

Sociality and cooperative breeding of red-cockaded woodpeckers, *Picoides borealis*

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Summary. Thirty groups of red-cockaded woodpeckers (*Picoides borealis*) were studied from 1976–1982 to (1) determine the demographic structure of groups, (2) identify the role helpers play in reproductive activities, and (3) investigate the selective pressures promoting sociality and helping behavior. Groups had only 1 mated pair and 0–2 helpers. Approximately half of all groups had helpers and a given group had helpers some years but not others. Helpers, with rare exception, were males 1 or 2 years old and progeny of 1 or both members of the breeding pair. As a result of higher nestling survival, groups with helpers fledged significantly more young per year than unassisted pairs ($\bar{X}=2.05$, $SD=0.97$, $n=43$ vs. $\bar{X}=1.40$, $SD=1.01$, $n=50$). Nesting success was also associated with size and quality of nesting period home range, but evidence suggested that the increased number of young fledged resulted directly from the action of helpers. There was a significant positive correlation between reproductive success and experience of breeding females among unassisted pairs but a significant negative correlation among pairs with helpers. In groups with experienced females, helpers were assisting both their mothers and fathers and, therefore, were related to the offspring on the average by 0.50. In groups with inexperienced females, helpers were assisting their fathers and unrelated females and were related to the offspring by 0.25. The red-cockaded woodpecker's unique habit of excavating nest and roost cavities in living pines and the extended period of time required for excavation may be an important ecological constraint that promotes the retention of helpers. Because helpers are related to the offspring they help rear, kin selection and gains in indirect fitness may provide a partial explanation of why red-cockaded woodpecker helpers help.

However, the negative correlation between the efficacy of helping behavior and the helpers' relatedness to the offspring they help rear implies that helpers are least effective in producing offspring which would represent greatest gains to indirect fitness. This raises questions about the relative importance of kin selection and indirect fitness in the evolution of helping behavior among red-cockaded woodpeckers.

Introduction

Avian cooperative breeding systems, especially those in which some individuals (helpers) seemingly delay or forgo reproduction while assisting others, have been the subject of much research. Avian helpers have proven to be convenient subjects for exploring the selection pressures that promote seemingly altruistic behavior (Brown 1974; Ricklefs 1975; Stacey 1979; Koenig and Pitelka 1981), specifically for evaluating the concept of inclusive fitness as an explanatory principle of why helpers aid in the rearing of offspring not their own (Brown 1978; Emlen 1978; Vehrencamp 1979; Brown and Brown 1981; Woolfenden 1981; Emlen and Vehrencamp 1983; Woolfenden and Fitzpatrick 1984).

Cooperative breeding has been reported in more than 150 species of birds (Fry 1972; Grimes 1976; Rowley 1976; Woolfenden 1976; Zahavi 1976; Emlen 1982a), and several species have been studied in detail (see Emlen 1978 and Koenig 1981 for reviews). The attention paid to such species has generated some common thinking among investigators: the many species that share cooperative breeding as a common trait are quite diverse

in terms of taxonomy, life history, and habitat association (Brown 1978); given the diversity among birds exhibiting cooperative breeding, it is likely that the selective backgrounds and evolutionary mechanisms are diverse as well (Ricklefs 1975; Brown 1978; Emlen 1982a; Emlen and Vehrencamp 1983); and the applicability of selected hypotheses for explaining the adaptive significance of cooperative breeding can only be evaluated with additional and more thorough long-term field studies (Bertram 1981; Emlen 1981; Fitzpatrick and Woolfenden 1981).

The purpose of this study was to examine the structure and social interactions of groups of red-cockaded woodpeckers (*Picoides borealis*), a cooperative breeding picid endemic to pine forests of the southern United States. Specific objectives were: (1) to determine the demographic structure of red-cockaded woodpecker groups, (2) identify the roles and influences of helpers in reproductive activities, and (3) identify or hypothesize the selection pressures which might promote sociality and helping behavior in this species.

Red-cockaded woodpeckers are nonmigratory and maintain large, all-purpose territories throughout the year (Ligon 1970; Hooper et al. 1982). During the nesting season, individual groups may consist of only a breeding pair or of a breeding pair plus 1 to 3 helpers (Ligon 1970; Baker 1971; Beckett 1971; Lay et al. 1971; Lennartz and Harlow 1979). Outside of the nesting season, a group may consist of only the breeding pair, but typically it also includes offspring of both sexes and frequently helper males. At the nest, helpers assist with incubating the clutch and feeding and brooding nestlings (Lennartz and Harlow 1979). After the young are fledged, helpers – along with the parents – continue to feed the young, and throughout the year they assist in territorial defense and cavity excavation (Ligon 1970; Hooper et al. 1982).

Methods

We studied group structure and reproductive success in 30 red-cockaded woodpecker groups on the Francis Marion National Forest in Charleston and Berkeley Counties, South Carolina, from 1976–1982. The Francis Marion was selected as a study site because it supports one of the largest and densest populations of red-cockaded woodpeckers, with approximately 400 groups (Lennartz et al. 1983) on 64,751 ha of loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pine stands (USDA Forest Service 1977), the principal nesting and foraging habitat of the bird.

