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COOPERATIVE ENHANCEMENT OF REPRODUCTIVE SUCCESS IN TROPICAL WREN SOCIETIES[1]

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Abstract. Stripe-backed Wrens, *Campylorhynchus nuchalis,* live in cooperative groups of up to 14 adults in which all members share in defense of the common territory, in construction and defense of roosting and breeding nests, and in the care of young produced by a single breeding pair. A 5-yr study of a completely marked population of 25–30 groups in the Venezuelan savanna shows that breeders (principals) assisted by two or more nonreproductive auxiliaries have much greater reproductive success than those with less help. Per capita production of independent juveniles is higher, as well. Only groups with at least two auxiliaries successfully rear two clutches in a season. The proportion of nesting attempts successful in producing fledglings is much higher for groups of four adults or more than for smaller groups, probably because of lesser predation on the nests of large groups. The success of large groups is not likely due to differences in territory quality or breeder experience.

Rates of food delivery to nestlings and number of fledglings per successful nest are as high for pairs and trios as for larger groups. However, feeding of nestlings and fledglings by auxiliaries frees the principals from these tasks and probably makes multiple successful clutches possible. Auxiliaries directly defend the breeding nest from predators and competitors, although the principal male is most active in defense. Feeding efforts of auxiliaries are probably linked to increased nesting success primarily through enabling the principal male to defend the nest better. Aid-giving by auxiliaries is explained (1) by its effectiveness in improving the reproductive success of close kin through reducing risk of predation for nestlings, (2) by the probability of reciprocation of such effective help, and (3) by the low productivity of breeding outside a large established group. Data from this population of wrens constitute some of the strongest evidence to date that group defense against predators can provide the impetus for cooperative breeding.

Key words: communal breeding; cooperation; delayed dispersal; kinship; predation; predator defense; reciprocity; reproduction; reproductive strategies; tropical birds; wrens.

INTRODUCTION

Cooperative breeding in birds often involves a single reproductive pair of adults aided by one or more nonreproductive adults on a communally defended territory (Skutch 1961, Rowley 1976, Woolfenden 1976, Brown 1978, Emlen 1978). The social organization of the Stripe-backed Wren, *Campylorhynchus nuchalis,* is typical of cooperative breeders in that groups of up to 14 adults collaborate in territory defense, nest construction, defense against predators, and in the care and feeding of nestlings and fledglings. Young wrens often remain on their natal territories beyond physiological maturity, rather than disperse to breed (Wiley and Wiley 1977, Rabenold and Christensen 1979). Understanding the adaptive significance of aid-giving that is linked with delayed dispersal and delayed reproduction requires study of both the effects of cooperation on the reproductive success of the breeders, and the opportunity for nonbreeding adults themselves to breed elsewhere (Selander 1964, Lack 1968, Brown 1974). Calculations of both the costs and the benefits of helping require knowledge of the comparative success of cooperative and unaided breeding, both by individuals that do disperse to breed in a new area and by the breeders left behind (Hamilton 1964, West-Eberhard 1975, Brown 1978, Brown and Brown 1981, Koenig and Pitelka 1981). This paper will assess the hypothesis that cooperation in a group of wrens enhances the reproductive success of breeders, and that this cooperation benefits all collaborators.

Breeding pairs among Stripe-backed Wrens are the principal participants in groups in activities like territorial displays, and are the only members active at a nest where eggs are being laid (Rabenold 1984). The descriptive term "principal" and the presumptive term "breeder" can therefore be used interchangeably. Similarly, the terms "auxiliary" and "helper" will both be used to refer to presumptive nonbreeding subordinates that always participate in activities related to rearing young as well as maintenance of nests, territory defense, vocal displays, and tactile interactions.

Enhancement of the reproductive success of breeders through the efforts of helpers would help explain the tolerance of potential competitors for mates and food on breeding territories. Otherwise, one could consider the presence of helpers a form of extended parental care by the breeders, or competitive interference by the helpers, under conditions somehow unfavorable for dispersal (Alexander 1974, Zahavi 1974). Helpers could cause increased reproductive success in a variety of ways. An obvious possibility is that aid provided by

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auxiliaries, especially in the form of food brought to developing young, increases the number of young that can be successfully raised.

When auxiliaries are kin to principals and their young, increasing the production of these nondescendent kin will contribute to the inclusive fitness (Hamilton 1964) of the auxiliaries, and such aid-giving will be favored by kin selection. This "indirect" benefit (Brown and Brown 1981) to auxiliaries could offset the loss in direct offspring production incurred by deferred breeding. Such compensation would be especially important when established groups greatly facilitate rearing young and when opportunities to breed in such groups are few.

Deferred reproduction resulting in higher probability of survival and eventual breeding success can be advantageous when environmental constraints limit the number or divisibility of breeding territories relative to the pool of potential breeders (Selander 1964, Brown 1974, Ricklefs 1975, Brown 1978, Koenig and Pitelka 1981, Emlen 1982). Colonization of unoccupied areas becomes a poor option when auxiliaries that wait to breed gain delayed benefits, such as enhancement of ability to gain a high-quality breeding position in an established group later, and reciprocation of aid by previous recipients. High levels of relatedness between auxiliaries and young will then favor aid-giving by nondispersers as an interim form of gene replication. The critical factor favoring cooperative breeding under these circumstances is group enhancement of reproductive success.

Previous studies of cooperative breeding in birds have shown that the effects of helpers on reproductive success vary considerably among species. In most species, larger groups produce more young per year (Rowley 1965, Ridpath 1972, Parry 1973, Mader 1975, Rowley 1978, Stacey 1979*b*, Dyer and Fry 1980, Reyer 1980, Woolfenden and Fitzpatrick 1980, Brown and Brown 1981, Emlen 1981, Koenig 1981, Kinnaird and Grant 1982; see also review by Brown 1978). However, helpers have in some cases not been shown to be consistently associated with increased reproductive success (Gaston 1973, Vehrencamp 1978, Craig 1980, Birkhead 1981, Ligon 1981). Helpers are sometimes associated with improved nesting success (Ridpath 1972, Rowley 1978, Dyer and Fry 1980, Reyer 1980, Emlen 1981, Woolfenden 1981, Kinnaird and Grant 1982) and energy savings for breeders (Rowley 1965, Parry 1973, Brown et al. 1978, Rowley 1978, Stacey 1979*b*, Lewis 1981, Ligon 1981, Kinnaird and Grant 1982). In only one study has a positive effect of auxiliaries been verified experimentally (Brown et al. 1982). Helpers in some species reduce risk of predation for young birds (Rowley 1978, Woolfenden and Fitzpatrick 1980). This paper presents 5 yr of data from a large, completely marked population of Stripe-backed Wrens to evaluate the roles of helpers in the reproductive success of breeders and to consider the advantages of aid-giving to the helpers.

FIG. 1. The Stripe-backed Wren, *Campylorhynchus nuchalis* (drawing by Kathy Shuster).

