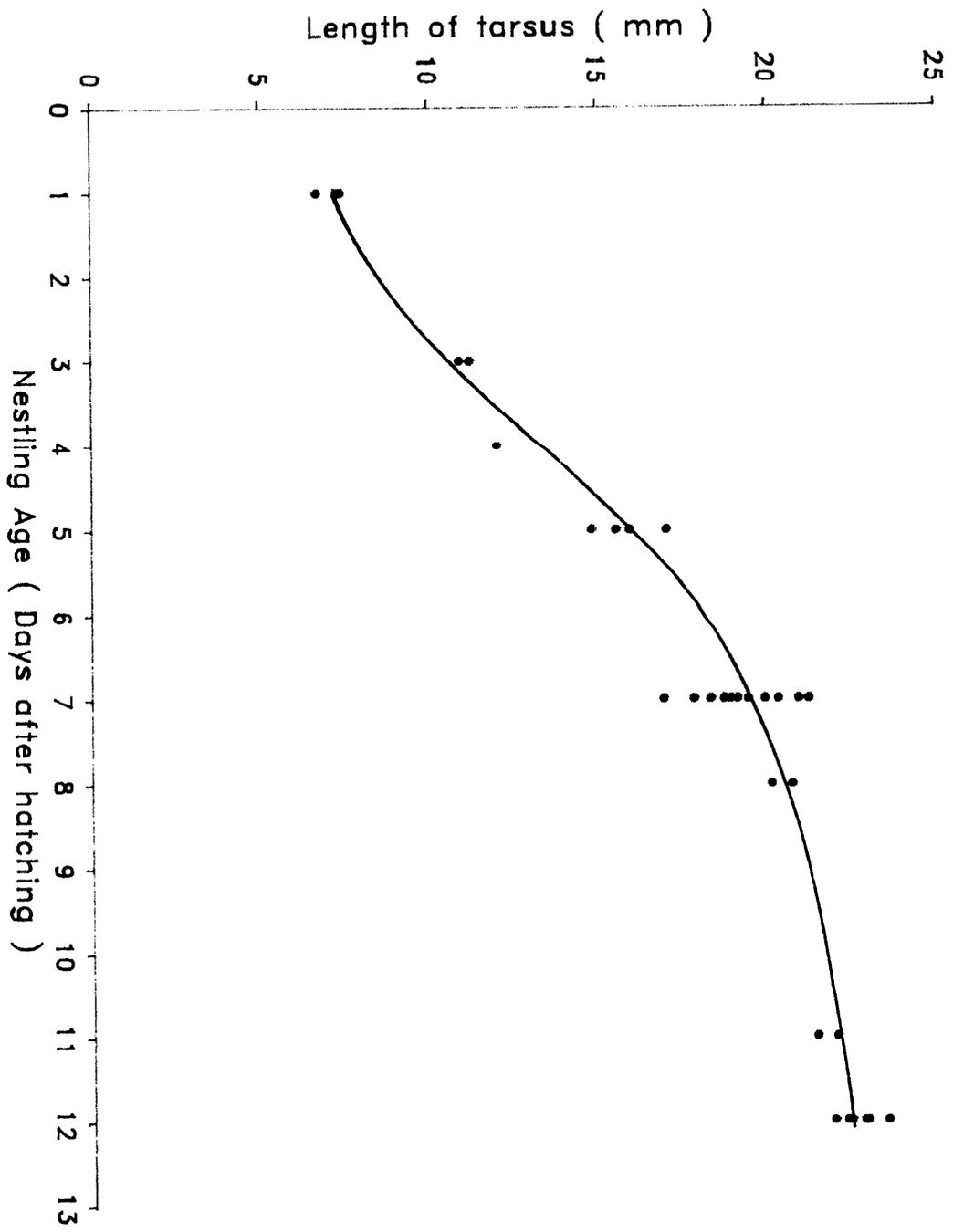
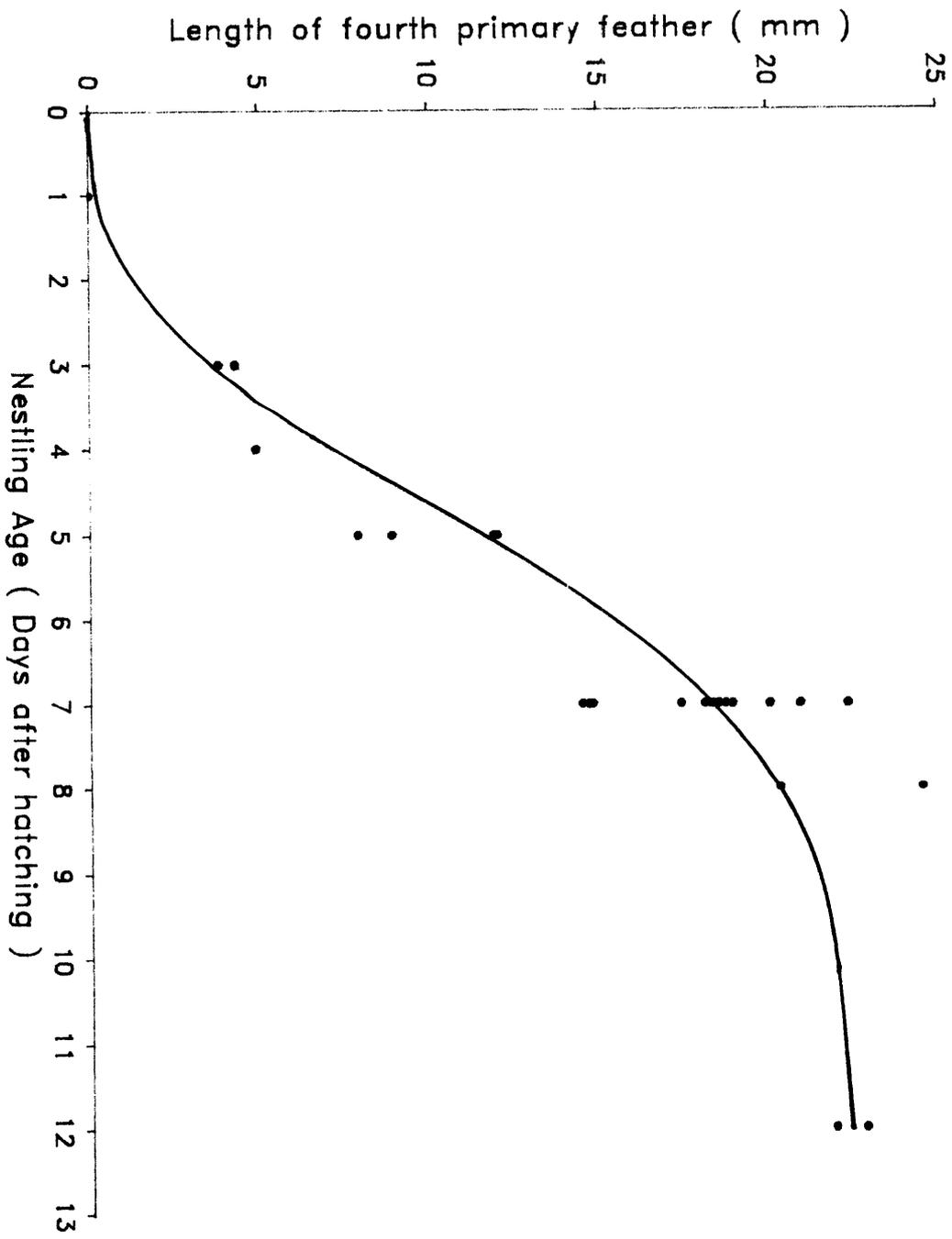


Fig. 6.4 The relationship between length of 4th primary feather and nestling age.



CHAPTER 7

NEST-SITE SELECTION

7.1 Introduction

One of the many factors that has been shown to influence the reproductive success of birds is nest placement (eg. Caccamise 1977, Best 1978, Wray and Whitmore 1979, Osborne and Osborne 1980, Murphy 1983). However, there is little published information on the importance of nest placement in the reproductive success of co-operative breeding species.

Predation is generally considered to be one of the major causes of nest failure in open - nesting passerines (Nice 1957, Nolan 1963, Ricklefs 1969). We should therefore expect nests of vulnerable species to be placed so as to minimise the chances of discovery by predators. In the present chapter I have investigated the relationship between some aspects of nest-site selection and reproductive success in the Eastwood population of the Superb Fairy-wren.

7.2 Methods

Each breeding season an attempt was made to locate all nests before eggs were laid. The subsequent reproductive effort was monitored and a number of nest-site characteristics were measured. The majority of nests were visited daily during the nesting cycle and many nestlings were banded and weighed. Successful nests were defined as those from

Footnote: part of this chapter has been published in Nias, R. C. 1986. *Emu* 86: 139-144.

which at least one fairy-wren fledged and nest productivity was defined as the number of fairy-wren fledglings per nesting attempt. Nests in which a complete loss of contents was recorded, including those subject to brood parasitism by cuckoos, were deemed unsuccessful.

In all breeding seasons the type of nest substrate used was recorded. During the 1983/84 breeding season, measurements were also made of a number of nest-site characteristics at all nests located.