All birds that roosted within cavities and therefore could be trapped were marked with colored plastic leg bands. Adults were trapped by placing mist netting on a wire frame over

the entrance of the woodpeckers' roost cavities early in the morning before they left the roost. Nestlings were captured with the aid of nylon monofilament nooses at age 5 to 7 days.

Reproductive success was monitored most intensively and systematically during 1977–1981. Additional observations made in 1976 and 1982 were used to augment the 5-year data set. Reproductive success was monitored for 5 years in 3 groups, 4 years in 17 groups, 3 years in 7 groups, 2 years in 2 groups, and 1 year in 1 group for a total of 109 group-years. To monitor reproductive success, we inspected nest cavities at 2- to 3-day intervals beginning approximately 1 week before anticipated egg laying and continuing until young had fledged.

Group size and composition were determined by trapping, banding, and observing the nest trees with spotting scopes while adults incubated and fed nestlings. Exact ages could be determined only for those group members that were banded as nestlings and for juvenile males that retain a distinctive patch of red crown feathers for approximately 6 months after fledging. We know of no reliable method for determining the age of adult red-cockaded.

In addition to monitoring reproductive success, home-range size and the use and availability of foraging habitat were determined for 18 groups. The detailed methodology used to determine home ranges and to study foraging behavior has been described by Hooper and Lennartz (1981) and Hooper et al. (1982). For these 18 groups, followed for 1 year from one nesting season to the next, we also derived estimates of juvenile survivorship through 3, 6, and 12 months after fledging.

Results

Composition of red-cockaded woodpecker clans

Although a given red-cockaded group may contain as many as 4 males during the nesting season, the species is presumed to be monogamous (Woolfenden 1976). There is little direct evidence in the literature to support this presumption other than the high frequency of solitary pairs as a breeding unit. Our observations indicate that the species is, indeed, monogamous. In the course of determining home ranges, monitoring nest attentiveness, and verifying group composition, we observed copulations and mountings involving marked birds in 12 different groups, 7 of which had male helpers. In no instance did we observe more than a single male to copulate with the group's resident female.

We monitored a total of 109 group nesting seasons for 30 individual woodpecker groups. For 93 of the nesting seasons, we were certain of group size and composition. The number of group nesting seasons with accurate information on group composition monitored per year ranged from a low of 14 groups to a high of 24. Among years, the proportion of groups with helpers ranged from 38 to 57%, averaging 46% over the 5 years. Of the 30 groups observed, 20 had helpers during at least one nesting season. The range in the number of helpers per group was quite narrow; 74% of the group nesting seasons attended by helpers had

only 1, and the remaining 26% had 2. Only 1 group had 3 helpers.

All helpers, with the exception of one, assisted with feeding nestlings. The one helper that did not feed nestlings was repeatedly observed with an intruding female, unrelated to resident group members. As will be noted later, intraspecific competitors may disrupt nesting efforts. Consequently, although this one helper was not observed attending the nest, it may well have contributed to the success of the nesting effort by occupying a potential competitor.

The 43 group nesting seasons attended by helpers involved 41 individual birds. Of the 41 individuals, 38 were male, 2 were female, and 1 was undetermined. The 2 females were both associated with the same pair of breeders but in 2 successive years. Thus, of 20 different groups that had helpers in 1 or more nesting seasons, only 1 group ever had female helpers. Ligon (1970) reported 1 female among the 4 helpers he observed at 2 nests, but female helpers were rare in our study area.

For 19 of the 43 group nesting seasons that involved helpers, we were able to calculate relatedness from banding histories of 19 individual helpers to both breeders and to nestlings. Twelve of the 19 helpers were progeny of the breeding pair and full siblings of the nestlings they cared for. Five helpers were genetically related to only 1 of the breeders, in four instances to the male and in one to the female, and half-sibs of the nestlings. We encountered two instances where helpers attended nests of breeders to which they were unrelated. Both cases involved the same group but in 2 successive years. In both years, the resident group consisted of the same mated pair plus a yearling female offspring. In addition to the 3 family members, a fourth bird was observed regularly feeding the group's nestlings. Banding and reproduction records indicate that this latter helper could not have been genetically related to the resident group members. In the first year the unrelated helper was unbanded and of undetermined sex and origin, whereas in the second year the unrelated helper was a male that had been banded just before the nesting season in an adjacent territory. It is possible that the same bird was involved both years. Because both events were associated with the presence of female helpers, possibly the unrelated helper(s) was attempting to consort with the auxiliary female. Also, because 2 males and 2 females were associated with the same nest, the actual parentage of the brood remains uncertain. Whatever the explanation, both behaviors – the presence of female helpers and helpers unrelated

to the breeding pair – are unique. In 93 nestings involving 30 groups over 5 years, this behavior was observed only twice and only within a single group.