STUDY POPULATION, METHODS, AND BACKGROUND

Stripe-backed Wrens (*Campylorhynchus nuchalis*; Fig. 1) range throughout the llanos (savannas) of Venezuela and Colombia to the foothills of the Andean uplands, in open woodlands (Selander 1964). Although temperature varies little over the year, the savannas are intensely seasonal habitats. At the study site, Hato Masaguaral, near Calabozo in Estado Guárico, Venezuela, an average of 1450 mm of rainfall is recorded annually, mostly falling during May to October. Little rain falls during November to April, and many trees then drop their leaves as a result. Most insectivorous birds, including the wrens, breed in the rainy season (Thomas 1979). Hato Masaguaral is a mosaic of distinct vegetation types ranging from very open savanna that is deeply flooded in the wet season and dominated by palms (*Copernicia tectorum*) and grasses and sedges, to dense forest near the Guárico River (Troth 1979). The Stripe-backed Wrens occur in intermediate vegetation types, especially in open shrubby woodland dominated by the trees *Cassia grandis, Albizia* sp. and *A. guachapele, Enterolobium cyclocarpum, Guazuma tomentosa, Ficus* spp., *Genipa americana,* and *Pithecellobium saman,* and shrubs such as *Annona* sp. and *A. jahnii, Trichilia trifolia, Randia venezuelensis,* and *Zanthoxylum culantrillo.* These woodlands are variably flooded in the wet season with up to 1 m of standing water and are interspersed with frequent grassy clearings.

The study population consisted of 25–30 groups of wrens ranging from 2 to 14 members. The wrens remained on year-round territories that have highly traditional boundaries (Fig. 2). Average group size was five adults, so that the total population in this roughly 120-ha area varied between 125 and 150 individuals (Rabenold and Christensen 1979). During this 5-yr study, territory boundaries changed little, except when neighboring groups' relative sizes changed dramati-

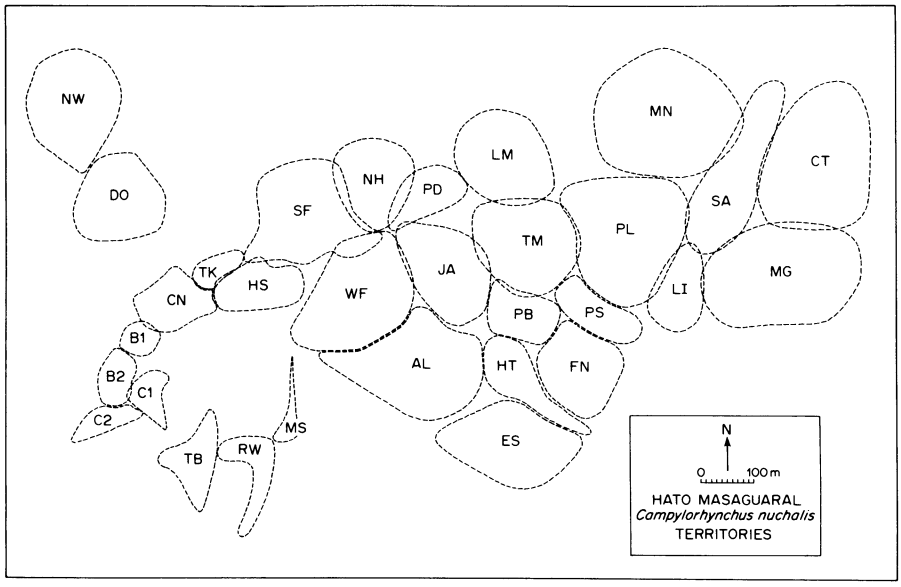

FIG. 2. Thirty-one Stripe-backed Wren territories in the main study area.

cally. All members of this population were color banded with individually unique combinations of plastic leg bands in 1977, and all subsequent recruits to the population, including all young produced and all immigrants, were also banded. In 5 yr, 358 wrens were banded in the study area, and all birds were individually recognizable during the observations described here.

I censused the population exhaustively twice each year, before and after the breeding season, including surrounding areas. The study area is bounded on three sides by open habitat unused by Stripe-backed Wrens. Migration into and out of the study population was fairly low: from 2 to 5% of the total population annually. For instance, in June and December 1981, 38 groups were censused outside the study area, using recordings of wren vocalizations to identify principals. In this census only five dispersers were found that had left the study population in 1981. In that time, only seven immigrants entered the 29 groups under study from the outside. Dispersal within the population usually involves only young females and is generally confined to one or two territories' distance. Males generally remain on their natal territories for life, often eventually breeding there. As a result of complete marking and the high viscosity of the population, parentage of 96% of the auxiliaries and 41% of the principals is known (Rabenold 1984). The sedentariness of the wrens and the traditional nature of group boundaries make it possible to treat groups as distinct entities across years.

Breeding status of all groups was monitored at weekly intervals through most of the breeding seasons of 1978 and 1979, and through roughly half of the seasons of 1980 and 1981. I lived in the study area for 8 mo in 1978, 6 mo in both 1977 and 1979, and 3 mo in both 1980 and 1981. With considerable help from C. Christensen, R. and M. Wiley, and P. Rabenold, >10 000 observer-hours were amassed.

Detailed observations of breeding behavior were made especially in 1978 and 1979, years in which breeding throughout the population was relatively productive. Observations of wrens feeding nestlings were made between 0600 and 1200 during the last week of the 17-d nestling phase, when feeding rates are maximal. Stripe-backed Wrens use two kinds of nests: nests built of sticks by Thornbirds (*Phacellodomus rufifrons*) and nests built by the wrens themselves using grasses and vines. Stick nests are usurped by the wrens and used for both breeding and roosting; they are conspicuous and often large and divided into several separate compartments (Fig. 3). Grass nests are more cryptic and are often worked into a matrix of mistletoe in the branches of a tree (Fig. 3). Deliveries of food to either type of nest are always readily observed, in part because the wrens habituate quickly to observers. Observers watched nests with binoculars, recording arrivals and departures of individuals, the identities of those taking food to the nestlings, the type and size of food, behavioral interactions of group members near the nest (especially allopreening, duetting, and aggressive encounters), and interspecific interactions near the nest.

Stripe-backed Wrens collaborate in territory defense and in nest building and defense, and all members of a group aid in feeding the young of a single breeding pair. All members perform the song of the species, a duet of rapidly alternated harsh notes. The two principal members of a group are conspicuous by their dominant role in duetting and allopreening, even in

FIG. 3. Two types of nests used by Stripe-backed Wrens for breeding and roosting. Upper-left arrow indicates a nest constructed of sticks by thornbirds that has been usurped by wrens. Lower-right arrow indicates clump of mistletoe in which an enclosed nest of grass has been constructed by the wrens. Note the position of both nests at the end of long slender branches, 10–15 m above ground. Tree is *Albizia* sp., the commonest tree used for nesting by the wrens.

the nonbreeding season (Wiley and Wiley 1977, Rabenold 1984). Only principals attend the breeding chamber during egg laying and incubation. Principal females (P♀) are identifiable when caught in the breeding season by the presence of a highly vascularized brood patch. Only the P♀ enters the chamber where eggs are laid and incubated, until the eggs hatch and others in the group begin to help feed the nestlings. Even then, she alone broods the nestlings during the day and spends the night in the nestling chamber. The other members of the group spend the night, generally together, in other chambers of the same nest or in another nest very close by. The principal male (P♂) is consistently closely associated with the P♀ especially during egg laying and incubation (Rabenold 1984). Although direct evidence of paternity is lacking, strong circumstantial evidence indicates that only one member of each sex breeds in groups of these wrens.

Nonbreeding members can be sexed behaviorally, especially by their duetting with the principals. Members of a group fall into one of two parts of a duet matrix: those that duet with the P♂ but not the P♀ (females) and those that duet with the P♀ and not the P♂ (males). Sexes assigned by the criterion of opposite-sex duetting partners have never been contradicted by later breeding roles. Age determinations by plumage and iris color are reliable only to 6 mo of age, so that individual histories must be used to determine age beyond juvenile status. Juveniles are considered "independent" 1 mo after leaving the nest, when they cease receiving appreciable quantities of food from adults. The number of juveniles raised to independence is used as the most basic currency of reproductive success.

