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Helper contributions to reproductive success in the splendid fairy-wren (*Malurus splendens*)

Eleanor Russell and Ian Rowley

CSIRO Division of Wildlife and Ecology, L.M.B. No. 4, P.O., Midland, 6056, Western Australia

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Summary. In *Malurus splendens*, helpers were present in 65% of 226 group-years with at least one helper female in 37% of group-years. Most females helped for only one year, while many males did so for at least two years. Most were offspring of one or both present breeders, and in 53% of helper-years, helped both parents. For 159 helpers of known age and parentage, the mean coefficient of relatedness to the offspring was 0.47. Novice females with or without helpers produced fewer fledglings per season than females with one year breeding experience and the same level of help. Helpers did not affect production of fledglings per year by females with one year of experience. Females with two or more years experience and at least two helpers produced more fledglings than equivalent birds with one or no helpers. Experience and helpers have little effect on production of fledglings per nest but they lead to more females renesting after a first brood has been raised. Fewer than 20% of novices renest after fledging one brood, while for females with at least two years experience, the percent renesting after success is 40% with no help, 56% with one helper and 69% with 2 or more helpers. Experienced females begin their first clutch earlier than novices, and helpers reduce the time to renest after success from 66 days for an experienced female with no helpers to 50 days for females with at least two years experience and two or more helpers. Breeding females with helpers survive better (76%) than those with no helpers (55%), and helpers thus gain future indirect fitness. Despite their close relatedness to breeders and offspring, in only 19% of group-years did helpers increase their indirect fitness from an increase in productivity.

Introduction

At first glance helping behaviour appears to be altruistic – assisting other individuals to raise their young when the helper could be raising its own. The problem has two parts, as was suggested by Brown (1974); why do some individuals not disperse from their natal group? and why do the non-dispersers help? There is no general agreement on the reasons why non-breeding adults help others to rear their young (see reviews by Koenig and Pitelka 1981; Emlen 1982a, b; Brown 1983, 1987; Woolfenden and Fitzpatrick 1984; Austad and Rabenold 1986). Some hypotheses explain why non-dispersers help mainly in terms of direct benefits to the helper while others consider that indirect fitness benefits are an important factor in the evolution of helping (see review by Brown 1987). An increase in the production of non-descendant kin increases the indirect component of fitness for helpers, and such aid-giving will be favoured by Kin Selection (Maynard-Smith 1964). The indirect fitness benefit to helpers (Brown 1980) could compensate for the loss of direct offspring production in situations where vacancies for new breeders are few, but there is no reason to assume that any one hypothesis is the sole explanation for even a single species, and Austad and Rabenold (1986) discuss alternative hypotheses.

Many studies have assessed the overall effect of helpers in individual nesting attempts or on the annual production of offspring by breeders, and have shown that although different species vary widely (see reviews by Rabenold 1984; Brown 1987), in most cases, larger groups produce more young per year (Rowley 1965, 1978; Ridpath 1972; Reyer 1980; Brown and Brown 1981; Koenig 1981; Wilkinson and Brown 1984; Woolfenden and Fitzpatrick 1984; Zack 1986), but not always (Craig 1980; Ligon 1981).

The contributions of helpers to increased reproductive success have been identified as one or more of the following: (a) reduced risk of predation of nests and fledglings (Rowley 1978; Rabenold 1984; Reyer 1984; Woolfenden and Fitzpatrick

1984); (b) reduced energetic burden on breeders (especially female; Brown and Brown 1981; Ligon 1981; Rowley 1981; Tidemann 1986); (c) increased food availability for nestlings (Reyer 1984); (d) feeding of the incubating female on the nest (Brown and Brown 1980; Zack 1986). Few studies have continued for long enough to assess the significance of this helping in the lifetime production by the breeder or the helper. In this paper we attempt to estimate the extent of the helper contribution to breeders in order to test the hypothesis that helping increases the indirect fitness of helpers.

We present an analysis of data on helping from a colour-banded population of splendid fairy-wrens *Malurus splendens* (= *splendens* for brevity), studied since 1973. These small (10 g) sedentary insectivores belong to the endemic Australasian Family Maluridae, and are only distantly related to wrens of the Family Troglodytidae (Sibley and Ahlquist 1985). In Western Australia, where we have studied *splendens*, they live in a dense and varied heathland, consisting mainly of xerophytic shrubs (Proteaceae and Myrtaceae), with scattered emergent eucalypts (*Eucalyptus calophylla* and *E. wandoo*). Rowley (1981) described their social system, typical of a cooperative breeder, with groups of up to eight adults. We are now able to consider in more detail the influence of helping on productivity by females of different age and experience and to suggest how this influence is exerted. In a later paper, we will present data on demography, dispersal and competition for breeding vacancies which will allow a full discussion of the evolution of cooperative breeding in *M. splendens*.