Group dynamics

We did not find red-cockaded groups to be stable social units. Of the 30 groups studied, 7 had a turnover of 1 breeder and 11 had a turnover of both breeders. The average (\pm SD) annual turnover rate for breeders was 21% (\pm 10%) for males and 23% (\pm 12%) for females. Also, 14 of the 30 groups had helpers some years but not others. Of the 16 groups that were consistently pairs or consistently pairs plus helpers, only 3 had the same breeding pair all years they were under observation. Generally an individual's tenure as a breeder was limited to a single group. Among 17 breeding females that disappeared from their original groups, only 1 was discovered functioning as a breeder in another group. The others were not found. We observed the disappearance or expulsion of 14 breeding males, none of which was subsequently encountered in other groups. Because our study groups represented an extremely small portion of the total red-cockaded population in our study area, it is possible the birds that disappeared from study groups could have become affiliated with other groups without our detecting them.

Birds that served as helpers also limited their association to a single group, their natal group as noted previously. Turnover in helpers was rapid, and few birds spent more than 1 or 2 years in helper status. We have precise data on the time spent in helper status for only 9 of the 41 individuals we observed as helpers. These are birds whose tenure as helpers began and ended within the time frame reported here. Of the 9, 7 remained with their natal groups as helpers for 1 nesting season, and 2 for 2 seasons. For the remaining 32 helpers, we lack information either on when they first became helpers or on when their tenure might end. Of these 32 individuals, 2 served as helpers for at least 3 years, 7 for at least 2 years, and 23 for at least 1 year. We observed no instances of birds leaving their natal territory and returning in subsequent years to serve as a helper. Consequently, most helpers were birds 1 to 2 years old.

Of 9 marked males that were observed to acquire breeding status, 4 became breeders in the territories where they had served as helpers following the disappearance of the breeding males. For 3 of the 4, the eventual breeding territory is known to have been the natal territory. At the time they became breeders, 2 of the males were 2 years old,

1 was 3 years old, and 1 was at least 4 years old. All had served as helpers the years prior to becoming breeders. In two cases, the new breeders replaced their fathers, attracted new females, and their mothers either left or were ejected from the territory. In a third case, the sequence of territory inheritance was from father to son to brother. Following loss of the original breeder, a 3-year-old son that had helped for 2 years attracted a new female and became the new breeder. When he disappeared a year later, his 2-year-old brother whom he had helped rear, and who in turn had assisted him as a helper for 1 year, became the breeder. The second breeding female, unfortunately, was unbanded, so we do not know if the last male attracted a new female or merely mated with the same female that had been paired with his brother. In the fourth case, a bird that had helped for at least the 3 previous years mated with the resident female when the breeding male disappeared. Because this bird had not been banded until in helper status, its relatedness to the original breeding male and female was not known.

In the cases noted above, when a breeding male disappeared and the breeding female and helper remained, it was the helper male that retained the territory. We observed one instance, however, in which a female and her male progeny both remained in their territory following disappearance of the original breeding male. The female mated with a new male, and her male offspring, which was not yet 1 year old at the time of turnover in breeding males, remained in the territory and subsequently functioned as a helper. Possibly this instance of both a male offspring and its mother remaining in their territory following loss of the breeding male was a function of the youth and inexperience of the male and its inability to compete successfully with older males for cavity trees, territory, and a mate.

The other 5 marked males that were observed to acquire breeding status replaced or overthrew breeding males in territories bordering their natal territories. All had served as helpers in their natal territories, and at the time of acquiring breeding status, 2 were 2 years old, 1 was 3 years old, 1 was at least 3 years old, and 1 was at least 4 years old. We do not know how these birds achieved breeding status. However, we saw two cases where resident breeding males were physically evicted from their territories and replaced by alien males. We suspect at least some of the 5 males obtained breeding status via contest with the resident male.

Our information on marked females acquiring breeding status is limited to data for 3 birds. This

paucity of information is related to the different dispersal patterns of males and females and to our inability to intensively monitor long-range movements. One female was originally banded in 1978 when roosting in the territory of a group with which she did not forage. Her group affiliation at that time, if any, was unknown. In 1979 she was recaptured in a second territory, approximately 0.9 km from the first, and again she was not part of the resident group. In 1980, she was recaptured in a third territory but was not yet a breeder as no nest was found that year. Finally, in 1981, she was observed as the resident breeder in this last territory. Consequently, at the time of becoming a breeder, she was at least 4 years old and had spent at least 3 years moving from one territory to another, presumably searching for an opportunity to mate and reproduce. A second female, banded as a nestling, was recaptured the year after fledging while roosting in a territory adjacent to her natal territory, but she was not a member of the resident group. In her second year, she was recaptured from another territory adjacent to her natal territory where she was observed as the resident breeder. The third female, whose age and origin were unknown, was captured from two different territories in 1981 before settling as a breeder in a third territory in 1982. The sketchy picture that emerges from the behavior of these 3 birds is that females apparently disperse more widely than males and wander from territory to territory searching for opportunities to breed. In contrast, males often remain in their natal territories and later become breeders either there or in adjacent territories.

We did not observe birds of either sex to become breeders as yearlings. However, subsequent to our studies in coastal South Carolina, we began studying a smaller population of red-cockadededs in the Piedmont of Georgia. The smaller population has allowed us to color-mark and monitor behavior of a much larger proportion of the birds. In the Georgia population, we have observed yearlings of both sexes as breeders.