RESULTS

Variance among groups in reproductive productivity

In 96 group-years, 101 breeding attempts were detected either in the incubation or in the nestling phase, and only 40 of these clutches resulted in at least one fledgling leaving the nest: an overall success rate of only 40%. Over the last 5 yr, 152 juveniles were produced in 32 groups under observation. For 26 groups that have been monitored most closely, the number of independent juveniles produced over 5 yr is strongly associated with mean group size over those years (Fig. 4). This association is produced by two major factors affecting the productivity of large groups: (1) a higher proportion of nesting attempts by large groups is successful in producing fledglings than is the case for attempts by small groups, and (2) large groups can produce two successful clutches in a single season. For example, the five most successful large groups (AL, MN, PB, TM, and WF) produced at least one fledgling

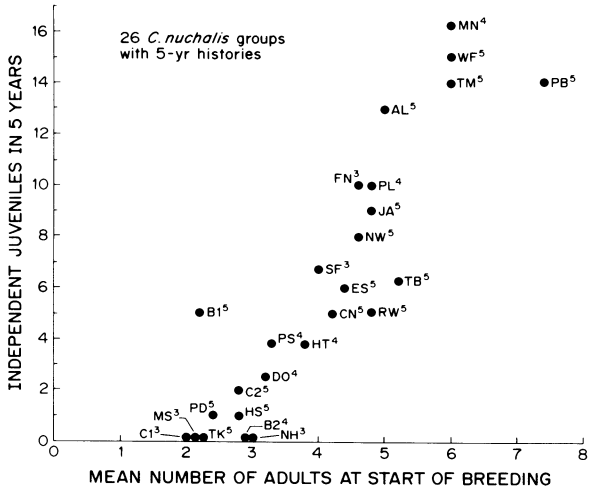

FIG. 4. The relationship between number of collaborating adults at the start of a breeding season and total juvenile production in 5 yr, for 26 Stripe-backed Wren territories. Superscripts indicate the number of years for which accurate data exist on the number of independent juveniles produced. Values have been extrapolated to 5 yr for groups that went extinct during the study or were added to the study population in 1978. Pearson correlation coefficient $r = 0.90$; $P < .001$.

in 80% of their attempts (16 of 20 clutches) including seven successful second clutches. In contrast, the five least successful small groups (B2, C1, MS, NH, and TK) failed in each of 19 attempts. This section will consider in turn the disparity in productivity between large and small groups, patterns of nesting success and failure, and abilities of breeders to produce additional young after losing nests or fledging young.

Annual reproductive success.—Groups with two or more auxiliary members produced on average six times as many independent juveniles per pair-season as did unaided pairs or those with only one auxiliary (2.4 vs. 0.4 juveniles per pair; $P < .0001$, $N = 96$, Mann-Whitney U test) (Fig. 5). Unaided pairs and trios rarely succeeded in raising any young in a breeding season. In comparison, groups with two or more auxiliaries often produced two broods of fledglings in a single season (Fig. 5). The relationship between number of auxiliaries and number of juveniles produced in a season is not a smooth one, but shows a sharp step increase between trios and groups with two auxiliaries. Quartets therefore seem to constitute a "critical mass" for breeding success. Trios on average produced only 0.40 juveniles per pair-season ($N = 25$), while the figure for quartets was 1.86 ($N = 21$), ($P < .001$, Mann-Whitney U test) (Fig. 5). Groups with more than two auxiliaries ($N = 28$) also showed increased productivity ($P < .005$, G log-likelihood ratio test [Sokal and Rohlf 1969]) compared to quartets, but the comparisons between larger group sizes are not as striking as the trio-quartet comparison (3.67 juveniles per pair for groups of ≥ 6 adults, $N = 15$, vs. 1.86 juveniles per pair for groups of 4 and 5 adults, $N = 34$) (Fig. 5).

Even if the number of independent juveniles per adult instead of the number per breeding pair is used to compare the productivity of groups of different sizes, groups with two or more auxiliaries do significantly better than smaller groups: 0.16 juveniles per adult for

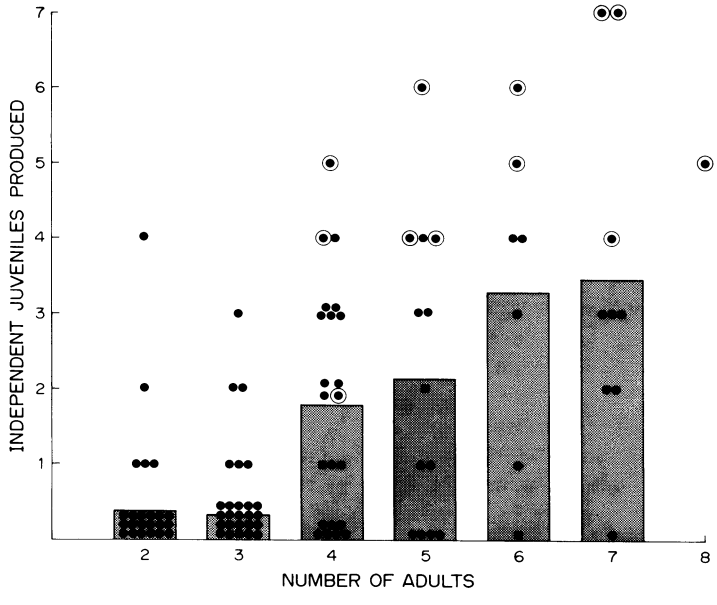

FIG. 5. Annual production of juveniles in groups of different sizes, 1978–1981. Each point represents the number of independent juveniles raised in 1 yr by the breeding pair in a group of a particular size. Circled points indicate two broods produced in a single season. Bars indicate mean number of juveniles per year for each group-size class.

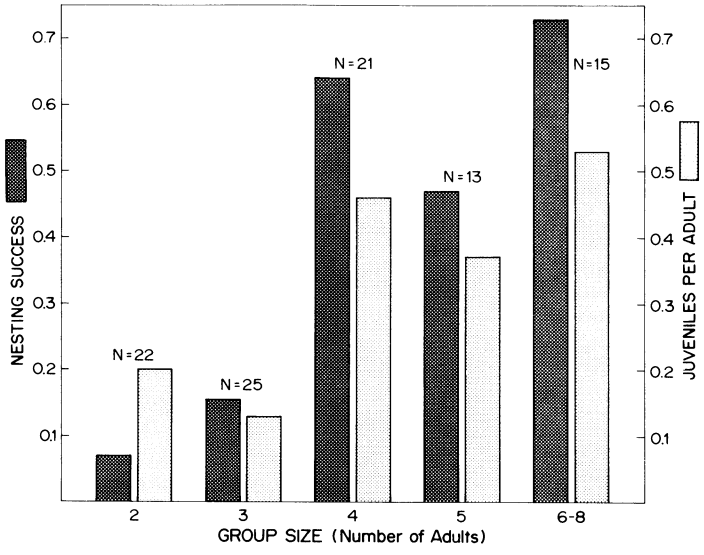

FIG. 6. The proportion of nesting attempts that produced one or more fledglings (nesting success), and independent juveniles produced per adult member for groups of different sizes. Bars indicate values calculated across N group-years.

pairs and trios ($N = 47$) vs. 0.47 juveniles per adult for larger groups ($N = 49$; $P < .0001$, Mann-Whitney U test) (Fig. 6). This measure of per capita productivity averages 0.53 juveniles per adult for groups with four or more adults and does not vary significantly among these group sizes.