The degree of concealment of each nest was estimated when viewing the nest, from above and from the sides, at a distance of about 1m. If I was not able to view the nest from above, then an estimate was made of vertical concealment by looking up at, and past, the nest. Concealment, both vertical and horizontal, was scored on a scale from 0 (nest entirely visible and exposed) to 6 (nest completely concealed from view), taking into account both the amount of nest visible, and the closeness with which the nest material resembled the colour and texture of the surrounding vegetation. Estimates of vertical and horizontal concealment were then combined as a single value (CONC) to express the total degree of nest concealment. An attempt was always made to assess nest concealment in the early stages of the nest cycle before nest outcome was recorded.

At each nest four (10m x 1m) quadrats were located radially from the nest, the direction of the first quadrat being chosen at random and the others at 90°

increments from the first. The number of sub-canopy height (TRA) and canopy height (TRB) trees present in the four quadrats was then recorded. Along the centre of each quadrat a line was positioned to radiate from the nest. The total length of this line intercepted by woodpiles and fallen trees (WOOD) and blackberry brambles (CBRA) was used to estimate the amount of area covered by these substrates near the nest. At points 0m, 5m and 10m from the nest along each line a visual estimate of canopy-cover was made and the values summed for each nest-site (CACO). The total area covered by the nest substrate was estimated by projection onto the ground (SUBS). Measurements were made of the depth of the nest in the substrate (VDE) and of the distance from the edge of the substrate to the nest entrance (LDE).

The rationale of this sampling technique, in which the quadrats or other sampling units radiated from the nest-site, was to sample more thoroughly in the immediate nest area at the expense of the area further from the nest. Sampling intensity therefore decreased in proportion to the square of the distance from the nest. Many of the nest-site variables showed highly skewed distributions and were transformed before statistical analysis. The following transformations were made; GSIZE (\log_{10}); HAG, SUBS, TRA, TRB (square root); WOOD and CBRA (arcsin percentage). Statistical procedures, using transformed data where appropriate, were performed using the SPSS statistical package (Nie et al. 1975).

7.3 Results and Discussion

Fairy-wren nests are typically built in dense vegetation from pieces of dry grass woven together with spider-webs. A large entrance is built in the oval nest about two-thirds from the base and a short roof, platform, or both may be built at the entrance. The inside of the nest is lined with finer pieces of grass and the bottom of the nest is covered with feathers or other soft materials (Rowley 1965, Beruldsen 1980). Nests have been found in thick grass, grass tussocks, small shrubs and other dense vegetation (Rowley 1965, Beruldsen 1980).

At Eastwood, nests were found in a variety of locations and substrates (see Chapter 6) but most commonly among the outer foliage of blackberry brambles. An attempt was made to record the outcome of all nests found in a four-year period (1981/82 to 1984/85 breeding seasons). The 1985/86 breeding season was omitted from this analysis because of extensive defoliation of brambles due to weed control measures within the forest. The outcome of all but three nests was recorded in the remaining four breeding seasons.

Brood parasitism, nest predation, and abandonment were all significant causes of complete, or partial, nest failure (Table 7.1). Some 23 out of 45 otherwise successful nests lost some of their contents during the nesting period. There was no evidence, however, to suggest that starvation had been the cause of nestling loss in any of

the breeding seasons. On the one occasion when dead nestlings were found undisturbed in the nest, there had been exceptionally low temperatures recorded in the previous 24 hours and snow had fallen in areas near the study-site. If nestlings had starved, then the bodies of the nestlings must have been removed by the adult birds. British tits (Parus sp.) may remove dead nestlings from the nest if they are small (Perrins 1979) but this was not observed for fairy-wrens.

Complete losses of nest contents were assumed to have been due to predation, and a number of nests showed obvious signs of disturbance. Although predation was never actually witnessed, a number of potential nest predators were observed at the study-site including Pied Currawongs Strepera graculina, Grey Shrike-thrushes Colluricincla harmonica, snakes, foxes and rats.

Table 7.2 compares the reproductive output of nests made in brambles with nests made in other substrates. Nests in brambles were more often successful ($\chi^2 = 5.43$; $p < 0.05$) and produced more fledglings per egg laid ($\chi^2 = 6.63$; $p < 0.05$) than those in non-bramble sites. Bramble nests were more successful in terms of the proportion of eggs that hatched ($\chi^2 = 5.28$, $p < 0.05$) and the proportion of nestlings that reached the age of 7 days ($\chi^2 = 5.12$, $p < 0.05$). However, bramble nests were no more successful than nests in other substrates in terms of the proportion of 7 day old nestlings that eventually fledged ($\chi^2 = 0.0$, n.s.).

A number of nest-site characteristics were recorded during the 1983/84 breeding season and these are summarised in Table 7.3. Tests were then made on these variables for differences between successful and failed nests. Successful nests were found to be better concealed ($t = 2.66, p < 0.05$) and surrounded by a higher coverage of brambles ($t = 2.13, p < 0.05$) than unsuccessful nests. In a comparison of only those nests built in brambles, successful nests were again better concealed than failed nests ($t = 2.11, p < 0.05$).

Correlations were made with the remaining nest-site variables in order to determine which physical features of the nest-site were associated with the degree of nest concealment. Nest concealment was negatively correlated with height above ground ($r = -0.36; p < 0.05$) and positively correlated with vertical depth in the substrate ($r = 0.35; p < 0.05$) and with substrate size ($r = 0.35; p < 0.05$).

Nest concealment has also been found to be an important influence on nest outcome in other species (Caccamise 1977, Wray and Whitmore 1979, Osborne and Osborne 1980, Joern and Jackson 1983). Nests concealed among dense foliage, for example, may be less likely to be found by predators, particularly those that hunt by sight such as birds. Better concealed nests may also be less accessible to predators. However concealment probably has little influence on predation by snakes and nocturnal mammals, which utilise non-visual clues when

searching for nests (Best 1978). Gottfried and Thompson (1978) however, in an experimental study of nest predation, could find no evidence that better concealed nests were less likely to be preyed upon. They suggested instead that predators may use subtle means of nest detection such as the observation of parental activity, rather than relying totally on visual searching.

Concealment of the nest in dense foliage, or selection of particular substrate types, may also reduce the rate of brood parasitism by cuckoos. A total of three out of 35 nests in brambles (8.6%), and four out of 17 nests in other substrate types (23.5%) were parasitised. As with their hosts, cuckoos were more often successful in brambles (100%) than in other nest-sites (25%).

A multiple regression analysis (Nie et al. 1975) was used to find the combination of variables that best explained the variation in the number of fairy-wren fledglings produced per nest. The resulting equation explained 36% of the variation in nest productivity (N of fledglings = $-1.13 + 0.22 \text{ CONC} + 0.02 \text{ CACO} - 0.05 \text{ WOOD}$; $R^2 = 0.36$, $F(3,33) = 6.23$; $P = 0.002$).

Secondly, a discriminant function analysis (DFA) was used to find the set of variables that best separated successful from unsuccessful nests. Discriminant function analysis is a technique that can be used to separate two groups of variables on the basis of some prior classification (eg. Green 1971, Whitmore 1977). In the present study for example, I have used DFA to separate successful from

failed nests on the basis of a number of nest-site characteristics. The discriminating power of the set of variables was measured in this study by the determination of Wilk's Lambda, a value inversely related to the overall multivariate F value (Nie et al. 1975). A minimum tolerance of 0.1 was enforced to reduce the problems associated with highly interrelated variables (Cavallaro et al. 1981).

Successful nests were separated from unsuccessful nests ($p < 0.01$) on the basis of being higher above the ground (HAG), closer to the edge of the substrate (LDE) and better concealed (CONC) than unsuccessful nests (Table 7.4). Nests placed higher above the ground may be less accessible to ground based predators, and better concealed nests should be less likely to be discovered. However, the significance (and negative influence) of the variable LDE (lateral depth of nest in substrate) could not be explained in these terms.

It is difficult to make meaningful comparisons between species, or even the same species at different locations, without controlling for variations in predator density, weather conditions, or other factors that may affect nesting success. In the present study, however, 34.6% of eggs were lost before hatching, while Rowley's figures for the Gungahlin population indicate a similar loss (34.2%, from Table 8, p.281, Rowley 1965). However, the losses between hatching and fledging at Eastwood (40.5%) and Gungahlin (18.4%) were considerably different.

The high loss of eggs during the incubation phase would suggest that nest predation was an important influence on the reproductive success of birds in both populations. Nest predation at the nestling stage would appear to be more important in the Eastwood population than at Gungahlin.

At Eastwood, brambles provided a greater degree of concealment for nests than did other substrate types and this may partially explain the greater success rate of nests placed in brambles. Brambles also possess protective thorns which may deter predators even if the nest is discovered. In a study of long-tailed Tits Aegithalos caudatus by Lack and Lack (1958) for example, it was found that nests placed in thorny brambles or shrubs were more likely to be successful than nests built on the smooth branches of trees.

The importance of nest predation as a cause of mortality in fairy-wren offspring argues for the importance of behavioural adaptations which minimise such losses. One of the most important adaptations would therefore appear to be nest-site selection. However, for good nest-sites to be chosen, they must be present within the territory to begin with. Therefore, strategies which enable birds to gain breeding positions in territories with potentially good nest-sites (ie. brambles) should be highly favoured by natural selection.

Table 7.1 Fates of nests in four breeding seasons (1981/82 to 1984/84). Only nests of known outcome included.