Roles and influence of helpers in reproduction

Every year, groups with helpers consistently fledged more young than unaided pairs (Table 1). The difference in any given year, however, was not statistically significant. The lack of statistical significance is not surprising, considering the small sample sizes and relatively small differences in number fledged (0.25–0.80 per year). Five-year av-

Table 1. Comparison of reproductive success between red-cockaded woodpecker groups with (H) and without (P) helpers, 1977–1981, Francis Marion National Forest, South Carolina. Numbers in parentheses indicate number of groups included in analyses

		1977	1978	1979	1980	1981	Five-year average
Proportion of groups nesting	P	1.00 (9)	0.82 (11)	0.93 (15)	0.89 (9)	0.83 (6)	0.90 (50)
	H	0.89 (9)	1.00 (9)	1.00 (9)	1.00 (8)	1.00 (8)	0.98 (43)
Clutch size	P	3.11 (9)	2.89 (9)*	3.20 (14)	3.12 (8)	3.20 (5)	3.10 (45)
	H	3.50 (8)	3.56 (9)	3.11 (9)	3.00 (8)	3.25 (8)	3.28 (42)
Hatching success	P	0.75 (9)	0.65 (9)	0.78 (14)	0.68 (8)	0.75 (5)	0.73 (45)
	H	0.75 (8)	0.66 (9)	0.78 (9)	0.79 (8)	0.81 (8)	0.75 (42)
Initial brood size	P	2.33 (9)	2.83 (6)	2.50 (14)	2.12 (8)	2.40 (5)	2.43 (42)
	H	2.62 (8)	2.62 (8)	2.75 (8)	2.38 (8)	2.62 (8)	2.60 (40)
Nestling survival	P	0.71 (9)	0.71 (6)	0.66 (14)*	0.82 (8)	0.50 (5)	0.69 (42)**
	H	0.90 (8)	0.81 (8)	0.91 (8)	0.84 (8)	0.76 (8)	0.85 (40)
Young fledged (all groups)	P	1.67 (9)	1.09 (11)	1.53 (15)	1.56 (9)	1.00 (6)	1.40 (50)**
	H	2.11 (9)	1.89 (9)	2.22 (9)	2.00 (8)	2.00 (8)	2.05 (43)
Young fledged (groups that nested)	P	1.67 (9)	1.33 (9)	1.64 (14)	1.75 (8)	1.20 (5)	1.56 (45)**
	H	2.38 (8)	1.89 (9)	2.22 (9)	2.00 (8)	2.00 (8)	2.10 (42)

* Means significantly different, $P \leq 0.05$, ** $P \leq 0.01$, 1-tailed, Mann-Whitney U -test (Siegel 1956)

Table 2. Correlations between number of red-cockaded woodpeckers fledged and stages of clutch and brood development, Francis Marion National Forest, South Carolina. Spearman's (r_s) and Pearson's (r) correlation coefficients

Clutch and brood development	1977 (r_s)	1978 (r_s)	1979 (r_s)	1980 (r_s)	1981 (r_s)	Five years cumulative (r)
Pairs						
Clutch size	-0.34	0.60	0.02	0.09	0.41	0.15
Hatching success	0.24	0.87**	0.43	0.81*	0.30	0.52*
Initial brood size	0.10	0.55	0.29	0.82*	-0.17	0.24
Nestling survival	0.65	0.98**	0.39	0.44	0.91*	0.74**
Helpers						
Clutch size	0.84**	-0.50	0.16	0.61	0.80*	0.29
Hatching success	0.91**	0.79*	0.89**	0.65	0.82*	0.80**
Initial brood size	0.95**	0.49	0.77*	0.80*	0.96*	0.74**
Nestling survival	-0.55	0.64	0.14	0.00	-0.41	0.27

* Probability of coefficient $\neq 0$, $P \leq 0.05$, ** $P \leq 0.01$

erages, however, confirm the yearly trend. Over all years, groups with helpers produced significantly ($P \leq 0.01$, 1-tailed test) more fledglings than did pairs.

Examining each stage in the nesting process (Table 1) indicates that the larger number of young fledged by groups with helpers is probably the result of the helpers' influence on nestling survival. This is the only stage in the nesting process prior to fledging where groups with helpers had significantly higher productivity or success than unassisted pairs. This inference is strengthened when we examine how productivity or success at various stages in the nesting process correlates with

number of young fledged (Table 2). Because of small sample sizes, the data for each year were tested for correlations with Spearman's rank correlation coefficient (Siegel 1956). The cumulative data for 5 years were tested with Pearson's correlation coefficient (Zar 1974). For unassisted pairs, among years, the number of young fledged was most highly correlated with nestling survival and hatching success. Over all years combined, the number of young fledged by pairs was most highly associated with nestling survival. In contrast, for pairs assisted by helpers, nestling survival was not correlated with fledging success in any year or for the 5 years combined. These distinctly different

Table 3. Forms of nestling mortality among broods of red-cockaded woodpeckers reared by parents with (H) and without (P) helpers, 1977–1981. Francis Marion National Forest, South Carolina