Methods

The study site covers 120 ha on Gooseberry Hill, east of Perth. The average annual rainfall is 880 mm, mostly falling from May to October. In 1973, the study population consisted of eight groups but since then the study has grown in area and population density; at peak density in 1984, we monitored 34 groups containing 115 adults. Rowley (1981) described the area and summarized data to 1979. The basic social unit is the monogamous breeding pair which remains together so long as both survive. Progeny tend to remain in the family group after they reach independence and stay on for at least a year after they reach sexual maturity (at one year old for both males and females). All group members take part in defence of the territory against conspecifics, both by singing and by engaging intruders, in defending the nest against predators such as snakes and lizards (Rowley 1981) and in mobbing cuckoos (Payne et al. 1985). Adult helpers, particularly females, contributed significantly to feeding the nestlings and to removing faecal sacs. After the nestlings fledge, the adults shepherd and feed them until they become independent. A few cases of plural breeding have occurred, generally when a female helper in her second year with the group built a nest at the same time as the primary female. These females were not included as helpers if they did not help the primary female. If they bred the following year, they were assigned one year of breeding experience.

The breeding season is from September to January and the birds are repeat breeders, sometimes nesting four times in the year, although twice is more usual. Clutch size is almost always three, with a range of two to four. The eggs take 14 days to hatch and the nestlings fledge when 10 days old. In some years they are heavily parasitised by Horsfield's bronze-cuckoo, *Chrysococcyx basalis*.

From 1973 to 1985, 763 *splendens* were individually colour-banded, most of them as nestlings whose pedigrees were known, assuming that the oldest male in the group was the father on the basis of mate-guarding behaviour at about the time of egg-laying. Electrophoretic studies at present in progress (M.G. Brooker unpublished) suggest that this assumption is not always justified. We censused the population thoroughly before and after the breeding season for changes in groups and survival of fledglings. During the breeding season, all groups were monitored, and we tried to follow the progress of all nests. The date when the first egg of a clutch was laid (unless known exactly) was calculated from the date of hatching (assuming 14 days incubation) or (if necessary) the age of nestlings when found (from growth curves). Some nests predated during incubation could not be dated so exactly. This intensive field work was accomplished with the help of Craig Bradley, Michael and Lesley Brooker, Graeme Chapman, Joe Leone and Bob and Laura Payne. In this paper we analyse data for 13 breeding seasons, from 1973/74 to 1985/86, and include data on the survival of fledglings to 1 September, 1986.

When comparisons of productivity across several categories of female made by Kruskal-Wallis One-way ANOVA indicated significant variation, Mann-Whitney *U* tests (one-tailed) were used to compare between pairs of categories.

Results

Occurrence of helpers

The composition of groups at the start of each breeding season (taken as 1 September) was extremely variable (Table 1). Almost every possible combination of males and females occurred, with a single male being the most common addition to the breeding pair (20% of group-years). Although a successful breeding season could lead to a group with more than 8 members in April/May, such groups did not remain intact, and groups with more than 8 adults during the breeding season did not occur. Helpers were not only male; at least one female helper was present in 83 out of 226 group-years (37%).

Most helpers were approaching one year old at the start of the breeding season (Fig. 1). Most females helped for only one breeding season whilst many males helped for at least 2 years and one for seven years; this reflects the greater dispersal of females (Rowley 1981). Of the 98 females known to have survived to 1 year old, 23 (23%) did not help at all, 58 (59%) helped for one year, 13 (13%) for at least 2 years, three for 3 years and one for

Table 1. Composition of 226 groups of *Malurus splendens*, Gooseberry Hill, 1973–1985

Total birds in group	Males	Females	Number of groups
2	1	1	78
3	2	1	46
	1	2	23
4	3	1	14
	2	2	19
	1	3	7
5	4	1	4
	3	2	17
	2	3	4
6	5	1	1
	4	2	3
	3	3	5
	2	4	2
7	4	3	2
8	5	3	1

Table 2. Who helps whom – relationships between helpers, breeders and the potential offspring. *r* is a minimum value, due to high level of inbreeding. The total is based on 159 individual wrens of known age and parentage over 210 helper-seasons