Success of nesting attempts.—Underlying the pattern of higher juvenile productivity in larger groups is greater nesting success. Most nesting attempts were detected in the incubation stage or in the very early nestling phase. Undoubtedly some attempts escaped detection if they failed early, but there should be no systematic bias with regard to group size in these cases. For unaided pairs and pairs with only one auxiliary, the proportion of clutches that produced at least one fledgling was only 0.13 (46 attempts), while the proportion of nestings succeeding for groups with two or more auxiliaries was 0.62 (55 attempts; $P < .001$, G test) (Fig. 6). No consistent effect of group size was found for groups larger than four, although lumping groups of 4 and 5 adults and comparing their nesting success to groups of 6, 7, and 8 suggests that very large groups might have a slight advantage over medium-sized groups (0.73 vs. 0.57 success per attempt, but $.1 > P > .05$, G test).

Several lines of evidence suggest that complete failures result from predation rather than from starvation (see also Ricklefs 1969). Nest failures occurred most often in the late nestling phase, when nests are most conspicuous owing to the frequent arrivals and departures of feeding adults, and to the movements and vocalizations of the nestlings (Skutch 1967). Failures were most often sudden; normal levels of feeding abruptly terminated on the day of failure rather than gradually decreasing to cessation. Feeding rates at nests that later failed did not differ from rates at those that resulted in fledglings. Nests were rarely physically torn apart, even though the suddenness of failures suggested complete removal of the nestlings. In 1978, when 42 breeding attempts were carefully monitored, the seasonal timing of nesting affected success in a way that implicates predation. Of 27 attempts at the peak of breeding activity in June and July, only 8 produced fledglings (29.6%). Of 15 attempts in May and August, early and late, respectively, in the breeding season, 12 (80%) were successful ($P < .005$, G test with Yates correction). This result is consistent with the hypothesis that predators switch to wren nests when they are most abundant.

Experience and recycling in nesting.—The age or history of breeding pairs had no significant effect on numbers of juveniles produced in a season. Newly established breeding pairs in 1978 and 1979 produced as many juveniles relative to their representation in the population as did pairs in their second breeding season together (Table 1). Similarly, young pairs breeding without helpers did not have different breeding success compared to older unaided pairs over the years.

The production of a second or third clutch of eggs in a season by breeding females following a nesting failure was not affected by group size, but females in pairs or trios never produced another clutch after fledging young. When nests failed, usually while nestlings were being actively fed, breeding females recycled quickly in groups of all sizes, often laying a new clutch of eggs within 10 d. Other group members have not been observed feeding breeding females. Because of repeated failures, breeding females in pairs and trios

TABLE 1. Number of independent juveniles produced by newly established (new) breeding pairs and by pairs that were together in the previous season (established). Data are pooled for 1978 and 1979. The fraction of breeding pairs in each category (new, established) was multiplied by the total number of juveniles produced to obtain the expected numbers. ($P > .05$, G test).

Breeding pairs	No. independent juveniles	
	Observed	Expected
New	27	19
Established	53	61

commonly produced three clutches of eggs in a season. Breeding females in larger groups did not lay more clutches in a season, but were capable of laying a second or third clutch after successfully rearing an earlier clutch.

Nestling feeding rates and contributions of individuals

In 4 yr of intensive monitoring of breeding in the study population, 54 nests were observed for at least 6 h each to establish rates of food delivery to nestlings and relative contributions of principals and auxiliaries. These observations have included >6000 deliveries of food items to nestlings. In addition, the provisioning of fledglings by adults was observed in 10 groups. One case is presented as an example in which four adults, including one male auxiliary and one female auxiliary, collaborated in feeding a clutch of nestlings and later in feeding the three young once they left the nest (Fig. 7). In this case, the auxiliaries provided somewhat less food to the nestlings than the principals (parents), but it is common for an auxiliary to provide more food than either parent, or occasionally to provide more than both parents combined. Of 91 individual auxiliaries whose helping efforts were quantified, 103 dyadic comparisons of auxiliary/principal showed the auxiliary contributing more feedings than the principal, and 79 showed the principal contributing more. On average, auxiliaries feed nestlings as often as principals do (variability in auxiliaries' contributions in Rabenold 1984). After the young leave the nest, they are still fed by all adults, usually for another month. While fledglings are being fed, auxiliaries often provide the bulk of the food. In the example presented here (Fig. 7), the principals subsequently produced another clutch while the fledglings were still being fed by the auxiliaries, and the second clutch was successfully raised.

Feeding rates and fledgling numbers.—Deliveries of food to nestlings become more frequent as the young birds grow, until they leave the nest. After 21 d of incubation, the nestlings are fed by all group members for 15–19 d. During the last week of this period, feeding rates average 18 deliveries/h for groups of all sizes, although there can be considerable variability from hour to hour. By observing six nests 1 h each day for >16 d of nestling feeding, I found that six observations of 1 h each over six consecutive mornings in the last

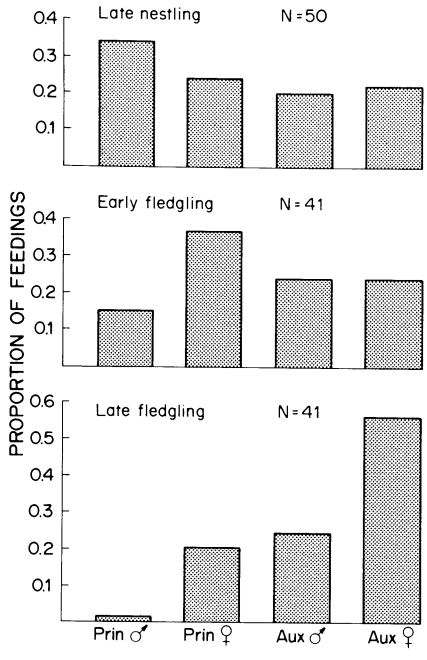

FIG. 7. Feedings provided by four adult members of one group (TM78) at three stages of development of the young. N = total number of feedings.

week of nestling feeding gave an accurate measure of overall feeding rates and of relative individual contributions. For each 6-h sample, two hour-long observations were made in the interval 0600–0800, two observations 0800–1000, and two observations 1000–1200. No effect of time of day was found. For 6-h samples, there was an average of 108 deliveries of food to nestlings.

Total nestling feeding rates did not vary significantly with group size. The number of items provided nestlings by pairs and trios ($\bar{x} \pm$ SD = 17.8 ± 5.8 items/h, $N = 12$ [for the 6-h sample]), did not differ significantly from provisioning by groups of four or five: 18.6 ± 5.2 items/h, $N = 24$ ($P > .05$, Mann-Whitney U test) (Fig. 8). All except one of the nesting attempts by pairs and trios included in this analysis eventually failed to fledge young. No consistent differences existed in the sizes or types of items provided by groups of different sizes. Slightly higher feeding rates were suggested in groups of six to eight adults compared to groups of four to five (Fig. 8; but $P = .12$, Mann-Whitney U test). Maximum feeding rates, in the 6-h samples taken during the last week of nestling feeding, did not vary significantly with group size. Thirty groups' feeding records were examined and the maximum hourly rate recorded. Pairs and trios averaged 24.6 ± 9.2 feedings/h ($N = 11$), while larger groups averaged 27.3 ± 6.6 ($N = 19$; $P > .05$, Mann-Whitney U test).