Year	Group type	Proportion of chicks that died		Proportion of total chick mortality from loss of entire brood	
		n	%	n	%
1981	P	6/12	50	5/6	83
	H	5/21	23	0/5	0
1980	P	3/17	18	1/3	33
	H	3/19	16	0/3	0
1979	P	12/35	34	4/12	33
	H	2/22	9	0/2	0
1978	P	5/17	29	0/5	0
	H	4/21	19	3/4	75
1977	P	6/21	28	4/6	67
	H	2/21	10	0/2	0
Total	P	32/102	31	14/32	44
	H	16/104	15	3/16	19

patterns of factors correlated with fledging success indicate that helpers not only increase nestling survival (Table 1), but also decrease variability in nestling survival to the extent that the number of young fledged is not strongly associated with survival of nestlings. This is, in fact, the case. Both unassisted pairs and pairs with helpers had similar brood size (2.43 and 2.60, respectively) and similar variability in brood size ($CV=0.34$ and 0.36 , respectively). Nestling survival, however, was both significantly lower (0.69 vs 0.85) and much higher in variability ($CV=0.47$ vs 0.23) for pairs than for pairs with helpers.

Helpers could increase nestling survival by a variety of mechanisms. Patterns of nestling mortality suggest one particular mechanism. Red-cockaded woodpecker broods hatch asynchronously (Ligon 1970 and personal observation), and some nestling mortality from starvation is to be anticipated. If starvation were the primary cause of nestling mortality, one would expect to observe partial brood reduction more frequently than total brood loss (Lack 1954). Partial brood reduction is the pattern of nestling mortality exhibited in most years by red-cockaded broods attended by helpers (Table 3). In groups with helpers, 81% of the total nestling mortality was in the form of partial brood reduction. Over 5 years, 16 chicks were lost from 14 broods. In 13 broods, the loss was always a single chick (1 of 3 or 1 of 4). Only 1 of 14 broods was lost entirely.

We observed a distinctly different pattern of nestling mortality in broods attended by only a pair of adults. In 4 of 5 years, a significant proportion of nestling mortality was associated with loss of entire broods, and total nestling mortality over 5 years was almost equally divided between partial brood reduction (56%) and total brood loss (44%). A total of 32 chicks was lost from 20 broods. Five broods (25%) were total losses. Of the other 15 broods, 12 lost single chicks and 3 lost 2 chicks. If total brood losses were deleted from our calculations of nestling mortality, the difference in nestling survival between pairs with and without helpers would have been much smaller (7% difference vs 16% difference shown in Table 1).

The higher incidence of total brood loss among unassisted pairs indicates that unassisted pairs are subject to additional forms of nestling mortality than pairs with helpers. Total brood loss could be the result of nest predation, nest abandonment, infanticide (Vehrencamp 1978; Trail et al. 1981; Emlen 1982b), or some form of disturbance or distraction to the adults causing them to disrupt feeding activities long enough for the total brood to starve. In 2 of the 5 brood losses, the chicks were observed dead within the nest cavity; we assume they would have been devoured had a predator been responsible for their demise. The chicks could possibly have been destroyed by a southern flying squirrel (*Glaucomys volans*) attempting to usurp the cavity, but we did not find squirrels using the cavities immediately following disappearance of the broods.

The other 3 brood losses were associated with loss of 1 of the breeders and with intraspecific intruders, suggesting that helpers may play a role either in provisioning the brood when 1 of the breeders is lost, and/or protecting the territory, the brood, and the parents against intraspecific intruders. Evidence suggests that helpers can at least compensate for a lost parent in feeding nestlings. We observed three instances where 1 of the breeders disappeared from groups with helpers while nestlings were being fed. In two instances, the remaining parent was assisted by 1 helper and in one instance by 2 helpers. In all 3 groups all chicks survived to fledging. This is in contrast to the 3 unassisted pairs that lost breeders, and none of the chicks survived. The fact that the loss of 3 broods was associated with the loss of breeders, and the loss of these breeders was in turn associated with the persistent presence of intraspecific intruders, leads us to hypothesize that intraspecific

competitors may be involved not only in breeder turnover but also, indirectly or directly, in brood mortality.

Post-fledging survivorship

In addition to examining differences in fledging success between pairs and pairs assisted by helpers, we attempted to determine if there were any differences in post-fledging survivorship. Survivorship is much more difficult to monitor because it is often impossible to determine whether the young died or dispersed from their groups. The problem is compounded in a communal species such as the red-cockaded woodpecker where only one sex is retained as helpers and where the different sexes have different dispersal patterns and, quite possibly, different mortality patterns. Given these problems, we approximated survivorship in a number of different ways.

Eighteen groups were followed throughout 1 year to determine home-range size and foraging habitat selection. Of the 18 groups, 15 fledged young the year that home-range work began; for 14, we were able to reliably monitor group composition throughout the year. For these 14 groups, we calculated the proportion of juveniles known to be alive at the end of September, the end of December, and the following breeding season. These dates represent survivorship to approximately 3 months, 6 months, and 1 year. Because females are usually not retained as helpers and, therefore, are not found in their natal groups the breeding season after fledging, we calculated 1-year survivorship only for males. In addition to calculating periodic and annual survivorship for the 14 groups that were followed throughout 1 year, we also calculated annual survivorship for males for all groups for each year and for all years combined over the period 1978–1981. The estimates for males probably provide the best approximation of survivorship, but these estimates are also confounded by our inability to identify disappearances as mortality or dispersion. The fact that males can remain in their natal group as helpers does not mean that all necessarily do.