Relationship of breeding pair to helper	*r* with nestlings	No. of helpers M	F	Total	%
Father × Mother	0.5	67	44	111	53.1
Parent × Sibling	0.5	15	10	25	12.0
Brother × Sister	0.5	1	1	2	1.0
Parent × 1/2 Sibling	0.38	8	4	12	5.7
Brother × 1/2 Sister	0.38	1	–	1	0.5
Father × Aunt	0.38	1	1	2	1.0
Parent × Grandparent	0.38	1	1	2	1.0
Brother × Aunt	0.38	3	–	3	1.4
Parent × Cousin	0.31	–	4	4	1.9
Grandfather × Aunt	0.25	1	–	1	0.5
Father × Unrelated	0.25	25	1	26	12.4
Unrelated × Mother	0.25	–	7	7	3.3
Sibling × Unrelated	0.25	5	5	10	4.8
Unrelated × Unrelated	0	2	2	4	1.9

Fig. 1. Frequency distribution of the age of helpers over 12 years 1974–1985 for 99 males and 75 females over 238 helper seasons

4 years. Of 120 males which survived to 1 year old, 21 (18%) did not help, 49 (41%) helped for 1 year, and 42 (35%) helped for at least 2 years.

Relationship between helpers and breeders

In 210 helper-seasons only four cases of helping unrelated breeders occurred. Most helpers were the offspring of one or both of the present breeders (Table 2) and by far the most common situation was for the helper (of either sex) to help both parents (53.1%; potential relationship to nestling $r=0.5$ or more, due to inbreeding). In all other cases they were helping various combinations of relatives, and their potential relationship to the nestlings was at least $r=0.25$. The level of inbreeding in this population is high (Rowley et al. 1986), and the average value of *r* between helpers and the offspring of the breeding pair was calculated from pedigrees to be 0.47; this is a minimum value, since the assumption that unknown immigrants were unrelated was probably not always justified.

Annual productivity, breeding experience and helpers

Annual productivity. The experience of the breeding pair may be an important factor influencing productivity. Females that had not bred before (= novices) produced fewer offspring per year than females with at least one year of breeding experience (Table 3). The experience of the male had no effect on production by either novice or experienced females and was not taken into account in subsequent analyses.

If females are classified as novice or experienced, with or without helpers, and their production of eggs, fledglings and yearlings compared (Table 4), the increased production due to experience is again evident; the presence of helpers does not significantly improve the production by novices and although there is a trend towards in-

Table 3. Effect of breeding experience on production of offspring by pairs of *Malurus splendens*. Experienced birds had at least one year experience as a breeder

Experience of breeding pair		N	Offspring production/year		
Male	Female		Eggs	Fledglings	Yearlings
Novice	Novice	24	4.5 ± 2.1^{a}	2.1 ± 1.7^{c}	0.8 ± 1.0^{e}
			***	**	N.S.
Novice	Experienced	20	7.2 ± 3.0^{b}	3.7 ± 1.7^{d}	1.4 ± 1.1^{f}
Experienced	Novice	33	4.7 ± 2.5^{a}	1.9 ± 1.4^{c}	0.6 ± 0.8^{e}
			**	***	***
Experienced	Experienced	72	6.2 ± 2.3^{b}	3.7 ± 2.0^{d}	1.4 ± 1.1^{f}

Pairs of means with the same superscript ($^{a-f}$) are not significantly different ($P > 0.05$, *t*-test). Significance of difference between adjacent means: ***: $P < 0.001$; **: $P < 0.01$

Table 4. Effect of breeding experience and presence of helpers on yearly production of offspring by female *Malurus splendens*. In this comparison, all experienced females are considered together and no distinction made between groups with one or more helpers. (Data from breeding seasons 1974–1985); in 1973, all were of unknown experience)

Female experience	Help	N	Offspring production/year		
			Eggs	Fledglings	Yearlings
Novice	0	41	4.4^{a}	1.7^{d}	0.6^{f}
			*	**	*
Experienced	0	31	5.6^{b}	3.1^{e}	1.2^{g}
Novice	+	32	4.5^{a}	2.1^{d}	0.8^{f}
			**	***	**
Experience	+	82	6.9^{c}	3.5^{e}	1.3^{g}
Novice and experienced	0	72	4.9	2.3	0.9
Novice and experienced	+	114	6.2	3.1	1.2

Pairs of means (in a column) which have the same superscript are not significantly different ($P > 0.05$, *t*-test). Significance of difference between adjacent means: *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$. Pairs of means with different superscripts (b, c) are significantly different ($P < 0.01$)

creased production by experienced females with helpers, only the production of eggs is significantly greater at this level of analysis. The analysis is carried further in Table 5, by dividing females into those with 0, 1 and 2 or more years of experience as a breeder, and by considering the effects of 0, 1 or 2 or more helpers. These categories are abbreviated:

N.0: Novice female with no helper
N.+ : Novice female with 1 or more helpers
E1.0: Female with 1 *y* breeding and no helpers
E1.1: Female with 1 *y* breeding and 1 helper
E1.2: Female with 1 *y* breeding and 2 or more helpers
E2.0: Female with at least 2 *y* breeding and no helpers
E2.1: Female with at least 2 *y* breeding and 1 helper
E2.2: Female with at least 2 *y* breeding and 2 or more helpers

These eight categories of female differed in their production of fledglings per year (Kruskal-Wallis One-way ANOVA, $P < 0.001$). There is some indication that N.+ females may produce more fledglings per year than N.0 females (2.1 vs 1.7, $P = 0.064$), and both classes produced significantly fewer fledglings than females with one year's experience (N.0 vs E1.0: $P = 0.04$; N.+ vs E1.1: $P = 0.004$). Helpers had no effect on the production of fledglings per year by E1 females (Kruskal-Wallis One-way ANOVA, $P > 0.05$). There was no difference between E2.0 and E2.1 ($P > 0.05$), but E2.2 produced significantly more fledglings per year than did E2.0 and E2.1 combined ($P = 0.02$). Once young fledged, there was no difference between groups in survival of fledglings to 1 year (calculated on pooled figures for each category of female; $\chi^2 = 6.9$, $P > 0.05$).

Productivity per nesting attempt. M. splendens may have more than one successful nest per year and the mean fledgling production by experienced females was > 3. This suggests that the effect of helpers may operate via the frequency of nesting rather than through an effect on the production of any individual nest. The mean clutch size was 2.9 ± 0.3 and there was no difference across four categories of female (N.0, N.+, E.0, E.+; Kruskal-Wallis One-way ANOVA, $P > 0.1$). Line 2 of Table 5 compares the production of fledglings per nesting attempt across all females. The difference was not significant (Kruskal-Wallis one-way ANOVA, $P > 0.05$), but novices were less successful than other females, and clearly helpers had no effect on production per nest by E1 and E2 females. Complete failure happened more often with novices (48%) than experienced females (40%), and they had more complete failures before hatching (29% of 126 nests as against 16% of 300 nests for all experienced females).

Across all levels of help and experience, the productivity of nests which hatched at least one wren was not significantly different, suggesting that once eggs hatched, even novices were no less efficient than experienced females at rearing nestlings to fledging and that the presence of helpers

Table 5. Effects of breeding experience and number of helpers on reproductive success in *Malurus splendens*. Significance of differences between groups and the code letters used is discussed in the text

Experience of ♀	Novice		1 year			2 or more years		
code	N.0	N.+	E1.0	E1.1	E1.2	E2.0	E2.1	E2.2
No. of helpers	0	⩾1	0	1	⩾2	0	1	⩾2
N	41	32	16	15	14	15	18	35
Fledglings/year	1.7	2.1	3.0	3.1	2.7	3.3	3.2	4.3
Fledglings/nest	1.1	1.3	1.5	1.6	1.2	1.8	1.4	1.6
Fledglings/nest which hatched wrens	2.1	2.3	2.3	2.5	2.4	2.3	2.1	2.2
Nests/♀/year	1.5	1.6	2.0	1.9	2.2	1.9	2.3	2.6
Survival of fledglings to lyo	0.33	0.38	0.33	0.45	0.47	0.45	0.30	0.34
Proportion of ♀♀ which renest after fledging wrens	0.15	0.13	0.38	0.33	0.43	0.40	0.56	0.69
Cuckoos/nest	0.17	0.22	0.19	0.32	0.19	0.14	0.26	0.15
% Females with:								
0 successful nests	37	19	19	0	14	0	17	3
1 successful nests	54	75	50	80	72	73	50	37
2 successful nests	9	6	25	20	14	27	28	49
3 successful nests	0	0	6	0	0	0	6	11

did not contribute to productivity. However, closer inspection of the data shows that whereas experienced females produced 3 fledglings more frequently than 1 or 2 (37% vs. 23%), novices produced 3 as often as they produced 1 or 2 fledglings (25% vs 27%), suggesting that they were not quite so good at rearing 3 nestlings.

We do not have enough data to compare feeding rates at nests of different classes of female. Most nestlings were banded at 7 days and we calculated an index of their condition as the cube root of body mass divided by the length of the fourth primary (after How and Kitchener 1983). There was no difference in this index across four categories of females (N.0, N.+, E.0 and E.+; Kruskal-Wallis One-way ANOVA, $P > 0.9$). However, it is still possible that nestlings of novices are less adequately fed during the 3 days of nest life from banding to fledging.