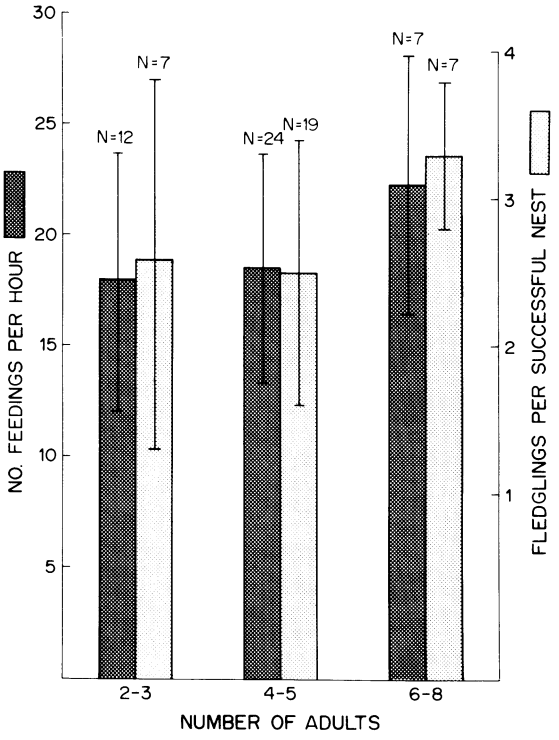

FIG. 8. Rates of feeding nestlings by all adults and numbers of fledglings produced in groups of different sizes. Bars indicate mean values calculated across N nestings. Feeding rates for each group were calculated from six 1-h samples in the 2nd wk of nestling feeding. Bracketed vertical lines indicate one standard deviation on either side of the mean.

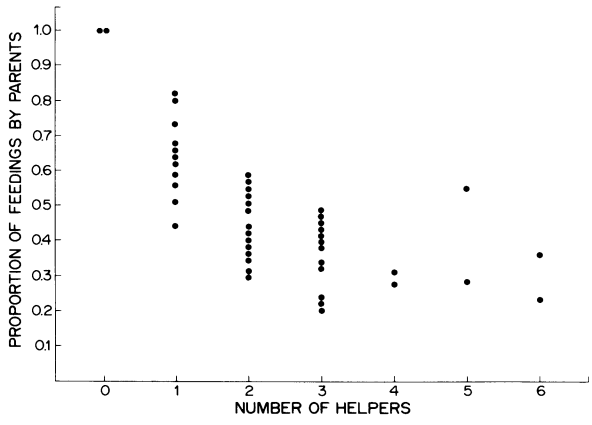

FIG. 9. Relative effort in feeding nestlings by principals in groups of different sizes. Each point represents the feeding effort of one principal pair as a proportion of total feedings by all adults.

The number of fledglings produced by successful nests did not differ for groups of different sizes (Fig. 8). Pairs and trios produced an average of 2.6 fledglings per successful nest, while the value for groups of four and five was 2.5. A slight increase was suggested in the number of fledglings per successful nest for groups larger than five adults (Fig. 8; but $P = .06$, Mann-Whitney U test).

Relative contributions of principals and auxiliaries.—All group members shared roughly equally in feeding nestlings, and as a result, contributions by principals diminished with increasing group size. Individual auxiliaries differed considerably in their helping efforts, but on average auxiliaries contributed feedings as frequently as principals (5 feedings/h for all). Principals taken together provided, on average, two-thirds of the food in trios, one-half in quartets, and two-fifths in groups of five, although there was considerable variation among groups of the same size (Fig. 9). Principals provided as little as 20% of the food for nestlings in some larger groups. As group size increased, the reduction in feeding trips was greater for male principals than for female principals (Fig. 10). Efforts of male principals in groups with two or more auxiliaries averaged nearly half those in pairs and trios ($\bar{x} = 3.9$ ($N =$ 30) vs. 7.3 trips/h ($N = 12$); $P < .0001$, Mann-Whitney U test), while females' efforts changed little (3.9 vs. 5.2 trips/h; $P > .10$).

Auxiliaries appear to contribute food similar to that provided by principals to nestlings. Food items brought to nests can usually be seen clearly with binoculars. In order to compare food items brought by auxiliaries to those brought by principals, I used sets of observations of 11 breeding attempts in eight different groups (three groups were analyzed in two different years). In all, 22 principals brought 708 food items in this survey, and 27 auxiliaries brought 810 items. Six of the data sets were chosen because they included >16 h of observation, and the other sets were chosen because of their relatively detailed descriptions of food items, usually because of a close observation point. Food items were classified by size (1-cm categories, using the 2-cm beak as a reference), taxonomic category (lepidopteran adult or larva, orthopteran, spider, miscellaneous adult insect [mantid, odonate, or unclassifiable], or pupa), and color (white, red-brown, yellow, light green, dark green, and dark brown). In each of the 11 groups, when cumulative proportions of items brought in each class of the three categories were compared between principals and auxiliaries, no significant difference emerged ($P >$ .05, Kolmogorov-Smirnov test). An example for one group is given in Table 2.

Wrens survive as well in small groups as in large ones, despite the fact that individuals feed young more often in small groups. Principals in groups with at least two auxiliaries have no greater survivorship (65% annually) than principals in smaller groups (61%; $P >$ .50, χ^2 test). Even though male principals could benefit more from nestling feeding by auxiliaries, male principals do not survive better than females (62% for males, 68% for females). Auxiliaries survive as well as principals (73% overall), but male auxiliaries survive better

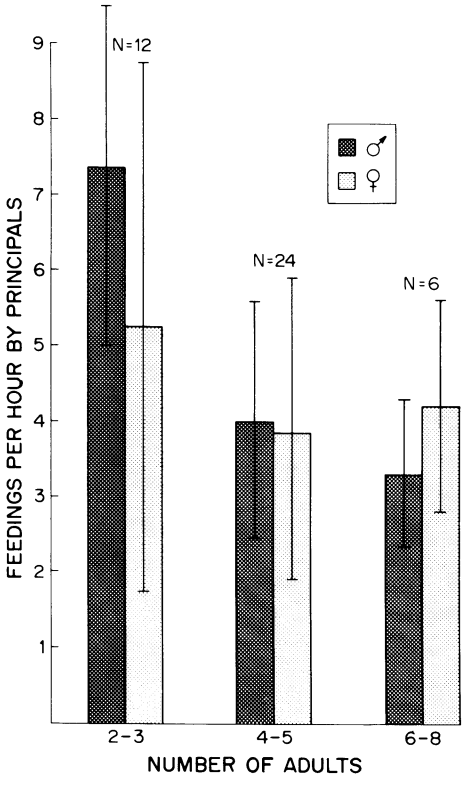

FIG. 10. Feeding trips per hour to nestlings by principals in groups of different sizes. Bars indicate mean delivery rates for N principals of each sex for each group-size class. Bracketed vertical lines indicate one standard deviation on either side of the mean.

(79%) than female auxiliaries (66%; $P < .05$, χ^2 test). Juvenile survival in the first 6 mo is not affected by group size. The rigors of nestling feeding and nest defense for unaided principal males may be more severe than for males with helpers, since in the only two cases of full clutches of four young successfully fledged by pairs, the male died shortly after the young fledged.