Fate of nest	N of nests	% of nests
Abandoned or destroyed before laying	24	20.7
Parasitised by cuckoo	12	10.3
Total contents missing		
(i) eggs	17	14.7
(ii) nestlings	18	15.5
Successful	45	38.8
Total nests of known outcome	116	100.0

Table 7.2 Reproductive variables measured over four breeding seasons (1981/82 to 1984/85) according to nest substrate type.

Substrate type	Eggs laid	Eggs hatched	7-day old nestlings	Fledglings produced	Fledglings per egg	Successful nests (%)
Blackberry brambles						
Total (77 nests)	209	146	112	92		
Mean per nest	2.71	1.90	1.45	1.19	0.44	47.4
S.D.	1.34	1.64	1.59	1.41		
Others¹						
Total (38 nests)	97	54	32	27		
Mean per nest	2.55	1.42	0.84	0.71	0.28	23.1
S.D.	1.62	1.78	1.52	1.35		
All nests	306	200	144	119	0.39	39.3

1. See text.

Table 7.3 Descriptions and values obtained for nest-site characteristics and nest placement in 1983/84 breeding season.

Variable measured	Mean	S.E.	Range	N
HAG: height of nest above ground (cm)	36.09	5.24	10-150	52
VDE: vertical depth of nest in substrate	54.47	5.45	5-200	43
LDE: distance from nest to edge of substrate (cm)	57.75	5.46	10-200	40
SUBS: area covered by nest substrate (sqm)	20.07	3.28	0.5-110	41
CONC: index of nest concealment	8.43	0.39	4-12	46
TRA: density of sub- canopy trees (N per 40 sqm)	10.63	1.47	0-40	51
TRB: density of canopy height trees (N per 40 sqm)	1.96	0.27	0-10	51
WOOD: % area covered by woodpiles/fallen trees	4.63	1.03	0-32	51
CBRA: % area covered by brambles	18.82	2.23	0-60	51
CACO: % canopy cover	45.95	3.38	0-80	51

Table 7.4

Results of Discriminant Function Analysis
between successful and failed nests.

Variable ¹	Standardised discriminant function coefficient	Wilk's lambda	level of sig.
HAG	0.65	0.70	p < 0.01
LDE	-0.37	0.68	p < 0.01
CONC	1.06	0.74	p < 0.01

1. Variables explained in Table 7.3.

CHAPTER 8

NESTLING FEEDING RATES

8.1 Introduction

In Chapter 6 I showed that helpers did not increase the seasonal reproductive output of breeding birds. However, the presence of helpers in any one breeding season may have some influence on the lifetime reproductive success of breeders. If, for example, helpers reduce some of the potential costs of reproduction, then the survivorship (and hence lifetime reproductive success) of breeders may be improved.

Co-operative breeding species are characterised by the presence of supernumerary birds which help to feed and care for the offspring of the breeding birds. In some species, helpers may increase the total amount of food delivered to nestlings (Dyer and Fry 1980, Sappington 1977, Ligon and Ligon 1978, Wilkinson and Brown 1984, Hunter 1985). The additional food supplied by helpers may be of particular importance when food is scarce (Reyer 1980). In other species, however, the total feeding rate may not be affected, but breeding birds may benefit by sharing the energy costs and risk associated with feeding nestlings (Brown 1972, Parry 1973, Gaston 1973, Rowley 1978, Vehrencamp 1978, Brown et al. 1978, Dow and Gill 1984).

In one study of nestling feeding in a co-operative breeding species, Brown et al. (1978) measured the influence of a number of social, physiological and environmental variables on the feeding rate of nestling Grey-crowned Babblers. Total feeding rates were found to be dependent on the energy needs of the nestlings, environmental factors such as temperature and previous rainfall but not the number of helpers present. Although helpers did not increase total feeding rates, the number of feeds delivered by parents was reduced in the presence of helpers. In the same species, Dow and Gill (1984) compared the growth rates of nestlings with the number of helpers present. Environmental variables such as temperature and rainfall were found to be more important influences on nestling growth rates than was the number of helpers feeding the brood.

Studies of the feeding rates of fairy-wren nestlings (Rowley 1965, 1981, Tidemann 1980) have largely been inconclusive due to small sample sizes and high variability. In the present study a total of sixty-nine nest-watches, of approximately one-hour duration each, were made at nests of the Superb Fairy-wren. A particular aim of the study was to identify the effect, if any, of helpers on the feeding rate of nestlings and the proportion of the feeds to nestlings made by each group member.

8.2 Methods

Nest-watches were made at nests which could easily be seen, with 10 x 50 binoculars or a small spotting-scope, from a distance of 30-50m. For some nests of particular interest a hide was erected 10-15m from the nest several days before a planned watch. Sixty-nine nest-watches were made with each lasting from 30 to 100 minutes, the majority (56) being at least 60 minutes in duration. All nest watches were made in the morning between 0800 and 1200h.

Nest-watches were made from day 0 (the day nestlings hatched) to day 11 (the day before fledging). Three watches were also made of groups feeding recently fledged young and these were assigned an arbitrary age of 12 days for statistical analysis.

The number of visits to the nest made by each group member was recorded and calculated in terms of number of visits per hour. In many nest-watches an estimate of the size of each food item brought to nestlings was made. Food-size was scored relative to the bill length of the individual on the following scale; 0 = food item either absent or too small to be visible, 1 = food item less than, or equal to, one bill length, 2 = food item between one and two bill lengths, and 3 = food item greater than two bill lengths. Food items were identified when possible.

Three different social groups of fairy-wrens were identified for this analysis; (1) simple pairs comprising only the breeding birds, (2) pairs with immatures from previous nests of the same year, but no adult helpers, and (3) pairs with adult helpers present, with or without immatures.

Estimates were made during each nest watch of cloud-cover (0 = zero cloud cover, 1 = up to 25% cloud cover, 2 = 25%-50% cloud cover, 3 = 50%-75% cloud cover, 4 = 75%-100% cloud cover) and wind speed (0 = calm conditions, 1 = slight breeze, 2 = moderate breeze). Nest-watches were not made during very windy conditions or in continuous rain.

8.3 Results

Of the sixty-nine nest-watches made, 34 involved simple pairs, 6 involved pairs with immatures only, and 29 involved pairs with adult helpers (16 with one helper and 13 with two helpers).

Since immatures contributed only about 3.6% of all nest visits, pairs with immatures only were combined with simple pairs in most analyses.

During the first few days after hatching females spent much of their time brooding the nestlings. The total percentage of each nest-watch spent brooding declined from about 90% on the first day down to about 15% on the third day after hatching. Major periods of brooding generally ceased when nestlings were 4 days old. When females were

brooding nestlings, males would occasionally perch near to the nest and call, the brooding female would then leave the nest to forage with the male. Food was often passed to the female while on the nest, or females would meet the male or helper near the nest and take the food from them. A 'wing-flutter' display (Tidemann 1980) by the breeding female was often seen when she encountered males or helpers near the nest. The female crouches with head and tail extended, and the wings are rapidly fluttered while being held out slightly from the body. Tidemann described this display in the White-winged Fairy-wren Malurus leucopterus and suggested that it was an agonistic display toward other birds near the nest. A similar function for this display may be possible in Superb Fairy-Wrens, although the display was not seen to deter the other group members from feeding the nestlings. On one occasion the food taken to the nest by a male helper was given to the female after she gave a 'wing-flutter' display. The food item was then passed on to the nestlings by the female.

All group members, including immatures and adult helpers were seen to attack other species that came near the nest, including Fuscous Honeyeaters Lichenostomus fuscus Grey Shrike Thrushes, and Eastern Spinebills Acanthorhynchus tenuirostris. Of these, the Grey Shrike Thrush may be a nest predator (Reilly 1966).

Faecal sacs were removed from the nest by all group members, usually being swallowed when nestlings were young and carried 15-20m from the nest when nestlings

were older. In all nest-watches, females were seen removing faecal sacs on 22 occasions and males on 13 occasions. For the 29 nest-watches involving adult helpers, faecal sacs were removed by adult helpers on only 4 occasions.

Only a small fraction of the food items delivered to nestlings could be identified with any certainty and it is likely that the results obtained are biased towards the larger and more easily identified species. Identified food items included adult and larval lepidopterans, other unidentified larvae and grub-like organisms, millipedes, ants, spiders, dragonflies (Odonata) and grasshoppers (Orthoptera).

The mean size of food items delivered to nestlings increased with nestling age. The relationship between mean food-particle size and nestling age did not appear to be exactly linear. Mean food-particle size tended toward an upper limit of about 1.5 at 6 days of age but correlation coefficients were not improved by transformation (food size squared). Food size was correlated with nestling age for deliveries by breeding males ($r = 0.58$, $p < 0.001$, $n = 40$ nest-watches), breeding females ($r = 0.56$, $p < 0.001$, $n = 44$ nest-watches) and adult helpers ($r = 0.56$, $p < 0.05$, $n = 14$ nest-watches). No correlation was attempted for immatures because of small sample size ($n = 3$ nest-watches).

The nest-visitation rate (number of nest-visits per hour) was significantly correlated with nestling age only for females ($r = 0.53$, $p < 0.001$, $n = 69$ nest-watches).