Juvenile survivorship within the groups followed throughout the course of 1 year is given in Table 4. The proportions were tested with Fisher's Exact Test (Zar 1974) to determine whether survivorship differed significantly between groups with and without helpers and between males and females. Survivorship of both sexes to 3 months and to 6 months and of males to 1 year did not differ

Table 4. Proportion of red-cockaded woodpecker juveniles observed alive within their natal home ranges throughout the year following fledging, Francis Marion National Forest, South Carolina

Parental group size	Time since fledging		
	3 months	6 months	12 months
Pairs			
Males ($n=8$)	0.88	0.88	0.38
Females ($n=6$)	0.33	0.17	0.00
Both sexes ($n=14$)	0.64	0.57	0.21
Pairs with helpers			
Males ($n=8$)	1.00	0.88	0.50
Females ($n=8$)	0.75	0.50	0.00
Both sexes ($n=16$)	0.88	0.69	0.25
All groups			
Males ($n=16$)	0.94	0.88	—
Females ($n=14$)	0.57	0.36	—
Both sexes ($n=30$)	0.77	0.63	—

significantly between groups of different group size. Also cumulative male survivorship ($n=61$) calculated over 4 years did not differ between pairs (0.33) and groups with helpers (0.35). Consequently, it would appear that the influence of helpers on group fitness, at least in terms of production and survival of young, is exerted most strongly on nestling survivorship.

More rapid disappearance, and perhaps higher mortality, of females is apparent from the figures in Table 4. For all groups, combining pairs and pairs with helpers, survivorship or retention of females at 3 months and at 6 months is significantly lower than for males ($P=0.0506$ and $P=0.0094$, respectively). This pattern seems to be more pronounced among pairs than among groups with helpers. Clans with helpers had lower survivorship of juvenile females than of juvenile males, though this difference was not significant. In contrast, among pairs without helpers, survivorship of juvenile females relative to that of juvenile males was almost significantly lower at 3 months ($P=0.0629$, 1-tailed) and definitely lower at 6 months ($P=0.0326$, 2-tailed). This suggests that groups with helpers are somewhat more hospitable to juvenile females than pairs.

Intercorrelations among group size, territory quality, and reproductive success

Positive correlations between group size and reproductive success have been reported for many coop-

erative breeders (Brown 1978; Emlen 1978; Koenig 1981). But as Brown (1978) emphasized, these correlations do not necessarily imply a cause and effect relationship. Reproductive success has also been shown to be correlated with territory quality (Gaston 1978; Brown and Brown 1981; Koenig 1981), and group size to be correlated with territory size (Ridpath 1972; Parry 1973; MacRoberts and MacRoberts 1976; Woolfenden and Fitzpatrick 1978) and territory quality (Brown and Balda 1977). Consequently, simple correlations between the presence or number of helpers and reproductive success are generally confounded by these intercorrelations of both reproductive success and group size with territory size and quality. Throughout the course of 1 year, for 15 of the 18 groups for which we measured home range, we examined correlations between reproductive success and home-range size and quality, and compared reproductive success and quantity and quality for foraging habitat between groups with and without helpers. Three groups were excluded from analyses because group composition was uncertain during the nesting season.

Reproductive success was measured as the number of young fledged during the nesting period when home-range monitoring began. Three measures of habitat quality (Table 5) were included in our analyses based on studies of foraging habitat preference (Hooper and Lennartz 1981; Hooper and Harlow, in press). These statistics were calculated from measurements of tree number and diameter taken from 1,540 point samples systematically distributed among 163 stands within the delineated nesting period home ranges which cumulatively totaled 415 ha.

The number of young fledged was associated with quality of home ranges and also probably with group size and size of nesting period home ranges (Table 5). Although fledging success was higher for groups with helpers than for unassisted pairs (Table 5), the difference was not significant. However, considering the small sample size and the consistently and significantly higher fledging production of groups with helpers over five years (Table 1), we feel the observed difference in number of young fledged is real, and the lack of statistical significance is due to the small sample size. Groups with helpers also had significantly larger nesting season home ranges ($P \leq 0.03$, 2-tailed t test) and significantly more preferred foraging substrate (number of pine stems ≥ 25 cm dbh, $P \leq 0.02$, 2-tailed t test). There was a positive curvilinear correlation (Pearson's correlation coefficient, $r = 0.52$, $P \leq 0.05$) between the number of

Table 5. Number of young fledged per group and habitat characteristics of red-cockaded woodpecker nesting season home ranges; Francis Marion National Forest, South Carolina