Nest defense

Stripe-backed Wrens aggressively defend the immediate vicinity of their nests against many other species of birds, especially during breeding. Raptors that are potential predators of adults and young include the Savanna Hawk (*Heterospizias meridionalis*), Roadside Hawk (*Buteo magnirostris*), Crane Hawk (*Geranospiza caerulescens*), and Yellow-headed Caracara (*Milvago chimachima*). Wrens often actively scold these raptors, loudly enough to attract other birds that join in harassing the predator vocally and physically. Species that collaborate in mobbing raptors include large flycatchers like the Greater and Lesser Kiskadees (*Pitangus sulphuratus* and *P. lictor*), smaller flycatchers like the Rusty-margined Flycatcher (*Myiozetetes cayanensis*), Blue-gray Tanagers (*Thraupis episcopus*), Yellow Orioles (*Icterus nigrogularis*), and Grayish Saltators (*Saltator coerulescens*). Just as often, however, the wrens will "ignore" a raptor in their nest tree and will quietly cease delivering food to nestlings if they have an active nest.

In contrast, brood parasites and nest competitors are always attacked when detected near the wrens' nest. Species chased include the brood-parasitic Shiny Cowbird (*Molothrus bonariensis*) and competitors for nests and nest material such as the Plain-fronted Thornbird (*Phacellodomus rufifrons*), Blue-gray Tanager, Greater and Lesser Kiskadees, Rusty-margined Flycatchers, Yellow-rumped Caciques (*Cacicus cela*), Troupials (*Icterus icterus*), and Yellow Orioles. When an individual wren discovers such an intruder, it often emits a train of harsh scolding notes before chasing the other bird while uttering a rapid series of chattering notes. Either of these vocalizations is effective in attracting other members of the group, who often join in the chase or the scolding.

TABLE 2. Comparison of food brought to nestlings by auxiliaries compared to principals for one group: ES78. Deliveries in 10 other groups were analyzed similarly.

Prey size					Prey type					Prey color				
Class	Principals		Auxiliaries			Principals		Auxiliaries			Principals		Auxiliaries	
(cm)	No.	Prop.	No.	Prop.	Class	No.	Prop.	No.	Prop.	Class	No.	Prop.	No.	Prop.
<1	29	.25	31	.31	Lepidopteran larvae	14	.29	12	.32	White	1	.01	1	.01
1	53	.47	35	.36	Spiders	10	.20	8	.21	Red-brown	14	.07	5	.04
2	30	.26	27	.28	Orthoptera	4	.08	5	.13	Yellow	16	.08	7	.05
3	2	.02	3	.03	Lepidopteran adults	3	.06	1	.03	Dk-green	33	.16	17	.13
4	0	0	1	.01	Miscellaneous adult insects	17	.35	12	.32	Dk-brown	67	.33	57	.43
5	0	0	1	.01	Pupae	1	.02	0	0	Lt-green	72	.35	47	.35
Total	114	1.00	98	1.00		49	1.00	38	1.01		203	1.00	134	1.01

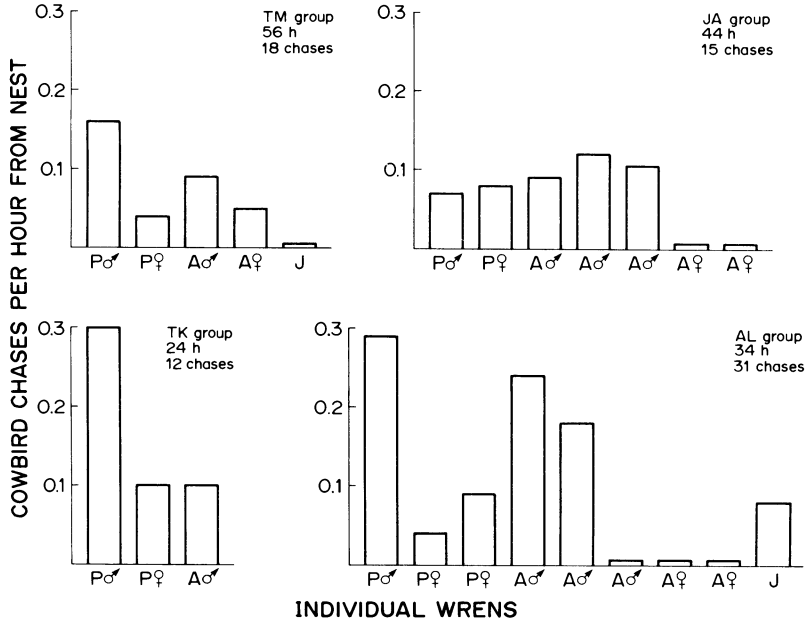

FIG. 11. Nest defense against cowbirds by individual wrens in four different groups. Individuals are listed by sex/status classes (A = auxiliary; P = principal; J = juvenile). All chases involved displacement of a cowbird from the vicinity of the nest. Despite variability, principal males are most active, and auxiliary males are more active than principal or auxiliary females.

Relative defense efforts by group members.—All members of a group participate in repelling intruders, but some classes of individuals are more active than others. Principal males are generally the most active defenders of the nest against cowbird encroachment. However, in some cases individual auxiliary males perform a large portion of the chases (Fig. 11). Principal females also chase cowbirds frequently, but auxiliary females generally participate little in this activity. In some larger groups, the majority of nest-defensive chases are performed by auxiliary males (Fig. 11). In >400 h of observation of active nests during the breeding season, 262 chases of cowbirds by wrens from the vicinity of the nest were witnessed, and 584 chases of other species, mostly those mentioned above. Principal males chased cowbirds more frequently than would be expected if their chases were proportional to their representation in groups (Fig. 12). Because there are always one principal male and one principal female in a group, expected values for the two classes are equal, but principal females chased cowbirds much less often. Auxiliary males also chase more often than would be expected according to their representation in groups when cases occurred, but auxiliary females and juveniles chased much less than expected (Fig. 12).

Chasing effort can be expressed as the proportion of exposures to intruders that are followed by chasing by an individual. In this way, chasing by a class of individuals is weighted by the frequency of the presence of an individual of that class. Principal males' chasing was nearly twice as frequent as the next most active class, auxiliary males (0.41 ($N = 109$) vs. 0.25 chases per exposure ($N = 87$); $P < .001$, χ^2 test). Auxiliary males and principal females did not chase cowbirds significantly differently, but both chased much more

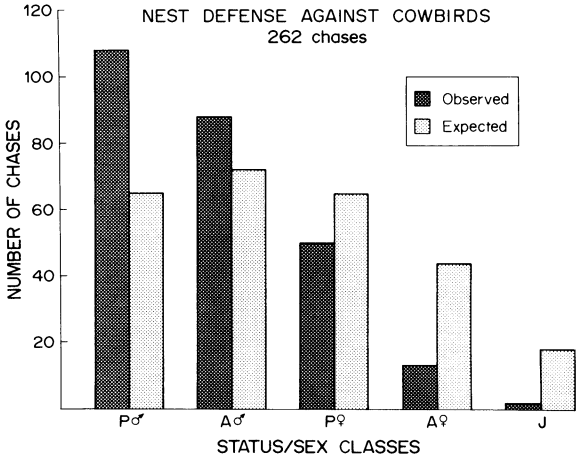

FIG. 12. Incidence of chasing cowbirds from the nest for different status/sex classes. Actual number of chases observed for each class (darker bars) is compared to the number of expected (lighter bar), if chases occurred in proportion to the representation of the class in the groups studied. Expected number of chases in a class equals total chases by all classes multiplied by the proportion of individuals in the population present during chases that belongs to the particular class.

TABLE 3. Combined chasing of cowbirds and other intruders.