One of the most significant causes of nesting failure in *splendens* is parasitism by cuckoos. Across all females, there was no significant difference in the proportion of nests parasitized ($\chi^2 = 7.3$, $P > 0.05$, $N = 365$), as Rowley (1981) found. It is interesting that for experienced females with one helper, regardless of experience, the proportion of nests with a cuckoo is nearly twice as high as for females with 0 or 2 helpers (Table 5), but we cannot explain this.

Helpers and the number of nests per season. The difference between females of most significance for yearly productivity lay in the number of nests which females had per year (Kruskal-Wallis one-way ANOVA, $P < 0.001$, Table 5). There was no difference between N.0 and N.+ ($P > 0.05$), and no difference between E1.0, E1.1 and E1.2 (Kruskal-Wallis one-way ANOVA, $P > 0.05$), but overall, novices had fewer nests than E1 females ($P < 0.001$). E2.2 females had more nests per year than E2.0 ($P < 0.05$). The difference between E2.1 and E2.2 was not significant although production of fledglings per year by E2.1 females was significantly less than that by E2.2 females and no different from that by any E1 or E2.0 females.

The percentage of females renesting after fledging a first brood of wrens increased with age and level of help. Fewer than 20% of novice females renested after fledging one brood of wrens, whereas 38% of E1 females did so, at all levels of help. For E2 females, the percentage renesting after a successful nest increased from 40% with no helpers to 56% with one helper and 69% with 2 or more helpers. Of the 18 E2.1, 6 succeeded in raising two broods of fledglings, with one female fledging three broods of two. For 35 E2.2, 20 succeeded in raising two broods of fledglings, and four raised three broods of three.

Helper effects on patterns of breeding. How are experience and the presence of helpers acting to increase the number of nests that a female has in a year? Three factors that may influence how many broods a female can fledge in one breeding season are discussed below: (1) the length of the breeding season; (2) the timing of the first nest; (3) how soon after fledging one brood can a female begin to lay another clutch. A fourth factor, how quickly a female can relay after failure at any stage is not considered because we seldom knew precisely when nests failed and so could not calculate the interval between nests after failure.

Length of the breeding season. The length of the breeding season of *splendens* on Gooseberry Hill varies considerably, depending on seasonal conditions. The mean time from the date of laying the first egg (eL.1) of the first clutch of the season to eL.1 of the last clutch of the season over the 14 years 1973 to 1986 was 109 ± 12 days (range 80–120 days). The date of the earliest eL.1 ranged from 19 August to 24 September, and that for the last clutch from 12 December to 8 January. The date when a female laid her first clutch for the season affected how much of the breeding season remained for her to lay repeat clutches.

Timing of the first nest. For novice females ($N=55$), the mean date of eL.1 for the first clutch was 12 October (S.D. = 22 days); for all experienced females ($N=89$), mean eL.1 was 22 September ± 16 days, 3 weeks earlier than for novices. The mean date for E2 females (20 September ± 16 days; $N=44$) is slightly earlier than for E1 females (25 September ± 13 days; $N=29$), but this difference is not significant ($t=1.48$, $P>0.05$). Once established as breeders, females rarely changed groups (<1% of breeding females), so that an experienced female was usually in a familiar territory, even if she had a new mate. Many novices were in strange territories and sometimes only moved from their natal group to fill a nearby vacancy after the start of the breeding season. For novices the start of the first nest was spread out through the breeding season, but for experienced females, almost all first nests were begun before mid-October (Fig. 2). For the first nest of the breeding season, eL.1 was known for enough E2 females ($N=44$) to allow comparison between females with 0, 1 and 2 helpers; no significant difference was found (Kruskal-Wallis One-way ANOVA, $P>0.3$). The mean date of eL.1 for novices with helpers was slightly earlier (6 October ± 23 days) than for novices without helpers (16 October ± 21 days), but timing was very variable and the difference was not significant.

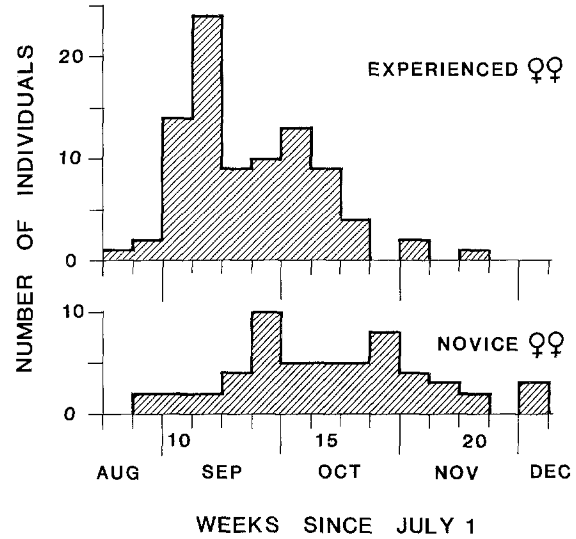

Fig. 2. Comparison between novice and experienced females of the dates when the first egg was laid in their first nests of the breeding season. The time scale is in weeks since 1 July