If the correlation is repeated only for nestling ages over 4 days (ie. when most brooding has finished) then the results remain significant ($r = 0.46$, $p < 0.01$, $n = 42$ nest-watches). Nest-visitation rates were not correlated with nestling age for males ($r = 0.19$, $n = 69$ nest-watches), adult helpers ($r = 0.15$, $n = 28$ nest-watches) or immatures ($r = 0.17$, $n = 9$ nest watches).

Negative, but non-significant, correlations were found between food-particle size and nest-visitation rate after controlling for nestling age with a partial correlation analysis (Males : $r = -0.15$, $p = 0.36$; Females: $r = -0.11$, $p = 0.48$).

A third measure of the amount of food delivered to nestlings, the relative biomass, was calculated to take into account both the delivery rate and size of food items. Using the regression equations obtained between food-size and age of nestlings for each group member, a standard mean food-size was calculated for each day of nestling age. The standard mean food-size was then multiplied by the nest-visitation rate to obtain the relative biomass of food delivered. Relative biomasses were correlated with nestling age for deliveries by breeding males ($r = 0.43$, $p < 0.001$), breeding females ($r = 0.62$, $p < 0.001$) and adult helpers ($r = 0.43$, $p < 0.05$). The total relative biomass of food delivered to nestlings by the whole group was correlated with nestling age ($r = 0.60$, $p < 0.001$).

Analyses of covariance (Nie et al. 1975) were used to test for the effects of a number of variables on the various measures of nestling feeding. A linear regression model was used in which covariates (nestling age) and effects (cloud-cover, year, wind-speed, brood size and group size) were tested individually while all other variables were held constant. The results of the analyses are summarised in Table 8.1. Immature and adult helpers were not included in these analyses because of small sample sizes in many categories.

Mean food-size delivered by males and females was not affected by any of the variables measured except nestling age. Although insufficient data were collected in some years for inter-year comparisons to be made, no obvious differences were noted.

Total nest visitation rates increased with nestling age and also varied between years with the highest rates being recorded in the 1985/86 breeding season. Inter-year variation may be due to a number of factors such as differences in the abundance or types of food organisms present, weather, or sampling error due to observer inconsistency between years. Total nest-visitiation rates declined with increasing wind strength. Nest-visitiation rates increased with brood size (Fig. 8.1) with broods of one nestling visited less frequently than broods of two ($t = 3.75, p < 0.01$) and broods of 3 nestlings visited less frequently than broods of 4 ($t = 2.34, p < 0.05$).

However, no significant difference was found in nest-visitation rates between broods of 2 and 3 nestlings ($t = 0.12$, $p = 0.90$).

Breeding males visited nests less frequently in groups with helpers than in simple pairs ($t = 3.12$, $p < 0.01$). However, results from the analysis of covariance (Table 8.1) indicate that the overall effect is marginally non-significant ($p = 0.054$). No effect of group size was seen on the nest-visitation rates of females, or on the total nest-visitation rate.

The relative biomass of food delivered to nestlings increased with nestling age as would be expected from earlier simple correlations. The relative biomass was also affected by inter-year variation, and by brood size in a similar manner to nest-visitation rates. The relative biomass of food, delivered by groups as a whole, was not affected by the presence of helpers. Males delivered a lower relative biomass of food on average in groups with helpers than when in simple pairs ($t = 3.4$, $p < 0.01$).

However, group size had a marginally non-significant effect on the relative biomass delivered by males, after controlling for all other factors ($p = 0.067$.)

Mean food-size over the whole of the nestling period did not differ significantly between breeding males and females ($t = 0.10$; n.s.) or between females and adult helpers ($t = 0.01$; n.s.). In contrast, mean nest-visitation rates were higher for females than for males

($t = 2.8$, $p < 0.01$), or adult helpers ($t = 2.3$, $p < 0.05$) and the relative biomass of food delivered to nestlings by females was, on average, greater than that for males ($t = 2.44$, $p < 0.05$) or adult helpers ($t = 3.67$, $p < 0.01$).

In order to determine more clearly the effect of helpers on nest-visitation rates, the proportion of visits made by each group member was calculated. Fig. 8.2 shows the relationship between the percentage of visits made by breeding males and breeding females in relation to the number of helpers present at each nest-watch. Adult helpers made an average of 19.9% (s.d. = 16.2%) of all nest visits. In groups with two adult helpers present, the combined efforts of the helpers averaged 35.5% (s.d. = 18.6%) of all nest visits. Male helpers made a lower proportion of all nest-visits than did female helpers ($t = 2.66$, $p < 0.05$). Immatures made only a small proportion (about 1.5% per individual) of all nest-visits.

Both males and females showed a decline in the percentage of nest-visits made as the number of helpers increased. Males made a slightly lower percentage of all visits when 2 helpers, rather than 1 helper, were present ($t = 1.84$, $0.1 > p < 0.05$); and fewer visits when 1 helper, rather than no helpers, were present ($t = 2.49$, $p < 0.05$). Overall, males made a lower percentage of all visits when in groups with adult helpers ($t = 3.72$, $p < 0.01$). The percentage of visits made by females did not differ significantly in comparisons between groups of different sizes, or between groups with, or without, helpers.

8.4 Discussion

In the present study, two variables (food-size and nest-visitation rate) were measured at watches of fairy-wren nests. The aim of the study was to relate the delivery of food to nestlings to social (group size), environmental (wind speed, cloud cover) and other variables (nestling age, brood size). In particular, an attempt was made to determine the role of helpers in the care of nestlings, and the effect of helping behaviour on the amount of parental care delivered by breeding birds.

Food-size increased with nestling age but was unaffected by the number of nestlings present, cloud cover, wind speed, or group size. An inter-year variation in food-particle size may have been due to differences in the abundance and type of prey organisms present, or to observer inconsistency. Increasing food size with nestling age has been documented in a number of studies (eg. Best 1977, Pinkowski 1978, Biermann and Sealy 1982, Bedard and Meunier 1983). Fairy-wrens chose food items consistent with the capacities of the nestlings and very young nestlings (1 or 2 days old) were fed on items generally too small to be seen by the observer, while older nestlings were often fed grasshoppers, moths, caterpillars and other items twice the length of the adult bill.

Nest-visitation rates increased with nestling age from a mean of 11.7 (s.d. = 6.3) visits per hour on the first day after hatching to a mean of 32.7 (s.d. = 5.0) visits per hour for young fledglings. Nest-visitation rates

also increased with brood size, decreased with wind speed, but were unaffected by cloud cover or the presence of helpers.

The percentage of visits made by adult helpers in total (0 to 56%) is generally lower than those recorded for Mexican Jays Aphelocoma ultramarina (46 to 68%, Brown 1972), Florida Scrub Jays (25 to 76%, Stallcup and Woolfenden 1978) and Grey-crowned Babblers (30 to 70% Brown et al. 1978) although comparisons are difficult because most of these species had more than two helpers in many groups. Immature helpers (ie. those from a previous brood in the same breeding season) made only a minor contribution towards the care of their siblings and were not a significant influence on the total nest-visitation rate.

A third variable, the relative biomass of food delivered per hour, was calculated by multiplying nest-visitation rates by standard food-sizes. Food-size was standardized for different group members (breeding males, breeding females, adult helpers) and for different nestling ages from regression equations. The relative biomass of food delivered to nestlings increased with brood size and nestling age and varied between years, but was unaffected by the other variables measured. The relative biomass of food delivered to nestlings was calculated in order to express better the actual amount of food delivered to nestlings over a given time period (ie. a product of both the size and rate of delivery of food items). Nest visitation rate alone may not always be a sufficient

indication of the amount of food delivered to nestlings. A number of studies (eg. Bedard and Meunier 1983) have pointed out that, for a given energy requirement, nestlings may be fed on many small items, or just a few large ones. In the present study however, no significant correlations were found between food size and nest-visitation rates.

Although no significant differences were found in the mean food-particle sizes delivered by different group members, breeding females visited nests more frequently than males or helpers and therefore made a higher overall contribution to nest provisioning. Breeding females also did all of the brooding of the nestlings and most frequently removed faecal sacs from the nest. Since females also build the nest, lay and incubate the eggs (Rowley 1965, see also Chapter 6) it can be seen that females assume by far the greatest portion of direct parental care. It might be expected therefore, that breeding females might gain the most from the presence of supernumerary birds which help feed and care for nestlings. There is probably a trade-off, for example, between the amount of care provided for nestlings and that required for self-maintenance (Ricklefs 1974, Drent 1975, Howe 1979) and that by 'lightening the load' associated with parental care, helpers may enhance the reproductive success and/or survival of the breeders (Rowley 1965, Brown 1978, Brown et al. 1978, Stallcup and Woolfenden 1978, Rabenold 1984). However, the amount of nest provisioning undertaken by the female was not significantly lower, either in absolute

terms or as a percentage, when helpers were present. Neither were there any differences in the survivorship of breeding birds with, or without, helpers over the breeding season.