	Sex/status class				
	P♂	P♀	A♂	A♀	All
Exposures					
Chase	870	870	1080	895	3715
Not chase	352	160	272	62	846
Chases per exposure*	518	710	808	833	2869
	0.40	0.18	0.25	0.07	0.23

* All differences between sex/status classes are significant at the $P < .001$ level (χ^2 test).

actively than auxiliary females or juveniles ($P < .001$, χ^2 test). The results for chases of species other than cowbirds from the vicinity of the nest were qualitatively identical to cowbird chases. In the complete sample of all chases, auxiliary males chased significantly more frequently than principal females, and all differences between sex/status classes were significant at the $P < .001$ level (χ^2 test; Table 3). In summary, males are more active defenders of the nest than are females, and within each sex, principals chase more than auxiliaries. Principal males, who are liberated from feeding duties by the efforts of auxiliaries in larger groups, are the main defenders against potential threats to the breeding nest, measured by response to passerine intruders.

Effectiveness of group defense.—Cowbird parasitism occurs most frequently in small wren groups. Of twelve wren nests that have produced cowbird fledglings, ten have been nests of pairs and trios, the others the nests of quartets. While cowbird parasitism only accounts for a small proportion of nest failures (<10%), this suggestion that small groups' nests are easier to parasitize raises the possibility that large groups defend their nests more effectively. However, I have not been able to demonstrate greater vigilance by large groups. Using cowbirds as indicators, small-groups' nests were not visited more frequently than large-groups' nests (0.30 visits/h in 293 h for pairs and trios vs. 0.26 visits/h in 548 h for larger groups), and unchallenged cowbird visits are not more frequent for small groups. The proportion of time that no wren is visible within 2 m of the nest is not different for groups of different sizes nor is maximum duration of nonattendance. However, it is difficult to determine when no wren is near enough to detect intruders. There is no tendency for larger groups to respond more quickly to cowbird intrusions, since almost all responses are virtually immediate.

A series of preliminary experimental presentations of live predators at active wren nests suggests that large groups probably provide more effective nest defense than do smaller groups. Presentations of a live (caged) boa constrictor and of a live opossum to nests with nestlings show that the rapid and sustained scolding of wrens in large groups in response to these predators was very effective in attracting birds of other species. These other species, including orioles, tanagers, flycatchers, and saltators took more active, aggressive attitudes toward the predator, repeatedly swooping close to the cage. These observations match those made of wrens mobbing naturally occurring snakes, raptors, and mammalian predators. In small groups, the wrens responded with avoidance of the nest; they stopped coming to the nest and lingered quietly in the outer parts of the nest-tree. This quiet avoidance has been observed often when raptors alight in a nest tree but show no obvious interest in the wrens' nest. Feeding rates in the large groups in the hour following half-hour presentations of predators were considerably higher than in the hour preceding presentation. Further experiments will test the possibility that groups of four or more wrens are effective, through sustained scolding, at recruiting other birds into mobbing predators.

DISCUSSION

The effect of aid provided by auxiliaries on the reproductive success of principals determines not only the advantage to the principal but also the tradeoff for the auxiliary between remaining on the natal territory to help raise siblings vs. the more uncertain course of breeding independently. The results of this study suggest strongly that unaided breeding is unproductive, so that options for auxiliaries are effectively limited to collaborating in the established natal group as a helper until an opportunity arises to breed in that group or in a similar established group. The option of dispersing to colonize and to breed in an open area with a mate only, or with a single auxiliary, is an unproductive one. In fact, in 5 yr not one small group has built itself up from a pair or trio to a productive larger group. As long as inheritance of breeding status and the services of younger helpers in either the natal group or a similarly productive group is predictable, delaying attempts at reproduction could be advantageous (Wiley and Rabenold 1984). In addition, the fact that the opportunity to assist in breeding attempts of others will occur in the company of predictably close kin will contribute to the helpers' inclusive fitness, so far as the assistance is effective.

The evidence that helpers' efforts are effective in increasing the reproductive success of breeders can be organized on three levels: (1) the correlation of both annual and long-term production of juveniles with number of collaborating adults and the ancillary correlation of nesting success with group size; (2) the association of helpers feeding appropriate food to the nestlings, with reduced levels of feeding effort by breeders and the incidence of multiple successful clutches; and (3) the link between helping and nest defense established by both direct defense and the indirect effect of freeing the breeding male from care of the young.

The correlation of group size with reproductive success

The high annual productivity of breeding pairs with more than one helper is produced mainly by high efficiency in nesting: a high probability that a nesting attempt will produce fledglings. This apparent effectiveness of helpers should favor, for instance, a young bird remaining in the natal territory as one of two auxiliaries helping its parents raise full siblings rather than dispersing to breed as a member of an unaided pair. The former course would contribute more to the helper's inclusive fitness because the per capita productivity of quartets is considerably higher than that of unaided pairs. More important, a disperser leaving a quartet to breed unaided would, on average, sacrifice the production of 1.46 siblings (the difference a second helper would make to the natal group) in order to produce only 0.41 offspring, clearly an unfavorable trade.

A nonbreeding auxiliary forfeits the aid of the mate that could have been attracted to collaborate in reproducing (Charnov 1981). When the auxiliary can increase the productivity of its parents by a factor greater than the combined potential of breeding with a mate's help, however, the loss of the mate's collaboration is compensated. In Stripe-backed Wrens, a helper in a quartet can produce more full siblings (absolutely and per capita) than offspring in combined effort with a mate. As long as the siblings are actually full siblings (mean relatedness by descent, $r = 0.5$ [Hamilton 1964]), then they will contribute as much to the helper's inclusive fitness as offspring would ($r = 0.5$ also). Helpers among Stripe-backed Wrens often do aid in raising full-siblings (Rabenold 1984), but even if only half-siblings were being produced, helping would still often be better than breeding.

An alternative explanation for the correlation between group size and reproductive success is that the causal relation is reversed: previous reproductive success and subsequent nondispersal produce large groups. If factors extrinsic to cooperation among the wrens, such as territory quality, allowed some groups to be more productive than others, large numbers of adults would accumulate as a result, not a cause, of juvenile productivity. Reproductive success could be a result of quality of resources in a territory, and associated large numbers of auxiliaries merely a reflection of past reproductive success (Lack 1968, Brown and Balda 1977). Several studies of cooperatively breeding birds have suggested that habitat variables can cloud the causal relationship between helping and reproductive success (Zahavi 1974, Gaston 1978*a*, Vehrencamp 1978, Craig 1979, Stacey 1979*a*, Reyer 1980, Trail 1980, Koenig 1981, Lewis 1981).

Determining which resources are most important in the territory of an insectivorous bird is difficult (Orians 1980). Resource characteristics that could be associated with successful nesting include abundance of appropriate food, nesting sites and nesting material, or vegetation structure inhibiting predators. In some studies, effects of indicators of probable territory quality have been separated from cooperative effects (Koenig 1981, Lewis 1981), but the difficulty usually remains of identifying important environmental variables. Experimental manipulations of group size and year-to-year comparisons of naturally occurring differences on the same territories have most convincingly demonstrated the effectiveness of cooperative breeding regardless of habitat variation (Woolfenden and Fitzpatrick 1980, Brown et al. 1982). A rough correlation exists between 5-yr productivity of groups of Stripe-backed Wrens and the physical and taxonomic complexity of the vegetation contained in their territories. In addition, wrens prefer foraging in types of vegetation that are characteristic of the most productive territories. Establishing the links between vegetation characteristics and nesting success requires further study, but the data available at this time suggest that any effect of territory quality is probably weak in a particular year, compared to the active cooperation of wrens in raising young.