Time to renest after success. Helpers affect productivity by reducing the time to re-nesting after one brood was successfully raised. Sample size was too small to consider E1 and E2 females separately, but for all experienced females with no helpers ($N=16$) the mean time from eL.1 of the first (successful) nest to eL.1 of the second nest was 65.9 ± 9.0 days, whilst for all experienced females with helpers ($N=34$), the mean time was significantly shorter (55.1 ± 10.1 days; Mann-Whitney U test, one-tailed, $P<0.001$); for E2.2 ($N=21$), renesting was even quicker (50.0 ± 7.4 days; $P<0.001$).

Although E2.2 renest sooner than E2 females with no helpers, our data are too few to establish directly that it was the presence of helpers rather than increased experience which allowed this. However, several other lines of evidence suggest that the helpers contributed to the greater success of E2.2. Time to renesting was not significantly different between E1.0 ($N=8$) and E2.0 ($N=6$) (Mann-Whitney U test, two-tailed, $P>0.05$). E2.2 produced more fledglings per year than E2.1 and E2.0, and had more nests per year than E2.0. After success, 69% of E2.2 renested compared with only 40% of E2.0, and 60% of E2.2 females had two or three successful nests, compared to only 34% of E2.1 (Table 5).

Parasitism by cuckoos is frequent in *splendens* and in this situation helpers can have an effect on productivity by reducing the interval between nests. We have only enough data to say that for experienced females with helpers, the time from eL.1 to eL.1 (after a nesting attempt has fledged a cuckoo) was 46.1 ± 12.7 days ($N=18$). We cannot separate the effect of different levels of help or

Table 6. Survival to the next breeding season of breeding male and female *Malurus splendens* with and without helpers, based on all breeding birds of known experience over breeding seasons 1974–1985

Experience	Helpers	Female		Male	
		N	% Survive	*N*	% Survive
N	0	38	58	28	79
N	+	35	77	31	77
E	0	37	51	32	66
E	+	93	75	101	69
All	0	75	55*	60	72**
All	+	128	76*	132	71**

* $P<0.001$; ** NS

experience; the high post-fledging mortality of cuckoos could have contributed to the shorter interval.

Effect of helpers on survival of breeders

The presence of helpers had no effect on the survival of breeding males (Table 6). Males in the four categories (N.0, N.+, E.0 and E.+) survived equally well to the next breeding season ($\chi^2=2.0$, $N=192$, $P>0.5$), with no difference between those with and without helpers (72% vs 71%). However, helpers did improve the chance that a breeding female would survive to the next breeding season; there was a significant difference across the four categories ($\chi^2=10.1$, $N=203$, $P<0.02$), and survival of females with helpers (76%) was significantly better than without (55%; $\chi^2=10.7$, $N=203$, $P<0.01$).

Effect of experience as a helper on later reproductive success

Since some females did not help at all, and others bred at two years old after one year of helping, it was possible to investigate the effect of one year's experience as a helper on reproductive success in the first year as a breeder. For females with no helpers, mean production in their first year as a breeder was 1.5 fledglings per year for 1 year old females ($N=14$) and 1.6 for a novice that had spent one year as a helper ($N=11$; $P>0.05$, NS). For females with helpers and one year's experience as a helper ($N=11$), mean production in the first year as a breeder was significantly higher than for novices ($N=7$) that first bred at one year old with helpers (2.8 vs 2.0 fledglings per year; Mann-Whitney *U* test one-tailed, $P<0.05$), but not significantly different from any of the E1 females in Table 5.

Discussion

Do helpers really help?

About 65% of groups on the Gooseberry Hill study area over the years 1973–1985 contained at least one helper. It has been shown for other species (Florida scrub jay: Woolfenden and Fitzpatrick 1984; Kittiwake: Coulson and Thomas 1985) that performance as a breeder improves with experience. Here we have a situation where experience as a breeder leads to an improvement in performance which is further enhanced by the presence of helpers.

All classes of female except novices were equivalent in production from one nest, and the difference in annual productivity came about because the more successful (E2.2) females had more nests irrespective of the experience of their mate. Before the fledglings were independent, the female had left them to the care of helpers, built a new nest and laid another clutch. We consider that it is not until two helpers are present that there are enough adults (two helpers and the breeding male) to take care of three fledglings and release the female to renest. We are not yet sure that a particular adult always takes care of the same fledgling (Smith 1978) but our observations suggest this.