Group size and group identifier	Number of young fledged	Home range size (ha)	Area of pine foraging habitat ≥ 20 yr (ha)	Number of pine stems ≥ 13 cm dbh	Number of pine stems ≥ 25 cm dbh
Pairs					
1	3	23.4	22.3	5,514	1,645
3	2	17.9	16.4	2,287	1,366
5	3	12.5	11.8	4,813	1,880
8	2	24.6	23.6	9,524	3,219
13	2	20.7	15.9	8,893	2,014
15	1	15.4	15.4	4,725	2,909
16A	2	36.7	26.8	8,132	3,208
17	1	27.6	8.8	7,357	688
Mean	2.0	22.4	17.6	6,406	2,116
Standard deviation	0.76	7.6	6.1	2,476	920
Pairs with helpers					
9	1	20.0	15.3	5,668	2,657
11A	3	47.9	43.9	6,770	4,283
12	3	39.0	39.0	16,579	3,249
16B	4	25.5	22.2	5,362	3,047
18	2	39.0	24.4	5,453	2,564
19	3	38.1	31.7	7,783	5,174
20	3	26.4	13.8	6,226	3,273
Mean	2.7	33.7	27.2	7,692	3,464
Standard deviation	0.95	9.9	11.5	4,011	941

young fledged and the area of pine foraging habitat ≥ 30 years old, but area of pine foraging habitat was also curvilinearly correlated with home-range size ($r = 0.77$, $P \leq 0.0007$), and number of pine stems ≥ 25 cm dbh ($r = 0.72$, $P \leq 0.002$). Consequently, it appears that fledging success is related to group size, home-range size, and home-range quality. However, because independent variables are intercorrelated, determining the relative importance of each variable cannot be done with available data and correlation procedures.

Additional comparisons suggest that it is indeed the efforts of helpers, over and above nesting period home-range size and quality, that improves reproductive success. First, although nesting period home-range size and quality were greater for groups with helpers than for pairs, the year-round home range was not (75.7 vs 74.4 ha, respectively, $P > 0.9$, 2-tailed t test). On the average, groups with helpers used 45% of their year-round home range during the nesting period compared with

30% for pairs. Clearly, both pairs and pairs with helpers had possession of more resources than they used to feed nestlings. Except for logistics, it is difficult to hypothesize constraints on breeding period home ranges within the boundaries of year-round home ranges. Thus, the larger breeding period home range for groups with helpers was most likely due to the presence of helpers and not vice versa. Therefore, the higher reproductive attainment appears to be the direct result of helpers.

Second, comparisons of reproductive success of the same pairs with and without helpers provide an indication of the influence of helpers less confounded with the influences of home-range size and quality. We have data for four such comparisons, 2 groups which were pairs the first year but were assisted by helpers the second, and 2 groups that had helpers the first year but not the second. In all instances, groups with helpers produced 1 more chick per group than those without, for a cumulative increase of 67% in number of young fledged. This increase would seem attributable to helpers whether we assume constancy of home range from 1 year to the next or consider that helpers might have effected changes in home-range size and quality.

Intercorrelations among group size, breeder experience, and reproductive success

Other studies of cooperatively breeding birds (Ridpath 1972; Woolfenden 1975; Koenig 1981) have shown that reproductive success can also be associated with age or experience of breeders. We could not determine the age of our red-cockaded breeders with any certainty, but from 1978 we could classify most breeders as having had zero or 1 or more years' prior breeding experience in the group they were associated with. Individuals were categorized as 0 (no prior experience) or 1 (prior experience), and pairs were categorized as 0, 1, or 2 according to the cumulative experience of the individual breeders. Using Spearman's rank correlation, we tested for associations between number of young fledged and the relative experience of males, females, and the pair together, with data from the 4 years combined. Differences in the relative experience of breeders associated with pairs and the breeders in groups with helpers were compared with the Wilcoxon-Mann-Whitney 2-sample ranked-signs test (Hollander and Wolfe 1973).

Among all groups the number of young fledged was not found to be correlated with any measure of breeder experience (Table 6). Considering the

Table 6. Correlations between breeder experience and number of young red-cockaded woodpeckers fledged, Francis Marion National Forest, South Carolina, 1978–1981. (Spearman's rank correlation coefficients)

	Male experience	Female experience	Pair experience
Pairs	0.12 ($n=27$)	0.52** ($n=24$)	0.40 ($n=23$)
Pairs with helpers	-0.22 ($n=29$)	-0.40* ($n=24$)	-0.43* ($n=24$)
All groups	0.06 ($n=56$)	0.14 ($n=48$)	0.09 ($n=47$)

* $P \leq 0.05$, ** probability of coefficient $\neq 0$, $P \leq 0.01$

2 group sizes separately, however, fledging success was significantly correlated with relative experience of females, positively among pairs and negatively among pairs with helpers. The mean rank of relative female experience was somewhat higher for groups with helpers than for pairs, but the difference was not statistically significant. Our conclusion is that because fledging success is not positively correlated with breeder experience among groups with helpers, and because groups with helpers were not found to have more experienced breeders than pairs, then the difference in fledging success between groups with and without helpers (Table 1) cannot be attributed to any association between group size and breeder experience.

The most intriguing aspect of these analyses, however, was the negative correlation between fledging success and relative experience of female breeders among groups with helpers. In an attempt to resolve this apparent enigma, we first examined the group of clans with inexperienced breeders ($n=5$) to determine if they shared some unique demographic parameter which might account for their higher reproductive success. Two of the groups had older helpers (3 and 4 years old) and 1 of these had 2 helpers instead of the customary 1. However, using Spearman's rank correlation procedure we found no relationship between number of young fledged and number of helpers and helper age ($r=0.21$, $P>0.10$ and $r=0.13$, $P>0.10$, respectively).