In a study of co-operative breeding in the Galapagos Mockingbird Nesominus parvulus, Kinnaird and Grant (1982) also found a situation in which breeding males, but not breeding females, visited nests less frequently in the presence of helpers. However, no explanation was attempted for this dichotomy. I suggest that among fairy-wrens, the difference may be due to the different roles of males and females during the breeding season, and in particular, the role of breeding males in territorial defence. Once freed from some of the responsibilities of feeding nestlings, breeding males may be able to devote more time to territorial defence. In this context, it would be interesting to know how breeding males in groups with, or without, helpers partition the relative amount of time spent on various activities such as territorial defence, self-maintenance, and in parental duties. Furthermore, Gaston (1978a) suggested that the assistance given to breeders may be a form of 'payment' for not being excluded from the group. Since it is generally assumed that helpers benefit by remaining within the group until suitable breeding positions become available in the population (Selander 1964, Brown 1978, Emlen 1982a, Emlen and Vehrencamp 1983) then the parents are in a position to 'demand' the provision of alloparental care by helpers

by excluding those that do not help. With respect to Superb Fairy-wrens however it is only the breeding male that seemed to benefit, at least in terms of the amount of parental care provided. Breeding males should therefore tolerate helpers which assume some of the parental care activities. It is possible that even though females do not seem to benefit directly in the presence of helpers, they may be unable to exclude male helpers from the group.

In some studies it has been suggested that the amount of alloparental care provided by helpers may be adjusted according to the amount of potential benefit they receive by remaining within the group, or their dominance in relation to the other helpers (Woolfenden and Fitzpatrick 1977, Carlisle and Zahavi 1986). Supernumerary birds in the Superb Fairy-wren may act as helpers as some form of 'payment' for not being excluded by the breeding male. This type of evidence is contrary to the view that helping behaviour may simply be mis-directed parental care (Price et al. 1983, Jamieson 1986) and of no adaptive significance in itself.

Table 8.1 Summary of analyses of covariance for effects of measured variables on nestling feeding rates.

Source of variation ¹	A: Food size		B: Nest-visitation rate		C: Relative biomass of food		
	Breeding males	Breeding females	Breeding males	Breeding females	Breeding males	Breeding females	
Nestling age	**	***	n.s.	**	***	***	***
MAIN EFFECTS							
Cloud cover	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Year	n.s.	n.s.	**	***	**	**	**
Wind speed	n.s.	n.s.	*	n.s.	*	n.s.	n.s.
Brood size	n.s.	n.s.	*	*	*	n.s.	*
Group size	n.s.	n.s.	p=0.05	n.s.	p=0.07	n.s.	n.s.
EXPLAINED	*	*	***	***	***	***	***

1. Variables explained in text.

* = p < 0.05

** = p < 0.01

*** = p < 0.001

Fig. 8.1 The relationship between the number of nest-visits made per hour and brood size. Data from all years combined. Vertical bars indicate standard error of the mean.

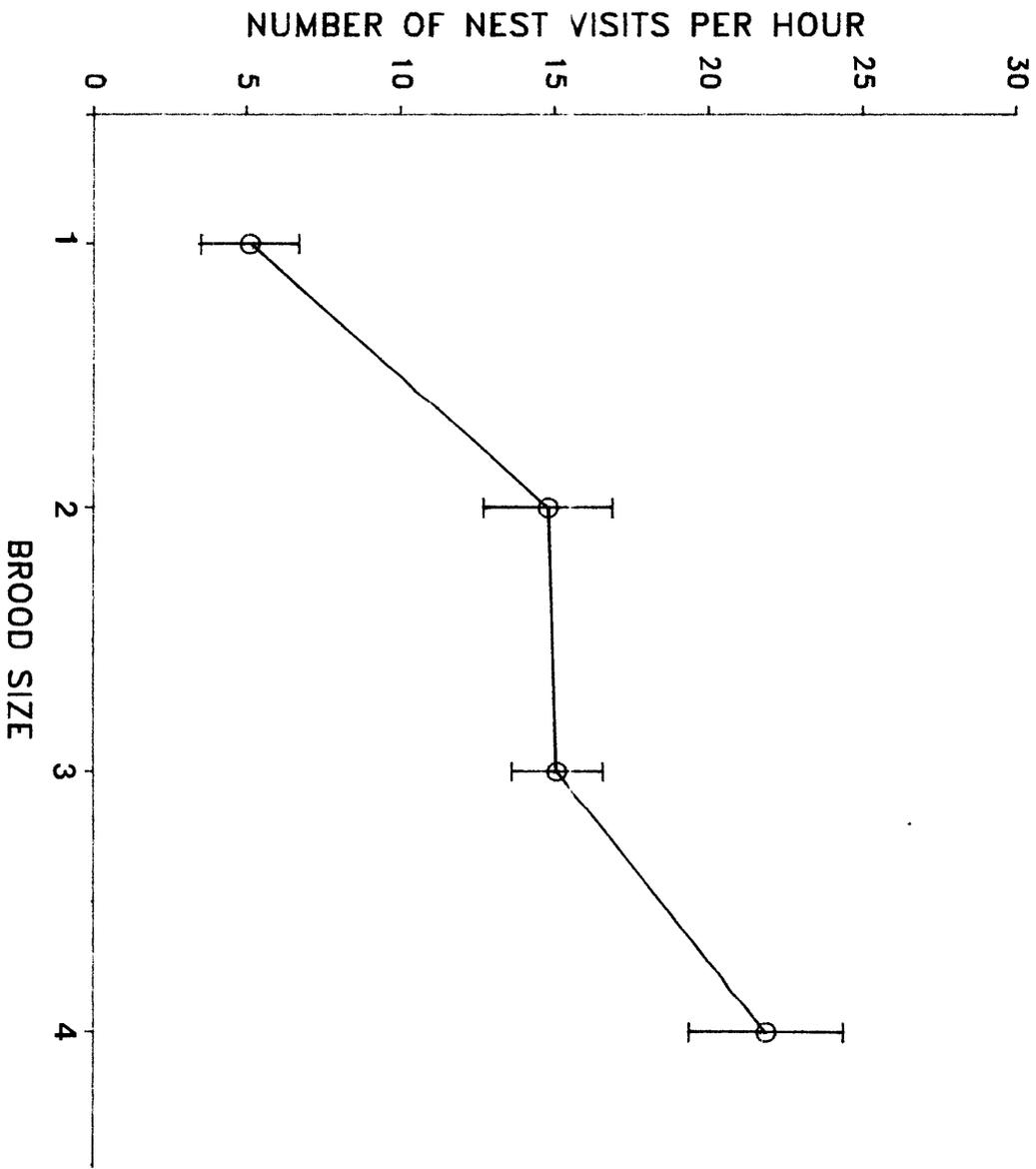
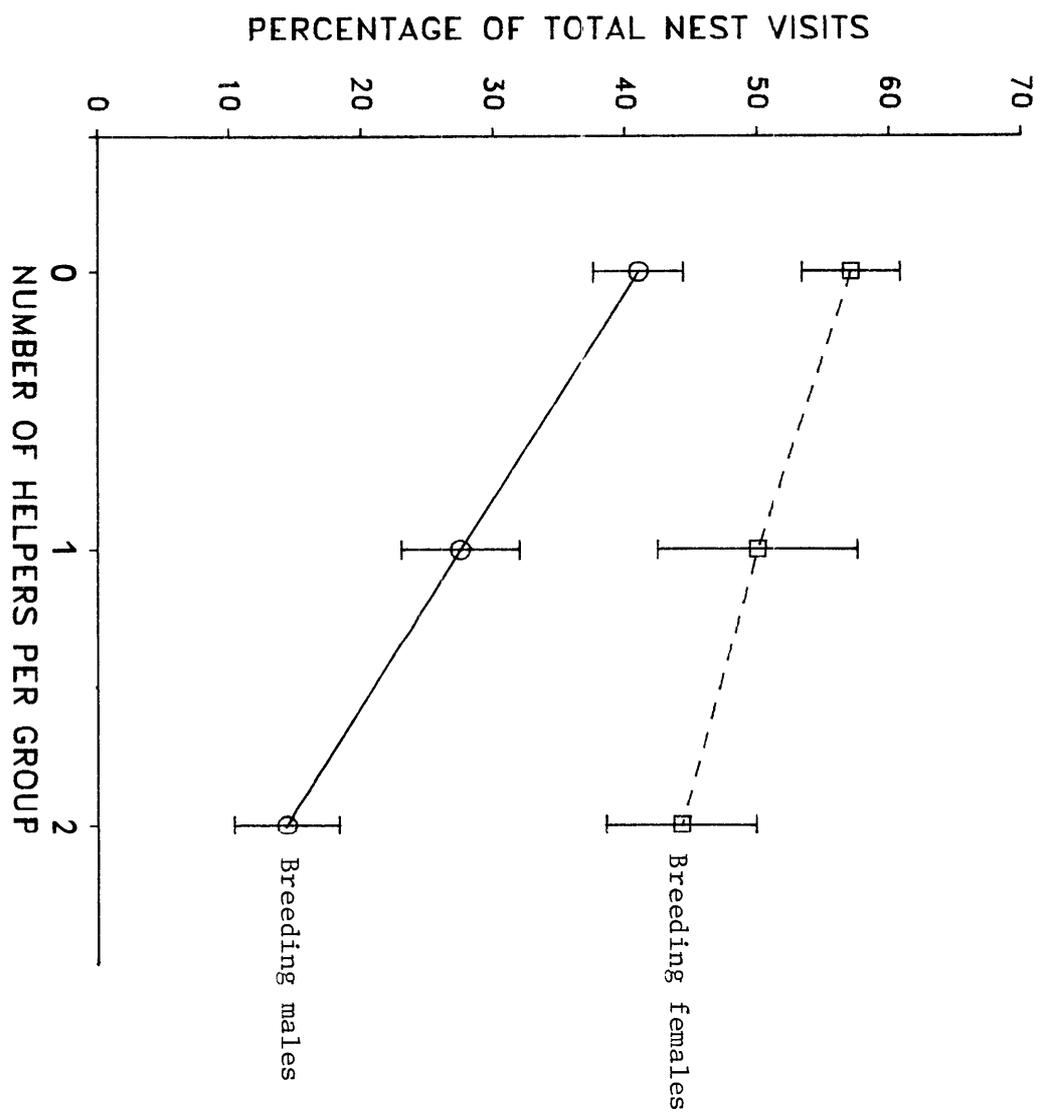


Fig. 8.2 Mean percentage of all nest visits made by breeding males and breeding females in groups with 0, 1 and 2 adult helpers. Vertical bars show standard-error of the mean.