The period September–December is adequate for two nesting attempts with a 65 day interval if there are no interruptions due to predation or cuckoos, but only experienced females with two helpers (and consequently smaller inter-brood interval) have time for two successful wren nests when another attempt has been predated or parasitized. Similar effects of helpers on the frequency of clutches and renesting after success are mentioned by Rowley (1965), Brown and Brown (1981) and Rabenold (1984). Helping may add to the effectiveness of the multi-brooded anti-cuckoo strategy, which has a higher probability of producing at least one fledgling than that of producing the same total of nestlings in one brood (Payne 1977; May and Robinson 1986).

For many species, the presence of helpers does not produce an increase in overall feeding rate, but reduces the contribution by breeders (especially the female) (Brown et al. 1978; Rowley 1978; Rabenold 1984; Wilkinson and Brown 1984; Tidemann 1986). This is true also for *splendens* (Rowley 1981), and when in addition, the female is released (by helpers) from feeding and shepherding fledglings, she is able to redirect her energy towards renesting sooner. Recent discussions of the contributions by helpers to reproductive success in *Malurus* spp. (Nias 1986; Tidemann 1986) considered only single nesting attempts, so it is not surprising that they failed to identify the helper effect on renesting.

Coulson and Thomas (1985) have shown that differences in female quality can be important for productivity. It is possible that females with two helpers are "good quality" females and that their increased productivity is partly due to the helpers and partly to their own characteristics. The data are few but in five cases out of six, the same females produced more fledglings when they had two or more helpers than when they had none; however, differences between years may be important with such a small sample. Variation in productivity from year to year has not been treated separately. In some years most birds do well, whilst in other years, very few do so; mean fledgling production per group ranged from 1.8 to 5.2 per year, with a mean of 3.1. It is the experienced females with helpers that are able to produce fledglings in years when most females are unsuccessful, with significant effects for their Lifetime Reproductive Success (Rowley and Russell 1988).

The enhanced reproductive success of larger groups could have resulted from a high quality territory, with increased group size the result of past success. Between December 1978 and January 1985, there were no major fires in the study area and vegetation cover, density and presumably territory quality increased steadily, but there was no corresponding increase in production of fledglings per group, although survival and population density did increase (authors' unpublished data). In January 1985, 99.5% of the study area was burnt by wildfire. Most adults survived, territories changed little, and the next breeding season produced 2.2 fledglings per female, compared with the pre-fire value of 2.5, despite a major reduction in cover, increased predation and parasitism (cuckoos), and a shortage of nesting material (Rowley and Brooker 1987). Any effect of territory quality is therefore probably weak compared with the effects of experience and helpers.

Why do helpers help?

Austad and Rabenold (1986) identified four general hypotheses to explain why helping in non-dispersers should be selected for. Can we provide evidence for or against any of these? The Parental Control hypothesis suggests that if it is advantageous for the juveniles to remain, but disadvantageous for the parents, parents only allow individuals to remain which help (Brown 1969; Gaston 1978; Emlen 1982b). In *splendens* the presence of helpers had no obvious detrimental effects on productivity but nevertheless imposed the costs of extra mouths to be fed and increased visibility at the nest. We have no evidence of parents evicting progeny from the group: if a female breeder was replaced by an immigrant female, surviving male helpers usually remained but female helpers left-presumably evicted.

The Experience hypothesis suggests that if individuals are prevented by environmental constraints from dispersing, they may gain useful experience in the rearing of young by helping. Female *splendens* which had helped for one year produced more fledglings in their first year as a breeder than females which had not helped, but only if helpers were present; they were also one year older. The cost of one year's delay in breeding was therefore to some extent offset by the experience gained.

The Reciprocity hypothesis suggests that helpers benefit from helping because they are rearing individuals which may later help them in breeding. This has recently been invoked as important in the evolution of helping (Ligon and Ligon 1983; Wiley and Rabenold 1984), but in *splendens* it is rare that a bird goes to a new group as a breeder with a younger sib as a helper. More than 50% of helpers help father and mother and 23% help a breeder who is a sib, generally a litter mate, so that the chances of reciprocity are few.