The relationship between group size and female experience and reproductive success is diagrammed in Table 7. Among groups with inexperienced females, those assisted by helpers produced three times as many fledglings as those without ($\bar{X}=2.80$, $SD=0.44$, $n=5$ vs $\bar{X}=0.89$, $SD=0.93$, $n=9$, $P<0.02$). In contrast, in groups with experienced females fledging success was virtually identical with or without helpers ($\bar{X}=2.00$, $SD=0.88$, $n=19$ vs $\bar{X}=1.93$, $SD=0.80$, $n=15$, $P>0.10$). These data suggest that helpers have a dramatic positive

Table 7. Relationship between number of young fledged per group and experience of breeding females in red-cockaded woodpecker groups with and without helpers. Francis Marion National Forest, South Carolina, 1978–1981. Comparisons between columns were made using two-tailed Mann-Whitney *U*-tests. Sample sizes are given in parentheses

Female breeding experience	Number of young fledged	
	Pairs	Pairs with helpers
None	0.89 (9) $P < 0.02$	2.80 (5)
Prior	1.93 (15) $P > 0.10$	2.00 (19)

influence on fledging success in groups with inexperienced females but do not enhance, and in fact may have a negative influence upon, reproductive success in groups with experienced females. Our sample size, however, especially for inexperienced females, is small, and the relationships need to be examined with a larger data set.

Discussion

Inquiries into the adaptive significance of cooperative breeding and helping behavior have emphasized two distinct, yet related, topics: (1) the environmental factors or pressures that promote the retention of juveniles and the aggregation of more than 2 adults into social units, and (2) the relative gains or losses in individual fitness among group members that explain how and why members of a group cooperate. Both topics have been explored by using cost-benefit analyses to assess the advantages and disadvantages of observed behaviors relative to the advantages and disadvantages of alternative behaviors. The major conclusions that have emerged from these analyses have been summarized by Emlen (1982a, 1982b). Among many cooperative breeding birds, social groups are extended family units formed by the retention of young in their natal territories. The social groups develop because the young are "ecologically constrained" (Emlen 1982a) from dispersing and breeding independently because of a shortage of resources required for reproduction (Brown 1974; Emlen 1978; Gaston 1978; Koenig and Pitelka 1981; Emlen 1982a). Once extended family units are formed, kin selection and gains in inclusive fitness to both breeders and helpers provide a parsimonious explanation for why helpers help (Brown 1978; Emlen 1978, 1982a).

Juvenile retention and group formation

The social system, behavior, and life history of red-cockaded woodpeckers seem to fit the models or

patterns summarized by Emlen (1982a) to explain when family social units will form. Red-cockaded woodpeckers have the unique habit of excavating their nest and roost cavities only in mature, living pines. Cavity excavation takes from several months to years to complete (Baker 1971; Jackson 1977; Jackson et al. 1979). Once completed, cavities are used for several years. In contrast, most other woodpeckers excavate cavities in dead trees; new nest cavities are excavated each year and take only a couple of weeks to complete (Jackson 1977).

We suggest that the use of living pines for cavities and the associated lengthy period of time required to excavate a cavity provide the ecological constraints that inhibit most male red-cockaded woodpeckers from dispersing and attempting to breed independently their first year. As noted earlier, we have observed yearling red-cockaded woodpeckers to acquire breeding status, but in all instances they moved into territories with completed cavities and replaced or displaced resident breeders.

Kin selection

Once the extended family unit has become established, the demographic environment is formed for the operation of kin selection. Because red-cockaded woodpecker helpers have been observed assisting primarily 1 or both parents and in one instance a brother, they are related to the young they help rear on the average by 0.25–0.50. Consequently, kin selection and gains in indirect fitness may provide a partial explanation of why helpers help. Table 6, however, would indicate that kin selection may not provide the entire answer.

The negative correlation between fledging success and female experience among groups with helpers is also a negative correlation between the efficacy of helping behavior and the relatedness between helpers and the chicks they help rear. In groups with helpers and inexperienced females, the female and the helper are, by definition, not related; he being a yearling or older in his natal territory, she making her first breeding effort in that territory. In contrast, in groups with experienced females, the breeding female and the helper are generally mother and son. The only exception to this was the one instance we observed of a female breeding in 2 different groups, and the second group she moved to had 2 helpers, offspring of the breeding male and his previous mate. In all instances, except one, in which relatedness between helpers and breeders was known, helpers have been either sons or, rarely, brothers of the breeding male. Consequently, in groups with experienced females, helpers were helping father and mother, and

were related to the young they helped rear on the average of 0.50. In contrast, in groups with inexperienced females, helpers were not helping father and mother, but rather father and a prospective mate. Should the father die, the helper is not inhibited by inbreeding from mating with the female. Helping under these conditions could conceivably have the multiple benefits of aiding in the production of half-sibs, establishing a bond with a prospective mate, and facilitating inheritance of a territory and cavity trees.

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