CHAPTER 9

GENERAL DISCUSSION

9.1 Introduction

Previous chapters have outlined the results of a four-year study of Superb Fairy-wrens at Eastwood State Forest. In the present chapter, the results are integrated into an adaptive explanation for the maintenance of cooperative breeding in this population.

9.2 The life-history of the Superb Fairy-wren

Data on the ecology and life-history of fairy-wrens were collected with particular emphasis on the following aspects; (i) the social, ecological, and demographic factors which affect breeding opportunities for immatures and helpers, (ii) factors which influence the reproductive output of breeding pairs, and (iii) the behaviour of non-dispersers in the natal group.

Fairy-wrens at Eastwood lived in social groups comprising a single, monogamous, breeding pair together with a variable number of non-breeding adult helpers and immatures. Helpers were the offspring of one, or both of the breeding birds that had failed to disperse from the natal group. Instead of breeding themselves, helpers aided the reproductive efforts of the breeding pair assisting in the defence of the breeding territory and in the raising of offspring.

Many helpers eventually gained access to breeding positions by dispersal to unoccupied habitat, filling vacancies in established groups, or (males only) by inheriting the breeding position within the natal group.

Each group of fairy-wrens occupied an exclusive, all-purpose territory during the breeding season (approximately September to February). Within each territory were patches of dense understory vegetation or thicket (mostly fallen trees, woodpiles, sapling regrowth and blackberry brambles) interspersed with relatively clear, open ground. Most nests were made in the available dense understory vegetation or thicket whereas fairy-wrens foraged mostly on the ground in the clear areas. In general, there was little understory vegetation present at Eastwood and fairy-wrens were largely confined to patches of blackberry brambles occurring along temporary water-courses or other disturbed areas.

The amount, or quality of essential resources contained within the territory is an important influence on the ecology and social organisation of many co-operative breeding species (eg. MacRoberts and MacRoberts 1976, Brown and Balda 1977, Craig 1979, Stacey 1979, Trail 1980, Lewis 1981). The communally breeding Acorn Woodpecker Melanerpes formicivorus, for example, relies on the presence of specially modified trees in which to store their food (acorns from trees of the genus Quercus) over the winter. The size and composition of breeding groups has been found to be correlated with the density of 'storage' trees (MacRoberts and MacRoberts 1976) as well as the size and reliability of

acorn crops (Trail 1980) and other ecological factors (Stacey and Bock 1978).

At Eastwood, the area of brambles present per territory was found to have an important influence on the ecology and social organisation of fairy-wrens. Groups on territories with large areas of brambles for example, had higher survivorship, greater reproductive success, and more helpers than did groups on territories with fewer brambles. Brambles were therefore considered to be an important component of fairy-wren territories and an indication of territory quality. Brambles provided refuge from predators and adverse weather and nests in brambles were more often successful, and produced more fledglings per nesting attempt, than nests in other substrate types. However, because the survivorship of fairy-wrens on territories with a large area of brambles was twice that recorded for adult birds on territories with small, or no areas of brambles, breeding opportunities on the best territories would occur less frequently. The area of brambles present within a territory was therefore an important influence on the lifetime reproductive success, and hence the fitness, of resident birds. Consequently, the potential fitness of immature fairy-wrens and helpers would depend, to some extent, on their ability to acquire breeding positions within good quality territories.

In the present study, I attempted to determine how, and when, fairy-wrens obtained breeding positions and which factors influenced the availability or suitability of such positions. Central to this question was the demography of the population, particularly mortality rates, dispersal, and recruitment to the population (Chapter 3) as well as the extent and variability of certain resources essential to reproduction (Chapter 4).

About 75% of annual adult mortality occurred during the winter months (May to July) when temperatures on the New England Tablelands regularly fell below 0°C and arthropods are relatively scarce (Bell 1985). However, there were no differences in the annual mortality rates of breeding males (56%), breeding females (56%), and adult male helpers (50%). Immatures seemed to survive less well during the non-breeding season than adults and this may have been partly due to their apparent inexperience in foraging techniques (Chapter 5).

Dispersal by all sex and age classes occurred most frequently in July and August, just before the start of the breeding season. Females dispersed more frequently, and further, than did the relatively sedentary males. These findings confirm the results obtained by Rowley (1965) in his study at Gungahlin and, in both the Eastwood and Gungahlin populations, the sex-ratio of birds arriving in the population after dispersal from other areas was similar (ie. about 1 male : 3.5 females). Most dispersal by males involved movement to nearby territories (in order to fill a breeding vacancy), whereas females rarely settled close

to their natal territory. Although dispersal in Splendid Fairy-wrens was much less frequent (Rowley 1981), there was again a preponderance of females among the dispersers. The ratio of male to female dispersal in Splendid Fairy-wrens was identical to that reported in the Superb and female-biased dispersal seems to be a characteristic feature of fairy-wrens.

If dispersal entails some risk of mortality, then it might be expected that female fairy-wrens should suffer greater mortality than males. The number of females arriving in the population (ie. immigrants) might therefore be lower than the number leaving (ie. emigrants). Skewed sex-ratios found in populations of Superb Fairy-wrens and other co-operative breeders (Fry 1972, Dow 1977, Woolfenden and Fitzpatrick 1978, Greenwood 1980, Reyer 1980) may therefore result from greater dispersal by one sex. Florida Scrub Jays, for example, show a male biased sex-ratio among adult helpers as well as greater long-distance dispersal by females (Woolfenden and Fitzpatrick 1984). However, a male biased sex-ratio in the Galapagos Mockingbird Nesomimus parvulus may be the result of greater mortality among female breeders, rather than dispersers (Kinnaird and Grant 1982). In general, a biased sex-ratio may be the result of (i) differences in the number of male and female fledglings produced, (ii) differential mortality in the immature stages, (iii) differential mortality during dispersal prior to breeding, or (iv) differential mortality among adults. Although no systematic attempt was made to identify the sex of immatures at Eastwood (mostly because of difficulties with re-capture

and lack of plumage differences) there were no obvious differences in the sex-ratio of birds captured at this stage. Similarly, Rowley (1965) found no difference in the number of male and female immatures prior to dispersal. There was also no difference in the mortality rates of male or female adults in either population. A skewed sex-ratio among adult fairy-wrens was therefore most likely to have arisen from differential mortality during the dispersal phase.

The ability of fairy-wrens to acquire breeding positions in the population was constrained by the limited extent of suitable habitat or, for males, a relative scarcity of sexual partners. A high degree of competition for breeding positions might therefore be expected among potential breeders and co-operative breeding may be one adaptation to such competition. A major benefit of delayed dispersal, for example, is the ability to monitor breeding vacancies within the population from the relative safety of the natal group (Brown 1978, Emlen 1982a, Emlen 1984 and others).

(1) Why do some birds delay dispersal from their natal group?

Potential breeders might delay dispersal from their natal group if their ability to acquire breeding positions within the population is limited by certain demographic or ecological 'constraints' (Emlen 1982a). Specifically, three factors should influence the likely success of potential breeders in their efforts to acquire

a breeding position; (i) the extent and quality of unoccupied habitat, and (ii) the probability of locating a mate and (iii) the probability of successful reproduction, should they become established as breeders. The first of these factors has generally been referred to as the 'habitat-saturation' hypothesis. The concept of habitat-saturation was first discussed by Selander (1964) in a taxonomic monograph of the Campylorhynchus wrens (Troglodytidae) and was brought to the attention of behavioural ecologists through the work of Brown (1974, 1978). Put simply, habitat saturation arises when the number of potential breeders in the population exceeds the number of breeding positions available. Habitat saturation should therefore be of particular relevance to a long-lived, permanently territorial species with specific habitat requirements such as the Superb Fairy-wren.

Koenig and Pitelka (1981) also suggested that marginal habitat, in which birds might live as 'floaters' while waiting for breeding opportunities to arise, should also be scarce if habitat saturation was to favour delayed dispersal. At Eastwood, fairy-wrens did not form into groups of non-breeding birds in marginal habitat. Any marginal habitat (ie. that which did not contain brambles) that was occupied usually contained other forms of understory such as fallen trees or woodpiles. Even if they made no nesting attempts, birds on marginal habitat were obviously unsuccessful 'breeding pairs' (eg. as in 1982/83) rather than 'floaters'.