If territory quality does control reproductive success, territories that have proven successful when occupied by a large group should remain successful even if the group's size dwindles because of emigration, fission, or mortality. However, in six cases over the last 5 yr in the wren population, reproduction in a once-productive territory has declined dramatically relative to other territories when group size slips below four adults. In one case, two immigrants (juveniles adopted from another group) joined a trio and raised the rank of the reproductive success of the principals to the level of other productive groups. Reproductive success seems to vary with number of auxiliaries even on the same territory.

If auxiliaries did not actually increase the reproductive success of principals, and if productivity were determined by resources in the group's territory, then helping could not affect the inclusive fitness of the helpers. Auxiliaries might not disperse because the habitat is saturated with wren territories and competitors for openings in those territories, or because existing territories contained essential resources (Selander 1964, Lack 1968, Brown 1974, Ricklefs 1975, Wilson 1975, Emlen 1978, Gaston 1978*b*, Stacey 1979*a*, Koenig and Pitelka 1981). In our study population of wrens, space for territories does not seem to be limiting. Four groups (B2, C1, HT, and SF) on territories that supported large groups (four to five adults) prior to 1978 subsequently dwindled to the point of extinction because of group fissioning and accidents of mortality. These vacated areas, although surrounded by wren groups with nonreproductive helpers, went virtually unutilized by neighboring groups, and were not recolonized by new breeders for 2 yr. In four other cases, pairs have disappeared and have not been replaced in 2–3 yr. In

contrast to the disinterest in colonizing vacated areas, competition is always keen for a breeding position in a large group. As many as 10 young females will engage in vigorous fighting, often lasting several days, in competition for the position of a deceased principal female in a large group. No such contests have been seen over a breeding position in a pair, trio, or vacant area. These openings are not treated by the wrens as desirable breeding opportunities.

Group fission is a possible solution to the "habitat saturation" predicament. If a territory contains the resources to support a single group of six adults, why could it not support two trios instead? Three instances of group fission have occurred since 1977, and in all cases the resulting groups were smaller than four adults and failed to breed successfully. This is consistent with the possibility that the minimum viable group size is four, but it is also possible that the territories became too small to provide a sufficient quantity or variety of resources. However, some territories are more than twice as large as those of other successful groups (Fig. 2), so that it remains puzzling why groups do not split more often. Possibly the integrity of a cooperating kin group is essential for breeding success.

If successful rearing of young were primarily a function of territory quality, then auxiliaries' apparent aid-giving would be superfluous unless there were some selfish gain in participating in the breeding effort (Emlen 1978, Woolfenden 1981, Ligon and Ligon 1982, Ligon 1983). Auxiliaries could be "practicing" for later breeding on their own, and principals might tolerate this because auxiliaries are their own offspring (Rowley 1965, Wilson 1975). However, no evidence exists that older or more practiced breeders do better than novice breeders among Stripe-backed Wrens. Second, auxiliaries could be forming alliances or improving their status in order to improve their chances of either emigrating successfully or taking over all or part of the natal territory. Sister-pairs have, on five occasions, emigrated together, but competition among siblings for breeding positions is the rule. In addition, a stable age-related hierarchy exists for males regarding priority to breeding status, so that only among same-age brothers could status competition become important (Rabenold 1984, Wiley and Rabenold 1984). Auxiliaries seldom cleave off a part of the natal territory for themselves, as is common in other species (Woolfenden and Fitzpatrick 1978).

A third possible explanation for helping even when aid is unnecessary is that auxiliaries could be either sabotaging the breeding attempts of the principals (Zahavi 1976) or making "payment" for acceptance in the group in order to enjoy survival advantages of waiting in a safe area for a breeding opportunity (Gaston 1978*b*). I have shown that auxiliaries provide appropriate food, and sabotage would not benefit the auxiliary unless it hastened turnover in the breeding position. However, principals survive just as well in large groups, and have high nesting success, so that any attempts at sabotage are at best ineffectual. Auxiliaries survive no better in large groups than in small ones, so that "payment" by auxiliaries brings no reward if it does not contribute to sibling production.

In general, corollary predictions of the hypothesis that auxiliaries do not actually contribute to the breeding success of principals, and that the correlation between group size and productivity is produced by variation in territory quality, are not verified by this study of Stripe-backed Wrens. It seems most plausible that helpers are effective in both providing necessary food to the young and contributing to the defense of the breeding nest. In fact, the degree of improvement in reproductive success attributable to helpers in Stripe-backed Wrens is matched only by Rowley's (1978) study of *Corcorax*. Koenig (1981) and Koenig and Pitelka (1981) have pointed out that the apparent effect of helpers among cooperative breeders is generally weak, so that reproductive success is not often greater per capita for groups compared to unaided pairs. However, for several species (Rowley 1965, Ridpath 1972, Rowley 1978, Stacey 1979*b*, Reyer 1980, Brown and Brown 1981, Emlen 1981) per capita productivity of groups is higher than for unaided pairs, and in these cases, rearing siblings in the role of helper can be more profitable than breeding. In Stripe-backed Wrens this is most striking since the extra 1.46 offspring produced on average by quartets compared to trios and pairs can be attributed to the activities of the helpers (Dawkins 1982). This sizeable increment in reproductive success of kin (usually parents) would be forfeited by a helper dispersing from a quartet to breed. In fact, a quartet is the typical group.

Auxiliaries' help in feeding nestlings, second clutches, and nest defense

Auxiliaries' feeding of nestlings and fledglings probably reduces the energetic burden on the principals, contributes to renesting by the female after a successful nesting, and increases vigilance at the nest by the principal male. These effects link the feeding efforts of the auxiliaries to the higher nesting success and productivity of the principals, even though nestlings do not receive more food nor are more young fledged from each successful nest in large groups than in small groups.

A possible link between auxiliary feeding and predators is that large groups could recover faster from interruptions in feeding caused by intrusions of predators. The savanna in which these wrens live supports a diverse and dense community of raptors, and these hawks favor the wrens' nest trees for perching and sometimes for nesting. Because the wrens commonly respond to raptors by ceasing deliveries of food to the nestlings, interruptions in feeding could be frequent. Although our experimental predator presentations suggest that compensation in feeding rates for such interruptions in large groups could be important, the anal-

ysis of maximum feeding rates showed no effect of group size. The 6-h samples from which these maxima were drawn are perhaps of insufficient duration to include bouts of recovery from interruption.

Data on feeding rates and information on nest failures do suggest that predation is the major cause of nestling loss and variation in nesting success, rather than starvation. Auxiliaries contribute to nest defense directly by joining in mobbing predators and competitors, and this cooperative effort is substantial in comparison to the level of effort of the principals. Furthermore, the principal male both defends the nest most and benefits most from auxiliaries' feeding efforts. By freeing the principal male from feeding, the auxiliaries probably contribute indirectly to nest defense and nesting success. Large groups of wrens are probably more effective in harassing predators directly, but the principal advantage of large numbers of wrens could be in their ability to cause sufficient disturbance around a threatening predator to draw other species. The wrens could be functioning as the main alarm in a predator-mobbing guild that includes larger species better able to harry raptors and snakes physically. Preliminary observations support this interpretation, and continuing experiments will test the effect more conclusively.

In conclusion, the most parsimonious explanation of the correlation between group size and reproductive productivity in Stripe-backed Wrens is that auxiliaries do contribute positively to the principals' breeding success by both feeding and defending nestlings and that they do so because (1) they have little opportunity themselves to breed successfully in large established groups, so the cost is small; and (2) they stand to benefit indirectly through substantial inclusive fitness gains and delayed reciprocation of aid by younger wrens once a breeding position is attained.

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