In what Austad and Rabenold (1986) call the Kin Selection hypothesis, helping behaviour may spread through the production of non-descendant kin that share the genes of the helpers. Because of the high level of inbreeding (Rowley et al. 1986), *splendens* helpers were involved in rearing nestlings that were on average related to them almost as closely as full sibs. The potential exists for significant enhancement of indirect fitness, which has a present (I) and a future (i) component (Brown 1980). According to the reformulation of Hamilton's original criterion (Hamilton 1964; Brown 1975; West-Eberhard 1975) a helper has a greater inclusive fitness when helping than when breeding if

$$r_h N_h > r_b N_b$$

where r_h is the helper's relatedness to the kin it is helping to rear, N_h is the number of young reared solely as a result of the helper's assistance, r_b is the relatedness of the breeder to the offspring, and N_b the number of offspring an unaided pair can raise. Based only on indirect present benefit from increased productivity in the current year by the

breeding female who is helped (data for all females from Table 4):
$I = r_h N_h = 0.47 \times (3.1-2.3) = 0.39$, which is less than $r_b N_b = 0.5 \times 2.3 = 1.2$.

An indirect future benefit, *i* (Brown 1980), arises from the increased survival of the breeding female, leading to an increased probability that she will breed again, and produce offspring more closely related to the helper than those of a new female that may be unrelated. An approximate calculation of the value of this benefit can be made. In the case of an individual helping its father and mother in year 1, there is a probability (P) $=0.72$ that she will survive to year 2 and produce 3.1 fledglings with $r_h = 0.5$, and $P = 0.28$ that she will be replaced by an unrelated novice who will produce 2.1 fledglings with $r_h = 0.25$ (assuming that both females have help in year 2). Without a helper the equivalent values of P are 0.55 and 0.45, and thus the difference due to helping in year 1 is $(0.72 \times 3.1 \times 0.5 + 0.28 \times 2.1 \times 0.25) - (0.55 \times 3.1 \times 0.5 + 0.45 \times 2.1 \times 0.25) = 0.17$ gene equivalents. This is obviously a significant addition to the value of I already calculated. There is a further indirect future benefit if this year's fledglings survive to next year to act as helpers and further improve the breeder's reproductive success.

Of the 186 yearly reproductive efforts of females with known experience, 39% were novices, for whom the effect of helpers on production is slight. In only 19% of group years were there females with at least two years experience and two or more helpers (E2.2), and it is only in those particular circumstances that the helper stands to gain any indirect benefit from increased fledgling production in that year. For all helpers there is also the indirect future benefit (*i*), and for the lone helper that is the sole benefit. Overall, helping does add to the inclusive fitness of helpers, and in one year the total indirect benefit from helping may be close to the direct genetic benefit from breeding as an unaided novice female ($r_b N_b \times P$ of establishment $= 1.7 \times 0.5 \times 0.8 = 0.68$). For a male, productivity as a novice is not so low, but the chance of a breeding vacancy is less (Rowley and Russell 1988).

In many species, such as the florida scrub jay (Woolfenden and Fitzpatrick 1984) and the stripe-backed wren (Rabenold 1984), increased survival and the chance of achieving breeding status are important direct benefits for the non-dispersers. These benefits, which also apply to *splendens*, depend upon the young bird being an integrated member of the group, and helping may be an important part of achieving social integration. It is much harder to identify any clear direct benefit to the young from actually helping; there is a slight gain in experience, but most benefit appears to be indirect. The increase in productivity due to helpers is similar to that found in other studies (Parry 1973; Reyer 1980; Woolfenden and Fitzpatrick 1984; Austad and Rabenold 1985; Zack 1986). Obviously, indirect future benefits are an important part of inclusive fitness which has previously been estimated only by Reyer (1984) and Rabenold (1985).

It is important to consider helping behaviour and delayed dispersal in the context of the lifetime fitness of the helpers and of the breeders in whose territories they help. The single most important factor contributing to Lifetime Reproductive Success (LRS) is lifespan as a breeder (Coulson and Thomas 1985; Fitzpatrick and Woolfenden 1988; Newton 1988; Rowley and Russell 1988). The benefit from helpers for the LRS of a breeding female may be substantial. If her survival is increased, she has a chance of surviving to breed for more than two years, accumulating helpers and becoming one of the few successful birds to produce replacement breeders. For a male, the benefit is less clear; there is no survival advantage, but it is to his advantage for his female to survive; a replacement novice would mean one or two years of reduced productivity. For both sexes, there is probably an added advantage in the ability to do well in a good year and to succeed in a poor year (Rowley and Russell 1988).

For helping by non-dispersers to be selected for, the total lifetime fitness of the helper strategy must exceed that of the non-helper strategy. If 1 or 2 years helping is followed by several years breeding, then the indirect contribution to fitness from one to two years helping is relatively insignificant. But for the significant number of birds which help but never get a chance to breed, inclusive fitness is entirely indirect. Those birds which disperse and do not achieve a breeding vacancy do not have even that. To compare these two strategies we need to relate the benefits of helping to aspects of demography, as well as mean and variance in LRS; this we hope to do in a future paper.

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