In the 1982/83 and 1983/84 breeding seasons at Eastwood, virtually all brambles were occupied by breeding pairs and only unsuitable habitat (ie. that which lacked any dense understory vegetation) was unoccupied by fairy-wrens. Some fairy-wrens occupied habitat which lacked brambles, but which contained other forms of understory such as fallen trees and woodpiles but these groups suffered higher mortality rates and had lower reproductive success than the population average. Of the 5 groups which occupied 'marginal' territories, 2 made no attempt to breed, and of the remainder, only one nest (out of a total of 9 nesting attempts) was successful. The success rate of these groups (11.1%) was therefore considerably lower than that achieved by the rest of the population over this period (45.2%). In addition, only one male (20.0%) and one female (20.0%) were still present as breeders in the following year compared with an average survival rate of 44% for all breeding adults in the population. As would be predicted from the habitat saturation hypothesis, helpers of both sexes were common in both breeding seasons in terms of absolute numbers (eg. 1982/83) or (as in 1983/84) when measured as a proportion of the fledglings produced in the previous year (see Table 3.5, Chapter 3).

In the 1984/85 and, to a lesser extent, the 1985/86 breeding seasons, some areas of apparently suitable habitat were not occupied by fairy-wrens. These areas contained substantial patches of brambles and had previously been occupied by successful breeding groups. Although no female

helpers were present, some males remained as helpers in both of these breeding seasons. The absence of females as helpers is therefore consistent with the habitat saturation hypothesis but the presence of male helpers is not. The occurrence of male helpers in the 1984/85 and 1985/86 breeding seasons may have resulted from an apparent shortage of mates. Unfortunately, no assessment of the number of unmated females in areas surrounding the study-site was made, but there were certainly fewer groups in close proximity (ie. within a radius of 1km or so) to Eastwood than were in the study-site itself. The number of females potentially able to enter the population through immigration might therefore have been less than the number of potential breeding males within the population. In addition, the pool of available females might have been further reduced by mortality during dispersal. A number of authors have also discussed the relationship between skewed sex-ratios and the presence of male helpers in the Superb Fairy-wren (eg. Brown 1975, Emlen 1978, 1984, Emlen and Vehrencamp 1983, 1985, Wittenberger 1984). In an analysis of data collected by Rowley at Gungahlin, for example, both Brown (1975) and Emlen (1978) suggested that delayed dispersal by male fairy-wrens was only favoured when there was a relative scarcity of females in the population. Furthermore, Emlen and Vehrencamp (1983, 1985) suggested that a correlation between the population sex-ratio and the proportion of groups with helpers was evidence for the

'skewed sex-ratio' hypothesis. However, this analysis needs to be considered in more detail. The inclusion of data from Splendid Fairy-wrens (Rowley 1981) for example, does not strengthen the argument as these points do not conform to the general correlation (eg. Emlen 1984, Fig. 12.5, p.322). Considered on their own, the data from Splendid Fairy-wrens do not support any correlation between sex-ratio and the presence of helpers. Female helpers were regularly recorded by Rowley in his study of Splendid Fairy-wrens although two different figures (19% and 38%) were given (Rowley 1981). A more important point, however, is whether or not the data are suitable for testing of the hypothesis. The population sex-ratio, for example, was calculated as the ratio between all adult males and females, but since virtually all helpers at Gungahlin were males, then it is simply an arithmetic truism to show that the number of helpers varied in accordance with the population sex-ratio. In other words, the skewed sex-ratio is a function of the number of male helpers present, rather than a measure of the number of females that are able to enter the population and breed.

Emlen (1982a) also argued that periods of poor environmental conditions may restrict breeding opportunities, and therefore favour delayed dispersal in co-operative breeding species. Studies of the White-fronted Bee-eater Merops bullockoides (Emlen 1982a, 1984, Emlen and Vehrencamp 1983, 1985) for example, have shown a correlation between pre-breeding season rainfall (and by inference the abundance of arthropods) and the presence of helpers. It was suggested

that during periods of low rainfall, the level of parental investment required to raise offspring successfully was prohibitive for novice breeders, and so delayed breeding would be favoured.

At Eastwood, rainfall was found to influence the reproductive output of fairy-wren groups. Again it can be assumed that during harsh periods (ie. the drought in 1982) there is a relative shortage of food and that breeding birds would experience some difficulty in feeding nestlings (see also Bell 1983). Although no direct evidence of starvation of nestlings could be found, the proportion of nestlings that eventually fledged was lowest in the 1982/83 breeding season. Drought conditions may also have reduced the ability of females to lay eggs and/or build new nests and replacement clutches. Therefore, the poor reproductive performance of many breeding groups in the 1982/83 breeding season suggests that food abundance is another factor that influences reproductive opportunities for fairy-wrens. However, it may still have been advantageous for potential breeders to acquire a territory and a mate, if these were available, even if the prospects for immediate breeding success were low. Earlier dispersers, for example, would be able to start reproducing immediately should favourable conditions return.

All immature Superb Fairy-wrens and adult helpers either disperse from their natal group, or remain (at least for a short-term) as non-breeding helpers. In this section

I have suggested that a decision to delay dispersal by immatures or adult helpers may be made if their probable success is lowered by habitat saturation or a shortage of sexual partners. In order to test the adaptive significance of delayed dispersal in co-operative breeding species, a number of authors have attempted to determine the relative costs and benefits of such behaviour (eg. Reyer 1984, Wiley and Rabenold 1984, Woolfender and Fitzpatrick 1984). The adaptive significance of delayed dispersal may then be assessed in terms of lifetime reproductive success.

In Table 9.1 the average lifetime reproductive success for fairy-wrens in the Eastwood population is estimated. Included in the table are differences in estimated lifetime reproductive success (ELRS) which can be attributed to differences in territory quality. The lifespan of an individual was taken to be three years. No effect of age on reproductive output, after the first year, nor any influence due to the presence of helpers, could be detected in this study. Therefore, Table 9.1 allows a simple comparison to be made of the ELRS for individuals following two different life-histories; (i) non-dispersal and non-breeding in the first year, followed by breeding in the second year (either by dispersal or inheritance), or (ii) breeding from the first year onwards, after dispersal or inheritance. The comparison suggests that the only difference in ELRS that arises from the alternatives is due to the reproductive output of first-year breeders. Therefore, delayed dispersal should not be favoured in this population

unless the advantages of doing so outweigh the cost due to not breeding in Year 1. In addition, the relative advantages of delayed dispersal depend to some extent on the quality of the territory that is eventually acquired for breeding. Immatures and helpers may therefore delay dispersal from their natal group if, by doing so, they can substantially improve their chances of gaining breeding positions in good quality territories in the future. By remaining as helpers on good quality territories, potential breeders experience better survivorship while waiting for breeding vacancies to occur. Resident helpers may also be better able to acquire a breeding vacancy through inheritance, than would a competitor from outside of the group seeking to fill the same vacancy. In summary, if breeding opportunities in the population are constrained by some factor, then delayed dispersal by fairy-wrens should be favoured over earlier dispersal if (i) survivorship is enhanced by remaining in the natal group, and (ii) if non-dispersers can inherit breeding positions. In addition, the advantages of delayed dispersal for some birds at Eastwood are enhanced by the disparity in quality of territories (see also Chapter 3).

(2) Why do non-dispersing birds help to raise the offspring of others?

In addition to the potential benefits to be gained by remaining within the natal group, non-breeding birds may also benefit by helping to raise their parents' offspring. There are four general hypotheses which suggest

why non-dispersers should help: (i) the 'payment' hypothesis. If non-dispersers benefit from remaining within the natal group then helping may be some form of payment, possibly to offset any disadvantages to the parents in allowing their offspring to remain (Brown 1969, Gaston 1978a).

(ii) experience gained by helping may later prove valuable as a parent (Rowley 1981, Woolfenden and Fitzpatrick 1984).

(iii) individuals raised by helpers may later reciprocate by assisting in the helpers own breeding efforts (Brown 1975, Woolfenden 1975, Wiley and Rabenold 1984).

(iv) the kin-selection hypothesis. Helpers may improve their inclusive fitness by raising non-descendant kin (Hamilton 1964, Brown 1974). However, it may not be possible to determine which, if any, of the proposed hypotheses best explain helping behaviour as they do not make mutually exclusive predictions. Two of these hypotheses are unlikely to be important for Superb Fairy-wrens for the following reasons; (i) experience gained as a helper did not seem to improve the reproductive success of breeders. No differences were found in the reproductive output of second-year birds that had helped, or not helped in their first year, (ii) individuals raised by helpers did not appear to reciprocate this help in later years. The 'payment' hypothesis is considered in a later section.

The importance of kin-selection in the evolution of co-operative breeding has often been discussed (Brown 1978, Brown and Brown 1981, Emlen 1978, 1981, Gaston 1978a, Ligon and Ligon 1978, Vehrencamp 1979, Koenig and Pitelka 1981 among others). The inclusive fitness of an individual

can be divided into two parts, the 'direct' component resulting from an individual's own reproductive efforts, and the 'indirect' component resulting from an enhanced production of genetically close relatives (Brown 1980). The indirect fitness component for fairy-wren helpers therefore arises as a function of the increased reproductive output of breeders that are helped, relative to those that are not helped, modified by the coefficient of relatedness between the helper and the breeders' offspring. The chance for non-dispersers to enhance their fitness through the production of extra relatives (ie. to increase their indirect fitness) is therefore another potential benefit to be derived from delayed dispersal. Analysis of Rowley's data for Superb Fairy-wrens at Gungahlin by Emlen and Vehrencamp (1983, 1985) however, have shown that the indirect fitness gained by helping behaviour is not sufficient, in itself, to compensate for direct fitness lost through delayed breeding. The importance of constraints on the reproductive opportunities for potential breeders are supported by this analysis of the Gungahlin population. However, this approach does not specifically address the problem of why non-dispersers should help, but rather the differences between the fitness of individuals when helping compared with their fitness when breeding. In order to test whether helping behaviour is beneficial to non-dispersers, it would simply be necessary to show that they enhanced their inclusive fitness (ie. by producing sufficient extra relatives) to an extent which compensated any loss in fitness acquired from providing such assistance.

In order to quantify the indirect fitness component arising from helping behaviour it is first necessary to establish the relationship between the presence of helpers, and the reproductive output of the breeders. Attempts to establish such a relationship have been a common goal in studies of co-operative breeding (see discussion in Chapter 6). For Superb Fairy-wrens in the Eastwood population however, there was no evidence to suggest that helpers enhanced the reproductive output of breeders. Simple pairs raised an average of 2.80 fledglings per season while groups with helpers raised an average of 2.30 fledglings per season (Table 6.7). Using an analysis of covariance it was shown that the presence of helpers was not a significant influence on group reproductive success after controlling for inter-year variation in rainfall and differences in territory quality. These results are apparently in contrast to those reported by Rowley for the Gungahlin population. However, in Chapter 6, I suggested that the effect of helpers on group reproductive success observed at Gungahlin may have been partly due to other factors, such as differences in territory quality. In particular, the difference in reproductive success of groups with, or without, helpers at Gungahlin was due to the proportion of eggs that hatched, rather than the number of nesting attempts per season, or the proportion of nestlings that fledged. I suggested that this difference in reproductive success was more likely to be a result of lower nest predation, than to any help given by non-dispersers. Rowley (1965, p. 281) also

hinted at the importance of territory quality to reproductive success, but in a somewhat different context. He argued that, in a year when the population was largest, some birds were forced to breed in sub-optimal habitat and, as a consequence, greater reproductive losses were recorded at the egg-stage. In a less crowded year, however, sub-optimal habitat was avoided and reproductive losses were lower.

Although there were no obvious benefits to helping behaviour in the Eastwood population, in terms of extra relatives being raised, neither were there any great costs. The only real cost that might occur would be additional energy expended in providing food to the nestlings. With no net fitness benefit to be gained, only two explanations appear to be able to account for the maintenance of helping behaviour in the Eastwood population. Either, (i) helping behaviour has some function other than increasing the production of offspring, such as a reduction in the amount of parental care given by breeding birds (see next section) or (ii) although not adaptive per se there are no reasons for it to be selected against. Several authors (eg. Price et al. 1983, Jamieson 1986) have suggested that helping behaviour is simply mis-directed parental care. Since parental care is an important suite of behavioural traits, any minor costs resulting from mis-directed parental care (eg. helping behaviour) would not be significant and selection against helping behaviour under these circumstances could be counter-productive (Brown and Brown 1984). Adaptive

explanations for the presence of helping behaviour in birds would be more easily invoked if it were shown that helpers adjusted the amount of aid given according to the amount of benefit which could be gained (eg. Clarke 1984, Carlisle and Zahavi 1986).

(3) Why should breeders tolerate grown offspring in the natal group?

There are three types of benefit which breeders might gain from co-operative breeding: (i) increased survival due to the presence of others, ie. in terms of better predator detection and/or food location (eg. Bertram 1978), (ii) increased seasonal reproductive output due to the presence of helpers, (iii) better prospects for the survival and ultimate breeding by their offspring (eg. Brown and Brown 1984). The degree to which any, or all, of these potential benefits contribute to the adaptive significance of co-operative breeding seems to vary between different species. In Pied Kingfishers, for example, helpers contribute to the survival of nestlings by increasing the amount of food delivered (Reyer 1984). In contrast, helpers in Campylorhynchus wrens (Austad and Rabenold 1985) and Florida Scrub Jays (Woolfenden 1975, Woolfenden and Fitzpatrick 1984) may reduce the levels of nest predation. Furthermore, helpers may reduce the level of parental care given by breeding birds, allowing more broods to be raised per breeding season (Rowley 1965, Brown and Brown 1981).

In Chapter 5, I suggested that benefits gained from group living may be most important to fairy-wrens during the non-breeding season. At this time individuals foraged widely for food over relatively large home ranges and occasionally wandered outside of the study-site into nearby cleared areas. Different groups often combined into foraging aggregations or semi-permanent 'super-groups' and joined other species in mixed flocks. This behaviour may have improved the survivorship of individuals during the non-breeding season. In the breeding season however, breeders did not survive better in groups with helpers, than in simple pairs.

Although there was no net increase in the amount of food delivered to nestlings, the proportion of feeding visits made by the breeders was lower in the presence of helpers. The greatest reduction in parental care was exhibited by breeding males (from about 40% of all nest visits in simple pairs to 15% in the presence of two helpers). Rowley (1965) also suggested that breeding females, relieved of much of the responsibility for dependent fledglings, would be able to begin re-nesting sooner than would be possible without helpers. This hypothesis was tested at Eastwood by comparing the inter-clutch intervals, following a successful nest, for helped and un-helped females. The presence of helpers was found to result in a significant reduction in the amount of time between clutches. Despite this help, however, the seasonal reproductive output of groups with helpers was not

greater than that of simple pairs. The evidence therefore suggests that direct benefits to breeders might arise from a reduction in the level of parental care (with possible long-term enhancement of survival or reproductive output) but that no seasonal increase in the number of offspring resulted. Such benefits to breeders could be considered a 'payment' made by helpers in exchange for residence in the natal group.

The payment hypothesis assumes that there is some cost to the breeders in allowing offspring to remain. If however, there is little or no cost to the breeders, then breeders may also benefit from delayed dispersal and helping behaviour by their offspring. As breeders, or at least one member of the pair, were the parents of their helpers, then any behaviour which improved the survival and lifetime reproductive success of helpers should also have benefited the genetic parent(s). Tolerance of grown offspring in the natal group might therefore be seen as extended parental care. The inheritance of a territory, for example, is of benefit to the helper (who gains a breeding position) and to the breeder (who ensures the reproductive success of his offspring). The 'extended parental-care' hypothesis makes an obvious prediction not necessarily shared by the 'payment' hypothesis; that is, helpers should only be tolerated if they are the offspring of the breeders and unrelated helpers should be ejected. At Eastwood, all male helpers were related to the male breeder (in one

case a sibling, rather than offspring). However, in at least half of the cases male helpers were not related to the female breeder. It would therefore be expected that females should not tolerate the presence of unrelated offspring unless; (i) unrelated helpers make some payment to the breeding female, (ii) breeding females are unable to exclude unrelated birds from the group, or (iii) if the breeding male is lost, the female is then able to mate with the unrelated male helper while retaining the territory. The results of this study suggest that all three factors may be relevant for fairy-wrens at Eastwood. Breeding males for example appeared to be the dominant group member and it may be only they that can determine group composition - this would also be consistent with the observation that breeding males did not have unrelated male helpers.

Although the origins of only a few female helpers could be determined, all were found to be the offspring of the breeding female, but unrelated to the breeding male. It would be easier to explain why breeding males tolerated unrelated females in the group if, for example, they represented a ready source of mates. Rowley (1981) found that unrelated Splendid Fairy-wren helpers were a ready source of mates for recently widowed birds. At Eastwood, however, female helpers did not inherit breeding positions within the group and all females dispersed some distance before breeding. It is unlikely, therefore, that breeding male fairy-wrens at Eastwood ever mated with their

unrelated female helpers. Therefore, the payment hypothesis is the most likely to explain why (unrelated) female helpers were tolerated in the group by breeding males.

9.3 Conclusion

Co-operative breeding in the Eastwood population of Superb Fairy-wrens occurred when breeding opportunities for potential breeders were limited. When all of the best quality habitat was occupied by breeding pairs, there was little opportunity for birds to form new breeding groups. Similarly, an apparent scarcity of females reduced the breeding opportunities for some males. For birds unable to gain access to a suitable breeding position within the population, the best alternative seemed to be delayed dispersal and helping behaviour in the natal group.

Table 9.1 A comparison of the Estimated Reproductive Success for two alternative reproductive histories.

Variable	A: Helper in year 1			B: Breeder in year 1		
	small	med.	large	small	med.	large
Bramble area per territory						
Reproductive output in year 1 (no. of fledglings)	0.0	0.0	0.0	1.00	3.25	3.50
Survivorship	0.29	0.45	0.60	0.29	0.45	0.60
Reproductive output in year 2 and 3 (no. of fledglings)	2.33	2.78	3.75	2.33	2.78	3.75
Potential reproductive output in 3 years (Total no. of fledglings)	4.66	5.56	7.40	5.66	9.81	10.90
Total reproductive output x survival to 3 years (E.L.R.S.)	0.87	1.04	3.60	1.87	4.29	7.10

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